Variation in hydraulic conductivity of mangroves: influence of species, salinity, and nitrogen and phosphorus availability

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We investigated how species identity and variation in salinity and nutrient availability influence the hydraulic conductivity of mangroves. Using a fertilization study of two species in Florida, we found that stem hydraulic conductivity expressed on a leaf area basis (K_{leaf}) was significantly different among species of differing salinity tolerance, but was not significantly altered by enrichment with limiting nutrients. Reviewing data from two additional sites (Panamá and Belize), we found an overall pattern of declining leaf-specific hydraulic conductivity (K_{leaf}) with increasing salinity. Over three sites, a general pattern emerges, indicating that native stem hydraulic conductivity (K_h) and K_{leaf} are less sensitive to nitrogen (N) fertilization when N limits growth, but more sensitive to phosphorus (P) fertilization when P limits growth. Processes leading to growth enhancement with N fertilization are probably associated with changes in allocation to leaf area and photosynthetic processes, whereas water uptake and transport processes could be more limiting when P limits growth. These findings suggest that whereas salinity and species identity place broad bounds on hydraulic conductivity, the effects of nutrient availability modulate hydraulic conductivity and growth in complex ways.

Introduction

Nutrient availability places constraints on plant growth that are often linked to limitations in photosynthetic carbon gain (e.g. Ellsworth and Reich 1993, Aber et al. 1996, Ryan et al. 1997). Because high rates of photosynthetic carbon gain are achieved at the expense of water lost in transpiration, photosynthetic carbon gain may be co-limited by water availability, water uptake by roots or transport to shoots in many environments. This might be particularly true of mangroves, which are trees that grow in saline, tidal wetlands. Mangroves typically have relatively low transpiration rates and high water use efficiencies (Ball and Farquhar 1984, Clough and Sim 1989). These water use characteristics become increasingly conservative with increase in salinity and with increase in the salt tolerance of the species (Ball 1988, Ball et al. 1988, 1997), with far-reaching consequences for the structure and function of mangrove forests along salinity gradients (Ball 1996). These

Abbreviations – K_h, native stem hydraulic conductivity; K_{leaf}, leaf-specific hydraulic conductivity; PSU, practical salinity units.

studies invite the question: what processes limit water use, and hence growth, in saline environments?

The role of stomata in regulating water loss and photosynthetic rates is well established (Givnish 1986), but the hydraulic architecture and hydraulic conductivity of xylem may also place underlying constraints on the productivity of trees (Hubbard et al. 1999, Brodribb and Field 2000, Brodribb et al. 2003). Studies investigating factors that limit the hydraulic conductivity of trees have considered both intrinsic characteristics such as deciduous or evergreen habits (Brodribb et al. 2003, Choat et al 2005), and environmental factors such as nutrients (Harvey and Van der Driessche1997, Ewers et al. 2000, Hubbard et al. 2004, Lovelock et al. 2004, 2005) and water availability (e.g. Ewers et al. 2000, Brodribb et al. 2003). Here we consider the role of species identity, salinity and nutrient availability in determining hydraulic conductivity in mangroves.

In mangrove forests, differing tolerances to salinity among mangrove tree species are proposed to lead to patterns of zonation, or spatial species replacement through the intertidal region (Lugo and Snedaker 1974, Ball 1996). In a previous study of coexisting species of mangroves in hypersaline conditions in Florida, rates of photosynthetic carbon gain were very similar in the two sympatric species, but water use efficiency, carbon gain efficiency and nutrient use efficiency differed (Lovelock and Feller 2003). The authors suggested that species coexistence was facilitated by variations in both salinity and nutrient availability. The less salt-tolerant species may achieve higher rates of photosynthetic carbon gain and growth under favorable conditions (e.g. mornings and in the wet season), while the more salt-tolerant species may have lower but sustained photosynthetic rates and growth over a wider range of conditions. Additionally, low nutrient concentrations in conjunction with hypersalinity were proposed to favor the persistence of the slower-growing, more salt-tolerant species, by preventing overshadowing by the faster-growing species, which may occur with alleviation of nutrient deficiency under less saline conditions. The differences in species traits, higher water use efficiency in the more salt-tolerant species, and higher nutrient use efficiency in the less salt-tolerant species, could be underpinned by fundamental differences in hydraulic architecture and conductivity that are linked to patterns in carbon and nutrient allocation.

