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ORIGINAL PAPER

Nutrient and salt relations of *Pterocarpus officinalis* L. in coastal wetlands of the Caribbean: assessment through leaf and soil analyses

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Abstract *Pterocarpus officinalis* L. is a dominant tree of freshwater coastal wetlands in the Caribbean and the Guiana regions. It is frequently associated with mangroves in areas with high rainfall and/or surface run-off. We hypothesized that *P. officinalis* is a freshwater swamp species that when occurring in association with mangroves occupies low-salinity soil microsites, or alternatively that it possesses mechanisms preventing accumulation of salt in photosynthetic tissues. To test this we compared the mineral composition of soils and leaves of several species in two *Pterocarpus* forests in Puerto Rico associated with coastal mangroves, Sabana Seca and Punta Viento. Results indicate that (1) Sabana Seca has low soil salinity values even in the *P. officinalis* and *Laguncularia racemosa* mixed zone. In Punta Viento, salinity in the mixed zone was higher than in the *Pterocarpus* forest, but much lower than in the mangrove area; (2) In both forests, leaves of *P. officinalis* showed much lower Na concentrations than mangrove species. The K/Na ratios were 16–20 times higher in *P. officinalis*, indicating preferential absorption of K against Na. The mangrove fern (*Acrostichum aureum*) growing side by side with *P. officinalis* and *L. racemosa* in Punta Viento also revealed high Na exclusion capacity. We found an asymmetric distribution of cations in the blade and rachis of the *P. officinalis* compound leaves in both sites. The rachis accumulates more Na and Ca, but less Mg than the leaf blade. This sequestration of Na in the rachis prevents salt damage of photosynthetic tissue in the leaf blade.

Keywords *Pterocarpus officinalis* · Mangroves · Caribbean · Salt tolerance · Cation compartmentation

Introduction

Pterocarpus officinalis L. is a ubiquitous tree species of coastal wetlands in the Caribbean and Guiana regions, and one of the main constituents of coastal freshwater-forested wetlands (Bacon 1990). It has been frequently reported to be associated with mangrove communities in high rainfall and/or abundant river run-off locations. Freshwater-forested wetlands occur right behind the mangrove belt and *P. officinalis* can grow in slightly brackish waters (Tomlinson 1986; Bonhême et al. 1998; Imbert et al. 2000; Rivera-Ocasio 2002). Álvarez-López (1990) described the structure of several *Pterocarpus* forests in Puerto Rico, two of them located within the mangrove fringe, with trees of *P. officinalis* and *Laguncularia racemosa* (L.) Gaertn. growing side by side. Eusse and Aide (1999), also in Puerto Rico, showed that litter production of *Pterocarpus* forests stands decreased along a salinity gradient delimited by

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Typha sp.–*Acrostichum* sp. associations at the freshwater side and *L. racemosa* at the brackish side. These studies suggest that *P. officinalis* is probably a species best adapted to flooding in freshwater-forested wetlands, showing, in addition, a degree of tolerance to soil salinity derived from seawater in coastal sites under tidal influence (Bacon 1990). In Costa Rica, Clark et al. (1999) showed that this species is restricted to swampy soils that are not associated with mangroves.

Tolerance to moderate interstitial soil water salinity can be based on salt exclusion at the root level, scavenging by xylem parenchyma along the transpiration stream or accumulation in specialized tissues in the leaves (Albert 1982; Medina et al. 1990; Popp 1995; Breckle 2002).

In this paper we study the salt–nutrient relations of *P. officinalis* forests in Puerto Rico. To that end we sampled and analyzed soils and leaves in two *P. officinalis* forests in Puerto Rico, the Sabana Seca site studied by Eusse and Aide (1999) and the Patillas site studied by Álvarez-López (1990) (Fig. 1). These sites were selected because of the association of *P. officinalis* stands with mangrove communities. We consider *P. officinalis* to be a freshwater swamp tree and hypothesize that when it grows in association with mangroves, it occupies ecological spaces with low salinity, or alternatively that it has mechanisms preventing direct accumulation of salt in photosynthetic tissues. To test these hypotheses, we compared soil chemistry within the selected forests and the nutrient composition and accumulation of Na in leaf tissues of *P. officinalis* and mangrove species growing nearby.

