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Nutrient relations of dwarf *Rhizophora mangle* L. mangroves on peat in eastern Puerto Rico

Ernesto Medina · Elvira Cuevas · Ariel E. Lugo

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Abstract Dwarf mangroves on peat substrate growing in eastern Puerto Rico (Los Machos, Ceiba State Forest) were analyzed for element concentration, leaf sap osmolality, and isotopic signatures of C and N in leaves and substrate. Mangrove communities behind the fringe presented poor structural development with maximum height below 1.5 m, lacked a main stem, and produced horizontal stems from which rhizophores developed. This growth form departs from other dwarf mangrove sites in Belize, Panama, and Florida. The dwarf mangroves were not stressed by salinity but by the low P availability reflected in low P concentrations in adult and senescent leaves. Low P availability was associated with reduced remobilization of N and accumulation of K in senescent leaves, contrasting with the behavior of this cation in terrestrial plants. Remobilization of N and P before leaf abscission on a weight basis indicated complete resorption of these nutrients. On an area basis, resorption was complete for P but not for N. Sulfur accumulated markedly with leaf age, reaching values up to 400%, compared with relatively modest accumulation of Na (40%) in the same leaves. This suggests a more effective rejection of Na than sulfate at the root level. Dwarf mangrove leaves had more positive δ^{13}C values, which were not related to salinity, but possibly to drought during the dry season due to reduced flooding, and/or reduced hydraulic conductance under P limitation. Negative leaf δ^{15}N values were associated with low leaf P concentrations. Comparison with other *R. mangle* communities showed that P concentration in adult leaves below 13 mmol kg^{-1} is associated with negative δ^{15}N values, whereas leaves with P concentrations above 30 mmol kg^{-1} in non-polluted environments had positive δ^{15}N values.

Keywords Mangroves · Nutrient resorption · Salinity · ^{13}C · ^{15}N

Introduction

Mangroves are tropical and subtropical intertidal communities, which grow along protected marine coastlines and in estuaries with a steady supply of nutrients and fresh water (Lugo and Snedaker 1974). The species *Rhizophora mangle* L. occurs along the Atlantic coast from the tropic of Cancer in Florida to

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E. Medina (✉)
Centro de Ecología, Instituto Venezolano de Investigaciones Científicas, Aptdo. 21827,
Caracas 1020 A, Venezuela
e-mail: medinage@gmail.com

E. Medina · A. E. Lugo
International Institute of Tropical Forestry, USDA Forest Service, Jardin Botánico Sur, 1201 Calle Ceiba, San Juan,
PR 00926-1119, USA

E. Cuevas
Department of Biology, University of Puerto Rico,
San Juan, PR 00931-3360, USA

the tropic of Capricorn in southern Brazil (Tomlinson 1986). The environments along this large geographic range vary from high nutrient and low salinity in the estuaries of many tropical rivers in Brazil and Venezuela, to hypersaline, low nutrient environments in many islands and continental coastlines in the Caribbean. Structural variations across these environments have been frequently attributed to availability of fresh water and salinity (Walter and Steiner 1936; Lugo and Snedaker 1974; Pool et al. 1977; Medina 1999). Reduction in structural development is well known in *R. mangle* communities found in the Florida and Yucatán peninsulas on calcareous substrate (Thom 1982; Tomlinson 1986). The morphological characteristics of these communities, however, are not uniform. In south Florida, mangrove communities on marl substrate show strongly reduced structural development (dwarf mangroves), with little accumulation of organic matter at the surface, and low interstitial soil salinity (Koch and Snedaker 1997). Sites located nearer to the sea, characterized by much higher interstitial soil salinity, also contained short mangroves (Lin and Sternberg 1992a, b, c). The former appeared to be mainly nutrient limited while the latter appeared to be affected by saline concentrations above seawater.

Nutrients have been identified as determinant of mangrove structural development. Boto and Wellington (1984) concluded that N and P availability regulate mangrove development, correlating soil parameters with community structure in transects through mangroves around Sydney, Australia. The effect of nutrients is somewhat hidden by lower salinity in estuarine environments (Lugo and Snedaker 1974; Medina and Francisco 1997). High freshwater runoff is naturally associated with higher nutrient supply, and the positive effects of both ecophysiological factors result in development of tall and dense estuarine mangrove communities (e.g., Rivera-Monroy et al. 2004). Feller (1995) established a long-term fertilization experiment in the Twin Cays in Belize and showed elegantly that for those communities on calcareous soils P availability was the ecological factor determining plant growth. Subsequent articles revealed complex relationships between P availability and N utilization in coastal mangroves throughout the Caribbean and the Gulf of Mexico (Feller et al. 1999, 2002; Koch and Snedaker 1997; Lovelock et al. 2006). Recent publications document the changes from P to N limitations in mangrove ecotones (Feller et al. 2002), and the analysis of stable isotopes showed that phosphorus limitation was the cause of large variations in δ^{15}N along the transects submitted to fertilization (McKee et al. 2002). The dwarf mangrove communities described so far are found behind fringes of *R. mangle*, their habit resulting from an inhibition of the growth in length of the terminal meristem. Therefore, the plants branch and produce adventitious roots from a shortened stalk resulting in two round-shaped, umbrella-like, superimposing structures, the canopy, and the adventitious root system (or rhizophore system, Feller 1995).

