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Photosynthetic capacity and intrinsic water-use efficiency of *Rhizophora mangle* at its southernmost western Atlantic range

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Abstract

The southernmost presence of *Rhizophora mangle* in the western Atlantic coast occurs in coastal wetlands between 27 and 28°S in the State of Santa Catarina, Brazil. We selected mangrove communities at the estuary of the River Tavares, Florianopolis, and the Sonho Beach, Palhosa, for measurement of photosynthetic performance and intrinsic water-use efficiency of *R. mangle* and coexisting individuals of *Avicennia schaueriana* and *Laguncularia racemosa*, during the spring season. We used gas-exchange techniques and isotopic signatures of C and N to estimate instantaneous water-use and carboxylation efficiency (CE), long-term water-use efficiency, and potential N limitation. Results showed that *R. mangle* had significantly lower photosynthetic rates but similar conductance values as the other two species resulting in lower intrinsic water use (WUE_i) and CE. WUE_i and CE were positively correlated in *L. racemosa* and *A. schaueriana*, but not in *R. mangle*. At each site, $\delta^{13}C$ values of *A. schaueriana* were consistently higher than those for the other species, indicating that these species are subjected to contrasting water stress conditions. Leaf concentrations of C were lower, whilst those of N were always higher in *A. schaueriana*, indicating accumulation of salts and nonprotein N-compounds in leaves. Nitrogen concentrations and moderate positive $\delta^{15}N$ values indicated that plant growth at the study sites was not inhibited by nutrient deficiency, and was not influenced by urban residual waters. Lower photosynthetic rates and values of CE of *R. mangle* compared to the other two species may constitute constraining factors preventing this species from establishing at higher latitudes.

Additional key words: intercellular CO_2 concentration; leaf temperature; photosynthesis; stable isotope.

Introduction

Mangrove ecosystems occupy a wide latitudinal range occurring in all continents from tropical to subtropical and warm temperate coastal sites. Their latitudinal limits of distribution generally match the 20°C winter isotherm, in areas usually not submitted to frost, and annual temperature amplitude below 5°C (Tomlinson 1986, Hutchings and Saenger 1987, Duke 1992). Along the Atlantic coast of the American continent mangroves occur from 29°N in the State of Florida (USA) down to nearly 29°S in the State of Santa Catarina, Brazil (Chapman 1976, Schaeffer-Novelli *et al.* 1990). Within this huge range only five mangrove species occur, *Rhizophora mangle* L., *R. racemosa* G.Mey, *Laguncularia racemosa* (L.) C.F. Gaertn, *Avicennia germinans* (L.) L., and *A. schaueriana* Stapf & Leechm. ex Moldenke (Tomlinson 1986). From phytogeographical and ecophysiological viewpoints it is

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Abbreviations: CE – carboxylation efficiency; C_i – intercellular CO_2 concentration; g_s – stomatal conductance; P_{Nmax} – light-saturated photosynthetic rate; Q_L – light intensity at the leaf surface; T_L – leaf temperature; WUE_i – intrinsic water-use efficiency.
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remarkable that *R. mangle* and *L. racemosa* cover the whole range from the Tropic of Cancer to Capricorn. *Avicennia germinans* covers mainly the northern range, and *A. schaueriana* appears to be more common in southern latitudes, but their distributions overlap from the southern Antilles (Imbert *et al.* 2000) down to 23°S in the Brazilian coast (Petri *et al.* 2011). *Rhizophora racemosa* is restricted to equatorial latitudes in the Atlantic and Caribbean coasts (Barreto and Barreto-Pittol 2012).

The latitudinal limits to the distribution of mangroves are probably determined by the occurrence of freezing temperatures during the winter causing xylem failure (Stuart *et al.* 2007). However, there seems to be interspecific differences in tolerance to frost. In the northernmost range, *A. germinans* is the species that occurs at the limit of mangrove distribution, occupying similar habitats together with *Spartina alterniflora* (Kangas and Lugo 1990). In the southern Atlantic coast, the species dominating at the latitudinal limit is *L. racemosa*, which co-occurs in salt marshes with sparsely occurring *A. schaueriana* and a few halophytic species such as *S. densiflora* (Schaeffer-Novelli *et al.* 1990, Soares *et al.* 2012).