Materials and methods

Sites

Sabana Seca

We sampled soils and leaves within a forest remnant described by Eusse and Aide (1999) located in Sabana Seca, Toa Baja, on the northern coastal plain of Puerto Rico (66°12′W, 18°27′N). Average rainfall reaches 1,693 mm. We selected plots located between a freshwater swamp and an *L. racemosa*-dominated mangrove forest.

Plot 1 was a relatively open *P. officinalis* stand, the neighboring disturbed areas being dominated by *Typha* sp. and several grass species. The site had multi-stemmed trees resulting from coppicing, apparently reflecting a history of disturbance in this plot. We observed several medium-sized (ca. 20 m^2) gaps dominated by *Acrostichum aureum* L. and numerous *P. officinalis* seedlings, some of them with scarcely nodulated roots. The soils were clayish and highly organic, with abundant, actively growing fine roots of *P. officinalis*. The larger roots were also superficial. We did not detect H_2S smell, suggesting adequate aeration.

Plot 2 was located within a dense *P. officinalis* stand, with single-stemmed trees less than 15 m tall and well-developed superficial roots. Many seedlings were germinating in a floating mat of litter, but these had no nodules. *A. aureum* individuals were present, developing vigorously in small gaps. Soils sampled had a similar texture to those of Plot 1, and no H_2S smell.

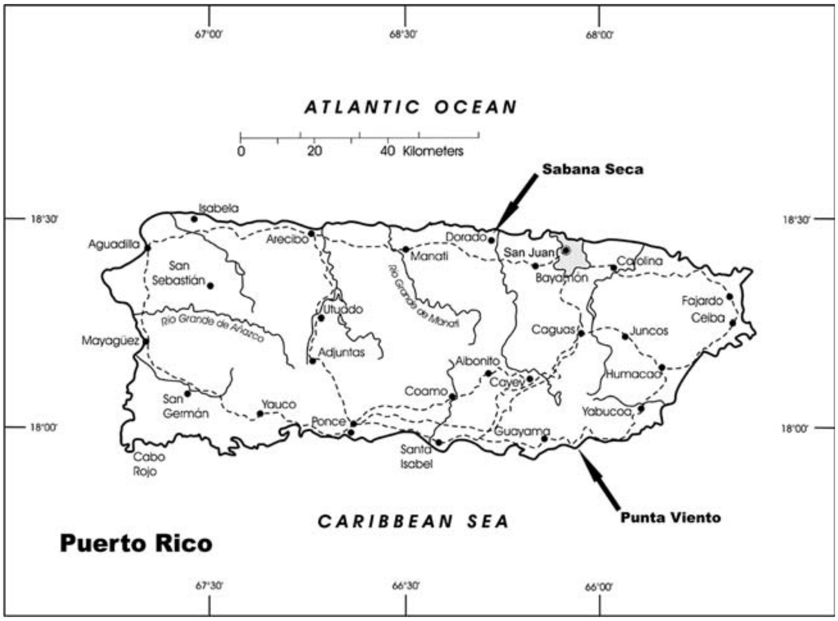

Fig. 1 Location of the stands of *Pterocarpus officinalis* sampled in Puerto Rico

Plot 3 was within the interface between *P. officinalis*-dominated and *L. racemosa*-dominated stands. *L. racemosa* was represented by large trees, more than 20 cm in diameter at breast height, several of them uprooted possibly by strong winds. We observed vigorous resprouting and branching on these trees. The plot also had *P. officinalis* trees (up to 4 m tall), partially shaded by *L. racemosa* and a few large *P. officinalis* trees. There was a clean separation between *L. racemosa* and *P. officinalis* along a natural drainage channel interrupted by the road. Soils sampled under water had a clay texture, were rich in organic matter and had a strong H_2S smell. Dense fine roots were found near the soil surface, mostly from *L. racemosa*.

Punta Viento

The stand is a remnant of a more extensive forest cut down probably more than 60 years ago for sugarcane plantations (Álvarez-López 1990). This forest relict is located in the County of Patillas in southern Puerto Rico (18°N 66°W) covering an area of 4.6 ha; average rainfall is 730 mm and mean annual temperature reaches 26.2 °C (http://www.ceducapr.com/pterocarpus.htm). The area receives water draining from the foothills of the southern mountain range, surfacing as freshwater springs and surrounded by large individuals of *Roystonea borinquena* O.F. Cook. The central part of the stand has a well-developed community of *P. officinalis*, described by Álvarez-López (1990). These communities interface toward the beach with mangrove communities located in areas 10–25 cm lower in elevation than that of the main *P. officinalis* stand. Along the border between *P. officinalis* and mangrove communities, we found individuals of *P. officinalis*, *Rhizophora mangle* L. and *L. racemosa* growing adjacent to each other. We differentiated four sampling areas, the *R. borinquena* + *P. officinalis* area (1, *Pterocarpus* forest); the *P. officinalis*–*L. racemosa* mixed zone (2) where these species grew side by side; the *R. mangle*-dominated area along a small creek (3); and finally the *Avicennia germinans* (L.)-dominated stand located within the lowest geomorphological position (4).

