

Flooding effects on phosphorus dynamics in an Amazonian mangrove forest, Northern Brazil

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Abstract

Aims and methods We examined porewater salinity, soil redox potential (Eh), soil extractable phosphate (extr.-P), leaf phosphorus (leaf-P) and plant growth in relation to inundation frequency (IF) and mangrove species distributions along a 600 m transect in the Bragança Peninsula, North Brazil.

Results The forest species composition changed across the tidal zone with *Avicennia germinans* dominating (99.1%) the high intertidal (HI) zone where the IF was 41–67 d.y⁻¹, *Rhizophora mangle*, *Laguncularia racemosa* and *A. germinans* co-occurred

in the mid intertidal (MI), and a mixed *R. mangle* (47.1%) - *A. germinans* (41.2%) stand occupied the low intertidal (LI) zone with an IF of 124–162 d.y⁻¹. Low IF resulted in high Eh levels (200 mV) in the HI zone relative to the LI where Eh ranged from 0–100 mV. The IF showed a significant positive correlation with extr.-P ($r=0.89$; $p=0.05$) and a negative association with Eh ($r=-0.75$; $p=0.05$).

Conclusion An ANCOVA confirmed that Eh and extr.P were influenced by flooding. Variations in these factors were reflected in patterns of P leaf tissue concentrations across the gradient; however, a MANCOVA showed that leaf-P was not related to tree height, tree volume or basal area. Water-logging conditions, porewater salinity, and P dynamics in the sediment appear to influence the forest structure. We suggest that P availability plays an important role in controlling mangrove species distributions but not their growth.

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Mangrove forest structure · Phosphorus availability ·
Redox potential

Introduction

A major issue in mangrove forest biogeochemistry is the role of tide-dependent processes, such as flushing time, inundation frequency (IF), degree of water-logging and extent of nutrient trapping and mobilization.

Phosphorus is present in plants as a constituent of nucleic acids, phospholipids and ATP (Marschner 1995). Although in mangrove sediments organic phosphorus (org.-P) comprises the largest phosphorus fraction, inorganic phosphorus (inorg.-P) is the largest pool of potentially plant-available P (Boto and Wellington 1988). The IF acts as a controller of nutrient availability by influencing salinity and anoxia (Boto and Wellington 1984). The few mangrove wetlands where fertilization experiments have been conducted appear to be either phosphorus limited (Feller 1995; Koch and Snedaker 1997) or differentially nitrogen and phosphorous limited across the tidal gradient (Boto and Wellington 1983; Feller et al. 2003). Mangrove forests have large geographic ranges which vary from high nutrient and low salinity environments, such as in the estuaries of many tropical rivers in Brazil and Venezuela, to hypersaline, low nutrient environments such as occur on many islands and continental coastlines in the Caribbean (Medina et al. 2010). Across mangrove forest inundation gradients, areas that are less exposed to marine water (high intertidal zone) are usually more P-limited (Boto and Wellington 1983; Medina et al. 2010). Thus, differential flood tolerance is one of the possible causes determining mangrove forest structure (Snedaker 1982). Mangrove forest structure and productivity along the tidal gradient have been correlated with the temporal and spatial variation of porewater salinity (Upkong 1991; Matthijs et al. 1999; Sherman et al. 2003), sediment phosphorus availability (Boto and Wellington 1983; Chen and Twilley 1999), and the interaction among sediment and growth factors (Lovelock et al. 2005).

In the Amazonian mangrove forest, a pioneer study showed that iron/aluminium-bound P (P-Fe/Al) is the main inorg.-P species, and tidal inundation appears to influence the chemical reactions involving P retention and release (Mendoza 2007). The hypothesis that differential flood tolerance is one of the possible causes determining the distribution of trees within a mangrove forest has been studied in the Bragança Peninsula, where macrotides (range ~4 m) constitute the main hydrodynamic feature of the coastal ecosystem (Cohen et al. 1999). Variation in forest structure, biomass, and productivity showed an interdependency between IF, bulk density, porewater salinity and total P content (Reise 2003). In addition,

regression analysis demonstrated that IF and competition amongst trees strongly influenced tree growth (Menezes 2006).

The aim of the present study was to evaluate the nutritional status of the Bragança mangrove forest, specifically P availability from sediments and P plant uptake, along a tide-maintained gradient of varying inundation frequencies. A very detailed set of Eh measurements were performed along the transect at several depths to investigate the Eh-dependence of P availability as influenced by inundation regimes and species-specific oxidation capacities of mangrove trees. Characteristics of the forest structure are detailed and correlated to the P content of the vegetation.

Material and methods

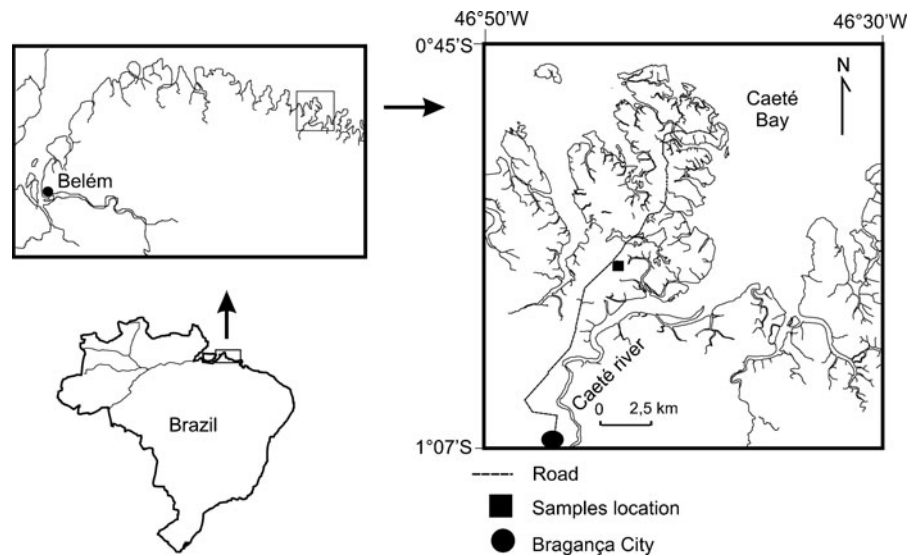
Study area

The investigated area is part of a large continuous mangrove forest belt at the northern coast of Pará State (Fig. 1) (Lara 2003). The study area is located at the upper intertidal central part of the 180 km² Bragança Peninsula (00°55'65"S, 46°40'09"W) which is in proximity to the Caeté River estuary and Bragança City limits (Fig. 1) (Behling et al. 2001). Several tidal channels cross the peninsula that allow macrotides, with ranges from 3 to 4 m, to flood most of the forest (Cohen et al. 1999). The dry season extends from July to November and the rainy season from December to June. The annual rainfall varies between 2,500 mm and 3,000 mm (Souza-Filho 1995). Mangrove forests are the dominant vegetation (90%) with the remaining area made up of salt-marshes, salt-flats, and restinga (sand vegetation) (Krause et al. 2001; Mehlig 2001). A road between the city of Bragança and the village Ajuruteua (on the northern part of the peninsula) crosses the peninsula and facilitates access to the study site. The distance from the nearest tidal creek or channels is about 2 km.

