THE INFLUENCE OF EDAPHIC FACTORS ON THE SCLEROPHYLLY OF MANGROVE TREE SPECIES IN SOUTHERN BRAZIL

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Received for publication: 22/05/2020 – Accepted for publication: 25/01/2022

Resumo

A influência dos fatores edáficos na esclerofilia de espécies arbóreas de manguezais no sul do Brasil. Manguezais são ecossistemas costeiros, sujeitos a condições ambientais limitantes e constituídos por comunidades arbóreas, cujas espécies apresentam adaptações morfológicas e fisiológicas para se desenvolver sob condições de estresse. A esclerofilia é uma resposta à ambientes com múltiplos estresses. Nas florestas de mangue, esses estresses são induzidos principalmente pela salinidade, frequência da maré, inundação do solo e limitação de nutrientes. O objetivo deste estudo foi estabelecer se o grau de esclerofilia foliar, expresso na morfologia das folhas e nos teores de nutrientes nas espécies arbóreas dos manguezais, está associado a condições edáficas e de salinidade. O estudo foi realizado em um manguezal no estado do Paraná, Brasil, onde foram amostradas duas áreas (franja e interior). Folhas de 15 indivíduos de cada espécie (*Avicennia schaueriana*, *Laguncularia racemosa* e *Rhizophora mangle*) e por área (franja e interior) foram coletadas para análises químicas e morfológicas. Amostras de solo adjacentes a cada árvore selecionada foram coletadas para análise de fertilidade. As amostras de solos da área da franja apresentaram maior teor de carbono, matéria orgânica, razão C:P, salinidade da água e predominância de areia que a área do interior do manguezal. A área foliar específica (AFE) mostrou que as espécies apresentam folhas escleróilas em diferentes graus: *L. racemosa >R. mangle >A. schaueriana*. Os diferentes graus de esclerofilia encontrados entre as espécies estudadas e entre as áreas indica que cada espécie possui estratégias próprias e que se manifestam distintamente em termos morfológicos e fisiológicos, mesmo desenvolvendo-se em condições ambientais similares.
Palavras-chave: área foliar específica, fósforo, nitrogênio, solo, salinidade.

Abstract

Mangroves are coastal ecosystems, subject to limiting environmental conditions and constituted by tree communities. The tree species have adaptations to develop under such stress conditions. The sclerophylly is a response to environments with multiple stresses. In the mangrove forests, these stresses are induced mainly by salinity, frequency of tidal influence, soil waterlogging, and nutrient limitation. The aim of the study was to establish if the degree of sclerophylly, expressed in leaf morphology and nutrient contents in tree species of mangroves is associated with edaphic and salinity conditions. The study was performed in one mangrove at Paraná state, Brazil, where two plots were sampled (fringe and interior). Leaves of 15 individuals of each species (*Avicennia schaueriana*, *Laguncularia racemosa* and *Rhizophora mangle*) for each plot (fringe and interior*)* were collected for chemical and morphological analysis. Soil samples adjacent to each selected tree were collected to perform fertility analyses. The fringe soils samples present higher carbon and organic matter, C:P ratio, pore water salinity and sand predominance. The specific leaf area (SLA) showed that species have sclerophyllous leaves in different degrees: *L. racemosa* > *R. mangle* > *A. schaueriana*. The different degrees of sclerophylly found among the studied species and among plots indicated that each species has its own strategies and that they manifest themselves distinctly in morphological and physiological terms, even when developing under similar environmental conditions.
Keywords: specific leaf area, nitrogen, phosphorus, soil, salinity

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INTRODUCTION

Mangroves are ecosystems that grow along protected sedimentary shores of tropical and subtropical coastlines (MITRA, 2013). The most important features of mangrove forests are defined by the periodic inundation by the tidal regime and the influence of both terrestrial and marine conditions. The soil of mangrove forests is permanently waterlogged, oligotrophic, unconsolidated, with fluctuating salinity, typically anoxic and rich in organic matter. Such environmental characteristics represent a stressful environment for the plant community and limit the development of mangrove forests (SPALDING *et al*., 2010). Although, mangrove tree species represent the most productive vegetal communities in world and can tolerate these limiting conditions by special adaptations, such as aerial roots, viviparous propagules, and sclerophyllous leaves (WANG *et al*., 2010; SERENESKI-LIMA *et al*., 2013; ARRIVABENE *et al*., 2014; NAIDOO, 2016). Thus, sclerophylly may have been a key adaptation to improve survival and allow high productivity in this environment.