The purpose of the present study was to: (1) test for differences in hydraulic properties among mangrove species; and (2) determine whether the hydraulic conductivity of mangroves varies with salinity and nutrient deficiency under natural field conditions. We first examined whether hydraulic conductivity and growth differ between coexisting mangrove species that have different levels of salinity tolerance at a hypersaline site in Florida: *Avicennia germinans*, which is highly salt tolerant, and the less salt-tolerant species *Laguncularia racemosa*. For this study, we fertilized pairs of *A. germinans* and *L. racemosa*. We then considered how these results from a single hypersaline site fit within the broader context of our recent results on the effects of alleviating nutrient deficiency on the hydraulic conductivity of other species at sites in Twin Cays, Belize and Bocas del Toro, Panamá (Lovelock et al. 2004, Lovelock et al. 2006, Lovelock et al. unpublished data). We used our collective dataset to address two questions: does salinity constrain hydraulic conductivity in mangroves, and are there differences between the effects of nitrogen and phosphorus limitations to growth on hydraulic conductivity?

Materials and methods

Species comparison

Our study of differences in hydraulic conductivity among species was conducted in the Indian River Lagoon, North Hutchinson Island, Florida (see Feller et al. 2003 and Lovelock and Feller 2003 for a full site description). The Indian River Lagoon site is an abandoned mosquito impoundment (number 23). At this site, taller *Rhizophora mangle* mangroves fringing the canal give way to dwarf forests that are dominated by *A. germinans*, but also include *Laguncularia racemosa*. In the scrub forest, *L. racemosa* and *A. germinans* coexist in patches. In May 1997, 18 pairs of similarly sized *A. germinans* and *L. racemosa* trees were randomly chosen from within the impoundment. A third of the pairs of trees were fertilized with nitrogen (N) by coring two 15-cm-diameter holes in the sediment between the paired trees, approximately equidistant from each tree, and inserting 200 g of urea (N:P:K, 45: 0: 0) into each hole and resealing it, a third were fertilized with phosphorus (P), using 200 g of triple superphosphate (P_2O_5, N:P:K, 0: 45 :0), and the final third were cored but not fertilized. These were designated as controls. Fertilizer was encased in dialysis tubing (Spectrapor Membrane Tubing, 40-mm diameter, 6000–8000 molecular weight cut off). All trees were fertilized at approximately 6-monthly intervals until July 1999. Salinity over the paired trees varied from 33 to 55 practical salinity units (PSU) and mean redox potential (eH) for the scrub mangrove was – 166 mV.

To determine whether nutrient availability limited plant growth, we assessed the effects of nutrient treatment (N, P or controls) on plant growth. We tracked the

stem extension and leaf production of five, initially unbranched, shoots (first order) in sunlit positions in the outer part of the canopy of each tree. Extension of shoots and the number of leaf scars were measured every 6 months over a 2-year period. Here we present the growth rates for the final year of measurement (1998–1999).

Hydraulic conductivity was measured for each tree in March 2004, using stem segments that were selected to have similar diameters and similar leaf areas. Branches of each experimental tree, cut at least 0.3 m from the target stem segment, were harvested in the early morning of the day of measurement. Stems were transported to the laboratory and re-cut under water prior to the measurement and trimmed with a razor blade. Stems were inserted inline with a perfusion solution of 95% distilled water augmented with 5% seawater, and allowed to equilibrate to steady state (approximately 5 min) before measurement. Native stem hydraulic conductivity (K_h, kg m^{-1} s^{-1} MPa^{-1}) was measured using a flow meter that measures the pressure drop across the stem segment relative to that across a capillary tube of known resistance (Brodribb & Feild 2000). We used calibrated tubes of differing resistance so as to match the resistance of the tube to that of the branch to minimize errors. The pressure applied to the stem varied between 2.2 and 2.7 kPa, and the pressure drop across the stem segment ranged between 0 and 0.16 kPa (mean 0.065 kPa). After measurement, leaves were detached from the stem and their area measured with a LiCor leaf area meter (LiCor Corp., Nebraska). Hydraulic conductivity of stems was expressed on a leaf area basis to give leaf area-specific hydraulic conductivity (K_{leaf}).