Topography and inundation frequency

In order to evaluate the IF along a 700-m transect perpendicular to the Caeté estuary, a topographic survey

Fig. 1 Study area on the central sector of the Bragança Peninsula



of the mangrove forest floor was undertaken during a spring tide in September 2001, following the methods of Cohen et al. (2001). The IF was calculated from the tide table and is expressed as the number of days per year at which the tide reached each topographic height along the transect (days/year, d.y^{-1}).

Forest structure

To characterize the composition and structure of the forest, eleven 10×10 m plots were positioned along the transect (4 plots at high intertidal, 4 plots at middle intertidal, 3 plots at low intertidal) according to the methods of Cintrón and Scheffer-Novelli (1984). In each plot, all trees with a stem diameter at breast height (dbh) >2.5 cm of each plot were measured, identified and tree height measured. Basal area ($\text{m}^2.\text{ha}^{-1}$), species density ($\text{trees}.\text{ha}^{-1}$), and tree volume as a cylinder ($\text{m}^3.\text{ha}^{-1}$) were calculated.

To examine the influence of individual tree species on the soil physical-chemical environment and how that varies across the tidal gradient, detailed measurements were taken near the base of selected trees in each plot. One canopy tree of the subdominant species in a plot was selected and labeled the “principal” tree. Three to five canopy trees of the dominant species near the principal tree were subsequently selected and labeled neighbors. Within the mixed-stand plots, subplots were established for an equal representation of the two co-dominant species.

Soil redox potential (Eh) analysis

From the eleven plots, nine plots (3 plots at high intertidal, 3 plots at middle intertidal, 3 plots at low intertidal) named as stations for the physico-chemical and chemical measurements were chosen. Measurements of soil redox potential were made during the rainy season (December 2001 to April 2002) using a platinum electrode. Along the 9 station transect, vertical profiles were carried out with electrodes during low tide at close proximity (50–100 cm) to pneumatophores (*Avicennia germinans*) and prop roots (*Rhizophora mangle*) of the principal tree and one of the neighbouring trees. The instrument employed was a 50 cm length Eh electrode (Microscale Measurements) connected to a separate reference electrode (Ag/AgCl) filled with a 3M KCl solution. The electrode was linked to a digital millivolt meter and fixed to a depth gauge up to a 50 cm depth. Each profile was measured in situ down to 50 cm with a resolution of 5 cm. The redox variation (ΔEh) relative to the soil aeration status for each mangroves species (species-specific), space between 0 and 40 cm-thick sediment profiles, corresponding to the root oxidation zone, was recorded. Non replicate profiles were made at each location. The electrode was inserted into the sediments for several minutes until near stable values were reached. The electrode was checked and calibrated using seven separate phosphate buffer (200 mM) in 50 ml de-ionized water

saturated with qinhydrone (~1 crystal/5 ml phosphate buffer) before, during, and after the field work. The seven pH-equidistant buffers were prepared taking into account the field pH range (6–8). The potential of this saturated redox buffer depends only on pH and temperature, thus after regression analysis, the millivolt (mV) values of the qinhydrone solution at each pH were compared to the respective standard solutions at 25°C and calculated according Nässer (1976).

Sediment analysis

At each station, a 1 m long stainless steel corer was used for sediment sampling. One core was taken between 50 to 100 cm from the trunk of the principal tree and one core between 50 to 100 cm from the base of one of the neighboring trees. At each station these paired stations, subjected to the same inundation frequency, allowed a comparison of the species-specific effects on the sediment chemistry. Cores were taken in five cm deep intervals to 50 cm (0–5, 5–10, 10–15, etc. up to 50 cm) and thereafter at 25 cm intervals down to 1 m depth. The samples were stored in dark airtight polyethylene bags at 4°C. Total soluble salts were extracted from a soil-water slurry 1:5 w/v (weight/volume) by homogenizing with a glass stirrer and allowing to stand 12 h. Conductivity was determined in the clear supernatant (WTW-LF 197) and used to calculate the salt content of the sediment sample after Ensminger (1996). The 5 cm sections of the sediment cores were homogenized, oven dried at 60°C to a constant weight, and then powdered in a porcelain mortar to pass through a 1 mm mesh. The fraction of total phosphorus (tot.-P) potentially readily available for biological uptake is the inorganic form termed extractable phosphorus (extr.-P). The method used for extr.-P (Hesse 1957; Hesse 1961) involves the extraction of 10 g DW sediments with 100 ml of a weak acid (pH 4.8) solution, containing 10% w/v sodium acetate in 3% v/v (volume/volume) acetic acid. This buffer solution is known as Morgan's extractant (Allen 1989). After shaking for 30 min the solution was filtered and analyzed by colorimetry after Grasshoff et al. (1983). The extr.-P data for the various depths were pooled, from which the 20–30 cm depth were presented here.

Leaf analyses

Green leaves of *A. germinans* and *R. mangle* were collected separately from the canopies of the principal tree and the two neighboring trees. To ensure a representative sample of each station, a batch of 8 leaves per tree in three width categories (3, 4 and 5 cm) from the penapical stem position of branches at the top (sun leaves) and middle of the canopy (shadow leaves) composed one sample. The samples were dried to a constant weight (60°C, 60 h) (Medina et al. 2001) and powdered (without petiole) in a porcelain mortar (~1 mm mesh). Total P in the leaves (leaf-P) was estimated as inorg.-P following a suitable dissolution procedure. The organic material was combusted (450°C, 24 h) (Allen 1989) and the ash material was digested after Solorzano and Sharp (1980). For the digestion, 5 ml of saturated acid persulphate solution diluted with 5 ml of de-ionized water was added to the 20 mg samples. The samples were autoclaved (115°C, 30 min) in closed teflon bottles (Grasshoff et al. 1983). Subsequently, 5 ml of the solution was transferred into reaction vials for colorimetry after Grasshoff et al. (1983) using a Hitachi U-2000 Spectrophotometer at a wavelength of 880 nm. The chemical analyses for extr.-P and leaf-P were conducted in duplicates and triplicates, respectively. The experimental errors are expressed as a variation coefficient (average of ~4.6%).

