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Hydraulic redistribution in dwarf *Rhizophora mangle* trees driven by interstitial soil water salinity gradients: impacts on hydraulic architecture and gas exchange

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Summary *Rhizophora mangle* L. trees of Biscayne National Park (Florida, USA) have two distinct growth forms: tall trees (5–10 m) growing along the coast and dwarf trees (1 m or less) growing in the adjacent inland zone. Sharp decreases in salinity and thus increases in soil water potential from surface soil to about a depth of 1 m were found at the dwarf mangrove site but not at the tall mangrove site. Consistent with our prediction, hydraulic redistribution detected by reverse sap flow in shallow prop roots was observed during nighttime, early morning and late afternoon in dwarf trees, but not in tall trees. In addition, hydraulic redistribution was observed throughout the 24-h period during a low temperature spell. Dwarf trees had significantly lower sapwood-specific hydraulic conductivity, smaller stem vessel diameter, lower leaf area to sapwood area ratio (LA/SA), smaller leaf size and higher leaf mass per area. Leaves of dwarf trees had lower CO_2 assimilation rate and lower stomatal conductance compared to tall trees. Leaf water potentials at midday were more negative in tall trees that are consistent with their substantially higher stomatal conductance and LA/SA. The substantially lower water transport efficiency and the more conservative water use of dwarf trees may be due to a combination of factors such as high salinity in the surface soil, particularly during dry periods, and substantial reverse sap flow in shallow roots that make upper soil layers with high salinity a competing sink of water to the transpiring leaves. There may also be a benefit for the dwarf trees in having hydraulic redistribution because the reverse flow and the release of water to upper soil layers should lead to dilution of the high salinity in the rhizosphere and thus relieve its potential harm to dwarf *R. mangle* trees.

Keywords: hydraulic lift, mangrove, sap flow, water relations.

Introduction

Water movement from deep wet soil to upper dry soil (from high to low soil water potentials), using plant root systems as the water transport pathway, has been termed hydraulic lift (Richards and Caldwell 1987). Although this description of hydraulic lift indicates only upward directionality in water movement between soil layers, water transport can also be downwards (Burgess et al. 1998, Schulze et al. 1998, Smith et al. 1999, Ryel et al. 2002, 2003, Scholz et al. 2002) and horizontal (Brooks et al. 2002, Warren et al. 2008). This process of water movement, which is more properly termed hydraulic redistribution, has been found in many terrestrial plants growing in dry environments but it has not been documented in wetlands such as in mangrove ecosystems.

Hydraulic redistribution can improve the water balance of the plants responsible for it and that of the neighboring plants (e.g., Dawson 1993, Ryel et al. 2002). The water released from the roots into the drier surface soil can be reabsorbed later when the water potential gradient between these roots and the soil is reversed during the daytime (Richards and Caldwell 1987). Hydraulic redistribution can also enhance nutrient uptake and the activity of mycorrhizae in the drought-prone surface roots, which is assumed to be beneficial to plants growing in environments with a dry season during which the nutrient-rich upper soil layers normally undergo desiccation (Caldwell et al. 1998, Brooks et al. 2002, Querejeta et al. 2003, Warren et al. 2008).

Rhizophora mangle L. trees are facultative halophytes that typically grow in saline coastal areas of tropical and subtropical regions, although they are capable of growing well in fresh water. They have several adaptations to saline conditions such as salt exclusion during water uptake, strong osmoregulation and ion compartmentation in leaves (Scholander 1968, Ball 1988, Werner and Stelzer 1990). Some mangrove species show variation in growth form: tall trees are found along the fringes of seashores or riverbanks and dwarf shrub-like growth forms are found in adjacent inland areas (Lugo and Snedaker 1974, Rao 1986, Lin and Sternberg 1992*a*, Feller 1995, Feller et al. 1999, 2003). Previous studies have shown that the difference in height between the coastal (tall) and inland (dwarf) *R. mangle* trees was neither due to differences in age (Feller 1995, Cheeseman and Lovelock 2004) nor due to differences in genetics (Lin and Sternberg 1992*b*). Abiotic factors including poor aeration and waterlogging (Davis 1940, Egler 1952), peat compaction (Craighead 1971), nutrient limitations (Lugo and Snedaker 1974, Feller 1995, McKee et al. 2002, Feller et al. 2003, Lovelock et al. 2004, 2006), fluctuations in salinity (Lin and Sternberg 1992*a*) and hypersalinity (Lin and Sternberg 1992*b*) have been suggested as factors contributing to mangrove dwarfism in the inland areas.