General site descriptions for additional studies reviewed

Additional data come from Twin Cays (16°50′ N, 88°06′ W), a 92-hectare archipelago of mangrove islands located approximately 1.6 km inside the Belizean Barrier Reef Complex (see Feller 1995 and McKee 1993 and references therein for a full site description) and Bocas del Toro, Panamá (9°21′ N, 82°15′ W; see

Lovelock et al. 2004, and Lovelock et al. 2005 for a full description of the site). At both sites, mangrove forests are growing on peat soils. At Twin Cays, forests are dominated by *R. mangle* in both the fringe and the dwarf zone, but dwarf *A. germinans* trees are also present. In Bocas del Toro, *R. mangle* is the dominant species.

To establish patterns of nutrient limitation at each site within each vegetation zone (taller fringing trees or dwarf trees) we fertilized eight or nine individual dwarf trees of either *A. germinans* or *R. mangle* with N or P, using the same methods as described above (see Feller 1995). Briefly, trees were fertilized at 6-month to 1-year intervals with 150–300 g of N fertilizer or P fertilizer, or were cored and not fertilized (controls). In Belize, pore water salinity was 35–37 PSU in fringing forests, and ranged between 37 and 40 PSU in dwarf *R. mangle* stands, and between 40 and 55 PSU in dwarf *A. germinans* forests. In Bocas del Toro, Panamá, mean pore water salinity in dwarf forests was 31 PSU.

Data analysis

For the species comparison experiment in Florida, we used a generalized linear model with species and nutrient treatment as fixed effects. Where a significant main effect or interaction between site and nutrient treatment occurred, we used Fisher's least significant difference post hoc hypothesis test to examine pairwise differences within and among the treatment levels. To analyze for heteroscedasticity, probability plots of all variables and residual plots were examined. For heterogeneous variances (K_h, K_{leaf} and stem extension), we transformed continuous data using logarithms. The relationship between K_{leaf} and salinity was assessed with regression analysis.

Results and discussion

The results of the present study show that there are interspecific differences in the hydraulic conductivity of coexisting mangrove species that apparently relate to their differences in salinity tolerance and that may contribute to their coexistence over at least part of a salinity gradient (Table 1). These results from a

Table 1. Differences in mean hydraulic conductivity of stems of the coexisting mangrove species *Avicennia germinans* and *Laguncularia racemosa* in a hypersaline scrub forest at Mosquito Impoundment no. 23, St Lucie County, Florida (n = 18 trees). Different superscripts across rows indicates species means are significantly different at $P < 0.05$.

Hydraulic conductivity	*Avicennia germinans* (high salinity tolerance)	*Laguncularia racemosa* (low salinity tolerance)
K_h [(kg m^{-1} s^{-1} MPa^{-1}) × 10^{-6}]	1.15 ± 0.23[a]	0.72 ± 0.12[a]
K_{leaf} [(kg m^{-1} s^{-1} MPa^{-1}) × 10^{-4}]	2.13 ± 0.48[a]	0.81 ± 0.15[b]

hypersaline site were combined with results from other species measured at sites with different environmental conditions. The combined dataset across three sites revealed patterns in hydraulic conductance related to variations in salinity and nutrient availability (Tables 2 and 3, Fig. 1). Hydraulic conductance declined with increasing salinity, but hydraulic characteristics were differentially affected, depending on whether growth limitations were due to N or P. These results are fundamental to understanding the physiologic bases of salinity tolerance and how such physiological attributes relate to the structure and function of mangrove forests along complex environmental gradients.