Dwarf *R. mangle* communities are also found in the eastern coast of Puerto Rico in areas subjected to a limited tidal flooding and not exposed to any wave action (Cintrón et al. 1978; Helmer et al. 2002; González et al. 2006). The dwarf mangrove communities at this site differ substantially in growth form from what has been described for Florida, Belize, and Panamá (Feller 1995; Koch and Snedaker 1997; Chen and Twilley 1999; Cheeseman and Lovelock 2004; Lovelock et al. 2004). They grow on 1–6 m deep peat, deposited on top of calcareous material of biological origin. The plants do not develop a main stem, but grow almost horizontally following the direction of the predominant winds and produce rhizophores that sustain the horizontal stems. Windward-oriented stem-ends dry out and die progressively. In addition, it appears that plants seldom flower, with the recruitment of new plants occurring through the eventual supply of propagules from the fringe belts surrounding the dwarf communities.

The peculiar growth form of *R. mangle* in Los Machos lagoon, and the probable association of dwarfing of this species with availability of nutrients or hypersaline conditions prompted us to perform an analysis of the nutritional and osmotic conditions of soil and vegetation in this area. We hypothesized that the extreme reduction in tree size and scarcity of propagules of these communities could result from nutrient limitation and possibly high salinity because of restricted tidal flushing determined by the topography of the site. The combination of these factors probably generated extreme low nutrient availability and physiologically detrimental K and Na concentrations in leaf sap, resulting in diminished capacity for organic matter production and canopy development.

Site description

The mangrove site selected belongs to the Ceiba State Forest of the Commonwealth of Puerto Rico, and is located south of the Nuevo Mundo Bay, connected to the sea through tidal channels, some of which were historically blocked by road constructions or hurricanes (Fig. 1). The tidal channels are lined by 3–6-m tall *R. mangle* mangrove communities, followed by dwarf mangroves of the same species, <1.5 m tall. The substrate is mangrove-derived peat that began to accumulate since around 4,500 years ago (E. Cuevas, personal communication). The area is under the influence of shallow tides typical of the Caribbean (around 30 cm, http://coops.nos.noaa.gov/tides06/), and is isolated from significant transport of allochthonous sediments.

Sampling area was selected after observation of aerial photographs, looking for accessible, undisturbed sectors showing a pattern of tall–dwarf communities from the berm along the main water channel to the area landwards. The area selected was near the center of the Los Machos lagoon and conformed a nearly peninsular shape, located between 18°14′42″N; 65°36′56″W and 18°14′37″N; 65°36′56″W (Fig. 1). A total of five points along a

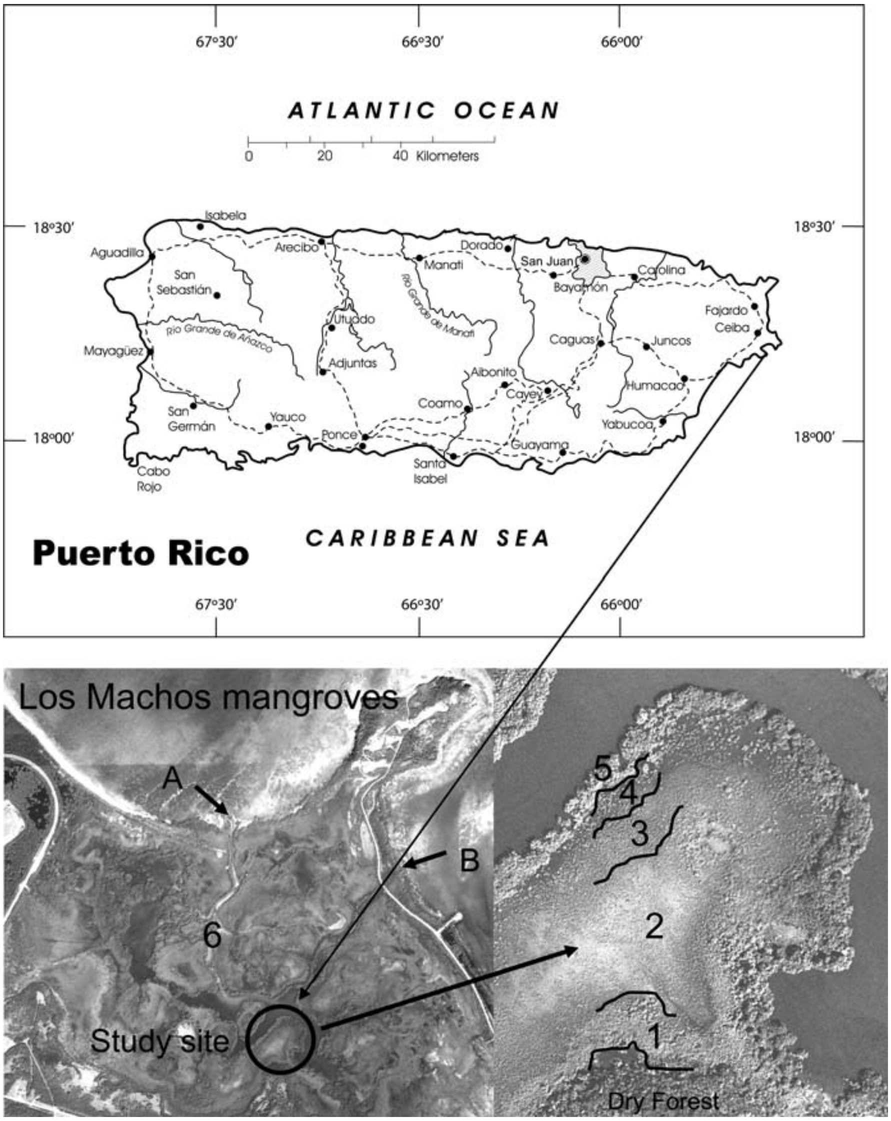


Fig. 1 Los Machos mangroves study site in the Ceiba State Forest, Humacao County, Puerto Rico. A and B showed the main water channels allowing the sea-water flushing of the wetland. The *numbers* indicate location of the points sampled in December 1995 for leaf area and nutrient analyses. A similar transect was sampled in March 1999 for estimation of leaf osmolality and measurement of carbon and nitrogen concentration, and isotope ratios in peat and leaves