Sclerophylly, by definition "hard-leaved", characterizes a non-specific response that plants develop to survive in an environment with a wide range of stresses (READ; SEASON, 2003). Sclerophyllous leaves are more resistant to herbivores, drought, and low soil fertility, due to features such as high leaf thickness and density, and low specific leaf area (sclerophylly index) (READ; SEASON, 2003). Sclerophylly is also linked to low water availability in xerophytic environments and, in mangroves, to conditions of high salinity (NAIDOO, 2010). Salinity is one of the most challenging conditions in the mangrove habitat and the plant community possesses a variety of mechanisms and strategies for salt management. Highly saline habitats induce in plants the development of mechanisms to aid in water conservation, such as an increase in epidermal and mesophyll thickness, compact palisade mesophyll, succulence, and small leaf area (WANG *et al*., 2010; NAIDOO, 2016), all of which are linked to sclerophylly and xeromorphy.

In mangroves, edaphic conditions are governed by the dynamics of tides, which results in an inundation gradient among areas within these forests. Along the floodplain gradient, physiographic plant types may be distinguished, with different structural and functional responses to dominant local physical processes (SCHAEFFER-NOVELLI *et al*., 2000; SEEDO *et al*., 2018). Fringes may be defined as mangroves that occur along seaward edges and experience the influence of regular flushing that maintains soil salinity close to that of seawater (SCHAEFFER-NOVELLI *et al*., 2000). Interior mangroves represent the mangrove forests that occur in the intertidal zone where there is infrequent tidal inundation, high evaporation, and consequently higher salinities (NAIDOO, 2010).

Fringe and interior mangroves frequently exhibit differences in species dominance and structure since a lower frequency of tidal flooding may result in a dominance of species with greater efficiencies of nutrient and water use (SCHAEFFER-NOVELLI *et al*., 2000; NAIDOO, 2010). Some interior mangroves (ex. Belize) are P limited because the increased waterlogging or other abiotic conditions result in soil nutrient transformations that reduce the availability of P relative to N (MEDINA *et al*., 2015). As consequence, trees in interior mangroves are more scrub-like with dwarfed, small and sparse vegetation (NAIDOO, 2010), while fringe mangroves have well developed trees.

In addition to inundation dynamics and zonation, some studies have indicated that the availability of nutrients, especially nitrogen (N) and phosphorus (P), plays an important role in mangrove growth (Lovelock *et al*., 2006a), and is linked to morphological and anatomical differences among species in environments of high or low nutrient availability. For example, mangrove species that grow in oligotrophic soils possess mechanisms for retaining and recycling nutrients, such as an increase in the sclerophylly of leaves over soils with low P (REEF *et al*., 2010).

Previous studies have shown that the three mangrove species in southern Brazil, *Avicennia schaueriana* Stapf and Leachman (Acanthaceae), *Laguncularia racemosa* (L.) C.F. Gaertn (Combretaceae) and *Rhizophora mangle* L. (Rhizophoraceae), are sclerophyllous to different degrees (SERENESKI-LIMA *et al*., 2013). Since sclerophylly is a response to a range of environmental conditions to which leaf morphology can respond, the aim of our study was to evaluate if differences in the edaphic conditions between the fringe and the interior of mangrove forests can affect leaf morphology and consequently the degree of sclerophylly of these species. Our hypotheses are: (1) the degree of sclerophylly is altered by changes in edaphic factors induced by tidal inundation; (2) the degree of sclerophylly is greater in the interior than in the fringe of the mangrove forest due the higher salinity at the interior plot.

MATERIAL AND METHODS

Study area: The study was performed on Rio Pinheiros, Guaratuba Bay, Paraná State (25º49' S and 48º35' W), southern coast of Brazil. Guaratuba Bay encompasses about 48.73 km^2 of the coast and has a subtropical mesothermic climate with hot summers and no dry season; it is classified as Cfa according Koopen's classification (MADI *et al*., 2015) The estimated average annual temperature varies between 20.8ºC and 22.0ºC and the annual precipitation is 2,520 mm (SIMEPAR, 2016). Three typical mangrove tree species occur in the study area: *Avicennia schaueriana*, *Laguncularia racemosa* and *Rhizophora mangle L.*

Avicennia schaueriana is a shrub, known as *siriúba* or black mangrove, and it is a native species from South America. Generally, this species occurs in areas with lower influence of tides. Their propagules are small, light, floating, and can travel long distances (TOMLINSON, 1994). *Laguncularia racemosa* is a mangrove tree, 12- 18 m tall, known as white mangrove. This species has a pantropical distribution and is typically restricted to the landward fringe of the mangrove communities**.** The single seed is sometimes viviparous (TOMLINSON, 1994). *Rhizophora mangle* is a tree species 5-10 m tall, known as red mangrove, distributed in estuarine ecosystems throughout the tropics. It is an important native species in coastal areas in tropical and subtropical America and is commonly found from low intertidal swamp margins. *R. mangle* is viviparous with high rates of propagule production (TOMLINSON, 1994).