Tall *R. mangle* trees along the coast of Biscayne National Park are continuously flooded and drained by the advance and retreat of tides, whereas the dwarf *R. mangle* trees at adjacent inland areas are only flooded by sea water during occasional high tides. Surface soils in the inland zones are inundated during the wet season but gradually dry out during the dry season. Based on this information, the following hypotheses were made: (1) a large water potential gradient, particularly during the dry season, in the soil profile at the inland sites drives hydraulic redistribution in dwarf *R. mangle*; however, no such soil water potential gradient and hydraulic redistribution could be observed in the tall *R. mangle* trees of coastal sites and (2) dwarf *R. mangle* trees are under less favorable conditions in terms of soil water availability compared to tall trees, and thus will have characteristics of plants that are more conservative in the use of soil water.

Materials and methods

Study site description

The study site was located at Biscayne National Park (25°39′ N and 80°5′ W), Florida, USA. The mean annual temperature is about 25 °C and the mean annual precipitation is about 1200 mm (Ross et al. 1998) with a dry season from December to May. The mangrove vegetation at the study site is characterized by two distinct zones: a tall (5–10 m) mangrove zone of about 100 m width fringing the seaward edge of the coast and an adjacent dwarf (1 m or less) mangrove zone of 300–500 m width located inland from the coastal fringe. A transition zone with mangroves of medium height is present but is indistinct. The coastal zone is dominated by *R. mangle* L. trees (red mangrove) and sparsely inhabited by *Laguncularia racemosa* (L.) Gaertn. (white mangrove) and *Avicennia germinans* (L.) Stearn. trees (black mangrove). The inland zone is almost a monospecific stand of *R. mangle* trees. The slightly higher elevation at the intermediate zone impeded the tides from reaching the inland site except during occasional high tides.

Soil water osmotic potential and leaf water potential

The osmotic potential of the interstitial soil water (Ψ_o) at different depths from the soil surface was determined in December 2001, February and May 2002 (the beginning, the middle and the peak of the dry season, respectively). In December, soil cores were taken at three randomly chosen points from both coastal and inland sites. Interstitial water was extracted from soil core samples at 10 cm intervals beginning at 10 cm and ending at 90 cm from the surface. In February and May, soil water samples were obtained using two sets of piezometers at each site. Piezometers were installed at random locations at 15 cm depth intervals between 15 and 105 cm from the surface, and the Ψ_o of all soil water samples was measured using a vapor–pressure osmometer (Model 5520, Wescor, Logan, UT) calibrated with standard salt solutions.

Leaf water potential (Ψ_l) was measured at predawn, mid-morning and midday for two clear days (December 18, 2001 and May 10, 2002), using a Scholander pressure chamber (PMS, Corvallis, OR). Leaves were wrapped with both plastic bags and aluminum foil the evening before the measurements and were kept wrapped when inserted into pressure chambers. Meanwhile, Ψ_l of freely transpiring leaves was also measured to calculate the water potential drop ($\Delta\Psi_l$) across the transpiring leaves (Richter 1973, Bauerle et al. 1999).

Sap flow

Sap flow in both dwarf and tall *R. mangle* trees was monitored from November 2001 to May 2002. The arching prop roots extending from the lower part of the main stem to the

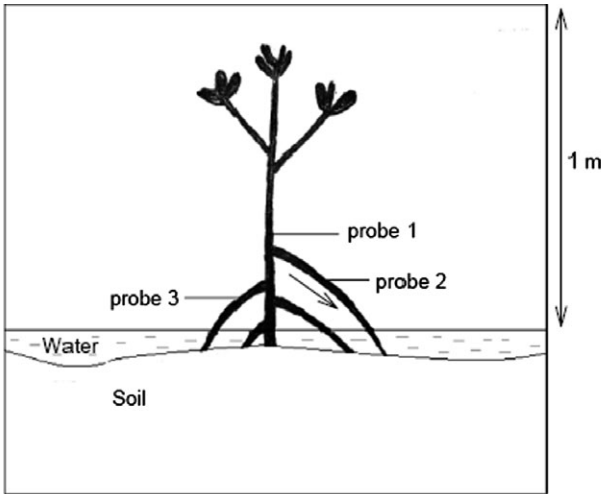

Figure 1. Diagram of a dwarf *R. mangle* tree. Locations of sap flow probes in the stem and two prop roots are indicated. The arrow indicates the reverse sap flow in a prop root. Root depth is not indicated in the diagram but the upper prop roots tap water from the upper soil layers while the lower prop roots and the tap root are able to acquire water from at least 50 cm below the soil surface. Water level in the diagram reflects hydrological conditions during the wet season. During the dry season the upper soil layer dries out.

substrate are the characteristics of *R. mangle* trees. At both the coastal and the inland sites, one data logger (CR10X, Campbell Scientific, Inc., Logan, UT) with three sets of probes was installed to monitor the sap flow in the main stem and in the two above-ground prop roots of an *R. mangle* tree simultaneously (Figure 1). Every 2–3 weeks, we moved the measuring systems to another randomly chosen individual at both sites. At the end of the experiment, sap flow of nine dwarf trees and eight tall trees was recorded.