transect from land to berm were sampled in December 1995 for the analysis of leaf morphology and nutrient concentrations. Point 1 was located at the inland-most border, where *R. mangle* grew together with *Avicennia germinans* and a few trees of *Laguncularia racemosa*. Substrate was composed of very dark-colored peat. Point 2 was located within a dwarf mangrove, dominated by *R. mangle* with a few scattered *A. germinans* shrubs, and the vegetation was dense (75% surface cover) and >1.5 m tall. Substrate was peat constituted almost exclusively by dead fine roots. Point 3 was a dwarf mangrove community constituted exclusively by *R. mangle*, <1 m tall, low density (surface cover <20%), with frequent and pronounced lack of apical dominance. The deep brown-colored peat was constituted by almost pure dead fine roots, >1 m deep. Point 4 was covered by a dwarf mangrove community of pure *R. mangle*, about 1.5 m tall, medium density (about 50% cover), with frequent lack of apical dominance. Substrate was peat constituted by almost pure dead fine roots. Point 5 was covered by a comparatively tall mangrove, along the berm lining the main channel, >2 m tall, and usual tree architecture. Point 6 was located in a fringe area along the main channel, where *R. mangle* impacted by hurricane Hugo in 1989 was regenerating. Plants were above 4 m tall, showing usual tree architecture.

In March 1999, the area was resampled along a nearly 200-m long transect from the fringe to the inland border of the mangrove vegetation, located in the same positions indicated in Fig. 1. The purpose was to measure the osmotic properties of interstitial water and leaf sap, and to determine the Carbon and Nitrogen isotopic signature in superficial substrate samples and leaves.

Climate data of the station at Roosevelt Roads, located <4 km east of the site, for the period 1959–2003 were obtained from the South East Regional Climate Center (http://www.sercc.com/). The mean monthly rainfall curve presents two maxima, in May (135 mm) and October (170 mm) as expected for a typical tropical climate at 18°N. Total rainfall amounted to 1,310 mm, and the first 4 months of the year received in average <100 mm each. Temperature averaged 26.6°, August being the hottest month with an average of 28.2°C, and February the coldest month with an average of 24.7°C.

Methods

Leaves were sampled without petioles in a sequence of relative ages from young (1st and 2nd pair), adult (3rd and 4th pair), old (5th pair and beyond), senescent (yellow-colored leaves) (two replicates of each leaf type from five different trees), separated according to their position in branch. Leaves were treated separately for area and weight, then pooled in one composite sample per type for chemical analyses. The field leaf categories differing in texture and color were confirmed by measurement of weight/area ratios (W/A, Specific Leaf Weight) and concentration of N and P. Samples were transported to the lab within 8 h after collection and dried in a ventilated oven at 60°C. Leaf area was measured in 10 fresh leaves (LiCor 1600 area meter) that were subsequently dried as above. Superficial peat samples (0–30 cm) for determination of concentration and stable isotopes of N and C were collected every 10–20 m along a 200-m transect from the fringe landwards. Analyses of C, N, and S were performed with a LECO CNS-2000 analyzer; total P, Na, K, Ca, and Mg were determined in a Beckmann SPECTRA SPAN DCP plasma spectrometer after digesting peat and leaf samples with a nitric-peroxide mixture; and ash percentage of leaves was calculated using oven dry weight (65°C) and weight of sample ash at 490°C (Medina et al. 2007).

In order to estimate sap osmolality, two samples per point of young, adult, and senescent leaves (each sample consisting of 2–3 leaves) were sealed into plastic centrifugation tubes and transported to the laboratory in a thermally isolated container filled with dry ice. Leaf sap was extracted by centrifugation after thawing. Parallel two interstitial water samples (50 ml) were taken from each point. Determination of osmolality and ion concentration in these samples followed procedures described in Medina and Francisco (1997). Natural abundances of ^{13}C and ^{15}N were measured using isotope ratio mass spectrometry in the Florida International University Stable Isotope Laboratory (methods described in http://www.fiu.edu/~sil/).

One-way analyses of variance were conducted to compare means applying an *a posteriori* Tukey–Cramer HSD test (JMP statistics program, SAS Institute Inc. 1989–2002). Variations in W/A ratios were higher than those of element concentration per unit weight. Therefore, we calculated the least significant difference (LSD) for W/A and applied it to the estimations of element concentrations per unit area.

Results

Leaf dimensions and element concentration in leaves

Leaf area differed significantly among plots (Fig. 2a). The largest leaves occurred in the fringe of the main collection area and in the regeneration site. Leaf weight varied linearly with area within each leaf category, but the W/A ratios differed significantly between sampling points and relative leaf age within each sampling point (Fig. 2b). Leaves from points 3–5 had larger W/A ratios interpreted as a higher degree of sclerophylly. Owing to these variations, we calculated nutrient concentration on an area basis for the plot—leaf age comparisons, and the estimation of relative element concentrations changes.

