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REGULAR ARTICLE

Distribution of mangrove vegetation along inundation, phosphorus, and salinity gradients on the Bragança Peninsula in Northern Brazil

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Abstract
Background and aims The Bragança Peninsula, in northern Brazil is characterized by macrotides (4 m) and specific edaphic conditions, which determine the local mangrove forest's development. This study, conducted during the dry season evaluated the spatial patterns of *Rhizophora mangle* and *Avicennia germinans* species across an inundation gradient.
Methods Along a transect of 700 m, measurements of structure forest, soil moisture, porewater salinity, extractable phosphorus (extr.-P) in sediments, and phosphorus in the leaves (leaf-P) were conducted.
Result The *A. germinans* (100 %) occurred in high intertidal (HI) zone. *A. germinans* (59 %) and *R. mangle* (41 %) co-occurred in mid intertidal (MI) zone, while *R. mangle* (58 %) predominated in low intertidal (LI) zone, followed by *A. germinans* (37 %) and *Laguncularia racemosa* (5 %). Covariance analysis (ANCOVA) indicated that salinity and soil moisture means are significantly different between the

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mangrove forests, but do not correlate with inundation frequency (IF). The means of extr.-P were significantly different in mangrove forests and correlated with IF and leaf-P.

Conclusion The inundation frequency, the availability of P in the sediments, phosphorus in the leaves and interstitial salinity are all important factors contributing to the distribution of the mangrove tree species *A. germinans* and *R. mangle* on the Bragança Peninsula.

Keywords Amazonia · Inundation · Mangrove · Phosphorus · Salinity

Introduction

The distribution of mangrove trees species within the intertidal zone has been discussed by a number of authors (Lugo and Snedaker 1974; Ukpong 2000; Satyanarayana et al. 2001; Feller 1995; Lovelock et al. 2005). Inter-related factors such as the pore-water salinity (Matthijs et al. 1999; Cuzzuol and Campos 2001), pH and Eh (McKee 1993) and the availability of phosphorus (P) (Boto and Wellington 1983; Feller et al. 1999) have been emphasized together with sediment morphology and edaphic conditions, which suggest that the different species of mangrove tree colonize and grow in specific tidal zones (Tomlinson 1986).

The adaptations of the genera *Avicennia* and *Rhizophora* to environments with moderate to high salinity are well understood (Nickerson and Thibodeau 1985; Thibodeau and Nickerson 1986; McKee 1993; Naidoo 1986; Naidoo et al. 1998; Sherman et al. 1998, 2003). These studies indicate that species of the genus *Avicennia* are more salt tolerant and may thus be able to colonize areas with relatively high levels of interstitial salinity, whereas *Rhizophora* predominate in less saline sediments, in the lower terrain, and where fresh or brackish water is more common (Sherman et al. 1998, 2003). However, the salinity gradient in itself does not account for the zoning of the mangrove forest, and other factors, such as the availability of nutrients and tidal inundation patterns must also be taken into account when analyzing the distribution patterns of the different mangrove species.

The physical and chemical properties of the soil and in particular the availability of nutrients, are important determinants of the spatial distribution of the vegetation (Vince and Snow 1984), and may also influence the concentrations of nutrients in the leaves (Vitousek 1982). Given this, the relationship between the concentration of phosphorus in the leaves and the availability of this element in the soil has been considered essential to the understanding of growth patterns (Boto and Wellington 1984; Medina 1984; Medina et al. 2001; McKee et al. 2002; Feller et al. 2003; Marchand et al. 2004; Lovelock et al. 2006; López-Hoffman et al. 2007), and the structure and productivity of mangrove forests (McKee 1995; Chen and Twilley 1999; Reef et al. 2010).

At Combu Island in northern Brazil, Silva and Sampaio (1998) found that the release of P into the silty-clayey sediment was related to the inundation gradient, which was determined by precise topographic variations. In the mangroves forests at Bragança, the strong hydrodynamics, together with the numerous tidal channels, indicate that the nutrient dynamics is dominated by the pattern of surface drainage and the influx of interstitial water (Lara and Dittmar 1999). The variation in the structure of the forest appears to be related closely to the fertility of the soil, frequency of flooding, salinity, and the availability of freshwater, as well as differences in the availability of nutrients or the efficiency of site-specific retranslocation (Reise et al. 2010). In this same region, Mendoza et al. (2012) recorded during rainy season high levels of P in the leaves of the red mangrove, *Rhizophora mangle*, in the most frequently flooded areas, associated with the highest levels of available P in the sediments. Based on these considerations, the present study tested the hypothesis that, during the dry season, the frequency of inundation, soil moisture, interstitial salinity, and phosphorus concentrations in the sediments and leaves determine the structure and distribution patterns of *A. germinans* and *R. mangle* in a mangrove forest on the Bragança Peninsula in northern Brazil.

Materials and methods

Study area

The study area is located in northern Brazil (00°55′65″ S, 46°83 40′09″ W), in the northeast of the State of Pará, on the Bragança Peninsula, adjacent to the estuary of the Caeté River (Fig. 1). The area is covered by a well-developed mangrove forest with trees of up to 20 m height. The principal tree species are *Rhizophora*

