



# Gas exchange and isotopic signature of mangrove species in Southern Brazil



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## ABSTRACT

The study measured leaf gas exchange parameters and abundance of stable isotopes of C and N of three mangrove species (*Rhizophora mangle* L., *Avicennia schaueriana* Stapf & Leechm. ex Moldenke. and *Laguncularia racemosa* (L.) Gaertn) to investigate how photosynthetic capacity and water use efficiency characterize salt tolerance along an environmental gradient, in the Guaratuba Bay Estuary, Brazil, around 25°S. Along the estuary, parallel to the river, nine 50 m<sup>2</sup> plots were marked: three plots at the fringe, three plots at the intermediary zone (around 150 m from the fringe), and three plots at the interior zone (around 350 m from the fringe), to represent the zonation pattern expressed by mangrove species. We used gas exchange parameters to calculate intrinsic water use efficiency ( $A_{max}/g_s$ ,  $WUE_i$ ). Long-term water use efficiency was calculated based on  $\delta^{13}C$  values, and  $\delta^{15}N$  values were related to source of N. *Avicennia schaueriana* showed the capacity to maintain high  $WUE_i$ , even with high  $g_s$ , under higher salinities. The foliar  $\delta^{13}C$  of *L. racemosa*, was lower than the other species and negatively correlated to pore-water salinity. *Rhizophora mangle* gas exchange parameters did not correlate to the measured soil variables. Although the difference was not significant in *R. mangle*,  $\delta^{15}N$  values indicate that fringe mangroves may use a marine source of N. How species respond to changes in pore-water salinity is expressed in both gas exchange parameters and isotopic signature through the floodplain gradient.

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## 1. Introduction

Mangroves are defined as tree communities that occur in intertidal zones, essentially in tropical coastal areas (Tomlinson, 1986). Mangroves are highly connected to other ecosystems, representing a source of subsidies for fauna and also source of organic matter to adjacent communities (Feller et al., 2010). With worldwide distribution, mangroves occupy the Atlantic coast in the American continents, from 29°N to 29°S. Five species occur in Atlantic tropical southern areas, but only three of these are able to occupy subtropical areas (Schaeffer-Novelli et al., 1990; Lüttge, 2008): *Rhizophora mangle* L., *Avicennia schaueriana* Stapf & Leechm. ex Moldenke., and *Laguncularia racemosa* (L.) Gaertn. Species distribution in subtropical mangroves are constrained by tolerance to freezing temperatures, establishment of seedlings, and the development of

saplings and trees (Schaeffer-Novelli et al., 2000; Kathiresan and Bingham, 2001; Kao et al., 2004; Krauss et al., 2008).

In the range of distribution of mangrove ecosystems, physiological differences drive alterations in forest species composition, structure, and function along environmental gradients (Ball, 1996; Krauss et al., 2008; Lima and Tognella, 2012). Physiological differences among species related to their tolerance of environmental conditions may play a part in mangrove species dominance and occurrence (Smith, 1992; Ball, 1996, 2002; Lüttge, 2008). Thus, each geographic zone shows a set of environmental features that results in forests with distinct physiognomies (Schaeffer-Novelli et al., 1990), since species occurrence and development may be affected by factors on a regional scale, e.g., water balance, wave regime, and tides (Smith, 1992; Schaeffer-Novelli et al., 2000).

Previous studies showed distinct forest structure along the Brazilian coast (Carmo et al., 2000; Bernini and Rezende, 2004; Silva et al., 2005; Petri et al., 2011; Lima and Tognella, 2012). Based on that, Schaeffer-Novelli et al. (1990) divided the coastline into eight units in a latitudinal range, which shows similar environmental conditions within each unit. We expect similar forest structures

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inside these latitudinal ranges as those delineated by Schaeffer-Novelli et al. (1990). However, within a mangrove forest occupying the same geomorphological settings, species occurrence and development may also be controlled by the degree of soil saturation and topography, which determines tidal and fresh-water runoff, sediment composition, and stability (Tomlinson, 1986). These factors impact tree species differently and may result in a zonation pattern, such as those observed in southern Brazil. In southern Brazil, under the 25°S coordinate, mangroves presented distinct species distribution (Sessegolo, 1997; Bigarella, 2001; Dornelles et al., 2006; Kilca et al., 2011; Madi et al., 2016). These distribution patterns may be influenced by the specific physiological tolerance of each species. However, ecophysiological studies that correlate structure and environmental conditions in Brazilian mangroves are insufficient to elucidate the absence or occurrence of zonation patterns in subtropical mangrove areas (Pascoalini et al., 2014; Soares et al., 2015).

Mangrove environments may characterize a physiological challenge for plants because of the salinity and, consequently, highly negative water potentials of soil pore water (Krauss et al., 2008; Cardona-Olarte et al., 2013). Therefore, the main issue to mangrove tree species is the tradeoff between water loss and carbon gain, since water acquisition is more energetically expensive than in non-saline soils (Reef and Lovelock, 2015). Ecophysiological parameters, such as water use efficiency (*WUE*), may reveal the ability of a plant to use water for biomass production. Considering the importance of stomatal closure as the first event restricting photosynthesis at water stress (Flexas et al., 2004), the intrinsic water use efficiency (*WUEi*), defined as the ratio between net CO<sub>2</sub> assimilation and stomatal conductance, may represent how much biomass is produced for a given amount of water related to gas exchange occurring during photosynthesis process (Farquhar et al., 1982).

