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Heterogeneity of elemental composition and natural abundance of stables isotopes of C and N in soils and leaves of mangroves at their southernmost West Atlantic range

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Abstract

Mangrove communities were selected in the state of Santa Catarina, Brazil, near their southernmost limit of distribution, to study mineral nutrient relation in soils and plants. Communities included three true mangrove species, *Rhizophora mangle, Laguncularia racemosa* and *Avicennia germinans*, and two associated species, the fern *Acrostichum danaeifolium*, and the grass *Spartina densiflora.* The sites included communities in the lower Río Tavares near Florianopolis city, Sonho beach near Palhoça city, and the Santo Antonio lagoon. These sites included a full range of mangroves under humid climate where winter temperatures, instead of salinity, may be the main factor regulating their productive capacity and species composition. Soil salinity was determined by the concentration of soluble Na, and soil C and N were linearly correlated indicating their association in organic matter. Tavares site showed higher specific conductivity, and concentrations of Na and Mg in the soil layer below 40 cm depth, indicating larger influence of marine water. Isotopic signature of C increased with soil depth suggesting that microorganisms decomposing organic matter are releasing ^{13}C depleted CO_2. Nitrogen isotopic signature decreased with soil depth, indicating enrichment in ^{15}N possibly as a result of denitrification in the upper soil layers. Mineral elements in leaf tissues showed *A. schaueriana* with higher concentrations of N, P, Na, K, Cu, Zn, and Na/Ca ratio. *Spartina densiflora* was characterized by the lowest N and K concentrations, and the highest concentrations of Al and Fe. *Rhizophora mangle* and *L. racemosa* had the highest Ca concentrations. Carbon isotopic signatures identified *S. densiflora* as a C4 plant, and *A. schaueriana* as the mangrove species occupying comparatively more water stressed microsites than the rest. Leaf nitrogen isotopic signatures were positive, in correspondence with the soil values. The results support the hypothesis that sites sampled were comparatively fertile, because sediment transport through fresh water run-off is predominant in humid coasts, and therefore plants were not limited by nutrient supply, nor particularly stressed by soil salinity.

Keywords: mangroves, soils, leaves, nutrients, stable isotopes, southwestern Atlantic latitudinal limit.

Heterogeneidade da composição elementar e abundância natural de isótopos estáveis de C e N no solo e folhas dos manguezais no extremo sul da sua distribuição na costa Atlântica ocidental

Resumo

Foram selecionadas florestas de mangue próximas ao limite sul de distribuição dos manguezais, no estado de Santa Catarina, Brasil, para o estudo do conteúdo de nutrientes no solo e em tecido vegetal. As comunidades estudadas eram compostas por três espécies típicas de mangue: *Rhizophora mangle, Laguncularia racemosa* e *Avicennia germinans*, e duas espécies associadas: a samambaia-do-brejo, *Acrostichum danaeifolium*, e a herbácea *Spartina densiflora.* Os locais de estudo incluiram comunidades no curso inferior do Rio Tavares na cidade de Florianópolis; Praia do Sonho, próxima à cidade de Palhoça e a Lagoa de Santo Antonio. Esses locais incluiram manguezais submetidos a clima úmido, onde as temperaturas do inverno, mais do que a salinidade, são o principal fator regulador da capacidade produtiva do sistema e da composição de espécies. A salinidade do solo foi determinada pela concentração de Na solúvel. Os conteúdos de Carbono e Nitrogênio no solo apresentaram correlação linear, indicando sua associação na matéria orgânica. A área do Rio Tavares apresentou maior influência marinha evidenciada pelas altas condutividade específica e concentrações de Na e Mg nas camadas do solo abaixo de 40 cm de profundidade. A assinatura isotópica do C aumentou com a profundidade no solo, o que sugere que microorganismos decompositores da matéria orgânica estão liberando CO_2 pobre em ^{13}C. A assinatura isotópica do Nitrogênio diminui com a profundidade do solo, indicando enriquecimento em ^{15}N, possivelmente como resultado de processo de denitrificação nos níveis superiores do solo. Os tecidos foliares de *A. schaueriana* apresentaram as maiores concentrações de N, P, Na, K, Cu, Zn, e da razão Na/Ca. *Spartina densiflora* apresentou as menores concentrações de N e K e as maiores concentrações de Al e Fe. *Rhizophora mangle* e *L. racemosa* apresentaram as maiores concentrações de Ca. Os resultados da assinatura isotópica de Carbono identificam *S. densiflora* como uma planta C4 e *A. schaueriana* como a espécie de mangue que ocupa os locais com maior estresse hidrico. As assinaturas isotópicas do Nitrogênio foram positivas, estando de acordo com os valores observados para o solo. Os resultados sustentam a hipótese de que os locais estudados são fertéis, pois o escoamento superficial de água doce é predominante em costas úmidas e, portanto, as plantas não estão sujeitas à limitação por aporte de nutrientes e não estão submetidas a estresse salino.