Statistical methods

For the statistical analysis the physico-chemical and chemical measurements of sediments considered the data pooled across the 20–30 cm depth. A Pearson correlation coefficient was used to evaluate the linear relationship among the study variables (IF, salinity, Eh, extr.-P, P-leaf, tree height, tree volume and basal area) (Davis 1973). We conducted an ANCOVA to compare differences in the mean salinity, Eh and extr.-P among the three mangroves forest stands without the influence of IF. Similarly, Eh was modeled as the covariate to evaluate the behavior of extr.-P among stands by minimizing the influence of Eh. Afterwards, to compare leaf-P concentrations among the three mangroves forests stands, IF, salinity, Eh and extr.-P were included as covariates to eliminate their

influence on leaf-P concentrations. Finally, a MANCOVA was used to compare the average tree height, tree volume, and basal area among stands adjusted for leaf-P concentrations with the intention of evaluating the possible influences of these biological parameters on forest structure across the gradient (Johnson and Wichern 1999).

Results

Topography and inundation frequency

Three main topographic characteristics were notated as high intertidal (HI), middle intertidal (MI) and low intertidal (LI) which may be recognized based on vegetation features along a well defined IF gradient (Table 1). At the boundaries of HI and LI with MI, slight topographic depressions of 5–8 cm were documented. These depressions were likely the remains of a paleochannel, here identified as depression one (D1) and two (D2), respectively. The HI zone (including D1) was delimited by an IF range of 41–67 d.y⁻¹ and was inundated only during spring tides. The MI zone was identified by an IF range of 80–101 d.y⁻¹, whereas LI (including D2) ending 2 km from the Caeté Estuary was inundated 124–162 d.y⁻¹. Inundation frequencies of the depressions indicate a

higher residence time of the flood water compared to the linear change across the transect.

Forest structure

The mangrove trees present in the study area were *Rhizophora mangle* (Rhizophoraceae), *Avicennia germinans* (Acanthaceae) and *Laguncularia racemosa* (Combretaceae) (Table 2). The dbh classes distribution indicates that the majority of trees belong to the smallest diameter size class (Fig. 2a). *A. germinans* occurs in all diameter classes (<2.5; <72.5–82.5 cm), but is most abundant in the smallest class. *R. mangle* occurs specifically in the <2.5 and >2.5–12.5 cm diameter classes, whereas *L. racemosa* occurred in the <2.5 and >2.5–12.5 cm size classes only. Concerning tree heights, the majority of trees belong to the second smallest height class (7.5 m) (Fig. 2b). *A. germinans* dominated all height classes. The majority of *R. mangle* trees occur between the heighest classes from >7.5–12.5 m and >17.5–22.5 m.

The species abundances and structural parameters varied among the three tidal zones (Table 2). The HI was dominated by *A. germinans* (99.1%) with numerous small trees with heights between 2 m and 19 m and stem diameters between 2.5 cm and 26 cm (Table 2). The MI was a mixed forest comprised of *A. germinans* (55.1%), *R. mangle* (39.1%) and *L.*

Table 1 Summary of the inundation frequency (IF) calculated as days per year, redox potential (Eh) and species-specific redox variation (Δ Eh), phosphorus concentrations (mgP.g⁻¹) in sediments as extractable P (extr.-P) and in 4-cm

leaves width as P-Leaf along the inundation gradient. Mean values are reported \pm SD ($n=9$ to 33) for the 0–40 cm-thick sediment profile ranges in parentheses

Stations	N	IF (d.y-1)	Extr.-P (mg P.g-1 DW)	Eh (mV)	Species	Δ Eh (mV)	Leaf-P (mg P.g-1 DW)
HI	2	51 \pm 14 (41–62)	0.05 \pm 0.02 (0.02–0.08)	225 \pm 44 (104 to 294)	<i>A. germinans</i> <i>R. mangle</i>	139 89	1.05 \pm 0.03
D1	1	67	0.10 \pm 0.05 (0.04–0.20)	11 \pm 77 (–110 to +141)	<i>A. germinans</i> <i>R. mangle</i>	25 76	1.10 \pm 0.05
MI	3	92 \pm 9 (80–101)	0.06 \pm 0.02 (0.05–0.10)	164 \pm 67 (256 to 57)	<i>A. germinans</i> <i>R. mangle</i>	22 50	1.16 \pm 0.04 1.23 \pm 0.02
D2	1	124	0.13 \pm 0.05 (0.06–0.19)	41 \pm 83 (–80 to +184)	<i>A. germinans</i> <i>R. mangle</i>	65 59	1.40 \pm 0.02
LI	3	145 \pm 17 (128–162)	0.05 \pm 0.01 (0.03–0.08)	46 \pm 71 (–121 to +145)	<i>A. germinans</i> <i>R. mangle</i>	193 66	1.40 \pm 0.10

Abbreviations: *HI* high intertidal, *MI* middle intertidal, *LI* low intertidal, *D* depressions

Table 2 Summary of mangrove forest structure data along the inundation gradient. Mean values are reported \pm SE, ranges in parentheses

Zone/Species	Stem N	dbh (cm)	Height (m)	Cylinder Volume (m ³ .ha ⁻¹)	Density (stems.ha ⁻¹)	Basal Area (m ² .ha ⁻¹)
HI						
<i>A. germinans</i>	115	7.1 \pm 4 (2.5–26)	7.7 \pm 7.6 (2–19)	46.8	2875.0	14.9
<i>R. mangle</i>	1	8.1	6.4	38	25.0	0.15
Total	116	7.1 \pm 3.9	7.1 \pm 3.5	84.8	2900	15.5
MI						
<i>A. germinans</i>	38	10.5 \pm 7.4 (2.5–42.5)	7.5 \pm 2.2 (4–16)	134.5	1266.7	16.3
<i>R. mangle</i>	27	14.6 \pm 4.9 (5.9–25.5)	10 \pm 3.2 (5–16)	210	900.0	16.7
<i>L. racemosa</i>	4	7.1 \pm 0.8 (5.9–7.6)	5.6 \pm 0.8 (5–6.6)	23	133.3	0.5
Total	69	11.9 \pm 6.6	8.4 \pm 2.9	367	2300	33.5
LI						
<i>A. germinans</i>	7	34.4 \pm 25.2 (6.5–81.8)	11.5 \pm 2.8 (6.5–15)	1683	233.3	31.7
<i>R. mangle</i>	8	14.5 \pm 5.6 (10.8–22)	8.9 \pm 2.3 (7–12)	27	266.7	5.0
<i>L. racemosa</i>	2	6.9 \pm 0.07 (6.9–7)	5.5 \pm 2.1 (4–7)	181	66.7	0.2
Total	17	21.8 \pm 19.4	9.6 \pm 3.1	1891	567	37