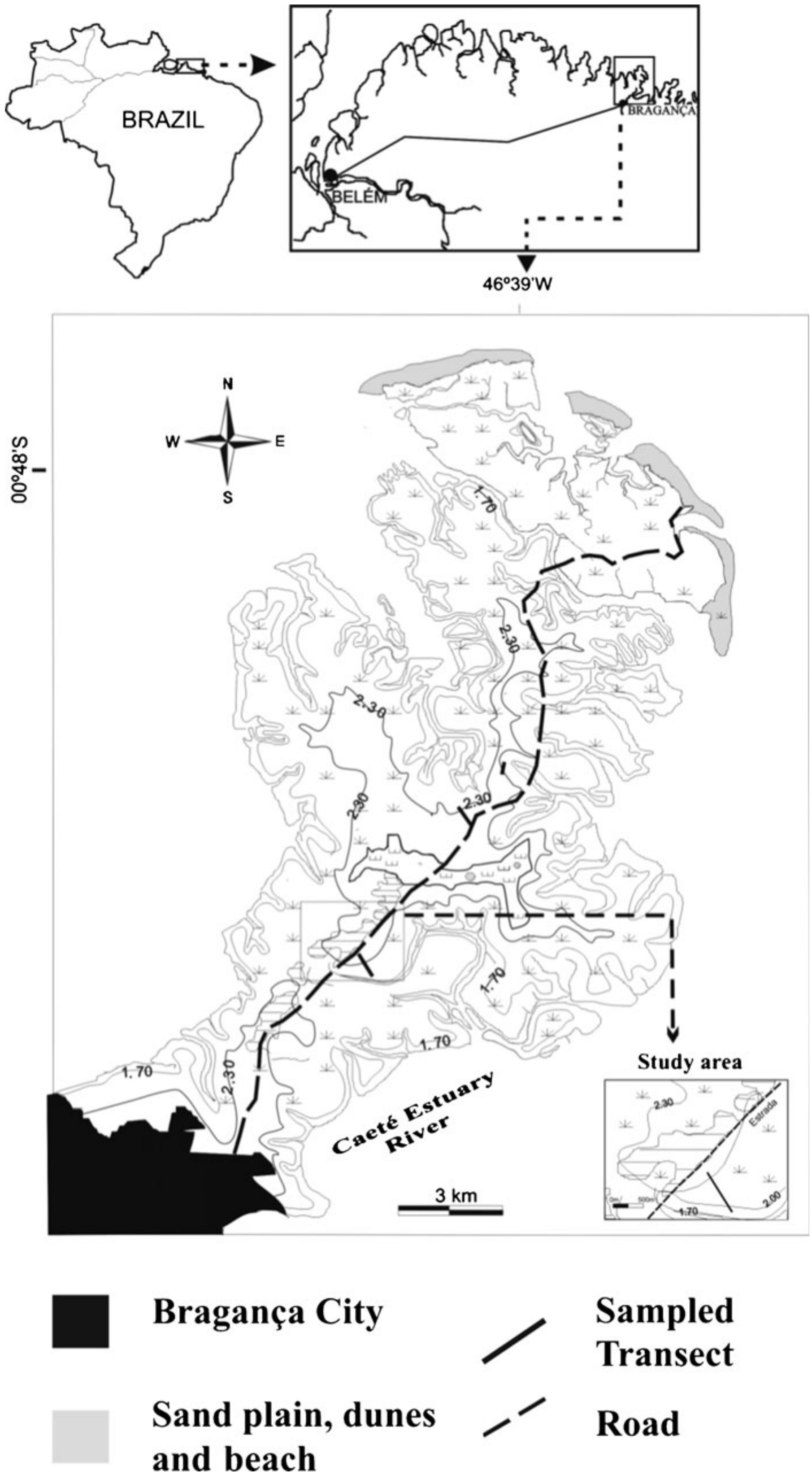

Fig. 1 Location of the study area in northern Brazil. Adapted from Cohen et al. (2005)

mangle (*R. mangle*), *Avicennia germinans* (*A. germinans*), and *Laguncularia racemosa* (*L. racemosa*). Mean annual temperature is 28 °C, and annual precipitation averages 2,550 mm, with 75 % of the rain falling between January and May (INMET 2009). Evaporation rates are higher during the three warmest months, that is, October, November, and December.

This coastal environment is characterized by a tidal range of approximately 4 m, and most of the mangrove forest is flooded during the spring tides (Cohen and Lara 2003). The region represents a Cretaceous coastal basin formed on Pre-Cambrian rocks. Outcrops are primarily of the Barreiras Formation (Costa et al. 2004; Behling and da Costa 2004). The geological characteristics, together with the variation in the relative sea level and the continuous influx of fluvial sediments, have led to the progradation of the mudflats and the development of mangrove systems (Souza Filho and El-Robrini 2000).

The sediments are predominantly clay-based (>80 %), with smaller proportions of silt (12 %) and sand (<4 %). The sandy fraction predominates in the lower-lying surfaces, where the hydrodynamics are more accentuated, whereas the silty and clay fractions are deposited primarily on the higher plain, where there is a reduced water flow (da Cruz 2009). The mineralogy encompasses quartz (dominant in the sand and silt fractions) and kaolinite, smectite, and illite (prevailing in the clay minerals). The presence of hematite, ilmenite, monazite, accessory minerals such as xenotime and trace elements indicate weathered sediments and soils (mainly oxisols) from the Barreiras Formation (Costa et al. 2004).

The presence in these sediments of authigenic minerals, such as pyrite, reflects the mineralization of the organic matter. The jarosite and halite, reflects the processes of the oxidation of the pyrite and evapotranspiration, respectively, in these environments. The mean levels of $SiO_2 + Al_2O_3$ (65 %) and Fe_2O_3 (6 to 7 %) reflect the influence of the products of tropical weathering on the mangrove forests sediments (da Cruz 2009). The enrichment of the muddy sediments with Na_2O and K_2O (3 % and 2 %, respectively), MgO (2 %), and CaO (0.2 %) in comparison with the detritus of the Barreiras Formation, corresponds to the contribution of oceanic waters to the constitution of the estuary (Costa et al. 2004). The enrichment of P_2O_5 (0.18 %) in these sediments is also consistent with the results of previous studies on the Bragança Peninsula (Costa et al. 2004), although their levels were higher than those obtained from another area of mangrove forests in northeastern Pará (Berrêdo et al. 2008).