The heat pulse system, described in detail by Scholz et al. (2002), was used to measure the sap flow (Marshall 1958, Burgess et al. 1998). Briefly, every hour a 6-s pulse of heat was produced by applying a known voltage across a line heater, and after the release of the heat pulse the temperature was measured for each second of a 100-s interval by two copper–constantan temperature probes placed at equal distances (0.6 cm) up- and downstream from the heater. Heat pulse velocity (V_h) was calculated according to Marshall (1958) as

$$V_h = (D/x)\ln(v_1/v_2), \tag{1}$$

where D is the thermal diffusivity of wet wood, x is the distance between the line heater and the temperature sensors, and v_1 and v_2 are the increase in temperature (relative to ambient) after the heat pulse is applied.

Heat pulse velocity was corrected for xylem wounding based on the estimated wound widths and coefficients provided by Burgess et al. (2001*a*). Sap velocity (V_s) was then calculated from the corrected heat pulse velocity (V_c) (Barrett et al. 1995) as

$$V_s = V_c \rho_{dw}(c_{dw} + mc_s)/(\rho_s c_s), \tag{2}$$

where V_c is the corrected heat pulse velocity, ρ_{dw} and ρ_s are the densities of dry wood and sap (water), respectively, m is the water fraction of the sapwood, and c_{dw} and c_s are the specific heat capacities of dry wood and sap, respectively. The sap flow from the soil into the plant was considered to be positive and the flow away from the stem base toward the soil was considered to be negative.

Thermal diffusivity of wet wood was calculated for both dwarf and tall *R. mangle* roots according to Marshall (1958):

$$D = K_{sw}/\rho_{sw}c_{sw}, \tag{3}$$

where K_{sw} is the thermal conductivity, ρ_{sw} is the sapwood density and c_{sw} is the specific heat capacity of the sapwood, estimated by weighing the density and the heat capacities of sap and woody matrix by volume fractions of each in fresh wood (Burgess et al. 2001*b*). The density and the heat capacity of the woody matrix were 1530 kg m^{-3} and 1380 J kg^{-1} K^{-1}, respectively (Edwards and Warwick 1984). The thermal conductivity of the sapwood was estimated using the equation (Swanson 1983, Burgess et al. 2001*a*):

$$K_{sw} = K_s m(\rho_{dw}/\rho_s) + K_{dw}[1 - m(\rho_{dw}/\rho_s)], \tag{4}$$

where K_s and K_{dw} are the thermal conductivities of sap (water, 4182 J kg^{-1} $°C^{-1}$ at 20 °C) and dry wood, respectively. The thermal conductivity of dry wood (W m^{-1} $°C^{-1}$) was calculated according to Swanson (1983) as

$$K_{dw} = 4.184 \times 10^{-2}(21 - 20F_v), \tag{5}$$

where F_v is the void fraction of the sapwood calculated as one minus the sum of solid and liquid fractions.

Environmental variables

Environmental variables at both study sites were recorded continuously throughout the study period. A quantum light sensor (Li-Cor Inc., Lincoln, NE) and humidity probes (HMP35C, Vaisala, Helsinki, Finland), which were connected to a data logger (CR10X, Campbell Scientific, Inc.), were used to measure photosynthetic photon flux density (PPFD), air temperature and relative humidity. The air saturation deficit (ASD) was calculated from air temperature and relative humidity.

Stem hydraulic conductivity and xylem anatomy

During the middle of the dry season (February 2006), the stem hydraulic conductivity (K_h) of 10 cm unbranched segments of branches from dwarf and tall *R. mangle* plants was measured. Six branches ca. 1 m in length, each from different individuals, were collected at predawn at both sites on two consecutive clear days. Branches were recut immediately under water to avoid embolisms and were transported to the laboratory with the cut end immersed in water and the free end tightly covered with opaque plastic bags.

Degassed and filtered 0.5 mmol l^{-1} KCl solution was used as the perfusion fluid. The hydrostatic pressure for the water flowing through the stem segments was generated by a constant hydraulic head of 70 cm. The active xylem area (A_{sw}) for water transport measured in the middle of stem segments was obtained by introducing indigo carmine dye to stem segments from one cutting end. Total leaf area (LA) terminal to each of the stem segments was measured using a LI-3100 leaf area meter (Li-Cor Inc., Lincoln, NE), and the leaf number per branch was counted to calculate the mean leaf size. To determine the leaf mass per area (LMA), the leaves were bagged separately for each branch and were oven dried for 48 h at 60 °C to determine the dry mass.