Palavras-chave: manguezais, solos, folhas, nutrientes, isótopos estáveis, limite latitudinal no Atlântico sul ocidental.

1. Introduction

Mangrove ecosystems occupy the intertidal zone in tropical and subtropical coasts. The mineral composition of their substrate is a result of the combination of sediments transported in fresh water runoff, and organic matter derived from the production of the mangrove system itself, including higher plants and marine microorganisms. Factors modulating local variations are decomposition rates of organic matter and export of particulates and dissolved minerals from mangroves to surrounding waters (Woodroffe, 1992; Lugo and Snedaker; 1974; Rezende et al. 2007; Lugo and Medina 2014).

Within their geographical distribution mangrove structural development is limited by salinity, correlated with climatic aridity, and nutrients, associated with fresh water runoff (Boto, 1983; Feller, 1995; Duke et al., 1998; Medina and Francisco, 1997; Rivera-Monroy et al., 2004), and may be also modified by anthropogenic influences, particularly sediment deposition (Soares, 1999). At their latitudinal limits of occurrence frost is added to the environmental constraints for mangrove establishment, survival, and structural development (Lugo and Zucca, 1977; McMillan and Sherrod, 1986; Lovelock et al., 2007; Soares et al., 2012).

In this paper we report on the elemental composition of soils and plants from mangrove ecosystems located in the southernmost reaches of mangrove ecosystems along the South American Atlantic coast, in Santa Catarina State, Brazil (Schaeffer-Novelli et al., 1990; Soares et al., 2012). The objective was to determine the nutritional profiles of mangrove sediments and species to assess differences determined by local hydrological conditions and species physiology. As the Santa Catarina coasts are under a humid subtropical climate (Schaeffer-Novelli et al., 1990) we hypothesized that mangroves substrates should be fertile, without restrictions in N and P availability, and that salinity effects should be partially counteracted by the availability of freshwater run-off. The results are compared with reports from other mangrove forests in contrasting latitudinal locations.

2. Material and Methods

2.1. Locations

Mangrove communities included in this study are enclosed within Segment VII described by Schaeffer-Novelli et al. (1990) (Cabo Frío to Torres) within 23°00’ and 23°20’ S, along the Santa Catarina state coastline. In this area “shelf sediment transport is very active… and rainfall increases southward from 1090 mm yr^{-1} in Rio de Janeiro to 1400 mm yr^{-1} in Torres and is higher than potential evapotranspiration”.

The study sites were: 1) Río Tavares (TA), located on the Ilha de Santa Catarina, near Florianopolis city between 27°35’and 27°40’S; 48°30’W; 2) Sonho beach near Palhoça city (PA), between 27°48’ and 27°49’S; 48°38’ and 48°47’ W; and 3) Santo Antônio Lagoon, Laguna Municipality, 28°30’ S (LA). In these sites the mangrove species *Avicennia schaueriana* Stapf & Leechm. ex Moldenke, *Rhizophora mangle* L., and *Laguncularia racemosa* (L.) C.F. Gaertn. coexist. *Avicennia schaueriana* occurs in the three sites, its height decreasing from Río Tavares to Laguna. In Sonho beach *R. mangle* is near to its southern latitudinal limit, whereas for *A. schaueriana* and *L. racemosa* this limit is located near the Laguna site (Schaeffer-Novelli et al., 1990; Soares et al., 2012). In Sonho beach and Laguna two salt tolerant species, *Acrostichum danaeifolium* Langsd. & Fisch. and *Spartina densiflora*

Brongn., coexist with mangrove communities, reaching high levels of cover.