Ecophysiological studies of Brazilian mangroves are still scarce (Lacerda *et al.* 1986, Medina *et al.* 2001, Falqueto *et al.* 2008, Mehlig *et al.* 2010), and so far no research has been carried out near the southernmost limit of their distribution. Our main objective was to explore the following question: Do constraints in photosynthetic capacity and intrinsic water-use efficiency of *R. mangle* help explain its distribution at higher latitudes?

In this article, we compared the photosynthetic performance of *R. mangle* at, or near its southernmost latitudinal range, with co-occurring mangrove species able to grow at much higher latitudes. We studied leaf gas exchange and natural abundance of stable isotopes of C and N, focusing on water-use and carboxylation efficiencies of dominant mangrove species in several communities occurring in the State of Santa Catarina, Brazil, around 28°S.

Materials and methods

Study area: The climate along the coast of the Santa Catarina State has been classified as mesothermal (Cfa) in the Köppen system (Santa Catarina 1986). The weather is influenced by polar air masses moving through its coast averaging three cold fronts per year (Rodrigues *et al.* 2004).

Measurements were carried out in October 2004 in two estuaries located in central and northeastern littoral, Florianopolis (the Tavares River, between 27°35' and 27°40'S; 48°30'W), and Palhoça (the Sonho Beach between 27°48' and 27°49'S; 48°38' and 48°37'W). Rainfall and average temperature during the measuring period were within the averages expected for the Cfa climate type of Santa Catarina (134.7 mm and 19.7°C, respectively) (Inmet 2014). The target of our study were mangrove communities described previously by de Souza Sobrinho *et al.* (1969), Schaeffer-Novelli *et al.* (1990), and Tognella-De-Rosa *et al.* (2004), where the mangroves of *A. schaueriana*, *L. racemosa*, and *R. mangle* are found growing together.

The Tavares River mangrove area is located in southwest coast of the Santa Catarina Island, inside the urban area of Florianopolis. At this site, average temperatures range from 17 to 25°C. The annual average precipitation is 1,470 mm, and the annual largest tidal amplitude is 1.4 m (Caruso 1990, Schettini *et al.*1996).

Measurements were carried out at two contiguous locations on the southern margin in the middle section of the Tavares River, a fringe forest along the water channel, with interstitial soil salinity of 20 ppt, and interior forest adjacent to a hypersaline area devoid of vegetation, locally denominated ‘apicum’, with interstitial soil salinity of 29–32 ppt. Measurements were performed on individuals of *R. mangle*, *L. racemosa*, and *A. schaueriana*, distant approximately 10 m from the river coast, and not shaded by surrounding trees. The fringe forest was a 90 m wide mangrove belt dominated by *L. racemosa* and *A. schaueriana*, with individuals surpassing 10 cm diameter at breast height. Individuals of *L. racemosa* were restricted to the river margin whereas those of *R. mangle* were located in the middle forest section interspersed with trees of *A. schaueriana*.

The Sonho Beach (Palhoça) area has a temperate climate with annual average temperature around 18°C in the winter and 27°C in the summer. Annual precipitation is 1,493 mm, and storms are well distributed throughout the year, a seasonal variation is small and similar to that of Florianopolis (Araújo *et al.* 2006). The mangrove forest studied is located in the north margin of the Massiambu River, near the mouth into the Sonho Beach. The river is not submitted to urban influence, but it is affected by agricultural activities. This place is the southernmost occurrence of *Rhizophora mangle* in Brasil (Schaeffer-Novelli *et al.* 1990). Measurements were carried out in a narrow band of mature mangrove community, about 70 m inland from the river margin, dominated by *A. schaueriana* with *L. racemosa* as the subdominant species. A few individuals of *R. mangle* were located near the interface of mangrove and nonhalophytic vegetation. *Spartina alterniflora* and *Acrostichum danaefolium* were associated with mangrove vegetation.