Nitrogen concentration increased from young to adult leaves and decreased significantly in senescent leaves (Fig. 3a). However, the N concentration in the senescent leaves remained similar to or above that of young leaves in sampling points 3 and 4, revealing an abnormal pattern of retranslocation. Sulfur concentration did not change significantly among plots in young and adult leaves (Fig. 3b), but in senescent leaves, S concentration increased markedly, more so at the points closer to the fringe. Phosphorus concentration declined slightly from young to old leaves, but it decreased abruptly in senescent leaves reaching concentrations of <1 mmol m^{-2} (Fig. 3c). Young leaves from point 3 showed significantly lower concentrations than those of points 1 and 6. Potassium increased significantly with leaf age in plots 3–5, an unusual result considering the mobility of this cation in the phloem—but in plots 1 and 6, it behaved as expected, being reduced by retranslocation or leaching from older leaves (Fig. 3d).

The sum of cations and ash concentrations showed a general pattern of increase with leaf age and were linearly correlated ($\sum$ions (mmol m^{-2}) = 13.59 + 13.19 Ash g m^{-2}; $r^2 = 0.972$). Sodium was always the dominant cation with 46% of the sum of cations, followed by Ca (23%), Mg (19%), and K (12%).

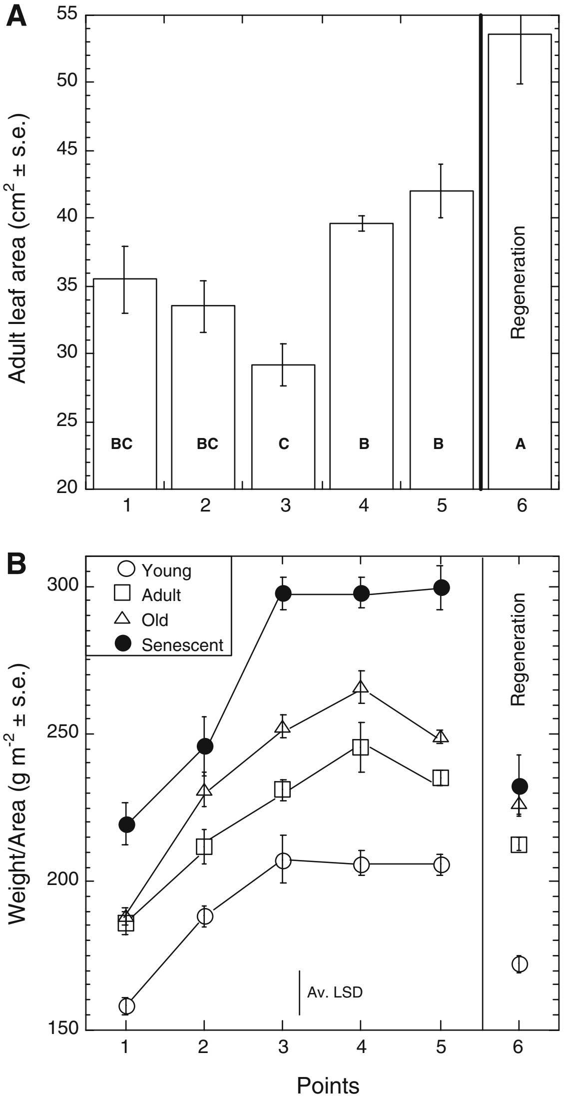


Fig. 2 Average size of adult leaves, and weight/area ratios of leaves of increasing age in the areas depicted in Fig. 1. **a** Columns with the same letter are not statistically different (Tukey–Cramer HSD Test, $P = 0.05$). **b** Points separated by distances greater than average. LSD are statistically different. In all these cases, $n = 10$

Element concentration and retranslocation before leaf shedding

The average percent change of relative element concentration from adult to senescent leaves, calculated per weight or per area were not statistically different, except for Ca (Table 1). However, the accumulation per unit weight is always lower than