2.2. Soil sampling and analysis

We evaluated the variables salinity and fertility in mangrove soils, and the influence of tide and rainfall on those parameters. We sampled soils at two contrasting depths: a) superficial soil (0-10 cm), assuming that at this depth salinity and nutrients that affect establishment and survival of mangrove propagules are more variable, and b) deeper layers (40-50 cm), beyond the volume directly influenced by root activity, expected to be less variable retaining the long term salinity and nutrient conditions of the site (Medina et al., 2001; Mehlig et al., 2010).

Soil analyses were carried out at the Center of Ecology, Instituto Venezolano de Investigaciones Científicas, using methods described elsewhere (Medina et al., 2008). Samples were dried at room temperature and subsequently disaggregated in large porcelain mortars and passed through a 2-mm^2 sieve. The soil powder was subjected to binary acid digestion and analyzed for Na, K, Ca, Mg using atomic absorption spectrophotometry; P was analyzed in acid digested soils using a colorimetric method. From each soil sample 1 g of air-dried material was dissolved in 50 mL distilled water and extracted during 24 h. Once the insoluble material settled down, the conductivity of the clear solution was determined using a Cole-Parmer conductivity meter with an Au-cell. Specific soil conductivity (SC) was calculated as: conductivity × 50/ air-dry mass [(mS cm^{-1}) g^{-1}].

2.3. Leaf sampling and chemical analyses

Mature, healthy leaves from three individual trees of the characteristic species were sampled, dried at 60° to constant weight, and analyzed for elemental concentrations using standard methods at the Department of Soil Science, Escola Superior de Agricultura "Luiz De Queiroz", Universidade de São Paulo). Briefly, samples were digested with sulfuric acid (N measured by Kjeldahl titration) and nitric-perchloric binary mixture for the other elements, which were measured by colorimetry (Al), turbidimetry (S), flame photometry (K and Na), and atomic absorption spectrophotometry (Ca, Mg, Cu, Fe, Mn e Zn).

The elemental concentrations for a given species were similar in the sampled sites, therefore specific intersite differences were disregarded. We lumped the set of data for each species and submitted the result to a variance analysis.

2.4. Natural abundance of stable isotopes (^{13}C and ^{15}N)

Subsamples of soils and leaves were analyzed for C and N, and their stable isotopes ratios ($\delta^{13}C$ and $\delta^{15}N$), in the laboratories of the Centro de Energia Nuclear na Agricultura (CENA, Piracicaba, University of São Paulo) using standard mass spectrometric techniques. Analysis of ^{13}C was intended to evaluate drought stress and water use efficiency (Farquhar et al., 1982; Lin and Sternberg 1992) whereas ^{15}N analysis was expected to indicate availability of mineral N in the soil and openness of the N cycle in the system (Martinelli et al., 1999).

2.5. Statistical analyses

We used a nonparametric one-way analysis of variance (Wilcoxon/Kruskal-Wallis test), the Tukey/Kramer HSD test to determine significance of differences between means (at $P \leq 0.05$), and linear regression to assess interelemental relationships for both soil and plant samples. All analyses were performed using JPM 8 (SAS Institute Inc.).

3. Results

3.1. Concentration of alkaline and earth-alkaline metals in mangrove soils

Specific conductivity and total ion concentration of the soil samples were linearly correlated. Sodium was the most abundant cation explaining 92% of the variation of SC [SC [(mmhos cm^{-1}) g^{-1}] = 0.272 + 1.58 Total Na 10^{-3} (mmol kg^{-1}); $r^2_{adj} = 0.92$, $F = 423.7$, Prob>F <0.0001). Samples from all sites and soil depths followed the same linear relationship (Figure 1)

The values of the soil parameters showed large differences among sites (Table 1). Specific Conductivity and Na concentration were much higher in deeper soil layers at TA, but similar for all sites in the superficial layer. Potassium and Mg showed a higher concentration in TA at both soil depths, whereas Ca was more concentrated in the superficial soil in LA.

The soil parameter values were significantly higher in the deeper soil layer for SC, Na, and Mg in TA, but not at the other two sites (Table 1). At PA, all parameters were consistently lower in the deeper soil layer but the differences were not significant, whereas at the LA site all parameters were higher in the superficial soil, although only differences of K, Ca, and Mg were significant.