Sampling and analyses

Soils

Samples taken from up to a depth of 20 cm were subsequently air dried, ground and sieved through a 0.85-mm mesh. The soils were digested using a modification of the procedure of Luh Huang and Schulte (1985). Concentrated HNO_3 (8 ml) was added to the sample (0.5 g) and left to stand overnight at room temperature. Afterwards, the mixture was heated to 60 °C (0.5 h), and after a cooling period, 4 ml 30% hydrogen peroxide was added and then heated to 165 °C for 1.2 h. The final step was the addition of concentrated HCl (2 ml) and heating to 165°C for 20 min. Sample digests were analyzed for Na, Mg, P, K and Ca by plasma emission spectrometry (Spectro Ciros CCD). Concentrations of C, N and S were measured by a dry combustion method using a LECO-CNS 2000 Analyzer, based on the modification of the Application Note (form 203-821-170) titled ‘‘Carbon, Nitrogen and Sulfur in Soils/Sands’’ Leco Corp. (St Joseph, MI, USA) 2000. To prevent interference of potential high chloride content in samples, these analyses were performed using a halogen trap (Portnoy and Giblin 1997). In addition, the soil pH was measured in water (1:2.5).

Leaves

Adult compound leaves were sampled from four to five trees from each plot. Most branches sampled were under partial shade (~70% full sun). The leaves showed frequently heavy herbivore damage. The leaves were cleaned in the lab and separated into folioles and rachises. Damaged leaf tissue, when present, was cut out. Clean leaf material (washed with distilled water) was oven-dried at 65 °C in a ventilated oven and subsequently ground. Leaf samples were acid-digested and analyzed using the same procedures described for soils, except the HCl step. Ash percentage of leaves was calculated using oven dry weight (65°C) and weight of sample ash at 490°C.

Statistical analysis

Concentrations measured in soils and leaf tissues were submitted to a one-way analysis of variance (ANOVA) (plots within sites, and species). Homogeneity of variances was tested with Bartlett test. In the case of unequal variances, a Welch’s ANOVA testing for equality of means, allowing for unequal standard deviations, was applied. When *F*-ratios were significant to $P = 0.05$, an a posteriori test was conducted to compare means (Tukey–Kramer HSD test). All statistical analyses were carried out using the JMP statistical program (SAS Institute Inc. 1989–2002).

Results

Soils

The sites sampled were characterized by highly organic soils with carbon concentrations ranging from 13 to 24 mol C kg^{-1} soil dry weight (Table 1). *P. officinalis* stands in Sabana Seca, however, had consistently lower concentrations of C and N, but similar S concentrations and lower pH values than the Punta Viento stands. Mangrove-dominated stands in both sites had higher S concentrations and lower pH values (Table 1). Cation concentrations were similar in the Sabana Seca soils, but differed significantly between *P. officinalis* and mangrove stands in Punta Viento (Table 2). In this site, Na, K and Mg concentrations increased, whereas Ca decreased from the *P. officinalis*-dominated stands to the mangrove stands (Table 2). The K/Na ratios were three to seven times larger in Sabana Seca, because in this site K concentrations within the *P. officinalis* zones were consistently higher. The Ca/Mg ratio, however, was three to four times larger in the *P. officinalis* stand of Punta Viento, derived from the Ca supply in the waters draining from the southern mountain range. In the mangrove zones, Na and Mg concentrations were higher reflecting the influence of marine water.