The hydraulic conductivity (kg m s^{-1} MPa^{-1}) was calculated as

$$K_h = J_v/(\Delta P/\Delta L),$$

where J_v is the flow rate through the segment (kg s^{-1}) and $\Delta P/\Delta L$ is the pressure gradient across the segment (MPa m^{-1}). The SA-specific hydraulic conductivity (K_s; kg m^{-1} s^{-1} MPa^{-1}) was calculated as the ratio of K_h to A_{sw} and the leaf-specific hydraulic conductivity (K_l; kg m^{-1} s^{-1} MPa^{-1}) was calculated as the ratio of K_h to LA distal to the stem segment.

Anatomical measurements of stem xylem were made on the cross-sections of six terminal branches each from a different individual. Under a 400× magnitude view, the lengths of the long and short axes of all the vessel lumens were measured in a sector of the transverse section (about 50 vessels). The lengths of the long and short axes were averaged and taken as the vessel lumen diameter (D_{vessel}). The mean D_{vessel} of all the measured vessels were then calculated for each branch sample.

Leaf gas exchange

During the dry season (May 10, 2006), leaf net CO_2 assimilation rate (A), transpiration rate (E), stomatal conductance (g_s) and intercellular CO_2 mole fraction (C_i) were measured using a LI-6400 photosynthesis system (Li-Cor Inc., Lincoln, NE) between 0900 and 1130 h EST. The PPFD in the cuvette was held at about 1500 μmol m^{-2} s^{-1}. Three sun-exposed mature leaves from each of the four randomly chosen individuals of both tall and dwarf trees were monitored under ambient CO_2 levels and temperature. Intrinsic photosynthetic water use efficiency (WUE) was calculated as the ratio of A to g_s (A/g_s).

Results

Interstitial soil water osmotic potential and leaf water potential

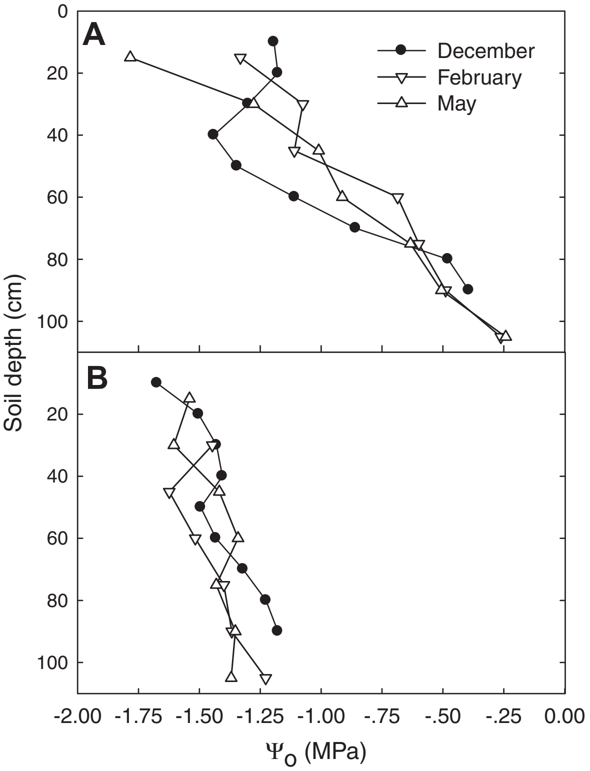

Figure 2. (A and B) Interstitial soil water osmotic potential (Ψ_o) at different depths across the soil profile at the inland site (A) and the coastal site (B) measured at the beginning (December 2001), the middle (February 2002) and the peak (May 2002) of the dry season.

Different patterns of Ψ_o across the soil profile were found at the coastal and the inland sites (Figure 2A and B). At the inland site, seasonal variation of Ψ_o across the soil profile was observed (Figure 2A). At the beginning of the dry season (December), Ψ_o in the upper 30 cm was around −1.25 MPa, which was higher than the lowest values found at 40 cm depth (−1.44 MPa). In soils deeper than 40 cm, Ψ_o gradually increased with depth and nearly fresh water was found at about 1 m depth. During the dry season, the Ψ_o of surface soil became more negative but it remained high at deeper soil layers. At the peak of the dry season (May), the most negative Ψ_o (ca. −1.8 MPa) was found near the soil surface. The first 10 cm of soil was very dry and no water was extracted for osmotic potential determination of interstitial soil water. The water potential of this layer should have been less than −1.8 MPa. On the other hand, no obvious seasonal variations in Ψ_o were found at the coastal sites and there were only minor changes in Ψ_o with an increase in depth, ranging from −1.2 to −1.7 within the soil profile of 110 cm depth (Figure 2B).