The Na/K ratios in Ta and La reveal mild salinity stress, compared to ratios in Pa.

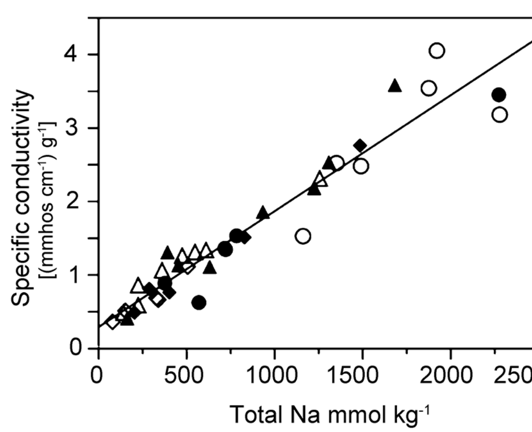

Figure 1. Correlation of total Na concentration and specific conductivity from different soil depths (closed symbols 0-10, cm; open symbols 40-50 cm), and sites (circles, Tavares; triangles Palhosa,; diamonds Laguna) in mangrove communities of Santa Catarina, Brazil.

Table 1. Average specific conductivity and cation concentrations in soil layer at different depth at each site.

	Depth	TA		PA	LA		W/K-W	
	cm	(6)		(8)	(5)		χ^2	P> χ^2
Spec. cond.	0-10	1.52	↓	1.76	1.25		0.96	ns
[(mmhos cm^{-1}) g^{-1}]	40-50	2.87		1.14	0.66		11.93	<0.01
Between depths	χ^2	4.33		1.59	1.84			
	P> χ^2	0.04		ns	ns			
Na	0-10	911	↓	854	647		0.69	ns
mmol kg^{-1}	40-50	1684		485	284		17.7	<0.01
Between depths	χ^2	4.33		2.16	1.32			
	P> χ^2	0.04		ns	ns			
K	0-10	166		47	114	↑	15.16	<0.01
mmol kg^{-1}	40-50	189		27	56		12.58	<0.01
Between depths	χ^2	1.09		2.16	5.77			
	P> χ^2	ns		ns	0.02			
Ca	0-10	50		46	91	↑	7.03	0,03
mmol kg^{-1}	40-50	44		23	35		4.32	ns
Between depths	χ^2	0.16		0.16	0.69			
	P> χ^2	ns		ns	<0.01			
Mg	0-10	128	↓	60	105	↑	6.96	0,03
mmol kg^{-1}	40-50	166		32	52		12.69	<0.01
Between depths	χ^2	3.69		1.22	6.82			
	P> χ^2	0.05		ns	<0.01			
Average Na/K	0-10	6		18	6			
	40-50	9		18	5			
Cation sequence								
	Ta			Na>K>Mg>Ca				
	Pa			Na>Mg>K=Ca				
	La			Na>K>Mg>Ca				

The arrows highlight the significance of parameter increase. In parenthesis sample number. Wilcoxon/Kruskal-Wallis (W/K-W) nonparametric analysis of variance test, ns not significant.

3.2. Concentration of non-metallic elements and isotopic signatures of soils

At all sites and soil depths the concentrations of C were positively and strongly correlated with those of N (R^2_{adj}= 0.767, P<0.0001) (Figure 2) and less so with those of P (R^2_{adj}= 0.117, P= 0.02). The concentrations of P, C, and N were higher in the superficial soil layers at all sites (Table 2). Phosphorus concentration in sediments differed between sites being higher in LA, followed by TA and lowest in PA, more markedly in the upper soil layer (Table 2). Carbon and N concentrations were similar and higher in LA and PA compared to TA.

The C isotopic signature decreased consistently from TA to LA at both soil depths, although means did not differed significantly (Table 2). This decrease was not expected considering the abundance of the C4 plant *S. densiflora* in PA and LA. There was a consistent tendency for the $\delta^{15}N$ values to decrease, and $\delta^{13}C$ values to increase, with depth at all sites.