Leaves

As soil Na concentrations were not significantly different among sampling plots in Sabana Seca, *P. officinalis* leaf samples were pooled together and compared with *L. racemosa*, as shown in Table 3. *P. officinalis* leaf tissues from Sabana Seca had higher concentrations than the soils of all elements with the exception of Na and Mg (compare Tables 1, 2, 3). However, *L. racemosa* also had higher Na concentration than the soil. Leaf–soil concentration ratio (LSR) of cations may be used as an indicator of relative accumulation or exclusion. Potassium was accumulated in leaf tissues of both species (LSR ~ 8), Na was excluded by *P. officinalis* (*R* = 0.1) and accumulated by *L. racemosa* (LSR = 3), Mg was relatively excluded by both species (LSR ~ 0.5), but Ca behaved neutral in *P. officinalis* (LSR ~ 1) and was accumulated in *L. racemosa* (LSR ~ 2.5). *P. officinalis* leaves showed higher N concentration than *L. racemosa*, but P, Na, Ca and percent ash were higher in the latter. Potassium and Mg concentrations were similar for both species. These differences were expected when comparing halophytes versus non-halophytes.

In the Punta Viento site, *P. officinalis* leaves showed consistently higher concentrations of all elements, except for Na, than the soils (compare Tables 1, 2, 3). Relative Na exclusion was lower than in Sabana Seca (LSR ~ 0.2). *Acrostichum* showed clear Na exclusion (*R* ~ 0.4); *L. racemosa* showed again Na accumulation (LSR ~ 2.2), but *Rhizophora* and *Avicennia* excluded this ion (LSR ~ 0.4 and 0.8, respectively). The latter two species grew on soils with Na concentrations at least twice as high as that of *L. racemosa.* Accumulation factors for K were much higher than in Sabana Seca for *P. officinalis* (LSR = 27.0) and *L. racemosa* (LSR = 26.6). *Acrostichum* showed a similar high

Table 1 pH and C, N, S concentrations of soils (0–20 cm) (in mmol kg^{-1}) from *Pterocarpus officinalis* communities in Sabana Seca and Punta Viento

Community location	*n*	pH (H_2O 1:25)	C	N	S
Sabana Seca					
Pterocarpus forest center	5	5.9	16,993	985	198
Pterocarpus–Laguncularia border	5	5.7	14,850	775	178
Pterocarpus–Laguncularia mixed zone	5	5.2	15,780	734	425
ANOVA *F* ratio		0.3	0.2	1.3	1.8
P-value		ns	ns	ns	ns
Punta Viento					
Pterocarpus forest	8	7.3a	23,236a	11,126a	208a
Pterocarpus–Laguncularia mixed zone	2	5.1b	24,147ab	980ab	708b
Rhizophora mangle	4	4.9b	19,680ab	810ab	870b
Avicennia germinans	2	5.2b	13,290b	665b	347a
ANOVA *F* ratio		263	4.5	4.9	59.1
P-value		<0.001	0.027	0.021	<0.001

In a column, numbers followed by the same letter are not statistically different. One-way ANOVA and Tukey–Kramer HSD at *P* = 0.05. By unequal variances (Bartlett test) the Welch ANOVA testing equality of means, allowing for unequal standard deviations, was applied (JMP-SAS 1989–2002)

ns not significant

Table 2 Cation concentrations of soils (0–20 cm) (in mmol kg^{-1}) from *Pterocarpus officinalis* communities in Sabana Seca and Punta Viento

Community location	*n*	P	Na	K	Mg	Ca	K/Na	Ca/Mg
Sabana Seca								
Pterocarpus forest	5	14	269ab	23a	258	219a	0.09	0.85
Pterocarpus–Laguncularia border	5	12	287a	32b	257	146b	0.11	0.57
Pterocarpus–Laguncularia mixed zone	5	10	200b	30b	252	188a	0.15	0.75
ANOVA *F* ratio		1.5	3.3	4.4	0.1	8.0	4.0	4.3
P-value		ns	0.08	0.042	ns	0.008	ns	0.05
Punta Viento								
Pterocarpus forest	8	17a	164a	12a	221a	1,136a	0.08	5.03a
Pterocarpus–Laguncularia mixed zone	2	10ab	531a	20a	305ab	512ab	0.05	1.73b
Rhizophora mangle	4	8b	1,656b	71b	519c	332b	0.04	0.64b
Avicennia germinans	2	11ab	1,431b	66b	408b	102b	0.05	0.61b
ANOVA *F* ratio		4.7	72.9	185.4	57.7	17.9	2.4	12.4
P-value		0.024	<0.001	<0.001	<0.001	0.009	ns	0.02