Abbreviations: *Dbh* diameter at breast height, *HI* high intertidal, *MI* middle intertidal, *LI* low intertidal

racemosa (5.8%) with a much lower density of trees than HI. Tree height varied between 4 m and 16 m, and tree diameters ranged from 2.5 cm to 42.5 cm. The LI also was a mixed forest with a higher occurrence of *R. mangle* (47.1%) and *A. germinans* (41.2%) whereas *L. racemosa* comprised 11.8% of the total. The tree height varied between 4 m and 15 m, tree diameters ranged between 6.5 cm and 81.8 cm, and stem density was the lowest of all three zones.

Physical-chemical patterns

In the 50-cm vertical profile sediment Eh varied widely ranging from –121 to +294 mV (Fig. 3a). The variation in Eh along the transect was strongly associated with the IF, vegetation zonation and vertical stratification of the root oxidation zone (0–40 cm depth). At LI, the lowest Eh value (–121 mV) occurred under *A. germinans* showing the highest

Δ Eh (193 mV) of the entire transect (Table 1). At D1, the lowest Eh values occurred beneath *R. mangle* (–110 mV) showing higher Δ Eh (76 mV) than *A. germinans*, in contrast to D2 with lowest Eh values occurring below *A. germinans* (–80 mV) showing higher Δ Eh (65 mV) than *R. mangle*.

In the Eh isopleth diagram of the sediments along the flooding gradient (0–50 cm depth), high Eh (200 mV) levels were found in the HI sediments in relation to sediments of the LI zone (0–100 mV) (Fig. 3a) whereas both the depressions had Eh values near 0 mV. Salinity levels in the surface sediments (<20 cm) were between 20 and 30‰ across the entire transect, whereas the salinity levels in the sub-surface sediments (20–30 cm) were maintained in 40‰ among the forest stands (Fig. 3b). Salinity increased to 50 and 70‰ in the deeper sediments (50–100 cm). In the HI zone, the salinity distribution showed a strong gradient with depth. Conversely, in the LI

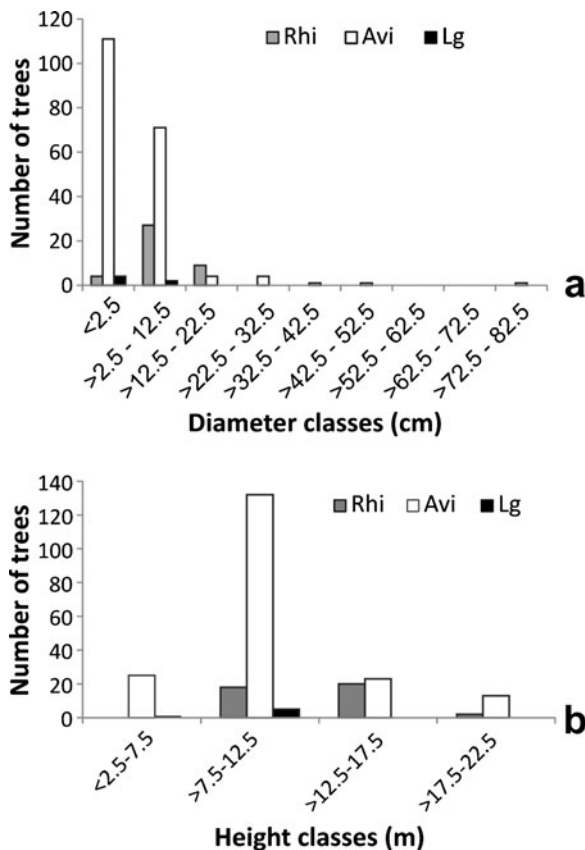


Fig. 2 Distribution of diameter classes (a) and height classes (b) of mangroves trees. Notes: Rhi, *R. mangle*; Avi, *A. germinans*; Lg, *L. racemosa*

zone, which is under continuous tidal influence, the salinity profile was less pronounced with the salinity decreasing to only 40‰ in the deeper sediments.

Phosphorus distribution patterns

Concentrations of extr.-P in the 40-cm vertical sediment profile varied from 0.02 to 0.20 mg P.g⁻¹ DW along the transect, with highest values (0.09–0.16 mg P.g⁻¹ DW) found in the depressions. Extr.-P concentrations in the 20 to 30 cm-depth showed a unique pattern along the tidal gradient, characterized by higher values in the *R. mangle*-dominated stand in the LI zone as compared to lower values found in the HI zone, an *A. germinans*-dominated stand (Fig. 4). The relationship between extr.-P (20–30 cm) and inundation frequency (IF) showed a significant Pearson correlation ($r=0.89$, $n=33$, $p<0.05$) indicating a trend of higher extr.-P levels towards LI (Table 3).

Phosphorous in leaves showed a clear trend of leaf-P depletion corresponding to three maturity stages: (1) young age class (3 cm) had the highest P content (2.0 ± 0.06 mg P.g⁻¹ DW), (2) immature to mature age class (4 cm) had depleted values of 1.4 ± 0.10 mg P.g⁻¹ DW, and (3) mature to senescent leaves (5 cm) had the lowest P content (1.35 ± 0.04 mg P.g⁻¹ DW). Considering the different types of forests, *Avicennia* stands presented the largest leaf-P value (1.6 ± 0.03 mg P.g⁻¹ DW) in D1, while *Rhizophora* stands showed the highest values (2.0 ± 0.06 mg P.g⁻¹ DW) in D2 (Fig. 5a). A leaf-P reduction ranging between 55% and 73% from mature/senescent (5 cm) to young (3 cm) leaves was observed, showing the lowest value (~55%) at D2 (Fig. 5b). There was a highly significant positive correlation between IF and P concentrations in mature leaves of *R. mangle* and *A. germinans* (Table 3) which was consistent with the strong correlation between extr.-P in sediment and leaf-P (4 cm) (Table 3). Leaf-P levels of *A. germinans* and *R. mangle* showed significant positive correlations with individual tree height, tree volume and basal area (Table 3).