During both December and May, predawn leaf water potentials (Ψ_{pd}) and midday leaf water potentials (Ψ_{md}) measured from covered leaves were not significantly different between dwarf and tall trees; however, the Ψ_{md} of the uncovered leaves were significantly lower in tall trees, which resulted in a significantly larger water potential gradient ($\Delta\Psi_l$) between the branch to which it is attached and the

Table 1. Predawn and midday leaf water potential of dwarf and tall *R. mangle* trees measured during December and May. Ψ_{pd} and Ψ_{md}, predawn and midday; $\Delta\Psi_{\text{l}}$, leaf water potential differences between covered and uncovered leaves measured at midday. Values are mean ± SE ($n = 6$). Letters a and b indicate significant differences between dwarf and tall trees on the same dates ($P < 0.05$).

Growth forms	Ψ_{pd} (MPa)	Ψ_{md} (MPa)		$\Delta\Psi_{\text{l}}$ (MPa)
	Covered	Covered	Uncovered	
December				
Dwarf	−1.94 ± 0.02 a	−2.30 ± 0.03 a	−2.45 ± 0.03 a	0.15
Tall	−1.71 ± 0.08 a	−2.08 ± 0.06 a	−3.01 ± 0.02 b	0.93
May				
Dwarf	−2.58 ± 0.05 a	−3.37 ± 0.09 a	−3.62 ± 0.02 a	0.35
Tall	−2.69 ± 0.06 a	−3.12 ± 0.07 a	−4.27 ± 0.07 b	1.15

leaf itself (Table 1). During midmorning, the estimated maximum leaf hydraulic conductance ($K_{\text{leaf}} = E/\Delta\Psi_{\text{l}}$) was significantly higher in tall trees than that in dwarf trees (2.08 and 1.20 mmol $\text{m}^{-2}\ \text{s}^{-1}\ \text{MPa}^{-1}$, respectively). In May, Ψ_{pd} and Ψ_{md} were all about 1 MPa more negative compared to the values measured during December.

Sap flow

No reverse sap flow was found in tall *R. mangle* trees; however, reverse sap flow was consistently recorded in prop roots of dwarf *R. mangle* trees during the whole study period from the end of the wet season to the end of the dry season. Reverse sap flow in dwarf trees was found on 93% of the sampled days. Most of the reverse sap flow in dwarf *R. mangle* trees occurred during the nighttime which is typical of plants that perform hydraulic redistribution (e.g., Richards and Caldwell 1987), and sometimes in the early morning and late afternoon (Figure 3A–C). During a low temperature spell on January 4 and 5, reverse sap flow occurred continuously 24 hours a day (Figure 4A).

The sap velocity (V_{s}) during daytime was typically higher in the main stems compared to that of the prop roots. The magnitude of V_{s} in the two prop roots of the same individual was sometimes quite different, which was likely due to the differences in size and location of the active part of the root within the soil profile (Figure 3A–E). Reverse sap flow (negative V_{s}) in dwarf mangroves was observed only in some prop roots, and V_{s} was between 0.5 and 2 cm h^{-1}, around 1/10 to 1/5 of the maximum positive V_{s} recorded during the day (Figures 3 and 4).

Stem and leaf characteristics

Dwarf trees had significantly lower K_{s} and smaller vessel lumen diameter compared to tall trees ($P < 0.01$; Table 2). The mean K_{s} values in dwarf and tall *R. mangle* trees were 0.18 kg m $\text{s}^{-1}\ \text{MPa}^{-1}$ and 0.67 kg m $\text{s}^{-1}\ \text{MPa}^{-1}$, respectively. Tall trees had twice more leaf area per unit sapwood area (LA/SA) than that of dwarf trees, 46.4 and 15.2 $\text{cm}^2\ \text{mm}^{-2}$, respectively. Higher LA/SA in tall trees resulted in a similar K_{l} between the two growth forms.