Hydraulic conductivity of coexisting species under hypersaline conditions

At our Florida site, *L. racemosa* and *A. germinans* coexist under hypersaline conditions, where they form a forest composed of dwarf or scrub trees. Under natural conditions, growth, measured as stem extension, was significantly greater in *L. racemosa* than in *A. germinans* (Fig. 2). Fertilization with P had no significant effect on growth of either species. In contrast, both species responded to fertilization with N, with the growth response of *A. germinans* being seven times greater than that of *L. racemosa*. Thus, whereas the occurrence of dwarf trees often correlates with hypersaline conditions, the lower height and productivity of dwarf mangroves is not a simple function of salinity, but also reflects the co-limitation by nutrient availability, which at the Florida site was alleviated by addition of N.

The marked growth response to N under hypersaline field conditions raised the possibility that fertilization with limiting nutrients might increase whole plant water use through alteration of hydraulic conductivity and architecture. However, despite the wide range of growth rates observed in the study, there were no

Table 2. Proportional changes in growth, hydraulic conductivity (native hydraulic conductance, K_h, and leaf-specific hydraulic conductance, K_{leaf}) and photosynthetic rates with fertilization as a proportion of control trees in tall fringing forest and scrub *Rhizophora mangle* mangrove trees in Belize and Panamá (original data are in Lovelock et al. 2004, and Lovelock et al. 2006), a scrub *Avicennia germinans* forest in Belize (Feller et al. unpublished data, Lovelock et al. unpublished data) and a scrub forest in Florida (data from this study, and Lovelock and Feller 2003). *Significant treatment effects ($P < 0.05$).

Site details	Variable	N fertilized	P fertilized
Florida, scrub forest, *Avicennia germinans*			
	Stem extension	102*	2.15
	K_h	0.70	0.65
	K_{leaf}	0.66	0.63
	Photosynthetic carbon gain	1.36*	1.14
Florida, scrub forest, *Laguncularia racemosa*			
	Stem extension	4.09*	1.39
	K_h	0.93	0.56
	K_{leaf}	0.64	0.40
	Photosynthetic carbon gain	1.06	1.07
Belize, tall fringing forest, *Rhizophora mangle*			
	Stem extension	2.30*	0.60
	K_h	0.81	1.18
	K_{leaf}	0.74	0.87
	Photosynthetic carbon gain	0.57	0.84
Belize, scrub forest, *Rhizophora mangle*			
	Stem extension	2.96	30.7*
	K_h	Not measured	1.86*
	K_{leaf}	Not measured	1.54*
	Photosynthetic carbon gain	0.96	1.51*
Belize, scrub forest, *Avicennia germinans*			
	Stem extension	1.25	10.5*
	K_h	1.41	2.94*
	K_{leaf}	1.16	1.36
	Photosynthetic carbon gain	0.98	1.51*
Panamá, scrub forest, *Rhizophora mangle*			
	Stem extension	2.29*	8.29*
	K_h	2.39*	6.18*
	K_{leaf}	1.87*	2.93*
	Photosynthetic carbon gain	1.02	1.08

Table 3. Summary of responses of hydraulic conductivity and photosynthetic carbon gain across mangrove sites where different nutrients limit growth. K_h, native hydraulic conductance; K_{leaf}, leaf-specific hydraulic conductance.

Nutrient limiting growth	Site	Tree form	Species	K_h	K_{leaf}	Photosynthetic carbon gain	Reference
N	Florida	Dwarf	*Avicennia germinans*	No	No	Yes[+] (seasonal)	This study
N	Florida	Dwarf	*Laguncularia racemosa*	No	No	No	This study
N	Panamá	Dwarf	*Rhizophora mangle*	Yes[+]	Yes[+]	No	Lovelock et al. 2004
N	Belize	Tall fringing	*R. mangle*	No	No	No	Lovelock et al. 2006
P	Belize	Dwarf	*R. mangle*	Yes[+]	Yes[+]	Yes+	Lovelock et al. 2006
P	Belize	Dwarf	*A. germinans*	Yes	Yes	Yes[+]	Lovelock et al. in review
P	Panamá	Dwarf	*R. mangle*	Yes[+]	Yes[+]	No	Lovelock et al. 2004