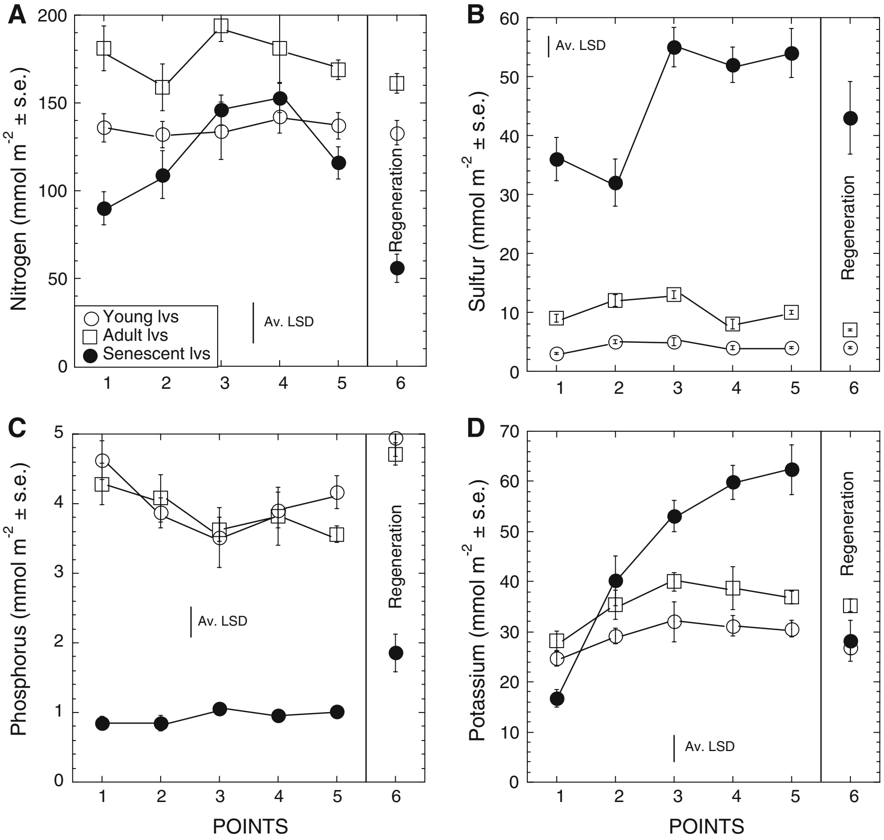


Fig. 3 Pattern of concentrations of N, P, S, and K (mmol m^{-2}) in leaves of increasing age in the areas depicted in Fig. 1. Points separated by distances greater than average. LSDs are statistically different (Tukey–Cramer HSD Test, $P = 0.05$). Standard errors are based on W/A ratios in Fig. 2 ($n = 10$)

Table 1 Average % change in nutrient in element concentration per unit area and weight, calculated as [Δ ([Senescent] − [Adult leaves])/[Adult leaves] × 100

Reference	N	S	P	K	Na	Ca	Mg
Area	−36	390	−73	18	73	73	69
Weight	−47	312	−77	−2	45	45	41
P	0.258	0.365	0.328	0.364	0.303	0.026	0.153

Positive values accumulation, *negative values* retranslocation or leaching. One-way ANOVA

per unit area, probably because of the W/A changes. On average per unit area, N and P concentrations were reduced before abscission by 36% and 73% respectively, whereas Na, Ca, and Mg increased by about 70%. Unexpectedly, K increased slightly but showed large variations between sampling points. The large% increment in S concentration was also unexpected. These values varied within plots for some elements. Potassium showed net retranslocation in points 1 and 6 and accumulation in the rest. Sodium accumulation was smaller in points 5 and 6, compared to points 1–4. Phosphorus was retranslocated similarly in all the sampling points, but retranslocation of N was more efficient in points 1 and 6 (compare values in Fig. 3).

Leaf sap and interstitial water osmolality

Osmolality of interstitial water increased from the normal sea water levels (≈1,000 mmol kg^{-1}, respectively) at the fringe to 1,450 mmol kg^{-1} at the inland border. Osmolality of leaf sap was always at least 200 mmol kg^{-1} higher than that of interstitial water, and followed a similar trend. Senescent leaves always had higher osmolalities than younger leaves (Fig. 4). Sodium was by far the dominant cation in leaf sap followed by Mg and K (Table 2). Potassium, Mg, and Ca were more concentrated in leaf saps, whereas Na was less concentrated in young and adult leaves, than in interstitial water. Potassium concentration of leaf sap did not change significantly with leaf age and was around nine times higher than that of interstitial water. Magnesium concentration was higher than that of Ca

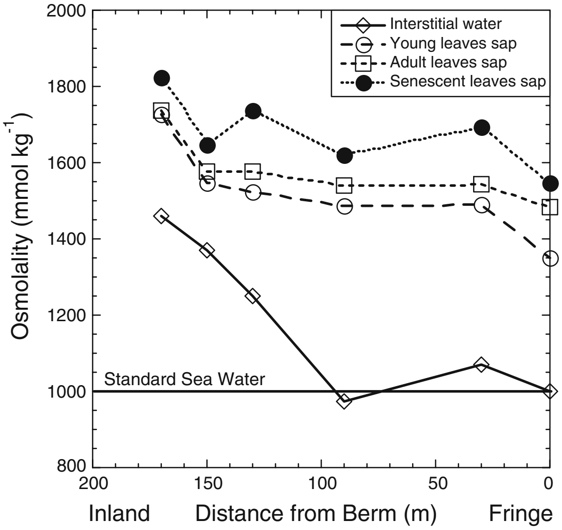


Fig. 4 Osmolality of soil interstitial water and leaf sap of leaves differing in relative age in the areas depicted in Fig. 1. Points represent the average of two leaf samples per leaf type (2–3 leaves each), and two interstitial water samples. Differences in osmolality between replicates was 10% for interstitial water, and <5% for leaf sap

in interstitial water (5 times), and in leaf saps (2–3.5 times). Leaf saps were more concentrated in Mg ($\approx$2 times) and Ca (3–5 times) than interstitial water. The leaf sap concentration of Na and Ca increased markedly in senescent leaves. Phosphorus concentration in leaf sap of adult leaves was higher in the fringe and inland samples (2–2.4 mmol l^{-1}) than in the dwarf mangrove community (1.5 mmol l^{-1}). In senescent leaves, P concentration did not vary with the distance from the fringe and averaged 0.5 mmol l^{-1}.