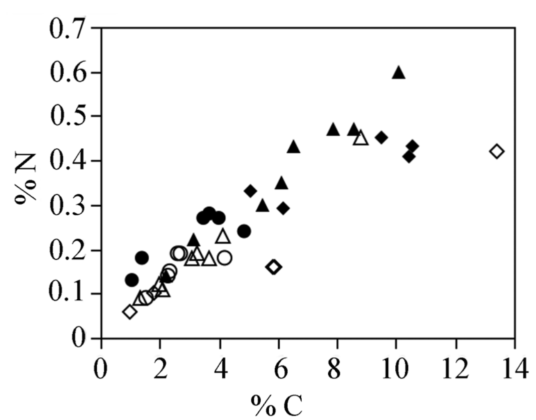

Figure 2. Concentration of C and N in % dry mass in soils from different depths and sites in Santa Catarina, Brazil. Symbols as in Figure 1.

3.3. Element concentration in leaves

Avicennia schaueriana showed higher concentration of the non-metallic elements N, P, and S, followed by *R. mangle*, and *L. racemosa*, while *S. alterniflora* showed the lowest concentrations of N and P (Table 3). The N/P ratios used as a relative indicator of P limitations in natural ecosystems was lower in the mangroves, compared to the associated species. Sulfur concentrations ranged from

Table 2. Average concentration of nonmetallic elements and isotopic signatures of C and N of soil layers at different depth at each site.

	Depth cm	TA		PA		LA		W/K-W	
		(6)		(8)		(5)		χ^2	$P>\chi^2$
P mmol kg^{-1}	0-10	16.5	↑	10.9	↑	23.4	↑	6.85	0.03
	40-50	11.6		5.2		9		9.73	0.01
Between depths	χ^2	3.1		6.35		4.81			
	$P>\chi^2$	0.08		0.01		0.03			
%C	0-10	3.1		6.3	↑	8.4		8.89	0.01
	40-50	2.6		3.6		5.6		0.65	ns
Between depths	χ^2	0.23		3.57		1.32			
	$P>\chi^2$	ns		0.06		ns			
% N	0-10	0.23	↑	0.37	↑	0.38	↑	6.98	0.03
	40-50	0.16		0.19		0.18		0.7	ns
Between depths	χ^2	2.86		5.35		3.96			
	$P>\chi^2$	0.09		0.02		0.05			
δ^{13}C ‰	0-10	–23		–24.3		–24.6		2.42	ns
	40-50	–21.9		–21.9		–23.2		0.33	ns
Between depths	χ^2	A		4.2		2.47			
	$P>\chi^2$	Ns		ns		Ns			
δ^{15}N ‰	0-10	5.6		4.4	↑	5		2.94	ns
	40-50	4.9		3.5		4.5		12.64	<0.01
Between depths	χ^2	0.78		9.66		0.89			
	$P>\chi^2$	ns		<0.01		Ns			

The arrows highlight the significance of parameter increase. In parenthesis sample number. Wilcoxon/Kruskal-Wallis (W/K-W) nonparametric analysis of variance test, ns not significant.

Table 3. Average leaf concentration (mmol kg^{-1}) of non metallic elements in plant species from Santa Catarina mangroves and accompanying halophytic species.

Species	Sites	n	N	P	S	N/P	N/S
Acrostichum danaeifolium	PA-LA	5	1291 b	36 c	60 ab	36	22
Avicennia schaueriana	PA-TA	8	1656 a	62 a	88 a	27	19
Laguncularia racemosa	TA-PA-LA	15	891 c	43 b	36 b	21	25
Rhizophora mangle	TA-PA	9	1110 c	40 bc	65 ab	28	17
Spartina densiflora	PA-LA	4	616 d	18 c	48 ab	34	13
Tests	W/K-W χ^2		31.77	17.85	15.47		
	$P>\chi^2$		<0.01	<0.01	<0.01		

Wilcoxon/Kruskal-Wallis (W/K-W) nonparametric analysis of variance test. Numbers followed by the same letter are statistically similar (Tukey-Cramer HSD test P=0.05).

36 to 88 mmol kg^{-1}, *L. racemosa* showing consistently lower values.