significant differences in stem hydraulic conductivity, K_h, between *A. germinans* and *L. racemosa* grown under control or fertilization conditions (Table 1). Both species had an equivalent capacity to conduct water that was not altered with nutrient enrichment. However, K_{leaf} in *A. germinans* was more than double that in *L. racemosa*. Thus, for a given hydraulic conductivity, *A. germinans* deploys much less leaf area than *L. racemosa*. A functional consequence of this difference in allocation may be lower vulnerability to xylem embolism in *A. germinans* than in *L. racemosa*, as *A. germinans* may maintain higher minimum shoot water potentials, thereby contributing to the higher level of salinity tolerance in *A. germinans* compared to *L. racemosa*. The
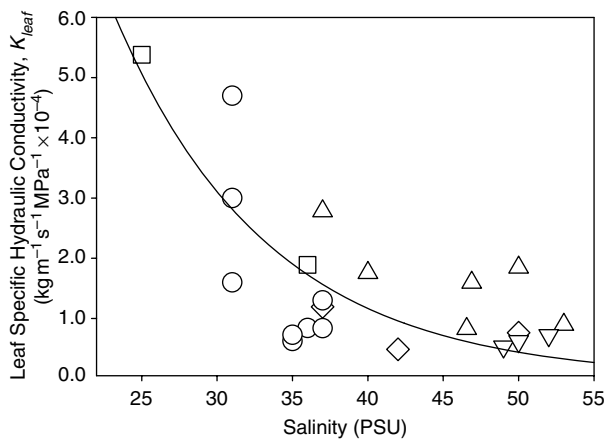
conservative leaf deployment per stem hydraulic conductivity in *A. germinans* may increase the capacity for photosynthetic carbon gain under conditions of high salinity and high evaporative demand, giving this species a competitive advantage in more arid or more saline conditions. Conversely, the higher leaf area of *L. racemosa* (lower K_{leaf}) will allow higher rates of whole plant photosynthetic carbon gain when water availability is high and salinity low. In an analogous study, a comparison of evergreen and deciduous species in a seasonally dry rainforest showed that K_{leaf} was higher in deciduous species that had high rates of photosynthesis during moist conditions, but lower in evergreen species that maintained lower photosynthetic rates in both wet and dry seasons (Brodribb et al. 2003).
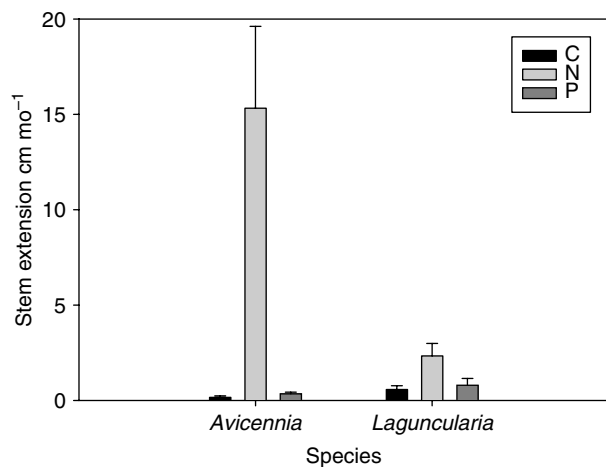

Fig. 1. Relationship between site salinity (practical salinity units, PSU) and leaf-specific hydraulic conductivity of mangrove stems for three mangrove species over three sites. Circles are treatment means (n = 6–9 trees) for control, nitrogen-fertilized and phosphorus-fertilized trees of *Rhizophora mangle* from Belize and Panama, triangles are *Avicennia germinans* trees from Belize and Florida, and diamonds are *Laguncularia racemosa* trees from Florida. The equation of the line is $Y = a \exp(-bX)$, where $a = -0.0058$, and $b = 0.0978$, $R^2 = 0.58$. We include two values from Melcher et al. (2001, squares) for Hawaii, assuming that in the study of Melcher et al. (2001) coastal and estuarine salinities are 36 and 25 PSU, respectively.

Fig. 2. Effect of fertilization with nitrogen (N) or phosphorus (P) on mean stem extension in coexisting trees of *Avicennia germinans* and *Laguncularia racemosa* in a hypersaline scrub forest in Florida. C, unfertilized control trees. Values are means ± SE, n = 6 trees.

