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ARTÍCULO DE INVESTIGACIÓN / ORIGINAL RESEARCH PAPER

SOIL-PLANT NUTRIENT INTERACTIONS IN TWO MANGROVE AREAS AT SOUTHERN BRAZIL

Interacciones de nutrientes entre suelo y planta en dos áreas de manglares en el sur de Brasil

Interação entre a composição química de solo e planta em dois manguezais no sul do Brasil

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ABSTRACT

Mangrove forests have a simple architecture. They shelter a few number of arboreal species that grow in a saline environment subject to tidal activity. The research objective was to evaluate possible interactions between physical-chemical soil attributes and plant-leaf nutrient concentrations of different mangrove species. Different mangrove species growing in the same soil, and the same mangrove species growing in two different soil classes were evaluated as to their leaf nutrient concentration patterns. The study was carried out in mangrove areas of the State of Paraná, southern Brazil, in two distinct soil classes: HISTOSOL THIOMORPHIC Salic sodic and GLEYSOL THIOMORPHIC Salic sodic; and three different species: *Avicennia schaueriana, Laguncularia racemosa* and *Rhizophora mangle*. Two subareas were delimited within each area from which soil and leaf samples were collected. Samplings from five individuals of each dominant mangrove species were taken from the soil (0-10 cm deep) under each tree crown projection. The data was submitted to statistical analysis using a set of simple and multivariate analysis in order to determine possible differences among mangrove species leaf nutrient concentrations, and whether these differences might be correlated with the soil attributes or not.

The results exposed that the nutritional state of the mangrove species is different and independent form the soil attributes in which they grow. Few correlations were found among leaf nutrient concentrations and soil attributes, suggesting differential selective nutrient uptake among species.

Keywords: Avicennia schaueriana, Laguncularia racemosa, mangrove, soil, plant nutrients, Rhizophora mangle, soil chemical attributes.

RESUMEN

Los manglares son bosques de arquitectura simple que albergan pocas especies arbóreas, creciendo en un ambiente salino sometido a la influencia de las mareas. El objetivo de este trabajo fue evaluar las posibles interacciones entre las propiedades fisicoquímicas del suelo y la concentración de nutrientes en hojas de diferentes especies de mangle. Se investigó si las diferentes especies que se desarrollan en la misma clase de suelo tienen concentraciones de nutrientes foliares similares, y si las plantas de mangles de la misma especie que



se desarrollan en diferentes tipos de suelos tienen concentraciones foliares similares. El estudio se desarrolló en manglares del Estado de Paraná, sur de Brasil, en dos tipos de suelos diferentes (HISTOSOL TIÓNICO Salino sódico y GLEYSOL TIÓNICO Salino sódico). Se analizaron tres especies vegetales diferentes (*Avicennia schaueriana, Laguncularia racemosa y Rhizophora mangle*). En cada área se delimitaron dos subáreas para recolectar el suelo y las hojas de cada una de las especies. Se tomaron cinco individuos de cada especie del dosel dominante para recoger hojas y muestras de suelo de 0-10 cm, en la proyección de la copa de los árboles seleccionados. Se realizaron análisis univariados y multivariados para probar si las especies de mangle tienen perfiles nutricionales diferentes, y si existe alguna correlación entre las propiedades del suelo con la composición química de las hojas. Los resultados mostraron que el estado nutricional de las especies de mangle es distinto e independiente de los atributos de los suelos en los que se encuentran. Las concentraciones de elementos en las hojas presentan poca correlación con los nutrientes del suelo, lo que sugiere que la absorción de nutrientes por las plantas es selectiva.

Palabras clave: atributos químicos del suelo, Avicennia schaueriana, Laguncularia racemosa, mangle, nutrientes, Rhizophora mangle.

RESUMO

Manguezais são florestas de arquitetura simples, abrigando poucas espécies arbóreas, vegetando em ambiente salino e sujeito ao regime de marés. O objetivo desta pesquisa foi avaliar as possíveis interações entre os atributos físico-químicos do solo e a concentração de nutrientes nas folhas de diferentes espécies de mangue. Assim, foi investigado se as diferentes espécies que se desenvolvem sobre a mesma classe de solo apresentam concentrações de nutrientes foliares similares, e se plantas de mangue da mesma espécie que ocorrem sobre diferentes classes de solo apresentam concentrações de nutrientes foliares similares. O estudo foi desenvolvido em manguezais no Estado do Paraná, Sul do Brasil, em duas classes distintas de solo (ORGANOSSOLO TIOMÓRFICO Sálico sódico e GLEISSOLO TIOMÓRFICO Sálico sódico), e três espécies diferentes de plantas (*Avicennia schaueriana, Laguncularia racemosa* and *Rhizophora mangle*). Em cada área foram delimitadas duas subáreas para coleta de solo e folhas das espécies. Cinco indivíduos do dossel dominante de cada espécie para coleta de folhas, na projeção da copa das árvores, e amostras de solo de 0-10 cm foram selecionados. Para testar se espécies de mangue apresentam perfis nutricionais distintos e se há correlação entre os atributos do solo com a composição química foliar um conjunto de análises univariadas multivariadas foram realizadas. Os resultados demonstraram que o estado nutricional das plantas é distinto e individualizado, independente dos atributos do solo em que se encontram as espécies. As concentrações dos elementos nas folhas pouco se correlacionaram com os nutrientes do solo, sugerindo absorção seletiva dos nutrientes pelas plantas.