All major metallic elements analyzed showed significant differences that appeared to be species specific. Concentrations of K, Mg, and particularly Na were consistently higher in *A. schaueriana* compared to the other two mangrove species (Table 4). Calcium concentrations in *L. racemosa* and *R. mangle* were twice higher than that of *S. densiflora*, three times compared to *A. schaueriana,* and 8 times compared to *A. danaeifolium*. The Na/K molar ratios decreased from *L. racemosa* and *S. densiflora* (≈3), to *A. schaueriana* (≈2), and *R. mangle* and *A. danaeifolium* (≈1). In contrast, the Mg/Ca ratios were higher in *A. danaeifolium* and *A. schaueriana* (≈3), and decreased to ≈ 1 in *L. racemosa* and *S. densiflora* and <1 in *L. racemosa.*

The set of species analyzed showed also differences in the concentrations of heavy metals (Table 5). *Rhizophora*

Table 4. Average leaf concentration (mmol kg^{-1}) of major metallic elements in plant species from Santa Catarina mangroves and accompanying halophytic species.

Species	Sites	n	Na	K	Ca	Mg	Na/K	Mg/Ca
Acrostichum danaeifolium	PA-LA	5	186 b	236bc	27 c	83 b	0.9	3.4
Avicennia schaueriana	PA-TA	8	975 a	411 a	76bc	227 a	2.4	2.9
Laguncularia racemosa	TA-PA-LA	15	424 b	167c	220a	105 b	3.4	0.6
Rhizophora mangle	TA-PA	9	335 b	220bc	221ab	210 a	1.5	1.2
Spartina densiflora	PA-LA	4	296 b	99 c	101abc	94 b	3.4	1
Tests	W/K-W χ^2		25.38	21.41	23.15	24.05		
	P>χ^2		<0.01	<0.01	<0.01	<0.01		

Wilcoxon/Kruskal-Wallis (W/K-W) nonparametric analysis of variance test. Numbers followed by the same letter are statistically similar (Tukey-Cramer HSD test P=0.05).

Table 5. Concentration of minor metallic elements of mangroves and accompanying halophytic species.

Species	Sites	n	Al	Fe	Mn	Cu	Zn
			------------------------		µmol kg^{-1}	----------------------	
Acrostichum danaeifolium	PA-LA	5	2.5 b	1.3 bc	1 b	85 bc	376 ab
Avicennia schaueriana	PA-TA	8	1 b	1.8 bc	3.6 ab	157 a	413 a
Laguncularia racemosa	TA-PA-LA	15	1 b	2.7 b	1 b	44 c	221 c
Rhizophora mangle	TA-PA	9	0.8 b	0.9 c	8.9 a	101 b	146 c
Spartina densiflora	PA-LA	4	7.1 a	5.2 a	1.7 b	31 c	264 bc
	W/K-W χ^2		10.13	14.36		27.36	
	P>χ^2		0.03	<0.01		<0.01	

Wilcoxon/Kruskal-Wallis (W/K-W) nonparametric analysis of variance test. Numbers followed by the same letter are statistically similar (Tukey-Cramer HSD test P=0.05).

Table 6. Average concentrations of C and N, and isotopic signatures of leaves from mangrove and accompanying halophytic species in mangroves communities in Santa Catarina, Brazil.

Species	Sites	n	C	N	$\delta^{15}N$	$\delta^{13}C$
			mol kg^{-1}	mmol kg^{-1}	‰	‰
Acrostichum danaeifolium	PA-LA	5	44.1 ab	1416 a	3.15 b	–25.6 bc
Avicennia schaueriana	PA-TA	8	41.8 b	1648 a	4.73 ab	–24.5 b
Laguncularia racemosa	TA-PA-LA	15	45.3 a	905 bc	5.58 a	–26.4 c
Rhizophora mangle	TA-PA	9	46.1 a	1084 b	3.59 b	–26.7 c
Spartina densiflora	PA-LA	4	46.3 a	687 c	4.31 ab	–12.7 a
	W/K-W χ^2		20.93	30.12	13.64	18.06
	P>c^2		<0.01	<0.01	<0.01	<0.01

Wilcoxon/Kruskal-Wallis (W/K-W) nonparametric analysis of variance test. Numbers followed by the same letter are statistically similar (Tukey-Cramer HSD test P=0.05).

mangle showed the highest Mn concentrations, *A. schaueriana* showed the highest values of Cu and Zn, whereas Al and Fe were more concentrated in *S. densiflora*.