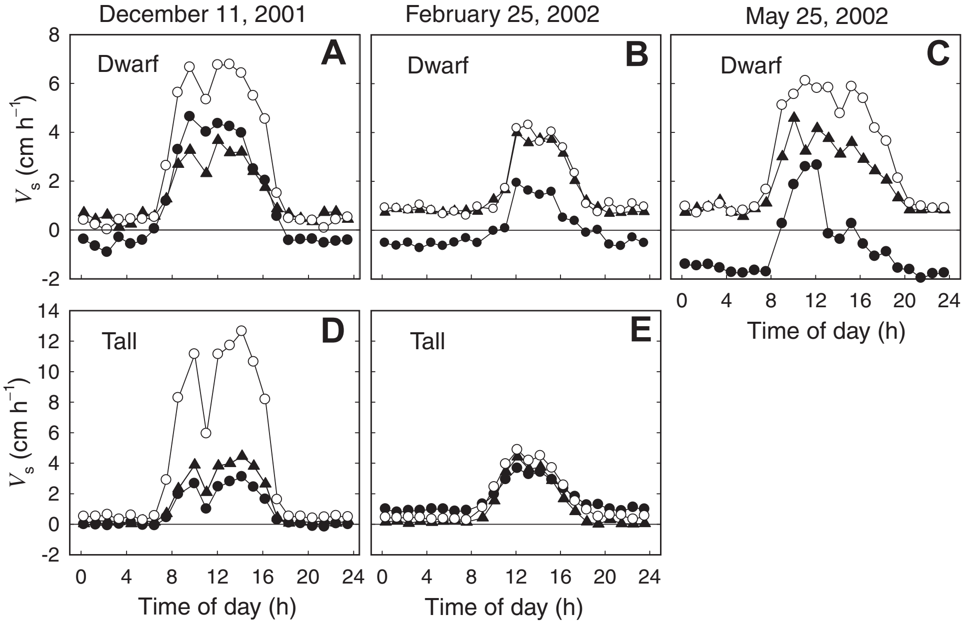

Figure 3. (A–E) Sap flow velocity (V_{s}) of *R. mangle* trees on representative days at the beginning (December 11, 2001), the middle (February 25, 2002) and the end (May 25, 2002) of the dry season, respectively. Open circles, filled circles and triangles represent V_{s} in the main stem and two prop roots, respectively.

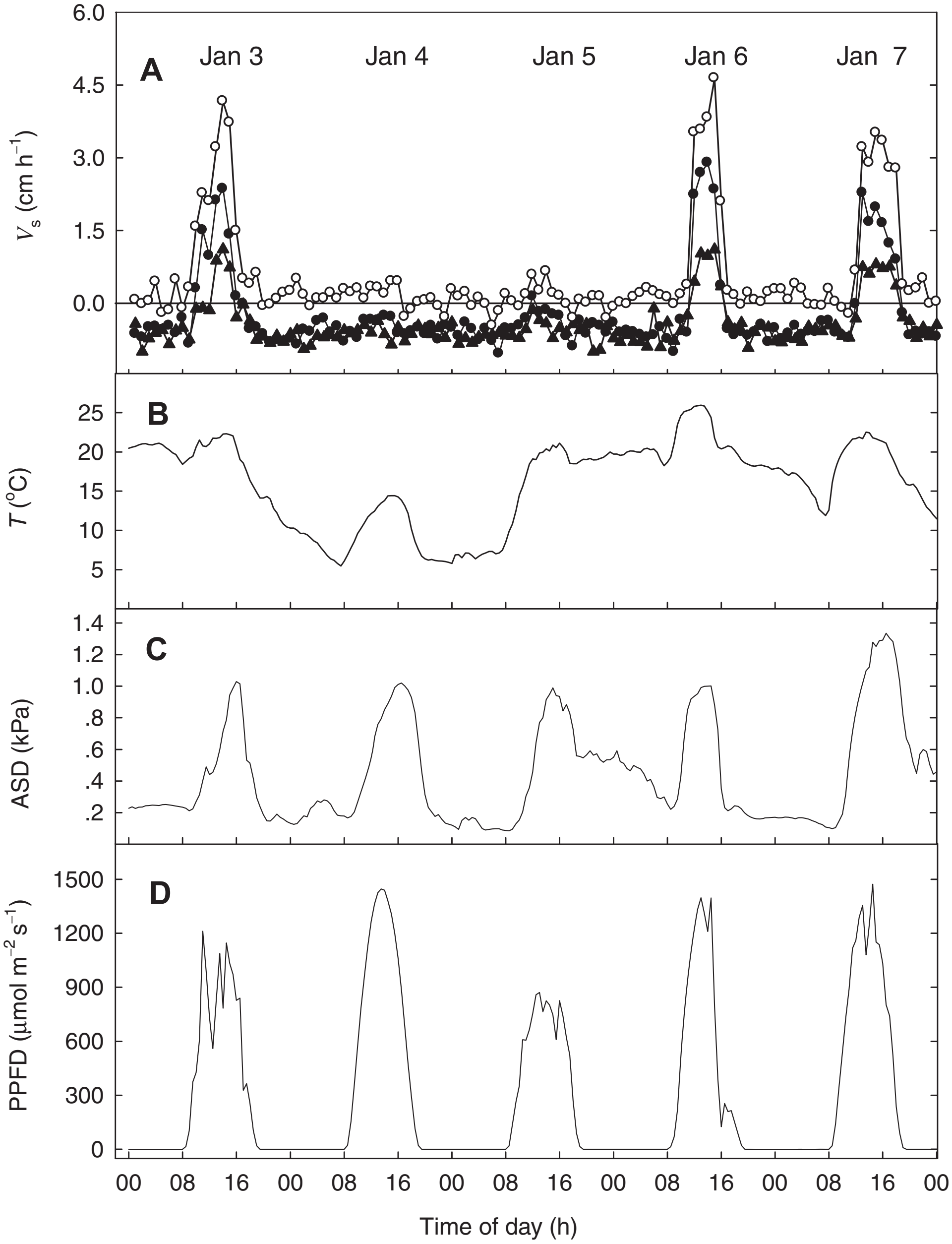

Figure 4. (A–D) Sap flow velocity, V_s in dwarf *R. mangle* trees (A), air temperature, T (B), air saturation deficit, ASD (C) and photosynthetic photon flux density, PPFD (D) measured from January 3 to January 7, 2002 showing day-time reverse flow during a low temperature spell. Symbols are as defined in Figure 3.