Topography and inundation frequency

The inundation frequency (IF) and topography were calculated according to Cohen et al. (2001), in which the number of days per year ($d.y^{-1}$) each zone of the forest is flooded by the tide was determined. These zones were demarcated along the 700 m transect perpendicular to the Caeté River (Mendoza et al. 2012).

Forest structure

The vegetation zones of the mangrove forest adopted in the present study were defined by Mendoza et al. (2012) based on the abundance of species and structural parameters that varied among the different tidal zones. From the access road towards the interior of the forest, the first mangrove zone is dominated by *A. germinans*, followed by a zone of mixed forest with both *A. germinans* and *R. mangle*. The subsequent zone is dominated by *R. mangle*, with some *A. germinans*, and a few *L. racemosa.* Three 20×20 m plots were established in each zone, with a total of nine plots being sampled along the 700 m transect during the dry season (November and December) of 2005. These plots were inventoried according to the procedures established by Mueller-Dembois and Ellenberg (1974), Schaeffer-Novelli and Cintrón (1986), and Martins (1991). All the trees with a diameter at breast height (DBH) greater than 2.5 cm were measured (diameter and estimated height) and identified. These data were used to calculate basal area ($m^2.ha^{-1}$), density, relative density, and the importance value (IV).

In order to analyze the variation in the structure of the forest in relation to the tidal sediment-plant gradient, a principal study tree and two neighboring trees were selected at each station within the plots, following the procedure defined by Mendoza et al. (2012). These trees were measured (height and DBH) and samples of the sediment were taken from the area around their base for the characterization of the environment.

Sediment analysis

Sediment samples were selected from two plots selected from each zone. Two stations were defined within each plot, and at each station, three neighboring trees (principal tree approach—see above) were sampled according to the species dominance in that forest zone. In the mixed zone, two sub-stations were selected for each of the co-dominant species. A total of eight stations were sampled. The cores were taken at a distance of 50–100 cm from the trunk of the principal tree, and from the base of one of the neighboring trees (Mendoza et al. 2012). Cores (30 cm depth) were sampled at intervals of 0–5, 5–10, 10–15, 15–20, and 20–30 cm.

At the laboratory, soil moisture was calculated in wet sediments (5 g) after drying for 24 h at 100 °C. The weight difference is equivalent to the water content. The conductivity of the interstitial water was measured from a wet sediment sample mixed with water (1:5 weight/volume) using a portable conductivity meter (WTW-LF 197). The samples were shaken and then settled for 12 h prior to the measurement. Salinity was calculated following Ensminger (1996).

In order to investigate the mechanism for the retention and availability of phosphorus, the sediments were dried at 60 °C and pulverized in an agate mortar and pestle prior to analysis. Leeg and Black (1995) ignition method was used to determine the levels of total (tot.-P), inorganic (inorg.-P), and organic phosphorus (org.-P). For total-P, 0.4 g of the dried sample was incinerated in a muffle furnace for 1 h at 240 °C. Once cooled, the ashes were hydrated with 1 ml of water, and were then added to 4 ml of concentrated hydrochloric acid (HCl) in a water bath at 60 °C for 20 min. Once the mixture had reached room temperature, a further 5 ml of HCl was added under agitation for 30 min and then centrifuged for 10 min. The supernatant was raised to a constant volume by the addition of de-ionized water, and aliquots were taken in order to determine P by colorimetry method (Grasshoff et al. 1983). Inorganic P was analyzed by the same procedure, except for the ignition stage. Organic P was calculated by the difference between tot-P and inorg.-P. The extractable phosphorus (extr.-P) was obtained with sodium acetate buffer solution, according Hesse (1957) and analyzed using the colorimetry method (Grasshoff et al. 1983).

Analysis of leaves

Twelve stations were sampled within the nine plots established for the measurement of forest structure. Within each plot, a station was defined for the collection of samples of leaves, except for the mixed forest zone, in which two distinct sub-stations were established in order to sample the two co-dominant species. A batch of 10 green leaves of *A. germinans* and *R. mangle* were collected separately from branch tips from the middle of the crown of each sample tree, with leaves being taken from all around the tree, including some on branches exposed to direct sunlight and others in the shade. A single sample of 30 leaves was thus collected for each species. Only healthy, mature, and well-formed leaves were collected. The leaves were washed and dried in paper bags in a oven at 60 °C until constant weight (Medina et al. 2001), and powdered (without petiole) in a porcelain mortar (~1 mm mesh). This material were then placed in a muffle furnace for 24 h at 400 °C, and the ash was digested with sodium persulfate in an acidic medium and analyzed by colorimetry (Grasshoff et al. 1983). More detailed information on the analysis of P in leaves is provided by Mendoza et al. (2012).

The chemical analyses for tot.-P, inorg.-P, and extr.-P were realizated on duplicates, and in the case of the leaves, on triplicates. Analytical error was estimated from the coefficient of variation of each sample, and was never higher than 5 %. The colorimetric method was used to evaluate the efficiency of the extraction of P from the vegetation, based on the Standard Reference Material—1515-Apple Leaves (National Institute of Standards & Technology).

Statistical methods

An analysis of covariance, or ANCOVA (Johnson and Wichern 1999) was used to adjust the response variable by observing the effect of one or more covariates in the mean comparison (Johnson and Wichern 1999). In this case, mean salinity, soil moisture, and extr.-P could be analyzed independently of the influence of IF. Similarly, in the case of the forest zones, the comparison of the mean extr.-P values was conducted considering salinity and soil moisture as covariates, and the behavior of leaf-P was evaluated independently of the influence of IF, soil moisture, salinity and extr.-P. The multivariate covariance analysis, MANCOVA

(Johnson and Wichern 1999) was used to compare the mean tree height and basal area between the different forests based on the adjusted values of leaf-P, with the objective of assessing the possible influence of these parameters on the structure of the forest along the gradient of inundation and salinity.