Statistics as in Table 1

Table 3 Mineral composition of mature leaves of *Pterocarpus officinalis* and mangrove species in the Sabana Seca and Punta Viento sites

Species	*n*	% Ash	N	P	Na	K	Mg	Ca	K/Na
Sabana Seca									
P. officinalis	14	4.9	2,448	36	19	236	143	228	23.2
Laguncularia racemosa	3	12.1	1,175	43	616	239	126	476	0.8
ANOVA *F* ratio		16	87	5	22	0	1	4	139
P-value		0.05	<0.001	0.047	0.04	ns	ns	ns	<0.001
Punta Viento[a]									
P. officinalis	7	6.9	1,967	30	27	325	240	502	15.6
Acrostichum aureum	1	6.1	907	38	200	618	308	87	3.1
L. racemosa	2	14.7	900	39	1,147	532	240	626	0.8
Rhizophora mangle	1	10.3	1,157	25	609	519	187	457	0.9
Avicennia germinans	1	9.8	1,489	25	1,075	364	81	161	0.3
ANOVA (*Pterocarpus* vs mangroves) *F* ratio		6	40	0.5	9	4	0.3	1	9
P-value		ns	<0.001	ns	0.04	ns	ns	ns	0.02

Concentrations in mmol kg^{-1}. Statistics as in Table 1

[a] In this site the *Pterocarpus* samples were run against the pooled mangroves samples

value (LSR = 30.9). Mangrove species showed lower K accumulation factors (LSR = 7.3 and 5.5 for *Rhizophora* and *Avicennia*, respectively). K/Na ratios distinguished *P. officinalis* from the other species (Table 3). Mangrove species had molar ratios below 1, whereas *P. officinalis* had values of 23 in Sabana Seca and 15.6 in Punta Viento. As expected, the *A. aureum* sample had a larger value than the true mangroves (sensu Tomlinson 1986; Medina et al. 1990). Leaf Ca/Mg ratios did not differ significantly at both sites.

Nitrogen concentration was always higher in *P. officinalis* leaves, a factor that may be associated with the reported symbiosis of this species with N_2-fixing bacteria (Saur et al. 1998). Among mangroves, the highest values were recorded for *Avicennia*, consistent with worldwide reports for species of this genus (Lugo 1999).

Cation compartmentation

Preliminary measurements indicated that the concentration of minerals was quite different in leaf blades and rachises of the *P. officinalis* compound leaves in spite of their similar ash content. We analyzed separately leaf blades and rachises of leaves from three trees from both sites (Table 4). The percentage of ash in both tissues was identical, but it was slightly higher in Punta Viento samples (5–6%). As expected, the concentrations of metabolically essential nutrients N, S and P were significantly higher in the leaf blades.

Table 4 Concentration of minerals (mmol kg^{-1}) in leaf blades and rachises of *Pterocarpus officinalis* leaves (n = 3)

	N	S	P	Na	K	Mg	Ca	K/Na
Sabana Seca								
Pterocarpus forest								
Leaves	2,343b	80b	35a	10b	225bc	122b	226c	22.5b
Rachis	886d	40c	18b	57a	206c	57d	341a	3.6c
Pterocarpus–Laguncularia interface								
Leaves	2,505a	100a	33a	5b	251ab	173a	270bc	53.7a
Rachis	969c	42c	20b	50a	284a	89c	312ab	5.8c
ANOVA *F* ratio	3,818	362	113	71	20	180	21	170
P-value	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Punta Viento								
Pterocarpus forest								
Leaves	2,564	85	40	13	354	181	305	27.3
Rachis	960	28	33	63	339	79	336	5.4
ANOVA *F* ratio	1,026	569	1	110	0	360	13	70
P-value	<0.001	<0.001	ns	<0.001	ns	0.002	0.022	<0.001

Statistics as in Table 1

Potassium was essentially similar in both tissues, Na and Ca were more concentrated in the rachis, and Mg was more concentrated in the leaf blades. In all cases, concentrations of alkaline and earth alkaline elements were higher in Punta Viento.