Table 2. Leaf and stem traits of dwarf and tall *R. mangle* trees. LS, leaf size; LMA, leaf mass per area; LA/SA, leaf area to sapwood area ratio; K_s, sapwood-specific hydraulic conductivity; K_l, leaf-specific hydraulic conductivity; and D_{vessel}, vessel lumen diameter. Values are mean ± SE ($n = 6$). Asterisks indicate statistically significant differences between the two growth forms: $^{**}P < 0.01$.

Growth forms	LS** (cm^2)	LMA** (kg m^{-2})	LA/SA** (cm^2 mm^{-2})	K_s** (kg m^{-1} s^{-1} MPa^{-1})	K_l (×10^{-4} kg m^{-1} s^{-1} MPa^{-1})	D_{vessel}** (µm)
Dwarf	18.69 ± 0.96	0.19 ± 0.01	15.2 ± 2.8	0.18 ± 0.02	1.24 ± 0.18	15.6 ± 0.8
Tall	37.24 ± 2.35	0.13 ± 0.01	46.4 ± 7.9	0.67 ± 0.18	1.42 ± 0.29	24.2 ± 2.8

Dwarf trees had significantly smaller leaf size but higher LMA ($P < 0.01$; Table 2). Tall trees had significantly higher maximum A, g_s, C_i than dwarf trees (Table 3). Intrinsic photosynthetic WUE was significantly higher in dwarf trees compared to tall trees.

Discussion

Hydraulic redistribution has been found in many plant species growing in dry environments where relatively large soil water potential gradient exists (Richards and Caldwell

Table 3. Leaf gas exchange traits of dwarf and tall *R. mangle* trees. A, net CO_2 assimilation rate at 1500 μmol m^{-2} s^{-1} quantum; g_s, stomatal conductance; C_i, intercellular CO_2 mol fraction; and A/g_s, intrinsic photosynthetic WUE. Asterisks indicate statistically significant differences between the two growth forms: $^*P < 0.05$ and $^{**}P < 0.01$.

Growth forms	A^{**} (μmol m^{-2} s^{-1})	g_s^* (mol m^{-2} s^{-1})	C_i^{**} (μmol mol^{-1})	A/g_s^{**} (μmol mol^{-1})
Dwarf	3.4 ± 0.9	0.034 ± 0.013	194.8 ± 17.8	106.8 ± 11.4
Tall	9.5 ± 2.8	0.159 ± 0.044	268.0 ± 8.9	59.6 ± 5.4

1987, Caldwell and Richards 1989, Dawson 1993, Scholz et al. 2002), but this is the first observation of hydraulic redistribution driven by interstitial soil salinity gradients in wetland environments with saturated soils. One prerequisite for hydraulic redistribution is the presence of a large water potential gradient across the soil profile (Richards and Caldwell 1987). The soil water potential gradient is usually developed during dry periods when surface soil dries out due to evapotranspiration, while deeper soil layers are still wet. But in dwarf mangrove ecosystems with saturated soils during most times of the year, the water potential gradient along the soil profile is not due to the differences in water content but due to the salinity of the interstitial soil water. In mangrove forests of southeast Florida, roots of *R. mangle* trees are found to occur throughout the soil profile from the soil surface to the bedrock (Lin 1992). The shallow and deep roots of dwarf *R. mangle* trees enabled them to reach both shallow and ground water layers differing in water potentials (Ewe et al. 2007).

The difference in Ψ_o patterns between the soils of coastal and inland mangrove sites is caused primarily by their difference in exposure to tides. During the dry season, the lack of fresh water input from rainfall caused the increase of salinity in the upper soil layers at the dwarf mangrove sites. Also, mangroves salinize the soil when they are extracting water from salty substrate (Passioura et al. 1992). When mangroves absorb water, 90–99% of salt is excluded by the roots (Scholander et al. 1968, Moon et al. 1986) and thus salt concentrates in the rhizosphere. The high soil water salinity (low Ψ_o) observed during the peak of the dry season in the upper soil profile of the inland site may thus result from both evapotranspiration and plant salinization of seawater in the poorly drained soils.