Results

Topography

According to the IF data three distinct topographic features were identified within the study area—low intertidal (LI), middle intertidal (MI) and high intertidal zones (HI). In the HI zone, the IF varied between 41 and 62 days per year (d.y^{-1}), whereas in the MI zone, it was 80–101 d.y^{-1}, and in the LI zone, it was between 128 and 162 d.y^{-1} (Mendoza et al. 2012).

Forest structure

The vegetation of the sample transect is composed of three species of mangrove trees, representing three distinct plant families—black mangrove, *A. germinans* (L.) L. (Acanthaceae), red mangrove, *R. mangle* L. (Rhizophoraceae) and white mangrove, *L. racemosa* (L.) C.F. Gaertn (Combretaceae). These species were recorded in at least one of the sample plots. The data collected in the different plots are summarized in Table 1.

Avicennia germinans was predominant (100 %) in the HI zone, with a mean height of 7.8±1.5 m and mean DBH of 14.11±4.54 cm. In the mixed mangrove forest (MI) the *A. germinans* is also the dominant species (59 %) with an importance value (IV) of 164 and a mean basal area of 19.55 m^2.h^{-1}. The rest of the individuals in this mangrove forest (41 %) were *R. mangle*, which presented a lower IV of 136, and basal area of 15.79 m^2.h^{-1}. While *A. germinans* dominates in this mangrove forest, the *R. mangle* trees are taller, with a mean height of 11.5±2.57 m and DBH of 15.4 ±3.85 cm. In LI the *A. germinans* decreases (37 %) and the *R. mangle* is the dominant species, with a much higher proportion (58 %) of the trees, with an IV of 141 and a mean basal area of 26.9 m^2.h^{-1}. Few stands of *L. racemosa* were measured (5 %).

Sediments

The highest mean salinity values were recorded in the HI (74.9±18.1‰), while the LI presented the lowest ones (33.4±1.5‰). In the MI zone, only a slight difference was observed in the values between *R. mangle* (40.51±0.4‰1) and *A. germinans* (43.36± 1.23‰). In contrast with salinity, soil moisture was lowest in the HI, with a mean of 37±3 %. Soil moisture was higher in the MI (48.36±1.54 %), although

Table 1 Mangrove forest structure along the inundation gradient on the Bragança Peninsula. Height (m); Density (ind/ha^{-1}), Basal area (m^2.ha^{-1}). Mean values ± SE, ranges in parentheses

Forest zone	IF n=12	n	DBH	Height	Density	Relative density	Basal area	IV
HI	51 (41–62)							
A. germinans		70	14.11±4.54 (7.2–26.2)	7.8±1.5 (3.43–11.0)	1750	100	30.17	300
Total		70				100	30.17	300
MI	92 (80–101)							
A. germinans		46	14.00±4.56 (8–36.4)	10.3±2.05 (7.1–16.5)	1150	59	19.55	164
R.mangle		32	15.39±3.85 (10.5–27.8)	11. 5±2.57 (6.25–18)	600	41	15.79	136
Total		78				100	35.33	300
LI	145 (128–162)							
A. germinans		21	21.50±6.60 (8.3–27.2)	13.5±4.00 (8.3–27.2)	525	37	29.24	124
R.mangle		33	19.5±2.84 (7–20.5)	12.8±2.84 (7–20.5)	625	58	26.97	141
L. racemosa		3	15.0±8.40 (10.2–21)	10.5±0.60 (9–12)	75	5	2.18	34
Total		57				100	58.40	299

IF inundation frequency (d.y^{-1}); *DBH* diameter at breast height (cm); *IV* importance value; *HI* high intertidal; *MI* middle intertidal; *LI* low intertidal; *n* number of individuals no difference was observed between the sediments occupied by *A. germinans* and *R. mangle* (Table 2).

The concentration of tot.-P in the flooding profile varied from 0.49 to 0.76 mg.g^{-1}, with the highest values (0.71±0.04 mg.g^{-1}) being recorded in the LI. Inorganic phosphorus varied in a manner similar to tot.-P, with the highest concentrations being recorded in the LI (0.67±0.04 mg.g^{-1}). In spatial terms, extr.-P presented the same distribution as tot.-P and inorg.-P. At the LI and HI zones, the mean values of tot.-P and inorg.-P were 0.037±0.002 mg.g^{-1} and 0.02±0.003 mg.g^{-1}, respectively (Fig. 2). The inorganic P is the most important fraction (80 %) of tot. P. The organic-P showed low concentrations along the profile with the highest values at HI (0.07±0.01 mg.g^{-1}) (Table 2).

The ANCOVA indicated that the mean salinity (F=11.74, p=0.00) and soil moisture (F=35.23, p=0.00) values were significantly different among the mangrove forest stands, although they were not correlated with IF (F=0.093, p=0.76 and F=0.22, p=0.64, respectively). In addition, the mean extr.-P values were significantly different among mangrove forest stands (F=15.32, p=0.00) and correlated with IF (F=7.19, p=0.01). However, when the effect of the correlation between soil moisture and extr.-P is removed, the mean extr.-P values were not longer significantly different among mangrove stands (F=1.81, p=0.177), which indicates that soil moisture must be a confounding factor for the analysis of this parameter.