The mean salinity among the three mangrove forest stands after adjusting for IF was not significant ($p=0.16$) nor was there a significant relationship between IF and salinity ($p=0.52$) (Table 4). However, when comparing the average Eh and extr.-P among the three mangroves forest stands a significant difference ($p<0.001$) was noted (Table 5). The ANCOVA also showed a linear relationship between IF and Eh ($p<0.001$) and IF and extr.-P ($p=0.00$) (Table 4). Although the results indicate an influence of IF on Eh and extr.-P, Eh and extr.-P show significant differences among forests stands independent of IF.

Concentrations of extr.-P without the effect of the Eh is significantly different along the three mangroves forests stands ($p=0.00$) (Table 5). The results indicated an Eh influence but does not confound the mean extr.-P variation along the stands. The Pearson correlation between these variables indicated a significant negative correlation ($p=-0.86$) (Table 3) which was supported by the ANCOVA.

Mean leaf-P concentrations among the three mangroves forests stands were not significantly different ($p=0.214$) (Table 6). A significant relationship of leaf-P with IF ($p=0.006$) and Eh ($p=0.005$) was observed (Table 6). These results suggest that the IF and Eh influence the outcome of the mean

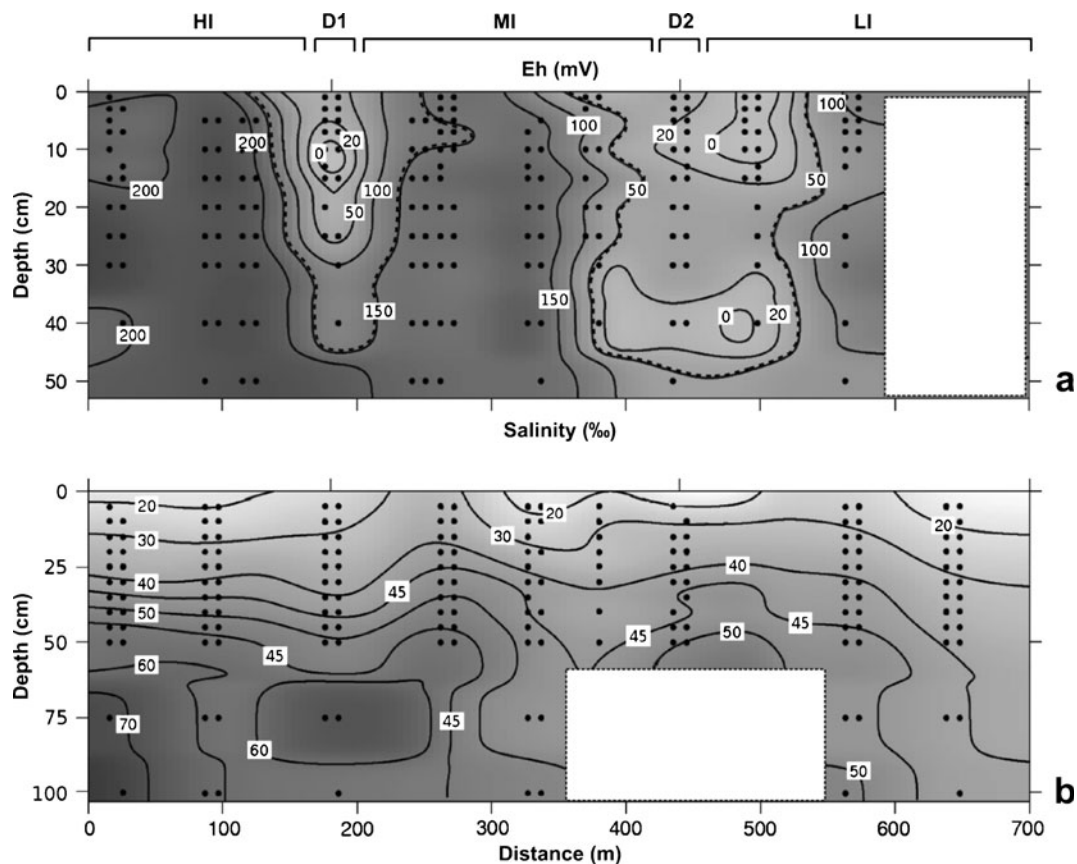


Fig. 3 Isopleth diagram of redox potential (Eh) (a) and salinity (b) measured in sediment along the tidal inundation gradient. Black points indicate the paired stations and blank squares

indicate no data. Notes: HI, high intertidal; MI, mid intertidal; LI, low intertidal; D, depression

comparison of leaf-P among stands and can be considered confounding factors for comparing the leaf-P along the mangroves forests stands.

The comparison of the vector averages of tree height, tree volume, and basal area to leaf-P concentrations was not significant indicating that the leaf-P does not influence the forest structure along the gradient (Table 7).

Discussion

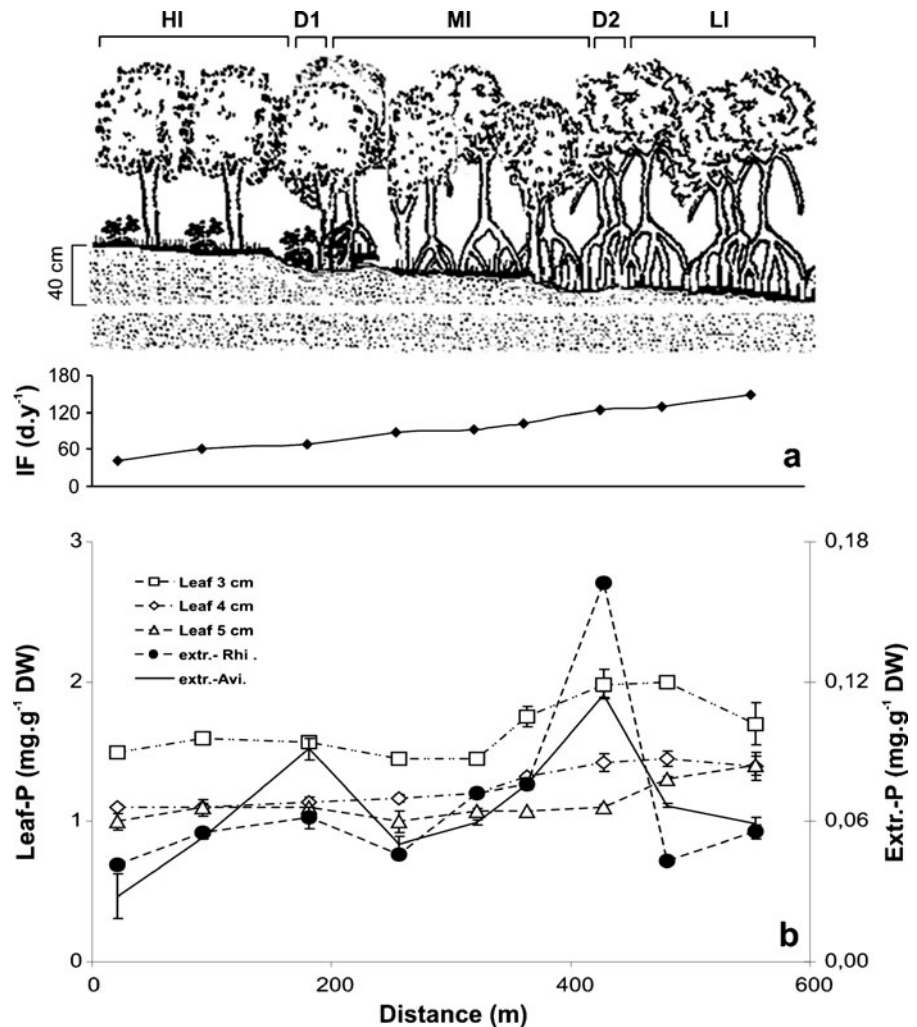
Inundation frequency, salinity and forest structure