Photosynthesis measurements: Three adult, healthy leaves of the second to third pair on separate branches of three trees of *A. schaueriana*, *L. racemosa*, and *R. mangle* were selected for measurement of gas exchange during the spring in October 2004. We used a portable infrared gas analyzer (*LCi*, *ADC BioScientific*, Hoddesdon, UK) that allowed fast measurements of CO_2 concentration, air relative humidity, temperature, and incoming photosynthetically active radiation (Q_L, μmol m^{-2} s^{-1}). These parameters were used to calculate net assimilation [P_N, µmol(CO$_2$) m^{-2} s^{-1}], leaf conductance [g_s, mol(H$_2$O) m^{-2} s^{-1}], leaf temperature (T$_L$, °C), and internal CO$_2$ concentration (C_i, [µmol(CO$_2$) mol^{-1}]) using a program provided by the manufacturers based on von Caemmerer and Farquhar (1981). Measurements were conducted around noon time (11–13 h), using atmospheric CO$_2$ concentrations (≈ 380 µmol mol^{-1}), under natural light, humidity, and temperature conditions.

We calculated WUE$_i$ [mmol(CO$_2$) mol^{-1}(H$_2$O)] as the ratio P_N/g_s (Osmond *et al.* 1980), when incoming Q$_L$ was above 1,000 µmol(photon) m^{-2} s^{-1}. At this Q$_L$, P_N in these species was light saturated and measured rates were designated as P_{Nmax}. An additional index related to the carboxylation efficiency (CE) was the ratio of P_{Nmax}/C_i (Kiran *et al.* 2013).

Leaf sampling and analyses: Leaves used for photosynthesis measurements were collected and transported to the laboratory, where they were dried in an oven at 60°C for several days to obtain leaf dry mass. Parallel leaf samples from the same trees were dried and grounded for the analysis of stables isotopes of C and N. These analyses were conducted in the Isotope Ecology laboratory of CENA-USP in Piracicaba, using a *Thermo-Quest-Finnigan Delta Plus* isotope ratio mass spectrometer (*Finnigan-MAT*, San Jose, CA, USA) interfaced with an Elemental Analyzer (*model 1110; Carla Erba*, Italy). The isotopic natural abundance is expressed in delta units (δ^{13}C and δ^{15}N) (Ometto et al. 2006). The δ^{13}C values are used as indicators of long-term leaf water-use efficiency (CO$_2$ taken up per unit of water transpired) (Farquhar *et al.* 1982), and δ^{15}N values are indicators of the origin and availability of N in soils (Fry *et al.* 2000).

Statistical analyses: Averages of photosynthetic parameters, WUE$_i$, and natural abundance of stable isotopes were submitted to one-way analysis of variance (*ANOVA*) grouping by species and sites. When variances were not homogeneous as tested with the *Bartlett*'s test, we used a *Welch*'s analysis of variance allowing for standard deviations being unequal. In addition, we conducted a regression analysis to explore the dependence of WUE$_i$ on P_{Nmax}, g_s, and C_i. All statistical analyses were conducted using the *JMP* statistical program (*SAS Institute Inc.*).

Results

Gas exchange: Both g_s and P_{Nmax} showed large variability, and overlapped between species and sites (Table 1). Compared to *A. schaueriana* and *L. racemosa*, *R. mangle* had lower P_{Nmax} values at the Tavares River fringe and Sonho Beach, but not at the Tavares River interior site. In addition, the average C_i values for every species were lower at the Tavares River fringe, and *R. mangle* values were consistently higher compared to the other species. Leaf temperatures, a factor that may affect WUE$_i$ values, were higher at the Sonho Beach.

Average WUE$_i$ varied for all sites within each species, but all species had their highest values at the Tavares River fringe (Fig. 1). Average WUE$_i$ and CE values were similar for *A. schaueriana* and *L. racemosa* at all sites, whereas *R. mangle* had lower WUE$_i$ values, at both sites in the Tavares River, but not at the Sonho Beach, and lower CE

Table 1. Gas-exchange properties of species at different sites. Light intensity (Q$_L$), leaf temperature (T$_L$), intercellular CO$_2$ concentration (C_i), stomatal conductance (g_s), and light-saturated photosynthetic rate (P_{Nmax}). Values followed by *the same letter* within column are not statistically different (P=0.05). Mean ± SD (n = 5–9 per species and site).