Palavras-Chave: atributos químicos do solo, Avicennia schaueriana, Laguncularia racemosa, mangue, nutrientes, Rhizophora mangle.

INTRODUCTION

Mangroves are ecosystems located between the highlands and ocean, characteristics of saline coastal habitats in the tropics and subtropics, occurring as an interface between land and sea (Schwarz, 2003). Such environments are dominated by many typical tree and shrub species adapted to a fine sediment substrate originated from periodical tide flood depositions, rich in organic matter, with varied salinity and low oxygen (Griffiths *et al.*, 2008).

The mangrove forest areas of the world occupy around 14.65 million hectares (Wilkie and Fortuna, 2003). Brazil ranks third with one of the world's largest mangrove areas, representing 7 % of the world (Giri *et al.*, 2011). The Brazilian mangroves are found along 6800 km of coast from the extreme north of Oiapoque (State of Amapá) until the southern region of Santa Catarina State (Schaeffer-Novelli *et al.*, 1990). Although it is considered a Permanent Preservation Area (PPA) according to the Brazilian directive CONAMA 303/02, this ecosystem is under continuous anthropic activity threat (Krug *et al.*, 2007). About 35 % of the Brazilian mangrove forests were lost between the 1980's and 1990's (Valiela *et al.*, 2001).

Mangrove forests show low tree species diversity when compared to other tropical forests (Kathiresan, 2008). At

southern Brazil, only three mangrove species are usually found: *Rhizophora mangle* L.; *Laguncularia racemosa* (L.) Gaertn; and *Avicennia schaueriana* Stapf & Leachman.

Despite the low plant diversity, mangroves play an important ecological role in the coastal areas (Kauffman *et al.*, 2011), because they are a source of organic matter for the ecosystem. They also provide goods and food for the human population, thereby demonstrating their socio-economic role (Soares *et al.*, 2003).

Species abundance is influenced by several factors such as geomorphology, climate, tide amplitude, salinity and edaphic characteristics (Boto and Wellington, 1984). Such abiotic factors are generally interrelated, as for instance soil salinity affecting leaf nutrient concentrations (Araujo *et al.*, 2010). Besides the complex interactions among abiotic factors, many mangrove species may present differences in the absolute plant nutrient concentrations and the relative ratios between nutrients due to different plant species abilities in nutrient selectivity and uptake (Bernini *et al.*, 2006).

Studies at the southern and northern coastal regions of Brazil showed that mangrove species presented differential nutrient concentrations. The *Avicennia* species was observed to show higher leaf concentrations of nitrogen (N), potassium (K) and magnesium (Mg) and lower concentrations of calcium (Ca) than *Rhizophora mangle* and *Laguncularia racemosa* (Cuzzuol and Campos, 2001; Bernini *et al.*, 2010). Such variation is expected considering that these species have differential selectivity for nutrients even growing in the same environment (Bernini *et al.*, 2006).

The spatial and temporal nutrient variability in the soil might also collaborate in differential nutrient uptake among species (Bernini *et al.*, 2010). Nevertheless, other studies have suggested that soil physical-chemical attributes might also affect plant leaf nutrient concentrations, mainly when plants share the same pool of soil nutrients (Vitousek and Sanford, 1986).

Soil salinity is considered a determinant factor affecting mangrove vegetation structure and development (Bernini *et al.*, 2006). Excessive soil sodium (Na) might induce other cation deficiencies in the plants. There are studies evidencing that mangrove foliar Ca concentrations are controlled by or dependent on the soil Na concentrations (Waisel, 1972). On the other hand, Ca is indispensable to the plant survival under mangrove environment conditions enhancing K uptake and Na inhibition (Lacerda *et al.*, 1986).

Mangrove soils are classified as allomorphic soils, developed by the deposition of sediments from the ocean, rivers and rain runoff. The main soil classes in these environments are: thiomorphic Gleysols and salic Gleysols, and Histosols (Vidal Torrado, 2005). These soils are mainly characterized by fine sediments (clay and silt), high organic matter and soluble salts (from sea water) (Citrón and Schaffer-Novelli, 1983).

In the State of Paraná, Brazil, Gleysols and Histosols are commonly found and both may present thiomorphism (Embrapa, 2009). The Gleysol class consists of hydromorphic soils characterized by a grey color as a consequence of the presence of reduced iron (Fe²⁺) due to constant (periodical or permanent) water saturation; the Gleysols are constituted by minerals of varied textures. The Histosol class consists of soils with high proportion of vegetal residues in different degrees of decomposition, poor drainage conditions, very low density and high porosity; they are extremely fragile soils, but with high organic-C and water storage capacity (Embrapa, 2009).