Discussion

To a casual observer, *P. officinalis* appears to tolerate high soil salinity and in fact, Álvarez-López (1990) reported *P. officinalis* growing in locations with soil salinity values of 12‰. However, our study shows these observations to be misleading. While *P. officinalis* can share the same geographic space with other halophytic species, the species in fact is occupying a different ecological space. *P. officinalis* also exhibits a number of ecophysiological responses to avoid a high-salinity environment. For example, the root system of *P. officinalis* is very shallow, roots spread laterally, and trees form organic matter mounds that elevate roots away from the denser saltwater in the soil. Seedlings normally grow and establish in the high watermarks of the forested wetland and no *P. officinalis* individuals grow in the lower elevations of saltwater wetlands. These field observations lend support to the hypothesis of *P. officinalis* restriction to oligo-saline microsites when associated with mangroves and explain why it does not occur as mangrove associate in semi-arid environments.

Both soil and leaf analyses reported here confirm that *P. officinalis* occupies oligo-haline or freshwater wetlands behind mangrove communities. In these communities, the influence of seawater intrusions may be experienced seasonally, as a result of reduced rainfall and surface run-off during the dry season, or occasionally as a result of strong winds causing seawater to flush coastland areas. Leaf analyses reveal that the proportion of cations accumulated in leaf blades allows the identification of true halophytes using K/Na ratios. Non-halophytes, even those occurring in oligosaline soils (salinity around 5‰), have physiological mechanisms accounting for Na exclusion at the root level, efficient K uptake in the presence of elevated Na and compartmentation of Na in specialized tissues (Breckle 2002). Non-halophytes have K/Na ratios well above 1 (Albert 1982), but the ratio can be reduced as the Na availability increases with soil salinization, or when K availability is reduced.

We interpret the large K/Na ratios measured in *P. officinalis* leaf blades compared to *L. racemosa* growing on soils of similar composition, as in Sabana Seca, as a result of a strong Na exclusion capacity. Na exclusion can take place at the root level, or result from accumulation of this cation along the transport in the xylem. The exclusion capacity for any higher plant depends on the soil K/Na ratios. Those are on average lower in Sabana Seca soils (Table 2). As a result, in spite of the higher leaf K concentration in *P. officinalis* leaf blades from Punta Viento, their K/Na ratio is smaller (Table 3). Mangroves sampled here are characterized by K/Na ratios below 1, as generally reported for many mangrove sites (Popp 1984; Lugo 1999).

We detected in *P. officinalis* an exclusion mechanism operating at the leaf level. Sodium transported in the transpiration stream is accumulated by a factor of 5 in the rachis compared to the blade, suggesting that it is partially retained in the woody rachis. The scavenging of salt along its path through the xylem probably occurs all the way from the root to the canopy. Such a process was shown in bean plants, cultivated in nutrient solutions to which salt was added up to 10^{-2} M concentrations (Jacoby 1964), shrubs (Jeschke and Wolf 1988) and grasses (Warwick and Halloran 1991). Waisel (1972, p. 120) showed the sequestration of Na in woody tissues of *Prosopis farcta* seedlings grown in 100 mM saline solutions exposed during 24 h to radioactive ^{22}NaCl.

The process apparently has not been documented in adult salt-tolerant trees (Popp 1995). It appears that exclusion and compartmentation of Na, and efficient K uptake, are not sufficient for *P. officinalis* to invade saline soils dominated by mangroves as those of Punta Viento. An additional protection that may be operating in *P. officinalis*, not measured in this work, is the cytoplasmatic protection based on the accumulation of the compatible solute glycinbetaine, a compound frequently associated with drought stress in legumes (Popp 1995; Rhodes et al. 2002). This compound is synthesized in herbaceous and woody legume species and it would be worthwhile to investigate its presence in *P. officinalis*.

We conclude that *P. officinalis* does not behave as a halophyte, as it does not accumulate Na in photosynthetic tissues. Regardless of its location, the individual trees will be elevated above the seawater, at an ecological space that allows it to function as a freshwater species surrounded by halophytes. However, the species has the capacity to tolerate some salinity, as evidenced by the accumulation of Na in the leaf rachis and its high capacity to accumulate K in the presence of Na, allowing the maintenance of high K/Na ratios in the leaf blades. These responses equip the species to exploit the narrow oligo-haline ecological spaces at the transition between saltwater and freshwater-forested wetlands. Comparative studies of salt relations in other mangrove-associated species are lacking. We expect that this mechanism of salt allocation detected in *P. officinalis* probably operates in other mangrove associates such as *Machaerium lunatum* and *Hibiscus pernambucensis* and the palms *Bactris major* in northern South America (Bacon 1990) and *Nypa fruticans* in Southeast Asia (Tomlinson 1986).

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