Due to the wide variation of IF along the transect, salinity ranges from hyper saline conditions (70‰) at HI to minimal salinities of 20‰ in the LI zone similar to that of the estuarine water salinity (Fig. 3a). Because the HI is flooded during the spring tides

only, evapotranspiration results in hyper saline conditions (60–70‰) in the deeper sediments (50–100 cm). Higher salinity (70‰) at deeper layers may suggest salt exclusion by roots (Gordon 1993). These results are consistent with Furtado da Costa (2000) who reported similar values in deep sediments near the study area of this work. Moreover the salinity in the sub-surface sediments (20–30 cm) did not vary among the forest stands (Fig. 3b) supported by the non correlation between salinity and IF (Tables 3 and 4).

Considering the entire depth salinity gradient (0–100 cm) and not only the non varying isoline of 40‰ at sub-surface sediments (20–30 cm), zonation of mangrove trees and characteristics of forest structure varied according to the inundation/salinity gradient. The dominance of small trees of *A. germinans* at HI is a consequence of the high salinity and infrequent tidal inundation. *A. germinans* is a more salt-tolerant

Fig. 4 **a** Variation of the inundation frequency (IF) calculated as the number of days in the year in which water height at high tide reached the topographic contour level. **b** Extractable phosphorus (Extr.-P) in sediments (20–30 cm) and leaves phosphorus (Leaf-P) of several width-sizes along the gradient distance. *Notes:* HI, high intertidal; MI, mid intertidal; LI, low intertidal; D, depression; Avi, *A. germinans*; Rhi, *R. mangle*



species able to colonize high saline areas (Tomlinson 1986). In the transition from HI to MI, the salinization of superficial as indicated by the 30‰ salinity isoline most likely allows for the continued dominance of *A. germinans* (Fig. 3b, Table 2). In the MI, heterogeneity in sediment salinity is consistent with the establishment of a mixed forest stand (Colonnello and Medina 1998). *L. racemosa* appear as scattered individuals throughout the MI and LI zones and appear to prefer the depressions, as they occur along these sites (Upkong 1991) as well as in areas with stagnated water (Medina and Francisco 1997). At the LI, the lower salinity allows for the dominance of the less salt-tolerant species *R. mangle* (Egler 1948). Along the transect, the mean tree height increases from 7.1 m (HI) to 9.6 m (LI), which may be associated with the porewater salinity gradient (Table 2). An

inverse relationship between salinity and vegetation height (Cintrón et al. 1978; Lara and Cohen 2006) and with above-ground biomass (Sherman et al. 2003) has also been reported.

Physical-chemical pattern

Phosphorus content in sediments was directly correlated with IF (Fig. 5a, Tables 3, 4). Under anoxic conditions there is a release of extr.-P attributed to reduction-induced solubilisation of P-Fe/Al (Shapiro 1958; Silva and Sampaio 1998; Mendoza 2007). The coastal bedrock of Brazil, the so-called Barreiras Formation, shows a pattern which reflects tropical lateritic weathering, where the lower unit consists of mud and sand deposited under tidal influence (Behling and Costa 2004). Here, the strong chemical weathering of

Table 3 Summary of Pearson correlations between extractable phosphorus (extr.-P) versus inundation frequency (IF), redox potential (Eh) vs. IF, leaves phosphorus (leaf-P) vs. IF, salinity vs. IF, salinity vs. extr.-P, leaf-P vs. tree volume, leaf-P vs. tree height, and leaf-P vs. basal area

Variables	r	p	n
extr.-P vs. IF	0.89	<0.05	33
Eh vs. IF	−0.75	<0.05	33
leaf-P vs. IF	0.96	<0.05	33
salinity vs. IF	−0.20	<0.05	33
salinity vs. extr.-P	−0.41	<0.05	33
Eh vs. extr.-P	−0.86	<0.05	33
Eh vs. Salinity	−0.40	<0.05	33
leaf-P vs. tree volume	0.60	<0.05	33
leaf-P vs. extr.-P	0.86	<0.05	33
leaf-P vs. tree height	0.77	<0.05	33
leaf-P vs. basal area	0.65	<0.05	33

Abbreviations: *r* Pearson's correlation, *p* p-value, *n* number of samples

the immature lateritic source supplies oxidized particles (Fe(hydr)oxides) (Costa 1991; Costa et al. 2004). The extr.-P concentrations reported in this study were consistent with previous studies in the Bragança Peninsula (Frizano et al. 2003), but higher than values reported in other studies (Hesse 1961; Boto and Wellington 1984).