Based on the soil-plant interaction evaluations, mainly on the relationships among soil physical-chemical attributes and plant leaf nutrient concentrations, two mangrove areas of southern Brazil with two distinct floristic structural organization such as tree abundance and basal area, were studied. The areas were characterized by two distinct soil classes (salic-sodic thiomorphic Histosol and salic-sodic thiomorphic Gleysol), with different organic-C contents. This study aimed to investigate if the leaf nutrient concentrations are soil class dependent, and if soil chemical-physical attributes would interrelate with leaf nutrients.

MATERIAL AND METHODS Research area

This study was carried out at Antonina and Guaratuba municipal districts, State of Paraná, Brazil. Antonina is located at the western region of Paranaguá Bay and covers an area of 460 km². Guaratuba is located at the Guaratuba Bay and represents the second greatest estuarine complex of Paraná coast with 48.72 km² (Fig. 1). The mangrove geographical position, edaphic and climatic characteristics are presented in Table 1. The average annual rainfall and daily temperature data is referred to the year of 2010,



Figure 1. Study areas analyzed in the mangrove of the estuary of Nhundiaquara River (Antonina, Paraná, Brazil) and mangrove of the estuary of Pinheiros River (Guaratuba, Paraná, Brazil).

registered by the Paranaguá Station of the Meteorological System of Paraná (SIMEPAR) (Table 1).

Material sampling

For each mangrove site an area of about 1000 m^2 ($10 \text{ m} \times 100 \text{ m}$), was established parallel to the shore line for soil and plant leaf samplings from *A. schaueriana*, *L. racemosa* and *R. mangle*. Five dominant individuals were randomly marked per area along the entire mangrove strip. At Antonina, the individuals were marked in the superior middle part of the Nhundiaquara River estuary; and at Guaratuba, in the middle part of Pinheiros River.

Intact mature leaves were collected from the middle of the tree crown at north face (Borille *et al.*, 2005), during July 2010, using pruning-scissors. Young and senescent leaves were not considered. Leaf samples were thoroughly rinsed and dried in a forced-air oven at 60 °C until constant weight, grinded to powder and submitted to nitric-perchloric digestion, according to Jones and Case (1990). Phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), sodium (Na) and sulfur (S) were determined by ICP-OES (inductively coupled plasma optical emission spectrometry) with argon plasma. Nitrogen (N) was determined by Kjeldahl method (Jones and Case, 1990).

Soil samples were collected at 0-10 cm deep (Nielsen and Andersen, 2003) in four selected points under each tree crown projection, during June 2010. Soil samples were air-dried at room temperature and passed through 2 mm sieve to obtain the air-dried fine soil fraction (< 2 mm). Soil samples were then analyzed for pH CaCl₂, P, K, Ca, Mg, Na and aluminum (Al), according to the "Manual of Methods for Soil Analysis" (Embrapa, 1997); Carbon (C) and N were determined by combustion using a VARIO-EL-III analyzer, Elementar® model. The mangrove thiomorphic character was confirmed according to classification of Embrapa (2009).

Statistical analysis

Plant and soil data were submitted to univariate and multivariate (data clustering and ordination) analyses in order to test whether mangrove species growing in different soil classes would show differential leaf nutrient concentrations. Univariate analysis was used to evaluate plant responses within and among mangrove areas. Statistical differences among areas were assured by means of two analyses of variance (*one-way* ANOVA), firstly including species as the variable factor, and secondly, the mangrove areas. Soil pedological attributes and leaf nutrient concentrations were the dependent variables. After ANOVA, variable means were compared by Fisher test LSD (p < 0.05). The variance homogeneity and Gaussian distribution were checked out by means of Bartlett test (p < 0.05) and Kolmogorov-Smirnov (p < 0.05) (Zar, 1999).

The K uptake efficiency in the presence of high Na concentrations was evaluated by means of the net selectivity efficiency index (net $S_{K:Na}$), according to Flowers and Colmer (2008), calculated by the following formula:

net
$$S_{K:Na} = \left[\frac{(leaf K / soil K)}{(leaf Na / soil Na)} \right]$$

Where leaf nutrient unities are in g.kg⁻¹ and soil nutrient unities in mg.kg⁻¹; the conversion factor for K is 0.391 and for Na is 0.230.