Emerging patterns over sites: effects of salinity on hydraulic conductivity

Although species differences in K_{leaf} are evident (Table 1), environmental factors can modulate K_{leaf} in complex ways, with consequences at both the plant and ecosystem levels (Mencuccini 2003). It is impossible to determine how the hypersaline conditions at the Florida site affected hydraulic conductivity, but a plot of our data combined with those from other field studies revealed that broadly, over all sites and species, K_{leaf} declined with increasing salinity (Fig. 1). Species apparently occupy different parts of the curve, reflecting interspecific differences in distribution along salinity. *R. mangle*, for example, is found at less saline sites, causing values for this species to be separated from those of other species found at higher soil salinities. The variation about the curve is also high ($R^2 = 0.58$), probably due to differences in other environmental parameters during growth. Nevertheless, the curve is suggestive of effects of salinity on K_{leaf}, and consistent with other studies (Melcher et al. 2001, Ewers et al. 2004, Lopez-Portillo et al. 2005).

We also assessed maximum rates of photosynthetic carbon assimilation per unit leaf area over sites and treatments to determine whether carbon assimilation could be tightly linked to hydraulic conductivity across a broad salinity gradient. Photosynthetic carbon assimilation was variable and did not show a declining trend with salinity over sites. Photosynthetic rates are dependent on a range of morphologic (e.g. specific leaf area) and physiologic processes that vary in response to environmental conditions and over species. But variation is relatively modest over broad variations in climate (Wright et al. 2004) and in response to variation in nutrient availability, particularly in comparison to the high variation observed in hydraulic traits (e.g. Lovelock et al. 2005). The apparent decline in K_{leaf} with increasing salinity implies that the water potential of sediments places strong constraints on hydraulic conductivity in mangroves, providing an additional mechanism for variation in water use and growth characteristics (Ball 1996) and forest productivity over gradients in salinity (Lugo and Snedaker 1974).

Emerging patterns over sites: effects of nutrients on hydraulic conductivity

Whereas salinity affects K_{leaf}, we found no significant effects of fertilization on either K_h or K_{leaf} in *A. germinans* and *L. racemosa* growing at the N-limited site in Florida. Similar results were obtained in a tall fringe forest dominated by *R. mangle* in Belize (Table 3), where growth was also limited by N availability. However, hydraulic conductivity increased significantly when N-limited *R. mangle* was fertilized with N in Panamá, although the response to fertilization with N was not as strong as that in P-fertilized plants at this site (Table 3). The basis for this site-specific difference in response to N is unknown. Thus, with one exception, fertilization of N-limited sites with N stimulated growth but had no effect on either K_h or K_{leaf}.

These results contrast with those induced by addition of P to P-limited sites. In Belize and Panamá, where growth of *R. mangle* was strongly limited by P, fertilization with P stimulated growth and enhanced hydraulic conductivity, as shown by significant increases in both K_h and K_{leaf} (Table 3). The physiological mechanisms underlying the different effects of N and P limitation on hydraulic conductivity are presently unknown, but may relate to the critical level of N or P required for differing physiological processes. The strong response of hydraulic conductivity to P fertilization in P-limited soils may be due to the absolute requirement of aquaporins in root membranes for P (Carvajal et al. 1996).

Conclusions

The results of the present study show that over a range of species and sites, hydraulic conductivity (K_{leaf}) in mangroves is constrained by salinity. The relationship between salinity and K_{leaf} was strong but variable, with the variation being at least partially due to species differences in K_{leaf} (e.g. Table 1) and to variation in nutrient availability (e.g. Table 3). From our comparison of data over sites with different limiting nutrients, we draw the preliminary conclusion that in P-limited sites, processes that control hydraulic conductivity are key to limitation in productivity. In contrast, in N-limited sites, allocation to leaf area, and in some cases increases in maximum photosynthetic rates, are more important processes leading to enhancements in primary productivity. A more targeted study directly contrasting hydraulic conductivity in P- and N-limited systems will be necessary to test this hypothesis. Understanding the mechanisms by which nutrients influence physiological processes over a broad range of salinities will bring new insights into the processes underlying hydraulic constraints on primary production in mangrove forests, and improve prediction of the effects of coastal eutrophication on mangrove ecosystems.

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