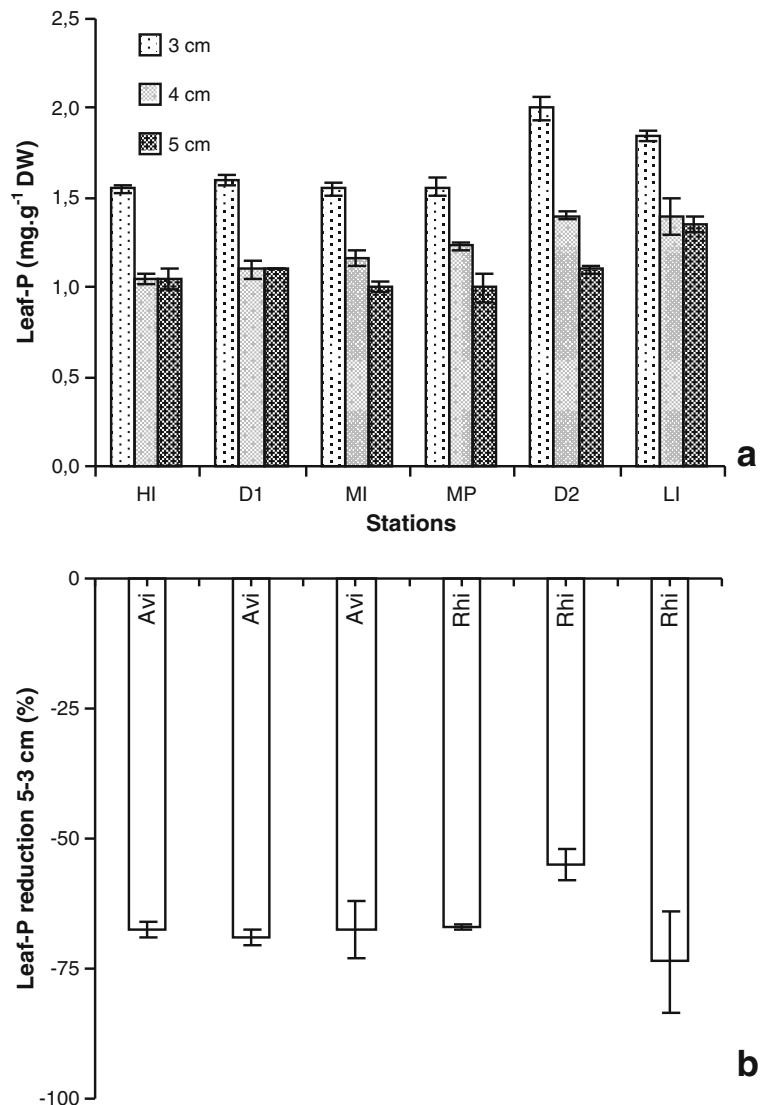
The less reducing conditions in sediments of the *Avicennia*-dominated forest (HI) reflect well-drained sediments exposed to low IF (Ponnamperuma 1972). At most stations, the Eh vertical profiles were characterized by two oxidation horizons similar to the redox stratification model proposed by Clark et al. (1998) for an *Avicennia*-dominated mangrove forest. The upper oxidation zone most likely was linked to the diffusion of atmosphere oxygen, whereas the lower oxidation zone was linked to the gas transport by mangrove root systems. The radial extension of this oxidized zone around the root tips, *i.e.*, higher redox potential near the root tips than the bulk sediment, was found to extend from <3 cm to 0.5 m (McKee 1993). Differences among species are of interest since they provide information with respect to their relative tolerance to flooding stresses.

The behaviour of extr.-P in the *R. mangle* and *A. germinans* stands differed in their responses to low sediment Eh conditions. Such differences may be partially explained by species distribution patterns

and species-specific oxidation abilities. Previous studies have revealed a significantly greater root-induced oxidation capacity for *A. germinans* in comparison to *R. mangle* under strongly reducing conditions (Nickerson and Thibodeau 1985; McKee et al. 1988; Andersen and Kristensen 1988; Alongi et al. 2000). At D2 and LI, a greater root-induced oxidation capacity for *A. germinans* was recorded under these highly reducing conditions (0–100 mV) (Table 1, Fig. 3a). The lower values of extr.-P under *A. germinans* as compared to *R. mangle* under these reducing conditions (Fig. 4b) suggests that the higher root-induced oxidation in *A. germinans* limits P availability and consequently the distribution of extr.-P in the frequently inundated zone (LI). Below *A. germinans* trees in the LI zone, the intense species-specific redox variation (ΔEh 193 mV) immobilized the extr.-P likely by increasing P-Fe/Al complexes, as freshly precipitated ferric hydroxide has a large P adsorption capacity (Saleque and Kirk 1995). In addition, the greater root-induced oxidation capacity of *A. germinans* at D2 was reflected in lower extr.-P concentrations (0.11 mg P.g^{−1} DW) in comparison to the higher extr.-P concentrations under *R. mangle* (0.16 mg P.g^{−1} DW) (Fig. 4b), consistent with findings by McKee (1996), and Ellison and Farnsworth (1997). Along the transect, porewater pH ranged from 6.3 to 7.5, showing slightly basic values in HI and MI, and slightly acidic values in LI (Mendoza 2007, data unpublished). Phosphorus availability is greatest in the pH range between 6 and 7 when interacting with Fe/Al- and Ca-P minerals (Havlin et al. 1999; Georgantas and Grigoropoulou 2006), and the slightly lower pH values in the LI zone (Mendoza 2007) should favor higher extr.-P concentrations which is supported by the strong correlation found between IF and extr.-P (Table 3). The diffuse supply of P would therefore depend on the balance between increased sorption by ferric hydroxide and an increased release from acid-soluble forms (Saleque and Kirk 1995).

In principle, anoxic conditions (Eh<0 mV) promotes the formation of iron sulphides (*i.e.* pyrite) via the polysulphide pathway (Wilkin et al. 1996; Rickard and Morse 2005). Studies of sulphur, iron (Fe), and P dynamics in other wetlands indicate that a strong sulphide/reactive Fe dependency controls P solubility under reducing conditions (Boto and Wellington 1984; Caraco et al. 1989). The latter hypothesis

Fig. 5 **a** Distribution of leaves phosphorus (leaf-P) of several width-sizes. **b** Range of leaf P reduction from mature/senescent (5 cm) to young (3 cm) leaves width-sizes. *Notes:* HI, high intertidal; MI, mid intertidal; LI, low intertidal; D, depression; Avi, *A. germinans*; Rhi, *R. mangle*



suggests that at $Eh < 0$ mV iron sulphides can prevent the re-supply of iron (hydr)oxides to surface

sediments, enhancing the bioavailability of reactive P for plant uptake. Previous studies (Lacerda et al.