Peat composition and isotopic signatures of substrate and leaves

The concentration of P in the upper peat layer decreased steadily landwards from the fringe, whereas that of N remained nearly constant up to 100 m from the fringe and then decreased linearly landwards (Fig. 5). Both N and P concentrations were linearly correlated with C (C–N $r^2 = 0.947$; C–P $r^2 = 0.837$; $n = 10$) indicating that those elements were bound to organic matter.

The δ^{13}C of the substrate changed along the transect within a narrow range, from −24.2 to −25‰ (Fig. 6a). Samples were slightly less negative in the center of the transect between 30 and 150 m from the fringe. Leaves showed more pronounced changes in δ^{13}C, with overall values ranging from −27.2 to −23.2‰ (Fig. 6b). Young leaves showed a clear trend toward more positive values, particularly the samples within 100–150 m distance from fringe. At the inland border of the wetland, values ranged from −27.2 (senescent and old leaves) to −26‰ (young leaves).

The δ^{15}N values of the substrate were similar throughout the transect, ranging from around 1.5‰ at the fringe to about 0.5‰ at 150-m distance from the fringe (Fig. 6c). Leaves collected between 90 and 150 m from fringe showed strong negative values contrasting to those at the fringe and inland extremes (Fig. 6d). Leaves of increasing age did not differ markedly in δ^{15}N.

Discussion

The mangrove communities sampled at Los Machos showed significant variations in structural development, leaf size, and W/A ratios associated with the distance from the interface with the water channel. Larger leaves were found near the fringe, whereas higher W/A characterized the dwarfed communities behind the fringe. These ratios increased markedly with leaf age, but the increases were significantly smaller near the fringe and the inland border of the

Table 2 Average interstitial water and leaf sap osmolality and concentration of P and osmotically active cations

	Osmolality (mmol kg $^{-1}$)	P (mmol l^{-1})	K (mmol l^{-1})	Na (mmol l^{-1})	Mg (mmol l^{-1})	Ca (mmol l^{-1})
Interstitial water	1,188 a	n.d.	13 a	461 a	65 a	13 a
Leaves						
Young	1,520 b	1.8 a	113 b	283 b	124 b	35 b
Adult	1,576 b	1.8 a	126 b	337 b	131 b	56 c
Senescent	1,678 b	0.5 b	126 b	461 a	154 b	72 c

$n = 6$. HSD Test Tukey–Kramer, $P = 0.05$ (JMP 5.0; 2002) (*n.d.* not detected)

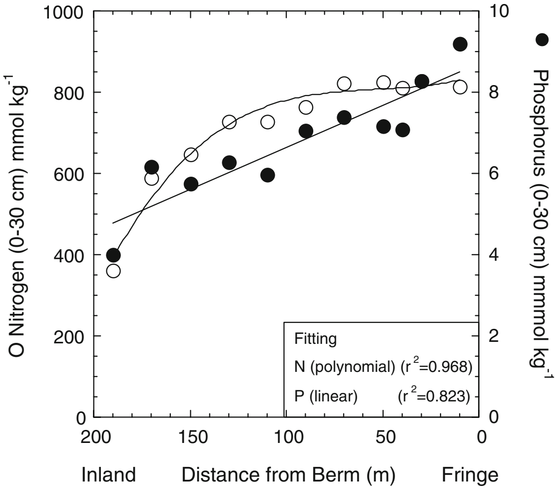
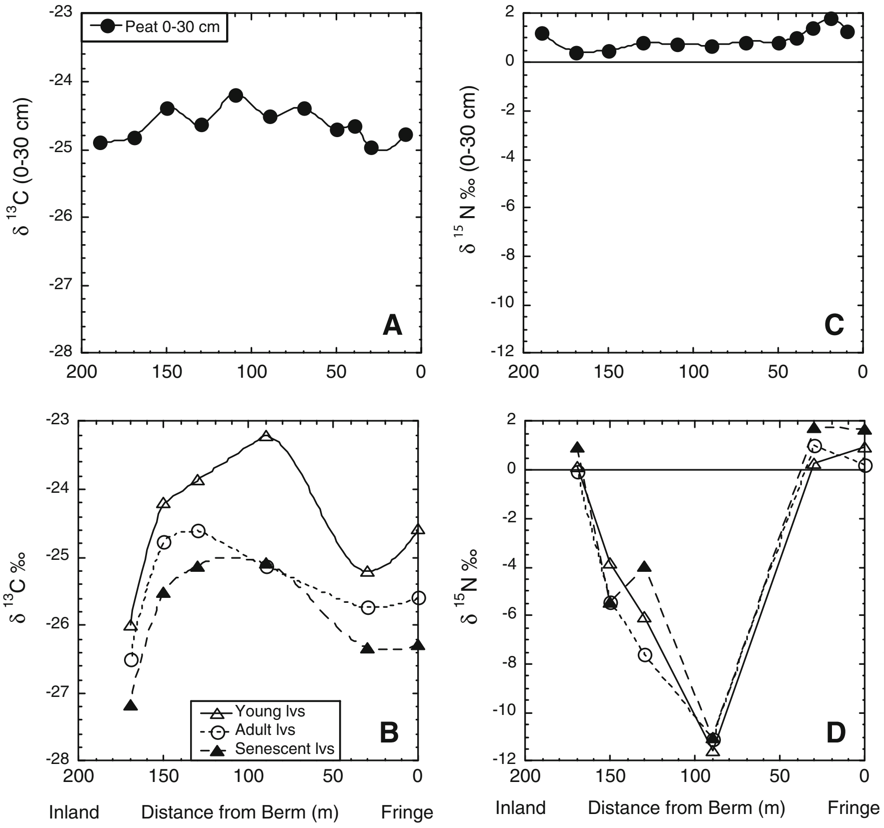