In order to detect differences among plant nutrient concentrations and soil chemical attributes in both mangrove areas, three Principal Components Analyses (PCA) were made with Euclidian distance. Pearson correlations among original variables and the PCA scores were made to identify which variables were the responsible for the variations. The number of axis was determined by the randomizing test with 999 permutations. Analyses were run by the PC-ORD 6.0 program (McCune and Mefford, 2011). In order to verify if the species present distinct strategies in nutrient absorption a hierarchical classification procedure was employed (cluster analysis, Euclidean distance and complete linkage-farthest neighbor), utilizing a matrix of leaf nutrient data, separately for each mangrove. The cophenetic correlation coefficient was calculated for each group with the objective to verify the deformation degree resulted from the dendrogram

Table	1. G	eographic	al loc	aliza	tion,	climate	and	eda	phic	cha	racter	istics	of s	studie	ed r	nang	rove	areas.	, State	of	Paraná	, Bra	ızil.

	Antonina	Guaratuba	
Geographical Coordinates **	25°29'S 48°42'W	25°50'S 48°34'W	
Temperature (°C) Mínima/máxima*	20.5 (16.7 - 26.4)	20.8 (18.0 -24.2)	
Climate	Cfa	Cfa	
Annual rainfall (mm)*	2733	3183	
Soil type**	Salic-sodic thiomorphic Histosol	Salic-sodic thiomorphic Gleysol	
Salinityof interstitial water (‰)**	16.3	24.4	
Redox potencial redox (mV)**	-327.2	-316.9	

* SIMEPAR (Meteorological System of Paraná). ** Boeger et al. (2011).

construction. In this study both coefficients were greater than 0.75. To test if the hierarquical classification could be significantly separated, a Permanova (Permutational Multivariate Analysis of Variance) with 999 permutations of the residuals in the full model was performed with the same distances used in the hierarchical classification (McCune and Grace, 2002).

RESULTS

Soil analysis

Soil samples from Antonina showed lower pH values than those from Guaratuba, but no differences among soil for each species, within each area, were observed. However, differences between soils were observed when each species was individually compared (Table 2).

Higher electrical conductivity (EC) was found in soil samples from Guaratuba than from Antonina, but no significant differences among the species soil samples within the same area were found (Table 2).

Significant higher organic matter concentration values (OM) were found in soil samples from Antonina than from Guaratuba. In addition, significant differences within each area were observed, among the three species (Table 2). In

the same way, higher soil carbon (C) values and C:N ratios were found in samples from Antonina, as expected, since these variables are related with organic matter.

No significant differences among the three species soil samples within each mangrove area were found for Ca, K, Mg, Na and P concentrations. But higher K and P concentrations were found in soil samples from Guaratuba than from Antonina. On the other hand, higher N concentrations were found in soil samples from Antonina, but only those collected under the *A. shaueriana* and *L. racemosa* species (Table 2).

Leaf analysis

The leaf nutrient concentrations were ranked according to the following decreasing values for the three mangrove species: N > K > S > Mg > Na > Ca > P for *A. shaueriana*, in both mangrove areas; Ca > N > K > Na> S > Mg > P for *L. racemosa* in Antonina and Ca > N > Na> S > K > Mg > P in Guaratuba; N > Ca> K > Na> S > Mg > P for *R. mangle*, in Antonina, and the opposite Na > K in Guaratuba (Table 3).

In general, considering the same soil type or location, the three species differ significantly according to their nutrient leaf concentrations (Antonia F = 49.94; p < 0.01 e Guaratuba F = 51.52; p < 0.01) (Fig. 5 and Fig. 6).

Table 2. Chemical characteristics (at 0-10 cm depth) of soil samples collected under the tree crown projection of *A. shaueriana*, *L. racemosa* and *R. mangle* species growing in mangrove areas, State of Paraná, Brazil.

		Antonina			Guaratuba	
	A. schaueriana	L. racemosa	R. mangle	A. schaueriana	L. racemosa	R. mangle
pH CaCl ₂	3.27±0.39aB	3.24±0.38aB	3.26±0.37aB	5.19±0.52aA	5.26±0.65aA	5.16±0.42aA
Al cmol _c dm ⁻³	4.38±2.46aA	3.62±1.72aA	4.16±2.09aA	0.30±0.45aB	0.55±0.88aB	0.21±0.59aB
H + Al cmol _c dm ⁻³	26.67±8.03aA	26.28±9.22aA	25.95±8.05aA	5.47±2.04aB	5.97±3.45aB	5.23±5.91aB
Ca cmol _c dm ⁻³	4.0±1.06aA	4.44±0.82aA	4.19±0.86aA	4.93±0.84aA	5.39±1.34aA	5.78±1.13aA
Mg cmol _c dm ⁻³	5.1±0.15aA	5.18±0.12aA	5.18±0.15aA	5.01±0.14aA	5.11±0.12aA	5.18±0.10aA
K cmol _c dm ⁻³	0.83±0.30aB	0.99±0.33aB	0.95±0.36aB	1.5±0.13aA	1.5±0.18aA	1.6±0.13aA
P ppm	19.29±3.98aB	19.99±3.82aB	21.43±5.07aB	33.82±3.72aA	36.57±5.31aA	38.12±4.87aA
N g dm ⁻³	4.54±0.65aA	4.14±0.54aA	4.21±0.61aA	3.17±0.73bB	3.55±0.68bB	4.07±0.57aA
C g dm ⁻³	89.53±1.26bA	80.32±1.63bA	91.52±2.19aA	53.95±1.64bB	59.77±1.21bB	70.99±1.18aB
Na cmol dm ⁻³	25.03±2.50aA	27.84±2.88aA	26.61±2.35aA	27.42±2.88aA	27.72±3.35aA	28.44±2.98aA
EC dSm ⁻¹	12.22±0.93aB	11.46±0.83aB	11.49±1.24aB	14.35±1.92aA	13.88±2.16aA	14.09±1.69aA
C/N	20.12±0.92abA	18.87±2.09bA	21.79±3.13aA	17.40±1.13aB	16.97±1.64aA	17.45±1.63aA
ОМ	15.40±2.16abA	13.81±2.81bA	15.74±3.76aA	9.28±2.82bB	10.28±2.08bB	12.21±2.04aB
S (Bases)	34.96±3.77aA	38.45±3.83aA	36.93±3.43aA	38.85±3.30aA	39.71±4.58aA	40.99±3.21aA
CEC	61.63±5.23aA	64.73±7.51aA	62.83±5.14aA	44.32±3.45aB	45.68±5.35aB	46.22±6.68aB
V%	58.76±9.53aB	60.58±10.10aB	60.06±9.43aB	86.63±4.00aA	87.13±6.20aA	87.59±7.08aA
m%	20.85±13.78aA	13.49±6.78aA	17.01±10.09aA	1.16±1.75aB	2.19±3.55aB	0.77±2.05aB