Despite the large representation of this parameter, *WUE* is estimated from leaf gas exchange, which makes it subject to temporal variance (Ferrio et al., 2003; Flexas et al., 2007). To avoid the effect of instantaneous measurements, *WUE* may also be estimated from stable carbon isotope composition ( $\delta^{13}\text{C}$ ), which is a time-integrated physiological indicator (Medina and Francisco, 1997).  $\delta^{13}\text{C}$  represents how much of the isotope <sup>13</sup>C, comparative to the amount of isotope <sup>12</sup>C, is discriminated in physicochemical process involved in leaf photosynthesis (Farquhar et al., 1989). Leaf  $\delta^{13}\text{C}$  reveals time-integrated *WUE* established on the duration of leaf lifespan, while *WUEi* only reflects water use efficiency instantly, in the recording procedure throughout gas exchange measurements (Cao et al., 2012). Thus, environmental factors that impact gas exchange components may reflect in  $\delta^{13}\text{C}$  variation, e.g., a higher discrimination against the heavier C isotope indicates a higher average conductance over the lifespan of the leaves and higher soil water potential (Cheeseman and Lovelock, 2004), while less negative  $\delta^{13}\text{C}$  values are correlated with higher water use efficiency (Medina and Francisco, 1997).

Although gas exchange characteristics of mangrove species have been explored considerably (Cintron et al., 1978; Clough and Sim, 1989; Lin and Sternberg, 1992a; Sobrado, 2000; Naidoo, 2010), the study of Soares et al. (2015) is, so far, the only ecophysiological research carried on the southernmost distribution of mangroves on the Atlantic coast, resulting in a lack of knowledge about how physiological tolerance impacts mangrove species distribution in subtropical areas. Soares et al. (2015) suggest ecophysiological responses of species, e.g., low photosynthetic rates and values of carboxylation index, as constraining factors to species distribution in higher latitudes, although they did not correlate their results with soil nutrient content.

Thus, this study aimed to investigate how photosynthetic capacity and water use efficiency characterize salt tolerance along an environmental gradient in a Brazilian subtropical mangrove for-

est. We addressed the following questions: Do leaf gas exchange parameters and isotopic signature of mangrove tree species differ among zones along the floodplain gradient? Also, are the ecophysiological responses to the environmental changes different among species? Overall, we hypothesized differences in gas exchange reflects photosynthetic capacity and differ among species, modulating differences in forest structure. For example, *A. schaueriana* seems to be more tolerant to salinity, thus exhibiting higher stomatal conductance in fringe mangroves and individuals with pronounced development, even where pore water salinity is higher, such as fringe areas.

## 2. Material and methods

### 2.1. Site description

The Pinheiros River Estuary is on the coast of Paraná State, Brazil, inside the Guaratuba Bay (25°50'S to 25°48'S and 48°34'W to 48°36'W). The climate is classified as *cfa* (mesothermal) in the Köppen system, with annual mean temperature of 20.8 °C and annual rainfall of 3183 mm during 2012. The estuary is close to the mouth of Guaratuba Bay. The soil is characterized as salic-sodic thiomorphic gleysol, showing high porewater salinity and organic matter content.

Along the estuary, parallel to the river, nine 50 m<sup>2</sup> plots were marked following a transect from fringe to inland: three plots at the fringe (5 m from the water body), three plots at the intermediary zone (around 150 m from the fringe), and three plots at the interior zone (around 350 m from the fringe), to represent the zonation pattern expressed by mangrove species. Forest structure was used to establish zones towards inland: *L. racemosa* shows higher density and dominance in fringe, whereas *R. mangle* is the most representative species in interior plots. In intermediary plots, both species were codominant. *Avicennia schaueriana* has higher density in fringe, decreasing towards interior plots.

### 2.2. Abiotic factors

Salinity of pore-water was measured at low tide with a digital hydrometer (Akso AK83) in five randomly selected points within each plot, 30 cm deep, during gas exchange measurements, totaling 45 samples *per zone* (fringe, intermediary and interior zone). Samples of sediment were collected at low tide with an auger, including one sample inside each plot and five samples around plots, totaling eight samples *per zone*.

To determine sediment nutrient composition, samples were collected at 10 cm depth. Particle-size distribution (fines and sand content, 30 cm deep) was determined using a particle analyzer (Camargo et al., 1986). Soil organic matter content (OM), pH, and soil cation exchange capacity (CEC) for the <2 mm fraction were measured according to standard procedures as described in Camargo et al. (1986).

### 2.3. Photosynthetic gas exchange and leaf water potentials

Measurements of gas exchange were conducted in the summer of 2013/2014, between December and January. The number individuals *per species* measured depended on the frequency of species, ranging from 2 to 5 individuals per species in each plot, with a total range for all plots varying from 2 to 14 individuals *per species*. Three sunlight exposed mature leaves were analyzed per individual. Measurements were conducted from 11:00 to 13:00 in sunny days (PAR > 1000  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), under natural humidity and temperature conditions.

We used a portable infrared gas analyzer open system (IRGA CI-340 model, BioScience), which performs measurements of CO<sub>2</sub>

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