Fig. 5 Concentration of N and P in the upper peat layer within a 200-m long transect in the dwarf mangrove community depicted in Fig. 1. Each point gives the value for a composite peat sample (two samples, 0–30 cm depth)

mangrove community. Larger W/A ratios have been associated with sclerophylly caused by P deficiency (Sobrado and Medina 1980, Medina et al. 1990). In this study, P concentration per unit area of young and adult leaves was consistently lower in the dwarf communities, whereas N, S, and K concentrations in those leaves' types did not change appreciably along the transect sampled. Those elements, however, showed characteristic concentration patterns in senescent leaves. In the dwarf communities N was more concentrated, reaching similar or higher values in senescent than in young leaves. Phosphorus was markedly depleted in senescent leaves indicating the high level of retranslocation for this element. Sulfur accumulated in senescent leaves in a pattern apparently associated with the proximity to the fringe. Potassium concentrations in senescent leaves increased from inland toward the fringe. We infer from these patterns that P is the limiting nutrient in these communities, affecting structural development and retranslocation of N and K.

The patterns of element concentration in leaves of increasing age along the transect revealed differences in accumulation and remobilization characteristics. The percent change in element concentrations per unit area showed the expected pattern of

Fig. 6 Distribution of δ^{13}C values in substrate (**a**) and leaves (**b**), and of δ^{15}N values in substrate (**c**) and leaves (**d**) along the transect in the dwarf mangrove community depicted in Fig. 1. Points give the values for a composite leaf sample (10 leaves) and a composite peat sample (two samples, 0–30-cm depth)



remobilization of P (>70%), but a reduced remobilization of N (<40%). Feller et al. (2002) found reduced remobilization of N in dwarf mangroves (41%) contrasting with the values for fringe mangroves not limited by P (62%). Feller et al. (1999) and Lovelock et al. (2004) also reported values of N remobilization below 50% in dwarf *R. mangle* communities in Belize and Panama. An unexpected result was the accumulation of K in senescent leaves of dwarf mangroves, as this element is readily mobile in phloem and can even be leached from intact leaves (Marschner 1986). Which physiological mechanisms may explain these patterns? In the case of N, we hypothesize that decreased remobilization may be associated with reduced sink strength due to P inhibition of growth and structural development. This statement will be considered further below when discussing ratios of N isotopes. Two processes may be involved in the case of K. One is the reduced energy available in P-deficient plants for loading K into the phloem (Marschner 1986). The other is that K leaching from leaves, a phenomenon that enrich K concentration in throughfall of many forest types (Tukey 1970; Jordan et al. 1980), may be impaired in the dwarf mangroves, possibly by reducing the diffusion of this ion through the leaf cuticle. This latter hypothesis can be easily tested with leaching experiments.

Percent accumulation of Na, Ca and Mg were similar and around 70%. The accumulation of Na, Mg, and S was expected because of the abundance of these elements in sea water. However, the higher relative accumulation of S in senescent leaves suggests that uptake of this element accelerates with leaf age. As Na is about 10 times more concentrated in sea water than S (Sverdrup et al. 1942), it seems that this mangrove is able to reject excess Na more effectively than sulfate or sulfide when present under waterlogged conditions. This and the chemical forms of S accumulation in *R. mangle* leaves form a topic worth exploring experimentally.

One environmental constraint frequently associated with reduced structural development of mangrove species is salinity. Our results showed that salinity increased from the fringe landwards. However, actual osmolalities measured in interstitial water do not qualify this environment as hypersaline. Leaves of all ages concentrated their sap by at least 200 mmol kg^{-1} above that of interstitial water indicating that there were no osmotic limitations for water uptake from substrate. Soluble Na and Ca concentrations increased by nearly 100% from young to senescent leaves (Table 2). Unexpectedly, and coinciding with measurement of total leaf K, concentration of this ion did not decrease with leaf age. Phosphorus concentration decreased by 75% in senescent leaves in agreement with the values calculated using total P concentration (Fig. 3).

The concentration of elements in senescent leaves has been proposed as an appropriate indicator of nutrient remobilization (resorption proficiency, Killingbeck 1996). In Belize, Feller et al. (1999, 2002) reported that senescent leaves of dwarf and fringe mangroves had N and P concentrations per unit weight well below the limits proposed by Killingbeck (1996) (Table 3). The average values on the same basis for Los Machos mangroves are also indicative of complete resorption and are quite similar to those of Belize. However, on an area basis average resorption is complete for P but not for N. This may be related to the increase of W/A ratios and the accumulation of ash material in senesced leaves, thus reducing the concentration of P and N by weight, but not for area. Therefore, if Killingbecks numbers are used for comparative purposes, then it is preferable to calculate them on an area basis to avoid errors induced by cation accumulation in saline environments.