Sampling design*:* We selected two mangrove areas along the shoreline of the Pinheiros River in Guaratuba Bay, and established a 300 m transect in each, extending from the fringe to the interior perpendicular to the shoreline. This 300 m transect represent the median point of the gradient between shoreline and forest transition. Two plots were delimited in each transect; fringe plot: adjacent to the margin of the river and interior plot: 250 m distant of the fringe plot (Figure 1). Light conditions are were similar between the two areas (fringe: 1563 ± 466 μmol.m^{-2}.s^{-1}; interior: 1415 ± 375 μmol.m^{-2}.s-1). Light intensity was measured with a light meter Li-250A (LICOR, USA). Fifteen individuals of each species, between 8-15 meters high, were selected in each plot. Twenty mature leaves were collected from each individual plant between the fourth and the sixth node from the apex and directly exposed to the sunlight. Of the total 1,200 leaves collected for each species (20 leaves x 30 individuals x 2 areas), 600 were used for analysis of leaf morphology and 600 were used for chemical analysis.

Soil analysis*:* In each plot, pore-water salinity was measured 30 cm deep at low tide with a digital hydrometer (Akso AK83), in five randomly selected points. Also at low tide, in each plot, five soil samples 30 cm deep were collected with an auger for chemical content and particle-size distribution analysis. The pH, the organic matter, carbon, and phosphorus content were estimated using an atomic absorption spectrophotometer (AAS), while nitrogen was estimated by the combustion method using an Elementar® model VARIO-EL-III analyzer. The distribution analysis of soil particle-size was performed by the pipette method. Soil samples were air-dried at room temperature and passed through a 2 mm sieve to obtain the air-dried fine soil fraction (< 2 mm). Triangle textural classes (IAC) were used for textural classification. Soil classification followed the *Sistema Brasileiro de Classificação de Solos* (EMBRAPA, 2009).

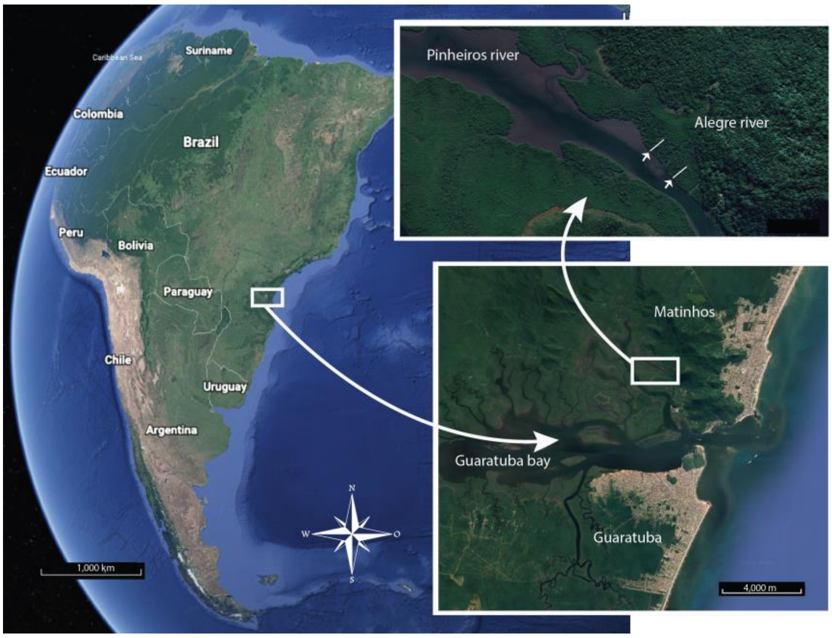

Figure 1. Transect position, indicated by white bars, at Pinheiros River, Guaratuba Bay, Paraná state, Brazil.
Figura 1. Posição dos transectos, indicados pelas e barras brancas, no Rio Pinheiros, Baía de Guaratuba, Paraná, Brasil.

Leaf morphological analysis: For each leaf collected, we measured the following morphological parameters: leaf thickness (mm) measured in the median region of the lamina with a digital caliper; leaf dry weight (g), estimated with a digital analytical balance from previously dehydrated leaves; leaf area (cm^2), estimated from images obtained with a flatbed scanner calibrated with Sigma Scan PRO software (version 5.0, SPSS Inc., Chicago, IL, USA); specific leaf area (leaf area/dry weigh; cm$^{2.}$.g^{-1}) and leaf density (specific leaf mass.1/thickness; mg.mm^{-3}). The density of salt secretory structures (no.mm^{-2}); and stomata density (no.mm^{-2}) were estimated from imprints made with nail polish of the median region of the epidermal surfaces of the leaves and using a light microscope coupled to a camera lucida. Specific leaf area was used as sclerophylly index (SI) (BOEGER; WISNIEWSKI, 2003). This index defines sclerophylly as SI< 60 and mesophylly as SI> 60.