Fisher test LSD (p < 0.05). Numbers followed by different small letters on the same line, within the same area, are statistically different. Numbers followed by different capital letters in the same line, between areas for the same species, are statistically different. Numbers are referred to mean \pm mean standard deviation.

No significant differences between areas for the same species leaf nutrient concentrations were found, except for *A. schaueriana* that showed higher leaf N concentration in Antonina (Table 3). Besides, leaf N concentrations were ranked in the same decreasing order for the species, within each mangrove area, as follows: *A. schaueriana* > *R. mangle* > *L. racemosa*. Potassium, Mg, S and Na showed higher and significant differences in *A. schaueriana* against *L. racemosa* and *R. mangle* (Table 3). Leaf P concentrations also showed the same tendency in both areas and within each area the following decreasing gradient was observed: *A. shaueriana* > *R. mangle* = *L. racemosa* for both Antonina and Guaratuba mangroves. As concerned to leaf Ca concentrations, *A. shaueriana* showed, in average, 3.5-fold lower Ca than *L. racemosa* in both mangrove areas (Table 3).

In Guaratuba, higher net selectivity efficiency index (net $S_{K:Na}$) values for K (in presence of Na) were found for A. shaueriana than for L. racemosa and R. mangle. In Antonina, A. shaueriana and R. mangle showed similar index values, which were higher than L. racemosa index (Table 3).

Soil-plant interaction

The data matrix analysis revealed few correlations among soil and plant variables. Positive correlations between soil Na and *R. mangle* leaf N in Guaratuba (r = 0.75; p < 0.05) and *L. racemosa* leaf N in Antonina (r = 0.72; p < 0.05) were found, respectively.

The principal coordinate analyses (PCA) of soil data collected under the three species crown projections and their respective leaf nutrient concentrations allowed clustering the species into two groups (Antonina and Guaratuba mangroves). The pedological attributes were the variables that mostly contributed, but correlation coefficients between principal coordinates and leaf nutrients were not above 0.70 (Table 4). This means that the data clustering and ordination

found for *A. shaueriana* explained 65.1 % of the data (PCA 1= 44.1 % and PCA 2 = 21 %) (Fig. 2). The soil pH, Al, H+Al, K, P, C, Na and OM showed higher correlations with the first coordinate. The second coordinate also separated the plots into two groups, but it was mostly correlated with Mg and N variables.

The ordination analysis for *L. racemosa* clustered the mangrove areas in two distinct groups (Fig. 3). The first and second coordinates together explained 60.1 % of data variation (PCA 1= 42 % and PCA 2 = 18.1 %). Soil pH, Al,



Figure 2. Principal component analysis (PCA) of soil chemical attributes and leaf nutrient concentrations of *A. shaueriana* (AV), from studied mangrove areas of Antonina (A) and Guaratuba (G), State of Paraná, Southern Brazil.