Leaves

The leaf-P concentrations varied from 1.03 to 1.55 mg.g^{-1}, with higher mean values being recorded in the leaves of *R. mangle* (1.55±0.1 mg.g^{-1}). In the MI, the lowest concentrations were recorded in the leaves of *A. germinans* (1.23±0.1 mg.g^{-1}), decreasing to 1.07±0.02 mg.g^{-1} in the leaves of the same species in the HI (Table 3). The distribution of leaf-P values accompanies the pattern of P availability in the sediments, and the highest concentrations (1.4 mg.g^{-1}) were associated with the highest levels of extr.-P (0.083 mg.g^{-1}) (Fig. 3).

Mean leaf-P showed significant differences between the mangrove forests (F=9.03, p=0.00) without the influence of extr.-P (F=22.54, p=0.00), soil moisture (F=10.78, p=0.00) and salinity (F=3.15, p=0.08) in the mean comparison. The MANCOVA

Table 2 Sediment characteristics along the forests zones. Phosphorus concentrations (mgP.g^{-1}) as total P (tot.-P), inorganic P (inorg.-P), organic P (org.-P), and extractable P (extr.-P). Soil moisture (%) and salinity (‰). Mean values ± SD for the 0–30 cm-thick sediment profile, ranges in parentheses

Forest zone	*n*	Tot.-P	Inorg.-P	Org.-P	Extr.-P	Soil moisture	Salinity
HI							
A.germinans	10	0.53±0.02 (0.49–0.57)	0.46±0.01 (0.44–0.50)	0.07±0.01 (0.052–0.086)	0.02±0.002 (0.015–0.025)	37±3.08 (31.42–0.79)	74.89±18.11 (61.38–108.6)
MI							
A.germinans	10	0.63±0.02 (0.60–0.67)	0.58±0.02 (0.56–0.61)	0.04±0.00 (0.038–0.048)	0.031±0.003 (0.026–0.036)	48.27±1.14 (47.08–0.00)	40.51±0.41 (38.8–42.8)
R.mangle	10	0.61±0.01 (0.60–0.63)	0.55±0.01 (0.53–0.57)	0.06±0.00 (0.056–0.063)	0.035±0.001 (0.033–0.037)	48.44±1.55 (47.08–0.00)	43.36±1.23 (42.02–45.2)
LI							
R.mangle	10	0.71±0.04 (0.63–0.76)	0.67±0.04 (0.61–0.73)	0.03±0.00 (0.020–0.044)	0.037±0.002 (0.034–.0.042)	50.52±1.72 (48.13–3.55)	33.41±1.50 (30.44–35.5)

HI high intertidal; *MI* middle intertidal; *LI* low intertidal; *n* number of samples