Table 4 Covariance analysis (ANCOVA) for salinity, redox potential (Eh) and extractable phosphorus (extr.-P) in sediments with inundation frequency (IF) as covariate parameter along the *A. germinans*-dominate stand, mixed stand and *R. mangle*-dominated stand

	Salinity					Eh				extr.-P			
	DF	SS	MS	F	p	SS	MS	F	p	SS	MS	F	p
IF	1	25.03	25.03	0.43	0.52	162670.5	162670.5	29.68	0.0000	0.0067	0.0067	40.66	0.0000
Forest	2	225.07	112.5	1.93	0.16	100271.9	50135.9	9.15	0.0000	0.0087	0.0044	26.77	0.0000
Erro	29	1694.6	58.4			158943.0	5480.8			0.0048	0.00016		
Total	32	2003.3				599657.7				0.0112			

Abbreviations: *DF* degrees of freedom, *SS* sum of squares, *M* mean, *F* statistic test, *p* p-value

Table 5 Covariance analysis (ANCOVA) of extractable phosphorus (extr.-P) in sediments with redox potential (Eh) as covariate parameter along the *A. germinans*-dominate stand, mixed stand and *R. mangle*-dominated stand

	DF	SS	MS	F	p
Eh	1	0.006783	0.006783	42.342	0.000
Forests	2	0.012227	0.006114	38.162	0.000
Error	29	0.004646	0.000160		

Abbreviations: *DF* degrees of freedom, *SS* sum of squares, *M* mean, *F* statistic test, *p* p-value

1995; Sherman et al. 1998) have attributed a large difference in sediment P to vegetation type and demonstrate that species composition shifts may result in large edaphic changes if strong plant-soil relationships exist. In Bragança Peninsula, in the same study area, the hypothesis that shifts in species composition, structure, and productivity also have a successional component which was recently supported by Berger et al. (2005) and Menezes (2006).

The leaf-P content was consistent with previous studies in the Bragança Peninsula (Medina et al. 2001), but was higher as compared to other studies (Boto and Wellington 1983; Gong and Ong 1990; Silva 1992), probably due to the abundant extr.-P (Frizano et al. 2003). The highest leaf-P concentrations in the more flooded zone (Fig. 4) is consistent with previous studies carried out in mangrove forests of North Australia (Cintron et al. 1978; Boto and Wellington 1983) and Southeast Brazil (Silva 1992). The mature (4 cm width) leaf group showed the most sensitive response to variations in available P as

Table 6 Covariance analysis (ANCOVA) of phosphorus in leaves (leaf-P) with inundation frequency (IF), salinity, redox potential (Eh) and extractable phosphorus (extr.-P) as covariate parameter as along the *A. germinans*-dominate stand, mixed stand and *R. mangle*-dominated stand

	SS	DF	MS	F	p
FI	54.620	1	54.620	87.439	0.006
Eh	57.934	1	57.934	92.745	0.005
Salinity	6.866	1	6.866	10.991	0.304
extr.-P	7.310	1	7.310	11.702	0.289
Forest	20.387	2	10.194	16.319	0.214962
Error	162.412	26	6.247		

Abbreviations: *DF* degrees of freedom, *SS* sum of squares, *M* mean, *F* statistic test, *p* p-value

Table 7 Multivariate covariance analysis (MANCOVA) of height and volume tree, and basal area with leaves phosphorus (leaf-P) as covariate parameter as along the *A. germinans*-dominate stand, mixed stand and *R. mangle*-dominated stand

	Test	Value	F	Effect DF	Error DF	p
leaf-P	Wilks	0.891	1.100846	3	27	0.365
Group	Wilks	0.734	1.499870	6	54	0.195

Abbreviations: *F* statistic test, *DF* degrees of freedom, *p* p-value

indicated by the highest correlation with extr.-P in comparison to the other leaf sizes (Table 3). The correlation between P in mature leaves and extr.-P in the sediments might be a useful indicator of nutrient status in mangrove forests (Boto and Wellington 1984; Medina 1984; Marchand et al. 2004).

The increase in P content from mature/senescent (5 cm) to young-leaves (3 cm) (Fig. 5b), termed here as leaf-P reduction, can be interpreted as a consequence of phosphate mobility in the phloem that is translocated from old to young leaves in response to nutrient stress. Consequently, old leaves may be a better indicator of deficiency of these elements than young leaves (Chapin and Cleve 1989). The leaf-P reduction was consistent with the P retranslocation value (60%) reported by Medina (1984). At D2, the leaf-P reduction in *R. mangle* decreased in the P resorption range (20–50%), reported by Feller et al. (1999), and is associated with the abundance of extr.-P due to the higher residence time of flooding water at this site. This nutrient-use efficiency is important to the within-stand nutrient cycling.

Initially the hypothesis that the IF was controlling the physical-chemical characteristics leading to the variation of salinity, Eh and extr.-P was considered. Thus the sediment-plant relationship could be consider given that the interaction between salinity, Eh and extr.-P in sediments, and the leaf-P along the flooding gradient may explain the mangrove zonation in Bragança. In this case, the extr.-P and leaf-P could be directly related to height and tree volume and basal area.

Although significant correlations between leaf-P and tree height, tree volume and basal area were found (Table 3), the ANCOVA results showed that Eh and extr.-P in sediments were the variables most influenced by flooding with a consequent influence on leaf-P concentrations (Tables 4, 5, 6). Fertilization experiments performed with *R. mangle* have found

that P promotes foliar and stem development (Koch and Snedaker 1997), and enhances the stem hydraulic conductivity area, which subsequently controls the growth of dwarf mangroves (Lovelock et al. 2006; Feller et al. 2007). In contrast, our data suggests that leaf-P does not influence patterns in tree height, tree volume nor basal area across the gradient in the Bragança Peninsula (Table 7). Even though numerous biotic and abiotic factors contribute to mangrove forest structure (Upkong 1991; Matthijs et al. 1999; Boto and Wellington 1983; Chen and Twilley 1999, Sherman et al. 2003; Lovelock et al. 2005), in Bragança Peninsula, at least during the rainy season, Eh and extr.-P were the factors controlling the leaf-P.

Conclusions

The mangrove forest showed a clear species zonation pattern with the dominance of *A. germinans* in the HI zone and *R. mangle* dominant in the LI zone. The species zonation patterns are determined by variations in IF and salinity. The interaction of different physical-chemical characteristics between sediment porewater and flood-water seems to control the concentration of P in the aqueous phase available to the mangroves.

Greater redox variation (ΔEh) and higher oxidation was found in the root zone of *A. germinans* as compared to *R. mangle* in the LI region which appears to control P availability. The higher root-induced oxidation of sediments under *A. germinans* limited the availability of P and consequently its distribution; whereas the much lower vertical redox gradient under *R. mangle* trees results in reducing conditions favoring the formation of extr.-P, and therefore can be considered as an adaptive response to nutrient uptake under waterlogging conditions. The conditions described could contribute to mangrove zonation and specie dominance in specific zones.

The interrelationships between waterlogging conditions, porewater salinity and P dynamics in sediments influence the forest structure; the relative importance of these factors varies according to the particular position along the tidal gradient. Moreover, the concentration of leaf-P does not appear to influence the tree height, tree volume or basal area. These results have significant implications for the

understanding of how flood gradients determine phosphorus status in mangrove ecosystems.

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