		Antonina			Guaratuba				
	Schaueriana	L. racemosa	R. mangle	schaueriana	L. racemosa	R. mangle			
N(g kg ⁻¹)	25.90 ± 2.59 aA	13.5 ±1.11 cA	18.16±1.88bA	22.23±2.23aB	13.3±1.02cA	18.89±1.15bA			
K(g kg ⁻¹)	11.92±2.83 aA	5.68±0.78 bA	6.99±0.99bA	13.09±2.43aA	5.50±0.97bA	6.70±0.70bA			
P(g kg ⁻¹)	1.95±0.34aA	1.60±0.26bA	1.37±0.27bA	1.63±0.19aA	1.34±0.11bA	1.36±0.09bA			
Ca(g kg ⁻¹)	4.22±0.58cA	14.28±2.49aA	10.30±1.21bA	4.86±0.42cA	16.43±2.58aA	10.34±1.75bA			
Mg(g kg ⁻¹)	9.2±1.67aA	4.3±0.52bA	4.65±1.26bA	9.71±1.26aA	4.10±0.43bA	4.40±0.81bA			
S (g kg ⁻¹)	10.78±2.92aA	5.10±1.15bA	4.36±1.59bA	10.23±2.25aA	5.83±1.29bA	4.91±0.75bA			
Na(g kg ⁻¹)	8.35±2.33aA	6.12±1.95bA	6.28±1.18bA	8.39±2.09aA	6.83±2.03bA	7.05±1.27bA			
net S _{K:Na}	17.37±2.05aB	8.32±1.05cB	10.61±1.11bB	22.5±aA 2.31	19.7±1.32bA	22.7±1.24aA			

Table 3. Leaf macronutrient and Na concentrations and net selectivity index for K (net $S_{K:Na}$) of three species (*A. shaueriana*, *L. racemosa* and *R. mangle* growing in mangrove areas, State of Paraná, Brazil.

Fisher test LSD (p < 0.05). Numbers followed by different small letters on the same line, within the same area, are statistically different. Numbers followed by different capital letters in the same line, between areas for the same species, are statistically different. Numbers are referred to mean ± mean standard deviation.

Soil and	Principal (<i>A. sha</i>	Component <i>ueriana</i>	Principal (<i>L. rac</i>	Component <i>cemosa</i>	Principal Component <i>R. mangle</i>		
plant variables	$\frac{1}{\lambda = 8.4}$	$\lambda = 3.84$	1 λ = 7.71	$\lambda = 3.40$	1 λ = 7.51	$\lambda = 3.00$	
рН	-0.97	-	-0.94	-	-0.99	-	
Al	0.97	-	0.97	-	0.98	-	
H+Al	0.98	-	0.97	-	0.96	-	
Ca	-0.63	-	-	-	-0.75	-	
Mg	0.10	-0.71	-	-0.62	-	-	
К	-0.92	-	-0.83	-	-0.87	-	
Р	-0.92	-	-0.92	-	-0.94	-	
N	-	-0.88	-	-0.65	-	-	
С	0.70	-0.66	0.86	-	0.62	0.64	
Na	-0.75	-	-	-0.86	-	-	
EC	-	-	-	-	-0.65	-	
C/N	0.79	-	-	-	-	-	
ОМ	0.71	-0.65	0.85	_	0.62	0.64	
N-p	-	-	-	-	-	-	
К-р	-	-	-	_	-	-	
Р-р	-	-	-	-0.60	-	-	
Ca-p	-	-	-	-	-	-	
Mg-p	-	-	-	-	-	-	
S-n	-	0.60	_	_	-	-	

Table 4. Correlation between the original variable values (of soil chemical attributes and leaf nutrient concentrations -p- of three adult plant species) and the two principal components used to detect differences between the mangrove areas, State of Paraná, Brazil.





Figure 3. Principal component analysis (PCA) of soil chemical attributes and leaf nutrient concentrations of *L. racemosa* (LAG), from studied mangrove areas of Antonina (A) and Guaratuba (G), State of Paraná, Southern Brazil.

Figure 4. Principal component analysis (PCA) of soil chemical attributes and leaf nutrient concentrations of *R. mangle* (RH), from studied mangrove areas of Antonina (A) and Guaratuba (G), State of Paraná, Southern Brazil.

H+Al, K, P, C, and OM were the attributes mostly correlated with the first coordinate, and Na with the second coordinate.

The ordination analysis for *R. mangle* also clustered the mangrove areas into two distinct groups (Fig. 4). Both coordinates together explained 55.6 % of the data variation

(PCA 1= 40.1 % and PCA 2 = 15.5 %). Soil pH, Al, H+Al, K, P and Na were the attributes mostly correlated with the first coordinate, and C and OM with the second coordinate (r < 0.70) (Table 4).



Figure 5. Cluster analysis for mangrove areas of Antonina, State of Paraná, Southern Brazil. AV - A. shaueriana; RH-R. mangle; LAG - L. racemosa.



Figure 6. Cluster analysis for mangrove areas of Guaratuba, State of Paraná, Southern Brazil. AV - A. shaueriana; RH-R. mangle; LAG - L. racemosa.

DISCUSSION

Soil analysis

The soil chemical analysis showed intra and interspecific variations, and the results were similar to the average values of other Brazilian mangroves (Cuzzuol and Campos, 2001; Bernini *et al.*, 2010; Bernini and Rezende, 2010). The main differential soil attributes between areas were Al, K, P, CEC, m % and V %, plus C-content that separated the soils in Histosol and Gleysol classes.