Site	Q$_L$ [µmol m^{-2} s^{-1}]	T$_L$ [°C]	C_i [µmol mol^{-1}]	g_s [mol m^{-2} s^{-1}]	P_{Nmax} [µmol m^{-2} s^{-1}]
Avicennia schaueriana					
Sonho Beach	1,997 ± 263	34.6 ± 0.9^{A}	198 ± 30^{AB}	0.36 ± 0.15^{AB}	17.2 ± 5.1^{A}
Tavares River interior	1,996 ± 109	29.0 ± 0.7^{E}	206 ± 30^{A}	0.24 ± 0.07^{BC}	13.9 ± 2.0^{AB}
Tavares River fringe	1,969 ± 145	32.6 ± 0.5^{BC}	152 ± 33^{BC}	0.20 ± 0.06^{C}	16.5 ± 2.4^{A}
Laguncularia racemosa					
Sonho Beach	1,954 ± 215	32.6 ± 2.1^{BC}	214 ± 24^{A}	0.25 ± 0.09^{BC}	13.3 ± 5.2^{AB}
Tavares River interior	2,005 ± 78	29.6 ± 0.7^{DE}	204 ± 40^{A}	0.24 ± 0.05^{BC}	14.1 ± 3.8^{AB}
Tavares River fringe	1,967 ± 77	32.3 ± 0.4^{C}	147 ± 33^{C}	0.20 ± 0.05^{C}	17.2 ± 1.1^{A}
Rhizophora mangle					
Sonho Beach	1,612 ± 584	34.6 ± 2.2^{AB}	225 ± 22^{A}	0.19 ± 0.09^{BC}	9.6 ± 3.2^{B}
Tavares River interior	1,882 ± 301	28.8 ± 1.1^{E}	239 ± 26^{A}	0.45 ± 0.13^{A}	15.7 ± 2.1^{AB}
Tavares River fringe	1,861 ± 132	31.0 ± 1.2^{CD}	209 ± 17^{A}	0.21 ± 0.05^{C}	12.7 ± 2.6^{AB}
ANOVA (P=0.05)	-	-	<0.0001	-	-
Welch's *ANOVA*	0.40349	< 0.0001	-	0.0023	< 0.0001