The patterns of δ^{13}C and δ^{15}N in leaves and substrate along the transect differed drastically from the monotonous decrease in peat concentration of both C (data not shown) and N from the fringe landwards. Leaves from the central points had more positive values of δ^{13}C revealing a certain degree of water stress, whereas variations in peat was within 1‰. δ^{13}C values also decreased from young to senescent leaves indicating decreasing water use efficiencies with leaf age. Salinity cannot be the cause of this pattern as the osmolalities of young and adult leaves differed little between points (Fig. 4). Lovelock et al. (2004) found that P fertilization of plants in a dwarf mangrove of Panama increased stem conductivity by a factor of six and leaf specific hydraulic conductivity by a factor of three. The lower hydraulic conductances were also correlated with stomata conductances. These results may explain the higher δ^{13}C values reported by Lin and Sternberg (1992a, b, c), McKee et al. (2002), Cheeseman and

Table 3 Average concentrations of elements in senescent leaves of *R. mangle* in the dwarf mangroves of Los Machos and other dwarf mangrove sites compared with resorption indices according to Killingbecks (1996)

		C	P	N	S	K	Na	Ca	Mg
Puerto Rico									
mmol m^{-2}	Ave.	10,102	0.8	120	49	41	194	84	70
	SD	1,578	0.1	44	11	14	61	12	9
mmol kg^{-1}	Ave.	36,071	2.9	427	178	144	704	309	258
Dry wt.	SD	1,255	0.7	113	28	31	199	45	35
Belize (Feller et al. 1999, 2002)									
Per weight			2	311					
Per weight			2	350					
Florida (Lin and Sternberg 2007)									
Per area			1	321					
Per weight			2	471					
Killingbecks complete resorption (1996)									
Per area			<1	<36					
Per weight			<13	<500					

Lovelock (2004), and this article. However, we did not find a linear relationship between leaf N concentration and δ^{13}C as reported by McKee et al. (2002).

Leaves from the dwarf mangrove communities had markedly negative δ^{15}N values, whereas those from the plots near the fringe or at the inland border had slightly positive values. The peat samples δ^{15}N values were all positive and slightly higher near the fringe. Similar pattern in both leaf and peat samples was reported by McKee et al. (2002) in Belize. Fry et al. (2000) surveyed three *R. mangle* sites in Florida for ^{15}N and did not find consistent differences between tall and dwarf mangroves. They found lower values as the distance from shore increased, but most values were positive. The highest δ^{15}N values and N concentrations in leaves were associated with anthropogenic N sources. The study by McKee et al. (2002) in Belize showed that long-term improvement in P availability through fertilization effectively increased the δ^{15}N values of the mangrove leaves. Those results provide strong support to the hypothesis that N fractionation is regulated by the demand generated by plant growth. Phosphorus limitation inhibits plant growth, resulting in more effective fractionation against the heavy N isotope. The relationship between P availability, as reflected by leaf P concentration and fractionation of N isotopes can be illustrated by a series of values collated from the literature compared with the results presented in this article (Table 4). Phosphorus-limited *R. mangle* mangroves in Belize and Puerto Rico have P concentrations in adult leaves between 11 and 12 mmol kg^{-1} (Feller 1995, Feller et al. 2002). Values range from 24 to 34 mmol kg^{-1} in mangrove sites with high P supply, such as those found in estuaries on the Caribbean coast of Venezuela and the northern Atlantic coast of South America (Medina and Francisco 1997; Medina et al. 2001; Barboza et al. 2006). Correspondingly, the δ^{15}N values of leaves from dwarf communities in Belize and Puerto Rico are below −5‰ whereas those of Bragança, Brasil are above +3‰. Strong N isotopic fractionation has been also related to P limitation in fresh water wetlands in New Zealand (Clarkson et al. 2005), Panamá (Troxler 2007), and Venezuela (Medina et al. 2008).

We conclude that the stunted growth of *R. mangle* in eastern Puerto Rico is probably caused by a combination of P limitation and seasonal water stress. Our results show that in addition to the negative δ^{15}N values shown in other dwarf mangrove areas in the Caribbean, the environmental stresses determining the stunting in these communities are causing abnormal patterns of K and N retranslocation and strong levels of S accumulation.

Table 4 Weight/area, nitrogen and phosphorus concentrations, and isotopic signatures of adult *R. mangle* leaves from sites with contrasting nutrient availability

Site	Type	W/A (kg m^{-2})	N (mmol kg^{-1})	P	$\delta^{13}C$ ‰	$\delta^{15}N$ ‰	Author
Puerto Rico	Fringe	213	978	13	−25.6	0.22	Present paper
Ceiba	Dwarf	245	897	11	−25.1	−11.13	
	Dwarf		941	12	−24.6	−7.59	
	Dwarf		922	12	−24.8	−5.47	
Belize	Dwarf	300	729	12			Feller (1995)
Belize	Fringe		636	19			Feller et al. (2002)
	Transition		650	17			
	Dwarf		686	12			
Belize	Fringe				−28.6	0.1	McKee et al. (2002)
	Transition				−27.9	−1.13	
	Dwarf				−26.4	−5.38	
Panama	Dwarf		864	23			Lovelock et al. (2004)
USA, Florida	Fringe		900	31			Feller et al. (2003)
Indian river	Transition		1,186	48			
	Dwarf		1,014	45			
Venezuela	Wet (Atlantic)	154	960	29	−27.6		Medina and Francisco (1997)
	Dry (Caribbean)	189	895	24	−26.3		
Venezuela	Center	147	1,058	27			Barboza et al. (2006)
Maracaibo lake	Border	150	1,091	32			
Brasil	Low salinity	131	1,360	31	−29.5	3.81	Medina et al. (2001)
Bragança	High salinity	145	1,460	34	−27.5	5.22	

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