The expressive differential percentages between the soil classes represented by m = 92 %; Al = 91 %; P = 44 %; K = 39 %; pH = 37 %; V% = 31 %; C and OM = 29 %; and CEC = 28 %, are coherent with the clusters expressed in Fig. 2-4. Significant differences for N were only found in Guaratuba and for C/N ratio in Antonina. Therefore, the statistical analysis among and within mangrove areas showed that significantly different soil variables were related with the distinct soil classification.

Carbon concentration was the main attribute responsible for the mangrove soil classification, characterizing a Histosol in Antonina and a Gleysol in Guaratuba. The Guaratuba soil profile did not show a sufficiently expressive histic horizon to be classified as a Histosol. However, the gleysol samples showed higher OM concentrations nearby the *R. mangle* individuals than nearby other species. This higher OM concentration resulted from its accumulation in the depressions, where *R. mangle* occurs when growing in inland sites, despite its frequently occurrence on coastal locations. The present data corroborated other authors' results, when high OM contents were observed nearby *R. mangle* plants in mangrove areas of Mexico (Lópes-Portillo and Ezcurra, 1989) and southern Brazil (Carmo *et al.*, 1998).

The lower pH values observed in Antonina's soil samples are probable due to the greater amount of sulfur radicals generated from OM and also to their greater potential acidity. However, two special considerations about Antonina's pH values must be done: (a) routine soil analysis showed very low pH values (3.5-4.5) indicating acidic medium; such low values are probably due to the soil sample procedure for chemical analysis, because oxidation of sulfur and derivates occur during soil drying (Bernini and Rezende, 2010); (b) under soil water saturation conditions (Embrapa, 2009), the same soil samples presented pH range of 6.8-7.4, which are more compatible with the high soil base saturation (V%) values found. Some of these mangrove soils may show pH \leq 4.0, when incubated for until eight weeks, and then, they are characterized as thiomorphic soils (Embrapa, 2009).

The higher soil exchangeable base (Ca, Mg, K and Na) concentrations (SBCS, 2004) corroborated the *in situ* higher pH values found (Cuzzuol and Rocha, 2012). The same is evidenced by soil CEC values, because soil charges are originated from the high OM concentrations and mineral colloids of sediments. The OM higher CEC in Antonina

than in Guaratuba soils is probably due to the organic constitution of Antonina's soils. Little variation of sum of bases (SB) was observed between areas and species. In this case Bases Saturation (V %), is inversely proportional to CEC, which in turn is dependent on the organic or mineral colloid characteristics.

The soil high electrical conductivity (EC) values (> 7dSm⁻¹ at 25 °C) conferred the Salic character to such mangrove soils (Embrapa, 2009). Furthermore, the high Na concentration values observed in these mangrove soils might be explained by the frequent flooding with saline waters in such areas, conferring the Sodic character to soil classification (Embrapa, 2009). Both studied areas presented high percentage of soil Na in the colloid exchange loci.

Leaf Analysis

Differential leaf nutrient concentrations were observed among mangrove species in both areas, although all three species were under the same synergistic and antagonistic relationships during root nutrient uptake from soil (Cuzzuol and Rocha, 2012).

In the present study, the leaf nutrient concentration means were within the range described in the literature for Brazilian mangroves (Cuzzuol and Campos, 2001; Bernini *et al.*, 2010; Bernini and Rezende, 2010). However, different nutrient concentration patterns were observed for the three species, contrarily to the results reported by Bernini *et al.* (2010). They found similar nutrient patterns in *L. racemosa* and *R. mangle* species, when studying the Espírito Santo mangroves, at southern Brazil. On the other hand, in the present study highest leaf N and lowest P and S concentrations were found in *A. shaueriana* and *R. mangle* species, corroborating the results of Cuzzuol and Campos (2001), when studying the Mucuri mangrove in the State of Bahia, Brazil.

The differential leaf nutrient concentration ranking among mangrove species (K > Mg > Ca in *A. shaueriana;* Ca > K > Mg in *L. racemosa* and *R. mangle*) appears to be related to the reciprocal antagonism among cations (Mengel, 1984), as well as to the seasonal variation that directly influences the leaf nutrient concentrations.

There was a clear distinction among species as to their leaf N concentrations, significantly higher in *A. shaueriana* leaves, independently of the soil type (Table 2). This species' higher leaf N concentration might be the result of glycinebetain (N-rich quaternary ammonium compound) accumulation in the cytoplasm that is supposed to contribute to plant salt tolerance (Popp, 1984; Medina and Francisco, 1997).