Leaf chemical analysis*:* Leaf samples were completely dried in a forced-air oven at 60ºC until constant weight. Phosphorus (P) analyses were carried out by nitric-perchloric digestion and argon plasma optical emission spectrometry (ICP OES). Nitrogen (N) and carbon (C) were determined by the combustion method in an

Elementar® model VARIO-EL-III analyzer. The NUE index was used to evaluate the efficiency of nitrogen use by each species (MADI *et al*., 2015).

Statistical analysis: Averages and respective standard deviations were calculated for all quantitative variables, and in all cases, data were tested for homogeneity of variances. One-way ANOVA tested leaf traits and edaphic differences between fringe and interior plots. Two-way ANOVA analyzed differences among species and among plots, and interactions of these two factors, with leaf traits and leaf nutrients as response variables. One-way and Two-way ANOVA was performed with 5% of significance using the “GAD” package in the R environment (Project for Statistical Computing 3.1.3). A multivariate analysis of variance model was constructed using Distance Based Redundancy Analysis (dbRDA) using Gower distance with the function “capscale” of the “vegan” package in the R environment to determine the most influential environmental variables (areas, plots and soil parameters: pore water salinity; clay, silt and sand content; organic matter content; pH; N, P and C soil content; and C:N, C:P and N:P ratios) and characteristics of leaf morphology (specific leaf area, leaf density, dry weight, leaf area and leaf thickness). Soil parameters were standardized by standard deviation. We tested the significance of each predictor with 999 permutations through ANOVA.

RESULTS

The soil of the studied mangroves was classified as an isomorphic, sapric, salic-sodic gleysol with high electric conductivity and Na content. Though the content of silt, clay and sand did not differ significantly between plots, the fringe exhibited sediment with a predominance of sand fractions, while the interior exhibited a predominance of silt fractions. Fringe plots had C and OM content and C:P ratio twice as high as the interior plots, as well as higher pore water salinity. The content of P and N, and the N:P and C:N ratios did not differ among plots (Table 1).

Table 1. Mean values and standard deviations of the chemical-physical traits of the soil. Legend: P = phosphorus, N = nitrogen, C = carbon, C:N = carbon nitrogen ratio, N:P = nitrogen phosphorus ratio, C:P = carbon phosphorus ratio, OM = organic matter. Values in bold denote statistical differences among plots (p < 0,05).

Tabela 1. Valores médios e desvios padrão das características físico-químicas do solo. Legenda: P = fósforo, N = nitrogênio, C = carbono, C:N = razão carbono/nitrogênio, N:P = razão nitrogênio/fósforo, C:P = razão carbono/fósforo, OM = matéria orgânica. Valores em negrito indicam diferença estatística entre as áreas (p < 0,05).

Soil variables	Fringe	Interior	*f*	CV
P (g/kg)	0.30 ± 0.01	0.36 ± 0.15	0.571	0.31
N (g/kg)	4.21 ± 1.94	2.54 ± 0.99	2.328	0.50
C (g/kg)	**119.80 ± 45.93**	**47.09 ± 8.16**	7.284	0.59
N:P	11.97 ± 6.12	8.01 ± 1.77	1.167	0.46
C:N	24.81 ± 0.26	22.97 ± 3.77	0.706	0.11
C:P	**399.32 ± 153.12**	**140.40 ± 43.39**	7.94	0.64
OM (g/dm)	**20.65 ± 7.91**	**8.11 ± 1.41**	7.284	0.59
Clay (g/kg)	162 ± 70.71	189 ± 111.72	0.083	0.44
Silt (g/kg)	330.5 ± 95.46	513.5 ± 61.52	5.193	0.29
Sand (g/kg)	507.5 ± 166.17	297.5 ± 17324	1.531	0.46
pH	5.22 ± 0.39	5.25 ± 0.37	0.009	0.07
Pore water salinity	**20.60 ± 0.29**	**16.87 ± 1.02**	49.31	0.11

All species in both plots were classified as sclerophyllous due to the low values for specific leaf area, which we used as sclerophylly index (Table 2). The most sclerophyllous species was *L. racemosa*, followed by *R. mangle* and *A. schaueriana*. Across species, *R. mangle* had higher leaf density, leaf area, and leaf dry weight. *L. racemosa* had larger leaf thickness and higher stomata density on the adaxial surface. *A. schaueriana* exhibited the higher number of salt-secreting structures per unit area on both sides of the leaves and higher stomata density on the abaxial surface (Table 2).