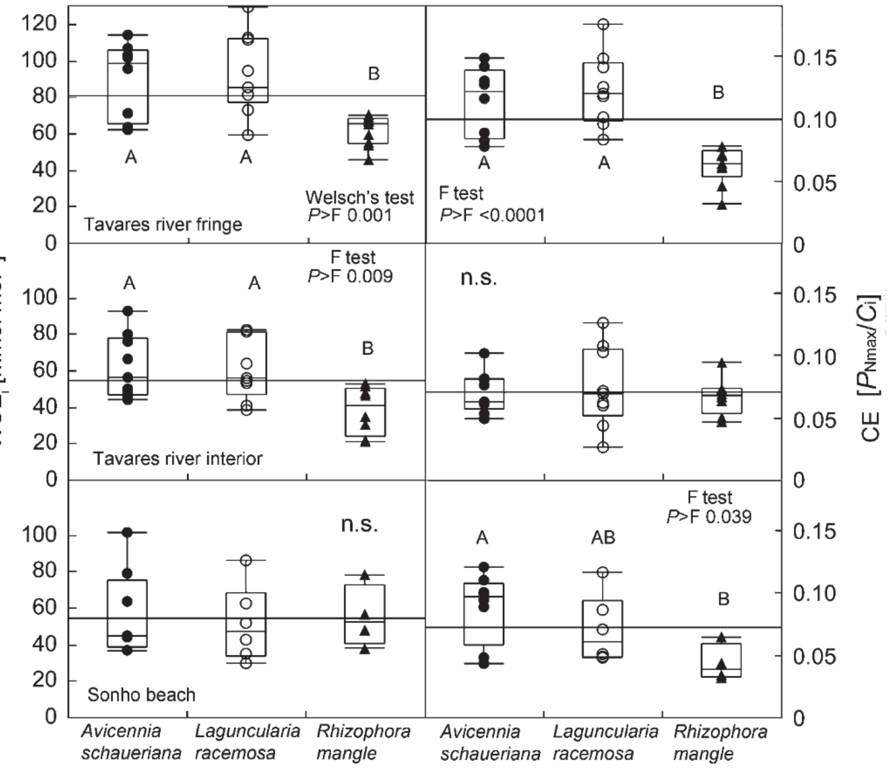

Fig. 1. Distribution of intrinsic water-use efficiency (WUE$_i$) and carboxylation index values (CE) calculated from field measurements of gas exchange. Box plots represent the median, and the 75th and 25th percentiles, whiskers are extended to extreme values. The horizontal line through the graph is the overall mean. *Different letters* on top of the box plots indicate significant difference of the mean (*Tukey*'s HSD test, P=0.05). *Filled circles*: *Avicennia schaueriana*, *empty circles*: *Laguncularia racemosa*, *black triangles*: *Rhizophora mangle*.

values at the Tavares River fringe and Sonho Beach, but not at the Tavares River interior site. All species had similar and lower values of WUE$_i$ at the Sonho Beach, the site, where higher leaf temperatures were recorded, and similar values of CE at the Tavares River interior, the site with higher salinity. WUE$_i$ was strongly and negatively correlated to C_i and the relationship did not differ between species (*A. schaueriana* r^2_{adj} = 0.88; *L. racemosa* r^2_{adj} = 0.93; *R. mangle* r^2_{adj} = 0.80), but overall WUE$_i$ average was higher for *A. schaueriana* (68.8 mmol mol^{-1}) and *L. racemosa* (66.4 mmol mol^{-1}), compared to *R. mangle* (50.4 mmol mol^{-1}). The linear relationship for the full data set indicated that C_i explained 89% of the variation in WUE$_i$ (WUE$_i$ = 171.9 – 0.546 C_i; r^2_{adj} = 0.89; F = 612, P >F < 0.0001; n = 78). Correlation between WUE$_i$ and g_s was negative and significant as expected, but much weaker, whereas the correlation between WUE$_i$ and P_{Nmax} was not significant. WUE$_i$ and CE were positively correlated, but regressions differed among the species (Fig. 2). The increase of CE with WUE$_i$ was negligible for *R. mangle* (P=0.385), intermediate for *A. schaueriana* (P=0.008), and the highest for *L. racemosa* (P<0.0001).

C and N concentrations and natural abundance of stable isotopes: Leaf C and N concentrations were similar for *L. racemosa* and *R. mangle*, but *A. schaueriana* had significantly lower C and higher N concentrations than the other species (Fig. 3).

All species had more negative δ^{13}C values at the Sonho Beach, corresponding to the lower WUE$_i$ values of *A. schaueriana* and *L. racemosa*, but not of *R. mangle*.

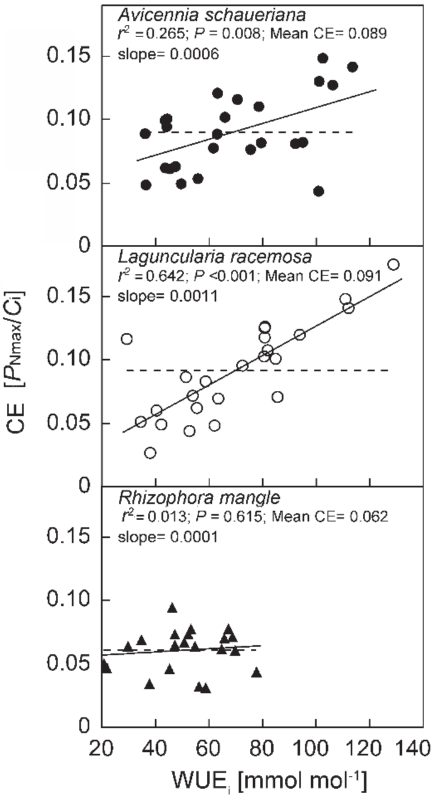

Fig. 2. Regressions of carboxylation efficiency (CE) *vs*. intrinsic water-use efficiency (WUE$_i$). The horizontal *dashed line* represents the overall mean. *Filled circles*: *Avicennia schaueriana*, *empty circles*: *Laguncularia racemosa*, *black triangles*: *Rhizophora mangle*.