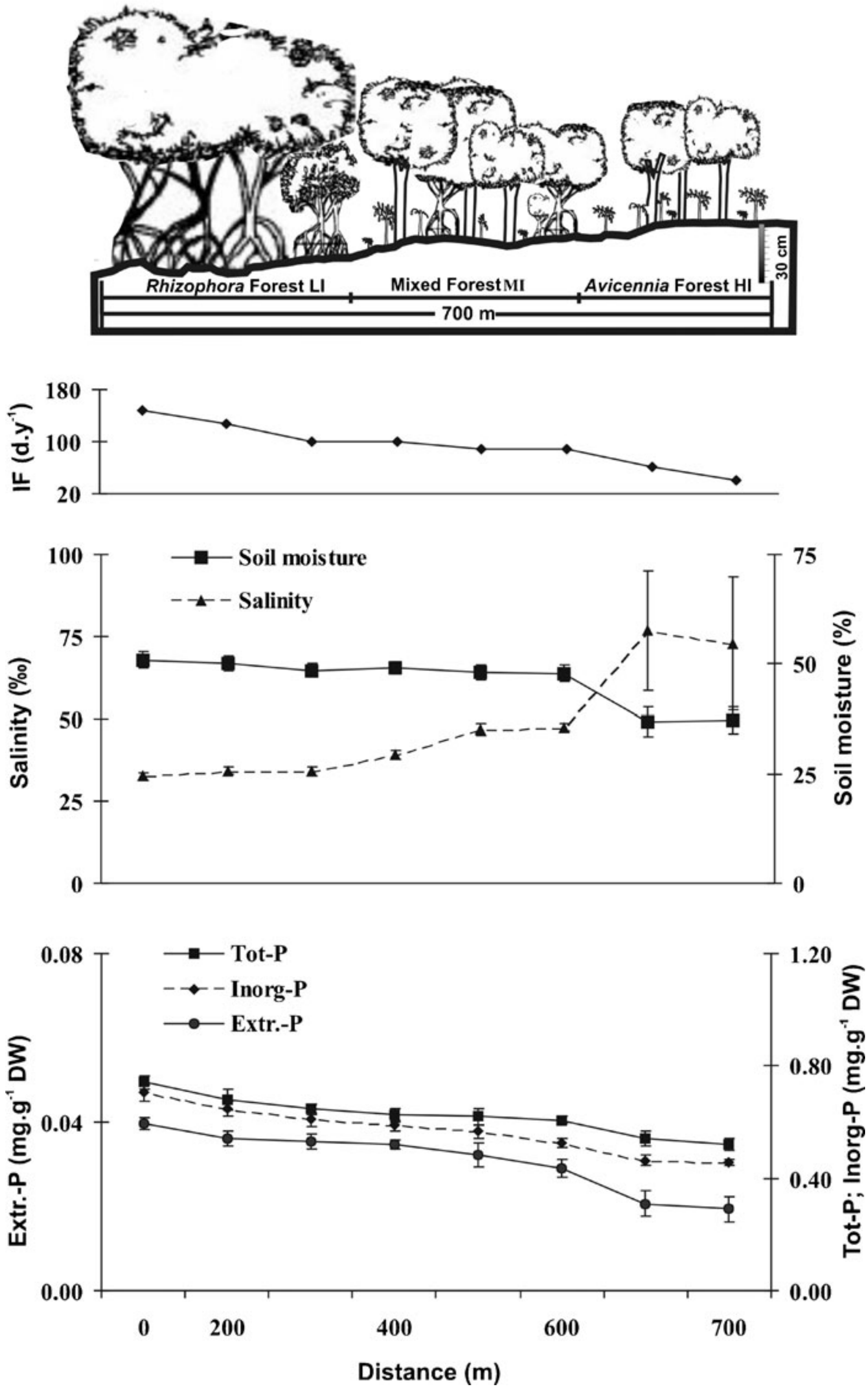

Fig. 2 **a** Variation of the inundation frequency (IF) and variation in **b** soil moisture (%), salinity (‰) **c** total P (tot.-P), inorganic phosphorus (inorg.-P), extractable phosphorus (extr.-P) ($mg.g^{-1}$) in the sediments (depth of 0–30 cm) along the study transect

demonstrated that the correlation between the vectors of tree height and basal area with leaf-P was significant (F=66.94, p=0.00), which indicates the importance of leaf-P in the forest structure along the topographic gradient.

Discussion

The results of the present study indicated a complete absence of any correlation between IF and either salinity or soil moisture, as observed by Mendoza et al.

Table 3 Forest structure and phosphorus in the leaves (leaf-P) data observed along the inundation gradient. Mean values ± SE, ranges in parentheses

Forest zone	*n*	DBH (cm)	Height (m)	Leaf-P (mg.g^{-1})
HI				
A.germinans	9	14.00±6.3 (7.2–24)	7.56±1.2 (5–9.3)	1.07±0.02 (1.03–1.10)
Total	9			
MI				
A.germinans	9	13.00±4.63 (8–24)	11.53±2.64 (7.1–16.5)	1.23±0.1 (1.09–1.33)
R.mangle	9	15.3±3.58 (10.5–22.5)	10±2.75 (8.3–16)	1.29±0.04 (1.23–1.53)
Total	18			
LI				
R.mangle	9	21.20±5.8 (14–30.5)	14.74±3.19 (9.5–20.5)	1.55±0.10 (1.45–1.72)
Total	9			

IF inundation frequency; *DBH* diameter at breast height; *leaf-P* phosphorus in the leaves; *HI* high intertidal; *MI* middle intertidal; *LI* low intertidal; *n* number of samples

(2012) in the same study area. This is despite the fact that a number of previous studies (De Leeuw et al. 1991; Lin and Stemberg 1992; Reef et al. 2010) have demonstrated the influence of the IF on salinity levels in the intertidal zone, as a process that contributes to the avoidance of the hypersalinization of the mangrove. By

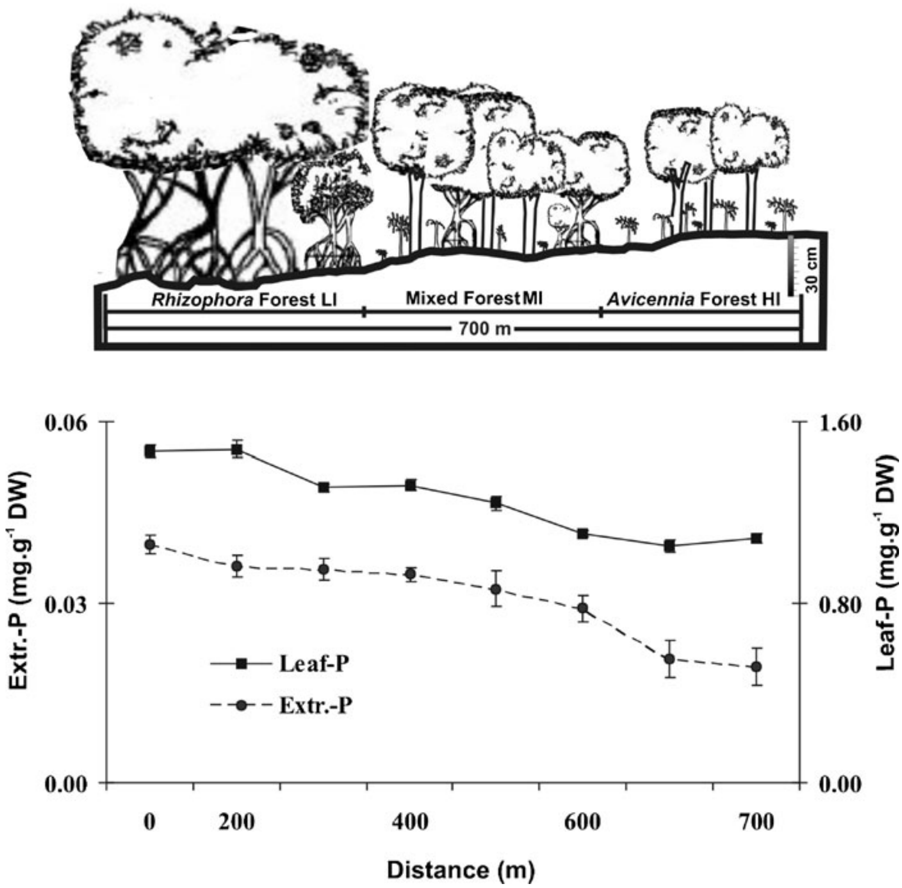

Fig. 3 Distribution of phosphorus in the leaves (leaf-P) in matures leaves and extractable phosphorus (extr.-P) in the sediments at 0–30 cm depth

contrast, the results of the present study reinforce the role of topography and evapotranspiration on the higher levels of interstitial salinity in some parts of the Bragança Peninsula, where solar radiation is particularly intense (Schwendenmann 1998), as observed in similar environments in other regions (Twilley and Chen 1998; Marchand et al. 2004; Lamb et al. 2008). The topographic variation observed between different areas of the Bragança Peninsula (Lara et al. 2010) may contribute to the predominance of evapotranspiration observed in some parts of the mangrove forest.