According to Two-way ANOVA, significant interaction factors were found among species, for all leaf traits, among plots for leaf density, leaf area, and leaf thickness (Table 3) and among the interaction of species and plot for all leaf traits, except leaf dry weight.

Comparing the fringe and interior plots, *A. schaueriana* had lower specific leaf area in the fringe plots, whereas *R. mangle* had lower specific leaf area in the interior plots. The leaf density of *A. schaueriana and R. mangle* were higher in the fringe plots, and individuals of *A. schaueriana* in the fringe plots showed a greater number of salt-secreting structures per unit area of both surfaces. *L. racemosa* individuals in the fringe plots exhibit a greater density of salt-secreting structures per unit area of the adaxial surface. Individuals of *L. racemosa* in the interior plots had higher stomatal density on the abaxial surface (Table 2).

Table 2. Mean values and standard deviation of leaf morphological traits of the studied species. Legend: SLA = specific leaf area. LD = leaf density. LA = leaf area. LT = leaf thickness. LDW = leaf dry weight. SG-AB = salt glands density on abaxial surface. SG-AD = salt glands density on adaxial surface. SD-AB = stomata density on abaxial surface. SD-AD = stomata density on adaxial surface. nf = not found. Values in bold denote statistical differences among plots ($p < 0,05$).

Tabela 2. Valores médios e desvios padrão das características morfológicas das espécies estudadas. Legenda: SLA = área foliar específica, LD = densidade foliar. LA = área foliar. LT = espessura foliar. LDW = massa seca foliar. SG-AB = densidade de glândulas de sal na superfície abaxial foliar. SG-AD = densidade de glândulas de sal na superfície adaxial. SD-AB = densidade de estômatos na superfície abaxial. SD-AD = densidade de estômatos na superfície adaxial. nf = não encontrado. Valores em negrito indicam diferença estatística entre as áreas ($p < 0,05$).

	Avicennia schaueriana		*Laguncularia racemosa*		*Rizophora mangle*	
Traits	Fringe	Interior	Fringe	Interior	Fringe	Interior
SLA ($cm^2.g^{-1}$)	**53.56 ± 9.00**	**57.11 ± 6.00**	38.29 ± 4.28	38.51 ± 4.92	**47.23 ± 4.55**	**44.75 ± 3.85**
LD ($mg.mm^{-3}$)	**0.43 ± 0.12**	**0.39 ± 0.05**	0.51 ± 0.06	0.51 ± 0.05	**0.57 ± 0.06**	**0.53 ± 0.05**
LA (cm^{-2})	20.39 ± 5.52	20.89 ± 4.44	23.20 ± 4.29	23.47 ± 3.77	31.89 ± 6.83	29.10 ± 6.97
LT (mm)	0.45 ± 0.04	0.44 ± 0.03	0.52 ± 0.06	0.51 ± 0.05	0.37 ± 0.03	0.42 ± 0.04
LDW (g)	0.39 ± 0.12	0.36 ± 0.09	0.61 ± 0.11	0.61 ± 0.12	0.67 ± 0.15	0.65 ± 0.14
SG-AB ($n.mm^{-2}$)	**40.39 ± 16.35**	**31.35 ± 11.92**	26.15 ± 5.28	25.62 ± 3.9	25.00 ± 1.01	26.78 ± 6.06
SG-AD ($n.mm^{-2}$)	**116.00 ± 43.37**	**75.0 ± 23.19**	**33.22 ± 3.11**	**25.56 ± 3.76**	nf	nf
SD-AB ($n.mm^{-2}$)	156.00 ± 44.55	166.87 ± 44.61	**89.83 ± 31.20**	**127.00 ± 46.62**	106.5 ± 32.05	109.67 ± 26.51
SD-AD ($n.mm^{-2}$)	nf	nf	149.16 ± 45.74	160.33 ± 64.90	nf	nf

Table 3. Results of Two-way ANOVA on specific leaf area (SLA), leaf density (LD), leaf area (LA), leaf thickness (LT) and leaf dry weight (LDW) of mangrove tree species *A. schaueriana*, *L. racemosa* and *R. mangle*. *f* -values are given and significant effects are denoted as: * $p = 0.05$; ** $p = 0.01$ and *** $p = 0,001$ probability level.

Tabela 3. Resultado da Two-way ANOVA da área específica foliar (SLA), densidade foliar (LD), área foliar, (LA), espessura da folha (LT) e massa seca foliar (LDW) das espécies estudadas. Valores de *f* são significantes quando denotados como: * $p = 0.05$; ** $p = 0.01$ and *** $p = 0,001$ em nível de probabilidade.