Hydraulic redistribution in the dwarf mangrove is mainly a passive process driven by different soil water potentials at different depths, which is mainly composed of Ψ_o, as the soil matric potential is close to zero in saturated soil during most times of the year. This redistribution occurred during the night or even during the day when transpiration of leaves was inhibited (e.g., by low temperatures). Fresh water movement to the surface saline soil at night may benefit the water balance of the plants during the daytime. The buildup of salt in the soil can be large enough to restrict water uptake by roots and to limit the growth of plants (Passioura et al. 1992). Also, leaf growth as well as the opening of stomata can be limited by elevated abscisic acid concentrations when roots are under high salinity. Hydraulic redistribution at night and parts of the day in dwarf *R. mangle* trees may function as a mechanism to dilute the salt that is accumulated during the daytime in the upper rhizosphere or even more importantly to promote the diffusion of salt from the root surface to the bulk soil and thus help to maintain the activity of roots in a nutrient-rich surface soil layer.

Reverse sap flow may also have a cost to dwarf *R. mangle* trees because it is analogous to nighttime transpirational water loss from leaves which may prevent or slow down the complete recovery of Ψ_l overnight (Donovan et al. 2003, Bucci et al. 2004). The delayed equilibrium in the water potential between the plant tissues and the bulk soil may negatively affect the refilling of embolized vessels in dwarf trees (Bucci et al. 2003) and the water economy of the plants in general. Therefore, to avoid hydraulic failure it might be more favorable from a water relation standpoint to have vessels with small lumen diameters and tighter stomatal control to water loss. The two traits will surely result in a cost in terms of reduced rates of photosynthetic carbon gain (Lovelock et al. 2006). Water movement to the soil via shallow roots constituted a competing sink of water to the transpiring leaves. Reverse flow was observed not only at nighttime but also during parts of the daytime (early morning and late afternoon), which is important for understanding the physiological and growth characteristics of dwarf *R. mangle* trees. Dwarf *R. mangle* trees have similar hydraulic traits (e.g., lower K_s and smaller vessel lumen diameters compared to tall trees) as that of the plants adapted to drought-prone environments (Abrams 1990, Bucci et al. 2005). These hydraulic traits may benefit dwarf mangrove plants growing under osmotic stress by reducing the risk of hydraulic failure (e.g., xylem cavitation) but at a cost of decreased water transport efficiency. Reduced hydraulic efficiency can have a negative impact on carbon assimilation by decreasing g_s (Santiago et al. 2004), which is consistent with the patterns observed in this study with dwarf *R. mangle* trees.

Large water potential gradients between the branch and the bulk leaf ($\Delta\Psi_l$) are usually associated with high rates of leaf transpiration and photosynthesis (Melcher et al. 2001, Franks 2006). The combination of lower K_{leaf} and smaller $\Delta\Psi_l$ in dwarf *R. mangle* trees resulted in its significantly lower values of transpiration ($E = K_{leaf} * \Delta\Psi_l$). The more conservative water use in dwarf *R. mangle* trees compared to tall trees may be due to the combination of several different factors. At the inland site, there were large seasonal variations in soil water salinity, particularly in the upper soil layers. Plants in such an environment may require continuous physiological adjustments that may result in slow growth. Lin and Sternberg (1993) observed that fluctuating salinity has significant negative effects on photosynthesis and plant growth in mangrove trees, relative to constant salinity with the same average salinity value. Nutrient limitations in the inland site could also influence hydraulic architectural traits and photosynthetic capacity of the dwarf *R. mangle* trees (Lugo and Snedaker 1974, Feller 1995, Lovelock et al. 2004, 2006). Nitrogen and phosphorous enrichment can significantly increase the growth of dwarf *R. mangle* trees mainly by increasing the stem hydraulic conductivity (Lovelock et al. 2004, 2006). Large water potential gradient across the soil profile and thus plant water loss to surface soil through reverse sap flow, and its interactions with other factors, such as the lack of N and P, may be an additional mechanism underlying the lower stem hydraulic conductivity, slower assimilation rate and eventually the dwarfism of *R. mangle* trees of the inland zones.

This is the first time that hydraulic redistribution in trees of wetland habitats has been observed. Reverse sap flow in dwarf *R. mangle* trees had a cost in terms of water loss to the upper soil layers which otherwise could be used for transpiration; however, it may help to relieve the adverse effect of high salinity in the rhizosphere, and thus could be of importance for the survival of dwarf *R. mangle* trees. Dwarf *R. mangle* trees at the inland site were under less favorable water conditions than tall trees at the coastal site. In tall *R. mangle* trees, more effective long distance stem xylem water transport and higher g_s were associated with higher CO_2 assimilation rates; whereas in dwarf trees significantly lower stem hydraulic conductivity and more conservative leaf water use were related to very low photosynthetic capacity and growth rates.

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