In the area of the present study, the values of extr.-P in the different forest stands were related significantly with the co-variable IF, which emphasizes the link between the IF and the availability of P in the sediments, as observed by Mendoza et al. (2012) during the rainy season. These authors considered that the values of the redox potential associated with IF play an important role in the control of the availability of this nutrient, as proposed for coastal sediments by Fenchel et al. (1998) and Kristensen et al. (2008).

Phosphorus associated to Fe and Al may be solubilized under anoxic conditions (Ponnamperuma 1972). Given this, in the LI zone, the greater availability of P may be related to the dissolving of the Fe/Al-P fraction present in the reducing sediments (Mendoza 2007). The principal source of Fe and Al is the sediments deposited on the mudflats of the Caeté estuary, which are rich in particles of aluminum phosphate, transported by the waters of the Gurupi River, which drains lateritic soils (Costa 1991). Sedimentation is thus the principal factor responsible for the increase in the levels of total-P observed in the present study, which is reinforced considerably by the inorg.-P fraction transported in suspension. This process accounts for the predominance of inorg.-P over org.-P on the Bragança Peninsula. A high percentage of inorg.-P has been recorded in mangroves by Fabre et al. (1999) and Prasad and Ramanathan (2010).

The leaf-P average concentration recorded in the present study (1.28±0.09 $mg.g^{-1}$) was very similar to that reported by Mendoza et al. (2012), who recorded values of 1.30±0.12 $mg.g^{-1}$. However, a one important feature here is the seasonal variation observed in extr.-P (Fig. 4). But, the results of the present study do not account for the negligible seasonal variation in the P content of the leaves, despite the clear association between this nutrient and of the forest gradient

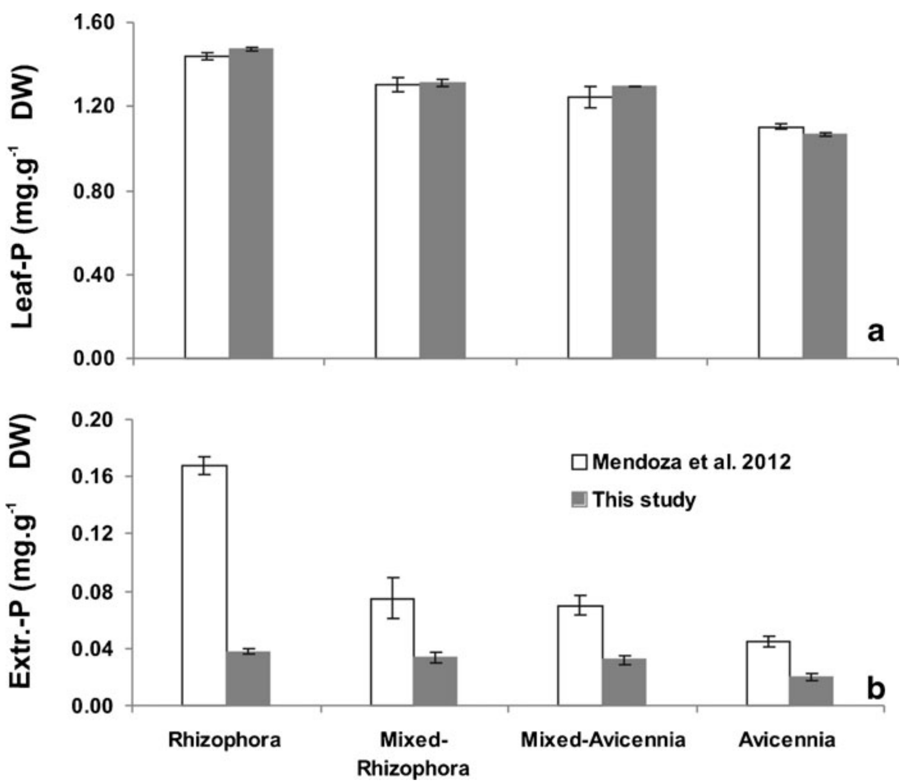

Fig. 4 Variation of phosphorus in the matures leaves (leaf-P) and extractable phosphorus (extr.-P) in the sediments **a** (25–30 cm) during rainy season (Mendoza et al. 2012), and **b** (0–30 cm) during the dry season (this study) in the mangrove forest stands

(Fig. 3). The highly significant correlation recorded between leaf-P and extr-P reinforces the interaction between these variables, which is associated with chemical, physiological, and climatic factors.

The lower extr.-P values observed in this study, suggest that during dry season the plant tends to maximize the use of this nutrient. Previous studies (Medina 1984; Jonasson and Chapin 1985) indicated that the increases of the use of the nutrients absorbed by the plant, reduces its dependence on nutrients supplied by the sediment. One fertilization experiment with P in Belize (Feller et al. 2003) showed that with increasing P availability, the mechanisms used by plants to recycle and conserve nutrient become less efficient.

Several authors consider that the tree ability to use and maintain nutrients is associated with the processes of translocation or resorption (Escudero et al. 1999; Son et al. 2000). According to Medina (1984) and Yuan and Chen (2009) approximately 53–60 % of the P is reabsorbed prior to leaf-fall. In the present study area, approximately 60 % of the phosphorus was transferred during the rainy season from the mature/-senescent leaves to the young leaves in response to nutrient stress (Mendoza et al. 2012). This is the period when leaf production is highest, probably due to the reduction in interstitial salinity (Mehlig 2006). This also suggests that a considerable proportion of the P is made available to the plant prior to the loss of the leaves.