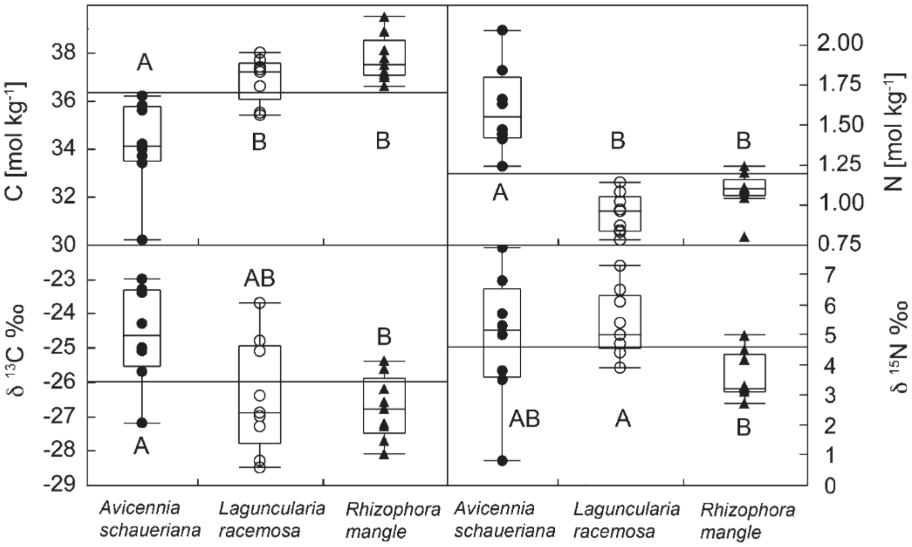

Fig. 3. Distribution of C and N concentrations and corresponding isotopic signatures. *Different letters* on top of the box plots indicate significant difference of the mean (*Tukey*'s HSD test, P=0.05). *Filled circles*: *Avicennia schaueriana*, *empty circles*: *Laguncularia racemosa*, *black triangles*: *Rhizophora mangle*.

Average δ^{13}C values for species from all sites showed that *R. mangle* had significantly lower values than those of *A. schaueriana*, whereas *L. racemosa* occupied an intermediate position (Fig. 3).

The δ^{15}N values varied among species and sites in a complex pattern. Pooling all sites and discriminating by species showed that *R. mangle* had consistently lower δ^{15}N values than the other two species (Fig. 3).

Discussion

Photosynthetic rates of *R. mangle* measured in our sites were within the range of those reported for mangrove species in the Caribbean (Moore *et al.* 1972, 1973; Azócar *et al.* 1992, Lin and Sternberg 1992, Sobrado 2000, Cheeseman and Lovelock 2004, Lugo *et al.* 2007), therefore photosynthesis in the Santa Catarina sites does not appear to be particularly constrained by salinity or drought during the period of measurements.

Avicennia schaueriana and *L. racemosa* showed a clear tendency to higher WUE_i than *R. mangle*, in spite of the overlapping values of P_{Nmax} and g_s. This result may be associated with the distribution of these species, *R. mangle* predominating near the coast line, and the other two species occupying landward positions with higher soil salinity and lower water potential of interstitial water (Schaeffer-Novelli *et al.* 1990).

The WUE_i values were low and similar for all species at the Sonho Beach, while the highest values were obtained at the Tavares River fringe site. These results indicated conditions favoring transpiration at the Sonho Beach, most probably caused by the higher leaf temperature recorded at this site for all species. Differences in WUE_i between the sites at the River Tavares were also significant. We expected lower WUE_i at the landward sites because they are usually more saline and drier, compared to fringe sites. Although not significantly different, the slightly higher maximum g_s, and lower P_{Nmax}, resulted in significantly smaller WUE_i at the interior site.

WUE_i and CE values were positively correlated but in the case of *R. mangle* the correlation was not significant and the range of variation was narrower than by the other two species. The slope of the regressions scarcely departed from zero in *R. mangle* and increased markedly in *A. schaueriana* and *L. racemosa*. The low values of CE, together with the lower P_{Nmax} of *R. mangle*, are possibly among the physiological constraints limiting its occurrence in coastal habitats at higher latitudes.