	Variation for Two-way ANOVA		
	Species (S)	Plot (P)	S x P
SLA	535,81***	0,03	17,41***
LT	424,15***	19,40***	22,06***
LD	234,09***	20,37***	4,27*
LA	237,71***	4,31*	7,68**
LDW	331,59***	1,99	1,74

The three studied species exhibited differences in leaf nutrients (Table 4), where *A. schaueriana* had a higher content of P and N and a higher N:P ratio than *R. mangle* and *L. racemosa*. *Rhizophora mangle* had higher content of C and *L. racemosa* had higher C:N and C:P ratios and NUE than both *A. schaueriana* and *R. mangle*. The comparison of leaf nutrient content between plots, *A. schaueriana* presented higher C content and NUE in fringe plots. *Laguncularia racemosa* exhibited high levels of P and C and high N:P and C:P ratios in fringe plots, and high NUE in interior plots (Table 4).

Table 4. Mean values and standard deviations of foliar nutrient concentrations of the studied species. Legend: P = phosphorous, N = nitrogen C = carbon, C: N = carbon/nitrogen ratio, N:P = nitrogen/phosphorous ratio, C:P = carbon/phosphorous ratio, NUE = nitrogen use efficiency. Values in bold denote statistical differences among plots ($p < 0.05$).

Tabela 4. Valores médios e desvio padrão das concentrações de nutrientes foliares das espécies estudadas. Legenda: P = fósforo; N = Nitrogênio, C = carbono; N:P = razão nitrogênio/fósforo, C:P = razão carbono/fósforo, NUE = eficiência do uso de Nitrogênio. Valores em negrito indicam diferença estatística entre as áreas ($p < 0,05$).

	Avicennia schaueriana		*Laguncularia racemosa*		*Rhizophora mangle*	
Variables	Fringe	Interior	Fringe	Interior	Fringe	Interior
P (g.kg^{-1})	1.62 ± 0.14	1.61 ± 0.21	**1.44 ± 0.35**	**1.15 ± 0.19**	1.34 ± 0.14	1.39 ± 0.15
N (g.kg^{-1})	20.11 ± 1.68	21.11 ± 2.56	11.47 ± 0.75	10.98 ± 1.84	16.38± 1.20	15.91 ± 2.43
C (g.kg^{-1})	**404.41 ± 9.95**	**394.33 ± 8.18**	**427.76 ± 7.57**	**441.86 ± 8.92**	449.82 ± 4.53	454.97 ± 7.81
N:P	12.46 ± 1.04	13.16 ± 1.24	**8.31 ± 1.56**	**9.55 ± 0.94**	12.30 ± 0.78	11.51 ± 1.62
C:N	20.22 ± 1.70	18.94 ± 2.55	37.48 ± 3.04	41.41 ± 7.87	27.58 ± 1.98	29.22 ± 4.63
C:P	251.14 ± 21.50	248.26 ± 31.26	**311.17 ± 61.89**	**393.73 ± 74.93**	339.46 ± 33.86	331.68 ± 36.10
NUE	**19 ± 0.1**	**16 ± 0.07**	**52 ± 0.2**	**70 ± 0.6**	41 ± 0.3	42 ± 0.6

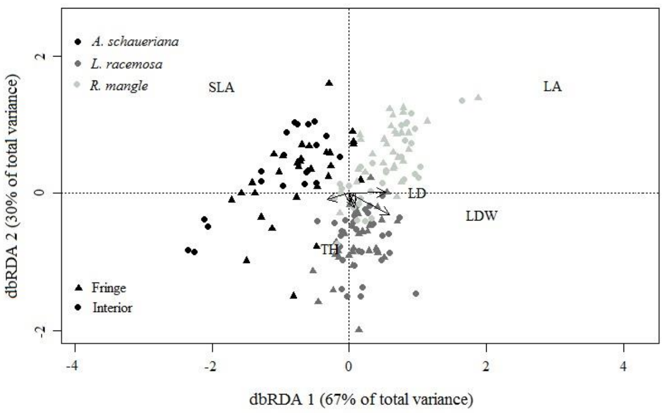

Figure 2. Biplot of the Distance-based Redundancy Analyses (dbRDA) showing the main variables on the leaf morphology in *Avicennia schaueriana*, *Laguncularia racemosa* and *Rhizophora mangle*, between plots. Legend: SLA = specific leaf area, LA = leaf area, LD = leaf density, LDW = leaf dry weight, LT = leaf thickness.