Avicennia shaueriana's higher leaf Mg and Na concentrations evidenced a selective root uptake for these nutrients, fact that is a characteristic salt excretion mechanism present in the species of this genus (Lacerda *et al.*, 1985; Medina and Francisco, 1997). On the other hand, the differential leaf K concentrations observed among species suggested diverse mechanisms affecting soil K movement to the rhizosphere, and else, distinct root K selectivity and uptake (Meurer, 2006). The net K selectivity index (net $S_{K:Na}$) values found (average = 19) were within the range indicated (9-60) by Flowers and Colmer (2008). The data evidenced that the medium physical characteristics might interfere on the K index values. High net $S_{K:Na}$ values for *A. shaueriana* in both studied areas expressed greater K uptake ability in the presence of high Na concentrations and higher K selectivity.

The high leaf Ca, superior than N concentrations observed *in L. racemosa* leaves do not represent the species usual nutrient pattern. Low leaf Ca was also found in *A. shaueriana* in mangroves of northern (Cuzzuol and Campos, 2001) and southern Brazil (Bernini *et al.*, 2006) and seemed to be a characteristic of species of this genus, independently of the soil type where the individuals are grown. Else, it would depend on which plant category the species would belong to, as concerned to Ca acquisition and accumulation, such as the so-called oxalate containing plants (Hawkesford *et al.*, 2012). The oxalate containing plants are characterized by the presence of free oxalate in the roots that would precipitate Ca and possibly restrict this nutrient transport to the xylem (Bernini *et al.*, 2006).

Soil- plant interaction

The ordination analysis and Pearson correlations between soil and plant nutrient variables evidenced the soil was not a conditioning factor for the species leaf nutrient concentrations in the studied mangrove areas.

Higher soil N and C concentrations were found in Antonina, indicating greater soil OM enrichment compared to Guaratuba mangrove, and characterizing the Histosol class. The significant increases in such soil attributes determined the soil ordination under the respective species. The highest OM concentration values in Antonina might be consequence of harbor activities and urban conglomerations nearby the experiment sampling area, because the organic matter seemed to be a mixture of autochthonous and allochthonous OM depositions from continental origin (Bittencourt, 1998; Lana, 1998).

The soil K and pH data ordination might be explained by the strong relationship between the soil base saturation and soil pH (Raij, 1983). It is highlighted that in Guaratuba, where soil base saturation was close to 90 % and pH was higher than at Antonina, the base saturation and pH values might also be due to potassium feldspars of regional sediments originated from elements of the "Serra do Mar" mountain ridge (Angulo, 2004).

On the other hand, Antonina's mangrove soil showed relatively high Al saturation, lower base saturation, and lower K concentrations, although K was high enough in terms of plant nutrition. However, even with K-rich feldspar depositions, Antonina's mangrove lower soil K concentrations might be explained by the lower K-OM binding affinity, suggesting greater K leaching and lower extractable K concentrations.

Mangrove soil ordination was strongly defined by soil Al and H+Al concentration values. Antonina's mangrove higher potential acidity, as already discussed, is probably due to this environment higher OM content (Lin *et al.*, 2009).

However, soil data ordination was not possible when using the variables responsible for mangrove soil classification (C, C/N and OM). This fact, in the case of R. mangle, might be attributed to its favorite localization at mangrove margins, which is a region of greater instability and more susceptible to tide action. Therefore, as this species follows along both mangrove margins, the spatial factor might have greatly influenced the *R. mangle* leaf chemical composition (Cuzzuol and Rocha, 2012). Contrarily to R. mangle, the other mangrove species seemed to more intensively respond to the soil matrix physical-chemical processes. Depending on the soil texture, soil factors such as redox potential, pH, CEC, C and EC might exert more or less influence on plant species nutrient uptake. The differential nutrient leaf composition of A. shaueriana and L. racemosa might also be attributed to the soil saturation degree and micro relief (limenez, 1988; Jimenez and Lugo, 1988).

From this study resulted that different mangrove species growing in the same soil class presented differential leaf nutrient concentrations. *Avicennia shaueriana* showed higher leaf nutrient concentrations, except for Ca, than the other two studied species (*R. mangle* and *L. racemosa*). Among the three species, *A. shaueriana* showed the highest net selectivity index for potassium in the presence of high saturation levels of sodium.

Differential and individual species nutritional patterns were observed, evaluated by the leaf nutrient concentrations, independently of the soil attributes in which they were growing. Differences observed in soil characteristics did not affect the species nutritional patterns. Few correlations were found between leaf and soil nutrient concentrations, suggesting differential selective nutrient uptake among mangrove plant species.

CONCLUSION

Different mangrove species growing in the same soil class presented differential leaf nutrient concentrations. *Avicennia shaueriana* showed higher leaf nutrient concentrations, except for Ca, than the other two studied species (*R. mangle* and *L. racemosa*). Among the three studied species, *A. shaueriana* showed highest values of selectivity index for potassium in the presence of high saturation levels of sodium.

Differential and individual species nutritional patterns were observed, evaluated by the leaf nutrient concentrations, independently of the soil attributes in which they were growing. Differences observed in soil characteristics did not affect the species nutritional patterns. Few correlations were found between leaf and soil nutrient concentrations, suggesting differential selective nutrient uptake among mangrove plant species.

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