Concentrations of C were lower in *A. schaueriana* leaves at all sites, probably as a result of a higher ash content in this species usually growing in more saline sites (Schaefer-Novelli *et al.* 1990, Medina *et al.* 2001). *Avicennia germinans* is less restrictive of salt uptake through the roots and regulates internal salt concentration through the activity of salt secreting glands in their leaves (Scholander *et al.* 1962).

The leaf N concentration data are similar to those of mangrove trees growing on N-rich sediments (Medina *et al.* 2001) indicating that the communities studied were not limited by N supply. In addition, N concentration of *A. schaueriana* was higher at all sites confirming reports for another *Avicennia* species from several locations in the Caribbean and the Atlantic coasts of South America (Medina and Francisco 1997, Medina *et al.* 2001, Mehlig *et al.* 2010) that attribute this to the accumulation of glycinbetaine, a nitrogen-containing compound that works as a compatible solute in leaves of *Avicennia* species, whereas *L. racemosa* accumulates mannitol and *R. mangle* accumulates cyclitols that do not contain N in their molecules (Popp *et al.* 1993).

The δ^{13}C values correlate with long-term water-use efficiency (Farquhar *et al.* 1982); higher values indicate higher water-use efficiency. Those values varied between sites and species, but the number of samples per species was not sufficient to separate them by usual statistical techniques. However, precision of individual measurements was sufficient to reveal a distinct pattern. We developed a table using average values for each species at each site and calculated the differences between species at each site, and between sites for each species (Table 2). Inter-site comparisons showed that the Sonho Beach was the site with the lower long-term water-use efficiency for all species, revealing relatively better water availability at this site. Differences between the River Tavares sites were comparatively minor. At all sites, *A. schaueriana* showed higher $\delta^{13}C$ values, indicating consistently higher long-term water-use efficiency in this species. As discussed above, this was not true for WUE_i calculated from gas exchange, that revealed similar values for *A. schaueriana* and *L. racemosa* at all sites. Isotopic signatures of *L. racemosa* were similar or slightly higher than those of *R. mangle.* Lacerda *et al.* (1986) found a similar pattern of isotopic signatures for the same species in the Sepetiba Bay in Rio de Janeiro, about 23°S, but Medina *et al.* (2001) did not report interspecific differences in tropical mangroves communities with high fresh water supply throughout the year in Bragança, Para, Brasil, at nearly 1°S. This suggests that increasing temperature seasonality from the tropics to the subtropics may affect the P_{Nmax}/g_s relationship leading to changes in short- and long-term water-use efficiencies.

The higher $\delta^{15}N$ values of *A. schaueriana* and *L. racemosa* leaves may indicate that these species are using N sources enriched in ^{15}N compared to the source used by *R. mangle*. The positive $\delta^{15}N$ values indicate that the N demand for plant growth was high, and that nutritional restrictions for nutrient uptake during leaf formation were negligible. These positive values are similar to those reported previously for the same species under tropical conditions in the State of Pará, Brazil (Medina *et al.* 2001). Negative values have been reported for *R. mangle* under conditions where growth is limited by P supply (McKee *et al.* 2002), and large positive values (> 10‰) have been reported in environments with large anthropogenic nitrogen inputs (Fry *et al.* 2000). Based on those reports, we suggest that the mangroves sites studied in Santa Catarina were neither limited by P, nor noticeably polluted by anthropogenic sources.

Table 2. Pair contrasts of averages $\delta^{13}C$ values of species and sites ($n = 3$). Δ values correspond to differences between sites (SB – Sonho Beach; Tf – Tavares fringe; Ti – Tavares interior) and species (*Avi – A. schaueriana*; *Rhi – R. mangle*; *Lag – L. racemosa*).

Species	Sonho beach	Tavares fringe	Tavares interior	Δ(SB – Tf)	Δ(SB – Ti)	Δ(Tf – Ti)
A. schaueriana	–25.2	–24.3	–24.2	–0.9	–1.0	–0.1
L. racemosa	–27.3	–25.7	–26.3	–1.6	–1.0	0.6
R. mangle	–27.7	–26.6	–26.1	–1.1	–1.6	–0.5
Δ*Avi – Lag*	2.1	1.4	2.1			
Δ*Avi – Rhi*	2.5	2.3	1.9			
Δ*Lag – Rhi*	0.4	0.9	–0.2			

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