Figura 2. Biplot da Análise de Reduntância baseada em Distância (dbRDA), mostrando as principais variáveis da morfologia foliar de *Avicennia schaueriana*, *Laguncularia racemosa* e *Rhizophora mangle*, entre as áreas. Legenda: SLA = área específica foliar, LA = área foliar, LD = densidade foliar, LDW = peso seco foliar, LT = espessura foliar.

The dbRDA based on model selection indicated that biological and environmental drivers shaped the leaf morphology of mangrove tree species in the studied mangroves (ANOVA, F = 43.97, $p = 0.001$, Figure 2). The first two constrained principal coordinates (dbRDA) were significant and explained 95% of the variance in leaf morphology. The dbRDA 1 explained 67% of the variance in leaf morphology and was related to leaf area (score 2.65) and specific leaf area (-score -1.88), while dbRDA 2 explained 30% of the variance and was related to leaf thickness (score 1.65) and leaf dry mass (score 1.80). Post-hoc tests also showed that the intrinsic variation among species (ANOVA, F = 101.60, $p < 0.0001$), along with P soil content (ANOVA, F = 9.24, $p < 0.0001$) and OM soil content (ANOVA, F = 4.09, $p < 0.001$) were the most significant factors affecting leaf morphology of mangrove tree species.

DISCUSSION

The studied mangroves reflect an oligotrophic condition due to the low contents of N and P in the soil (READ; SANSON, 2003), similar to the levels of P and N found in other studies in mangroves in the Paraná state (MADI *et al*., 2015) and other Brazilian regions (BERNINI *et al*., 2006). These nutrient contents are considered low and limiting in mangroves (MEDINA *et al*., 2015). This oligotrophic condition was also confirmed by the N:P ratio in the interior and fringe plots, indicating that fringe and interior trees are especially limited by N (KOERSELMAN; MEULEMAN ,1996).

Limitation in N and P was listed as one of the conditions that can induce sclerophylly in forests (READ; SEASON, 2003). Sclerophylly can also be linked to habitats with higher salinity (REEF *et al*., 2010), because the excess salt hinders the water absorption from the soil. For this reason, mangrove plants present similar characteristics of terrestrial xerophytes (PARIDA; JHA, 2010).

The adverse environmental conditions imposed by salinity and N and P limitation on the allocation of resources in plants have a direct effect on plant structure (READ; SANSON, 2003; NAIDOO, 2016). Specific leaf area, that denotes the investment of mass by area unit, represents plant productivity because it is related to production of photosynthetic tissues (VOGELMANN *et al*., 1996). Leaves that exhibit high values of specific leaf area are more productive because they invested more in photosynthesis than structural tissues. On the other hand, leaves with low values of specific leaf area are less productive, although they have greater resistance to scarcity of resources in the soil (WANG *et al*., 2010). The three species exhibited low values of SLA, indicating sclerophylly in all individuals at fringe and interior areas, despite de differences in the degree of sclerophylly, specially in *A. schaueriana* and *R. mangle*. These results support our previous study at the Antonina Bay, Paraná, Brazil (25°29'57" S, 48°42'44" W), a mangrove located close to Rio Pinheiros (SERENESKI-LIMA *et al*., 2013), where all tree species presented sclerophyllous leaves: *R. mangle* > *L. racemosa* > *A. schaueriana,* in decreasing order of sclerophylly.

However, leaf traits such as leaf area, leaf dry weight and leaf thickness showed no significant differences among plots. We had expected to find differences in these leaf traits because they are related with specific leaf area (sclerophylly index). Therefore, the evaluation of sclerophylly in plants cannot be based just on indexes, but also must consider the foliar morphology and nutrient content such as leaf thickness, presence of sub-epidermal layer, N and P contents (SERENESKI-LIMA *et al*., 2013).

The leaf nutrient contents found in this study are similar to those reported for subtropical mangroves at Paraná state (SERENESKI-LIMA *et al*., 2013; MADI *et al*., 2015) and other Brazilian tropical mangroves (BERNINI *et al*., 2006). The different patterns of leaf nutrient content among species are related to different strategies for the accumulation and utilization of nutrients. Despite being subjected to the same nutrient availability, the studied species have distinctively efficient methods of absorption (MADI *et al*., 2015).

The availability of nutrients, specifically N and P, can influence plant efficiency by altering the synthesis of enzymes for several photosynthetic processes. However, this effect cannot be disconnected from salinity and freshwater balance under natural conditions (MEDINA *et al*., 2015). Salinity tolerance also embodies physiological and morphological traits such as in *A. schaueriana*. The high N content in the leaves of *A. schaueriana* is probably the result of the accumulation of glycine betaine, a nitrogenized compound that works as a compatible solute in leaves of species of *Avicennia* and functions as a salt tolerance mechanism (SOARES *et al*., 2015).