The significant relationship observed between leaf-P and the structural characteristics (tree height and basal area) of the mangrove forest of the Bragança Peninsula, demonstrated by MANCOVA, indicates that leaf-P may be related to the nutrition of the *A. germinans* and *R. mangle* trees due to the relative efficiency of the use of P during the dry season, which is characterized by reduced precipitation levels, intense solar radiation, and high interstitial salinity. The structural variables, such as the tree height (F=8.74, p<0.00) and the basal area of the mangrove forest (F=4.11, p<0.05) were correlated significantly with the adjusted salinity values, which are associated with the more intense evapotranspiration that occurred during the study period (Fig. 5).

The larger number of small-sized *A. germinans* in the HI zone may be related to the hypersaline character of the sediments in this tidal zone. This is supported by

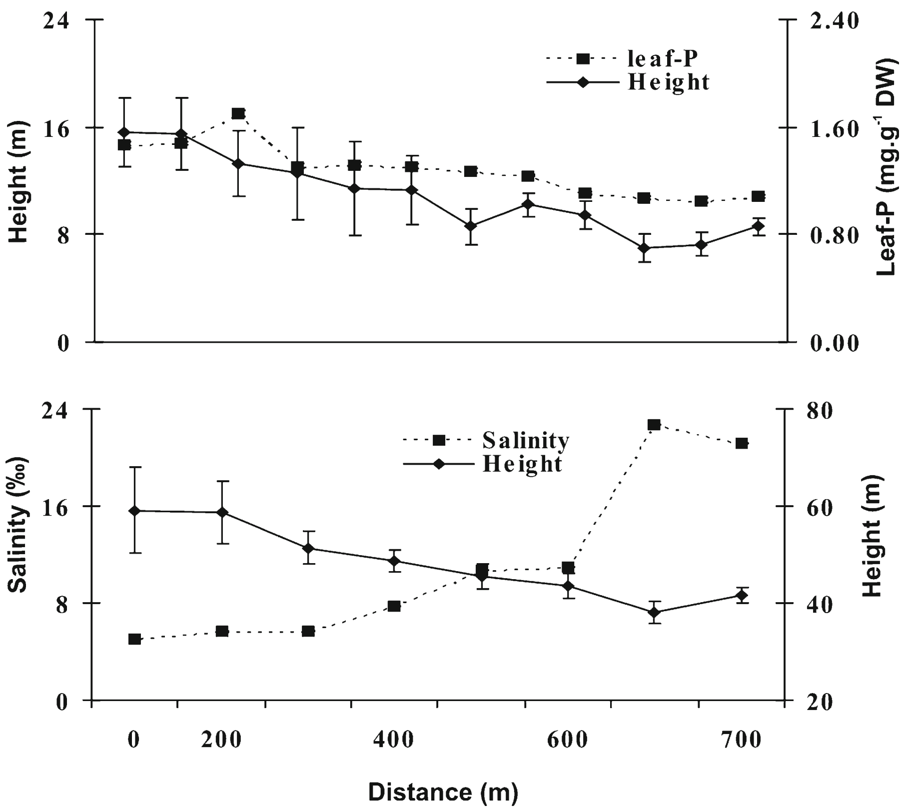

Fig. 5 Variation of phosphorus in the leaves (leaf-P) and sediment salinity (0–30 cm depth) with tree height along the transect

the increase in average tree height from 7.8±1.5 m in HI to 10.3±2.05 m in the MI (Table 1). For *R. mangle* the relative density increased from the MI where it was 41 to 58 % in the LI zone, with an accompanying increase in basal area from 16 $m^2.ha^{-1}$ to 27 $m^2.ha^{-1}$. The species *A. germinans* and *R. mangle* presented different degrees of tolerance to inundation and interstitial salinity levels. While they are able to tolerate high levels of salinity, the survival of these species in different tidal zones is influenced not only by interspecific differences in root aeration (McKee 1993, 1996), but also their physiological adaptations to different salinity levels (Tomlinson 1986; Hogartth 1999). The results of the present study coincide with those Reise et al. (2010) for the same study area, which also demonstrated the tolerance of both species (*Rhizophora* and *Avicennia*) to regular inundation with low to moderately saline water, but also the presence of monospecific stands of *A. germinans* in hypersaline zones. Similar results have been found by Ball (1988), Medina and Francisco (1997), Sobrado (2000), and Lopez-Hoffman et al. (2006).

The sediments conditions become more stressful to plant growth where drainage of water at low tide is restricted (Feller et al. 2003). In Bragança Peninsula the $\delta^{13}C$ isotopes data in the leaves of *R. mangle* and *A. germinans* (Schmitt 2006) correlated positively with salinity and negatively with the IF, indicating that the area most frequently inundated is less stressful for plants in comparison with areas of high salinity and low concentrations of extr.-P.

While leaf-P did not correlated with IF, it was related to the availability of P in the sediments, and the highest concentration were associated with the highest levels of extr.-P in LI, and also reflected the nutritional status of the vegetation—specifically, *R. mangle* and *A. germinans*—within the study area, as observed in other mangrove forests (Boto and Wellington 1984; Medina 1984; Marchand et al. 2004). In the HI zone, by contrast, the much higher salinity and hydrological deficit indicate reduced absorption of P by the plants, probably due to the reduction in the activity of the phosphorus in the soil solution (Marschner 1995). Overall, then, the results of the present study support the conclusion that the inundation frequency, availability of P in the sediments, phosphorus in the leaves, and interstitial salinity are the primary factors determining the distribution of *A. germinans* and *R. mangle* on the Bragança Peninsula.

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