3.4. Leaf isotopic signatures

Both C and N concentrations of the material used for determination of isotope signatures differed significantly among species (Table 6). Among the mangroves, *A. schaueriana* had lower C concentration, a fact probably associated with the higher concentrations of alkaline metals in this species. Its N concentration was much higher than in the other two mangrove species but similar to that of *A. danaeifolium*. There are small differences in the N concentrations given in Table 6 and those of Table 3. The reason is that values in Table 3 were measured in acid digested samples (microKjeldahl), whereas in Table 6, values were estimated using an elemental analyzer. Differences in δ^{15}N values were small with *L. racemosa* showing higher values followed by *A. schaueriana* and *S. densiflora*, the lowest values corresponding to *R. mangle* and *A. danaeifolum*. *Spartina densiflora* sampled in PA and LA, showed the most positive δ^{13}C values, typical of a plant with C4 metabolism. Within the other species, the δ^{13}C values of *A. schaueriana* were distinctly more positive, a result expected if this species is growing under higher salt stress than the two other mangrove species.

4. Discussion

4.1. Soils

At all sites the electrical conductivity of the soil extract (SC) from both depths was linearly correlated with the total concentration of Na. This element was then predominantly in water-soluble form, as expected if its presence is determined primarily by the influx of marine water. Analyses of soil samples located within and below the depth of distribution of fine roots reveal contrasting hydrological dynamics between sites. The more stable deeper soils indicate that marine influence is more pronounced in TA, whereas in LA more fresh water runoff reduces salinity. Further evidence of this conclusion is that SC, Na, and Mg concentrations increased significantly with depth in TA but not in PA and LA.

Some differences between sites are observed on the basis of main cation concentrations at the upper soil layer, where most fine-root activity is expected. Following Na as the main cation in all sites, was K in Ta and La, and Mg in Pa. This sequence points to differences in the composition of sediment supply to each of the mangrove communities studied. The proportions of these elements are potentially significant to the nutritional relationships of mangrove species, related to their specific requirements, and also to the cation interactions that modify the salinity effects. Calcium ions in the rhizosphere are indispensable to maintain K uptake in the presence of large concentrations of Na (Epstein 1998), counteracting the toxic effects of this ion within the plant. These cations sequences have a wide range of variations among mangroves that are associated with the influence of marine waters. In São Matheus, Brasil (≈18ºS) Bernini et al. (2006) reported K concentrations in sediments of 5.9 mmol kg^{-1}, well below the values obtained in our sites in Santa Catarina, and the cation sequence was Mg>Ca>K. In Bragança peninsula (Para, Brasil, ≈1ºS) K concentrations decreased towards to coast but were always higher than Ca concentrations (Medina et al. 2001)

The average Na/K molar ratios are larger for PA (18), followed by TA (7) and LA (2), differing markedly from the Na/K ratio of standard sea water (46). This indicates that all three sites are within a humid climate zone, rainfall counteracting Na accumulation in the superficial soil layer. Differences in the Na/K ratios at the upper soil layer, are mainly determined by significantly different concentrations of K among sites, with similar Na concentrations. The PA site has clearly lower concentration of K at both soil depths, pointing to restricted supply of this element by terrestrial runoff.

The distribution of P and N at different depths appeared to be coupled, because both parameters are associated with organic matter, and decreased significantly with soil depth at all sites. Differences among sites are comparatively small, and may be associated with contrasting sedimentation patterns and underground biomass accumulation. In TA and PA, mangroves are under a riverine dynamics, fine sediments accumulating in TA, whereas coarser sediments accumulate in PA. In LA the hydrologic dynamics is less energetic, hypoxic conditions are probably of large duration, therefore its concentration of organic C and N tend to be larger in the upper soil layer. Marinho et al. (2012) found similar results in Sepetiba Bay, Rio de Janeiro, Brazil and suggested that mangrove organic matter and methane concentrations are correlated.

Concentration of C in soils varied from about 3 to a little above 8%, within the range expected for wetlands (Ember et al., 1987). The δ^{13}C ranged from about -22 to -24.6 ‰, with a tendency for more positive values in the lower soil layer. This pattern is expected if ^{13}C depleted CO_2 is preferentially released during the decomposition process of organic matter. These values are more positive in general compared to those reported by Lacerda et al. (1986b) for the Sepetiba bay in Río do Janeiro, and may indicate the influence of carbon from marine organisms (Bouillon et al., 2003). We expected differences in carbon isotopic signatures to appear in those mangroves where *S. densiflora* made up a significant fraction of the vegetation cover due to its C4-photosynthesis (Ember et al., 1987), but it was not the case.