Even with little variation in specific leaf area among individuals of *A. schauerianna* in fringe and interior plots, the greater sclerophylly observed in the fringe is probably related to the high tolerance and distinct physiological mechanisms of this species. Fringe regions seem to be directly impacted by tides, even of low amplitude, which may explain the higher salinity observed there (FELLER *et al*., 2010). The higher salinity found at fringe areas was not expected, because interior mangroves usually have higher salinities due the infrequent tidal inundations and high evaporation (NAIDOO, 2010). Many plant species respond to adverse environmental conditions, such as salinity, by increasing sclerophylly. In a mangrove in Espírito Santo state, Brazil, individuals of *A. schaueriana* showed a positive correlation with salinity, as reveled by dry mass: leaf area ratio (LMA) (ARRIVABENE *et al*., 2014).

The sclerophylly index in *L. racemosa* was similar between fringe and interior plots. It is possible that the higher degree of sclerophylly found in *L. racemosa* is related to their adaptability to different abiotic conditions. Despite *L. racemosa* having the lowest N content, it had the highest NUE among the three species. The NUE values indicate the degree of efficiency in obtaining N by plants (MEDINA *et al*., 2015); as leaf nutrients decrease, the mechanism used to store this nutrient becomes more efficient, which may explain the low nitrogen content yet high NUE in *L. racemosa* (FELLER *et al*., 2010).

ISSN eletrônico 1982-4688
DOI: 10.5380/rf.v52 i2. 73959

Individuals of *R. mangle* located in the interior plots appeared as dwarf formations with short trees (~2 m) and twisted sclerophyllous leaves (FELLER *et al*., 2010). It is probable that the higher degree of sclerophylly observed in the individuals of *R. mangle* in the interior plots was a consequence of specific environmental conditions. Dwarf formations are usually associated with low tidal variation and high evaporation (NAIDOO, 2010; MEDINA *et al*., 2015), characteristics frequently observed in interior mangroves. However, the higher values for leaf density found at the fringe cannot be explained by these environmental variations. Leaf density usually is a response to the presence of structural tissues of the leaves and can be related to high ratios of C:N, as observed in fringe area (SEEDO *et al*., 2018).

The Distance Based Redundancy Analysis and Two-way ANOVA revealed that despite some similar environmental conditions (N and P concentration, N:P and C:N ratios, soil texture and pH) that mangrove trees are submitted in fringe and interior plots, these species showed distinct morphological and physiological mechanisms to deal with the adverse conditions of either type of mangrove plot. Therefore, there is not a single pattern for all plants located in fringe and interior plots, but a specific pattern for each species in each mangrove condition. Nevertheless, the intrinsic features of each species are apparently prevalent when compared to the environmental variables. Arrivabene *et al.* (2014) found that individuals of *A. schaueriana* could be considered appropriate bioindicators because they can indicate changes in environmental conditions. *Avicennia schaueriana* showed variation in dry mass per leaf area (LMA) that was positively correlated with salinity, manganese content, and pH, and negatively correlated with phosphorus content.

Besides differences in leaf morphology and physiological strategies, the evaluated species exhibited another intrinsic species-specific pattern: distribution and zonation. In the same mangrove areas, Madi *et al*. (2015) observed that *R. mangle* and *L. racemosa* tend to occupy plots with low salinity, whereas *A. schaueriana* exhibited a tendency to occupy plots with higher salinity.

Despite the different environmental conditions observed between fringe and transition plots the intrinsic factor of each species was determinant in the leaf morphological traits and the degree of sclerophylly observed. We could not establish a single pattern for the species in each plot, once each species responds differently to similar environmental conditions and exhibit distinct morphological, structural, and physiological strategies.

CONCLUSIONS

- Our hypotheses were partially supported by the results. Changes in edaphic factors induced by tidal inundation affected the growth of trees in fringe and interior areas in different ways: A. *schaueriana* presented higher degree of sclerophylly in the fringe plot; while *R. mangle* present higher values at the interior plot. *L. racemosa* presented similar sclerophylly in both plots. These results support the premise that each species has a distinct adaptability to abiotic conditions.
- The higher values of salinity in fringe plots are associated only with the higher degree of sclerophylly in *A. schaueriana*.
- A single pattern of sclerophylly for the tree species in each plot could not be established because each species responds differently to similar environmental conditions and exhibit distinct morphological, structural, and physiological strategies.

ACKNOWLEDGEMENTS

We would like to thank to the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for granted a scholarship to the first author and CNPq for providing fellowship to M.R.T.B. (301971/2013-7). We also would like to thank Dr. Carlos Bruno Reissmann for his assistance on the leaf and soil nutrient analysis.

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