The N isotopic signature of soils was always quite positive, with only slight differences between depths and sites. This result indicates that the three sites are characterized by an open nitrogen cycle (Martinelli et al., 1999), and that denitrification promotes the accumulation of the heavier isotope of N. This accumulation is also reflected in the isotopic composition of plants leaves as discussed below.

4.2. Plants

The N and P concentrations are within the upper range of variation in mangroves elsewhere indicating that the sediments in these mangrove sites are quite fertile as suggested also by the soil analyses (Lacerda et al., 1985; Medina et al., 2001; Bernini et al., 2006; Lugo et al., 2007; Medina et al., 2010). Besides, the N/P molar ratios are all below 30 for the mangrove species, and slightly above 30 in the associated species, well below the values reported from P-limited mangroves in the Caribbean (Medina et al. 2010). Sodium concentrations are lower than those reported for mangroves in drier climates (Medina et al., 2001; Alongi et al., 2003; Barboza et al., 2006) revealing the high fresh water availability of the communities studied. The Na/K molar relationships are larger than one, in the mangrove species and the grass *S. densiflora,* as expected for true halophytes (Medina, 1999). The fern *A. danaeifolium*, probably occupies less saline microsites, or restricts Na uptake effectively as reported for mangroves associates species (Wang et al., 2011).

Sulfur concentrations are well below concentrations reported for *Avicennia* and *Rhizophora* species elsewhere (Fry and Smith III 2002; Alongi et al., 2003; Bernini et al., 2006; Medina et al., 2010). We do not have an explanation for this fact but hypothesize that the mesic, humid climate where these communities are growing, reduces the stress of high level of available sulfate from marine waters through leaching brought about by rain and superficial run-off.

The differences in Ca concentrations among the species studied confirm previous reports from tropical mangrove sites where these species occur together (Lacerda et al., 1986a; Medina et al., 2001; Barboza et al., 2006; Lugo et al., 2007). Calcium is an element capable of counteracting excess of Na ions in the interstitial water surrounding the roots by stabilizing membranes in root cells (Epstein, 1998) supporting the absorption of K, therefore, its presence in the soil solution may improve tolerance to high levels of salinity. However, differences may be also associated with specific physiological requirements of Ca. Higher plants species differ in the amount of soluble Ca that they contain in their cell sap, and may be differentiated between calciotrophic and calciophobic physiotypes (Kinzel and Lechner, 1992). Species of the genus *Avicennia* contain high levels of soluble oxalate in their cells preventing absorption and accumulation of Ca within their cells (Popp et al., 1993) resulting in Mg/Ca ratios >2. This might be in our study the case of *A. danaeifolium* with a molar Mg/Ca >3, similar as reported for the mangrove fern, *A. aureum* (Medina et al., 1990). Oxalic acid concentration in leaf sap of these species deserves further analysis.

There are few data to compare the concentrations of Al and Fe of our species, elements that are most probably transported in terrestrial run-off. *Spartina densiflora* appears not to be capable of preventing Al absorption through the roots and is more permeable to Fe.

In general the concentrations of the heavy metals (Fe, Mn, Cu, and Zn) appear to be within the lower range of concentrations reported for other mangrove sites in Brazil (Machado et al., 2002; Bernini et al., 2010) and elsewhere (Alongi et al., 2003; MacFarlane et al., 2007).

The $\delta^{13}C$ values separated *S. densiflora* from the rest because of its C4 photosynthesis. The C isotopic signatures of C3 species corresponded to leaves grown under fully sun exposure, being more positive in *A. schaueriana*, an indication that the sampled trees were more water stressed (Soares et al., 2015). All $\delta^{15}N$ values were positive indicating that N was not limiting for plant growth and that plants were obtaining their N from sufficiently aerated soil layers where denitrification accounts for relative accumulation of ^{15}N (Craine et al., 2009).

The results support the hypothesis advanced in the introduction, that the mangrove sites reported here where comparative fertile, with high levels of N and P, and essential cations such as K and Ca. Nutrient rich sediments are transported by the abundant fresh water run-off characteristic of humid coasts. Therefore, plants were not limited by nutrient supply, nor particularly stressed by soil salinity.

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