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Regulation of water balance in mangroves

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• **Background** Mangroves are a group of highly salt-tolerant woody plants. The high water use efficiency of mangroves under saline conditions suggests that regulation of water transport is a crucial component of their salinity tolerance.

• **Scope** This review focuses on the processes that contribute to the ability of mangroves to maintain water uptake and limit water loss to the soil and the atmosphere under saline conditions, from micro to macro scales. These processes include: (1) efficient filtering of the incoming water to exclude salt; (2) maintenance of internal osmotic potentials lower than that of the rhizosphere; (3) water-saving properties; and (4) efficient exploitation of less-saline water sources when these become available.

• **Conclusions** Mangroves are inherently plastic and can change their structure at the root, leaf and stand levels in response to salinity in order to exclude salt from the xylem stream, maintain leaf hydraulic conductance, avoid cavitation and regulate water loss (e.g. suberization of roots and alterations of leaf size, succulence and angle, hydraulic anatomy and biomass partitioning). However, much is still unknown about the regulation of water uptake in mangroves, such as how they sense and respond to heterogeneity in root zone salinity, the extent to which they utilize non-stomatally derived CO_2 as a water-saving measure and whether they can exploit atmospheric water sources.

Key words: Mangrove, salinity tolerance, water uptake, hydraulic anatomy, salt secretion, aquaporins, halophyte, water use efficiency, WUE, *Avicennia*, *Rhizophora*, vapour pressure deficit.

INTRODUCTION

Mangroves are a diverse group of ∼70 tree species that grow in saline, tidal wetlands on tropical and subtropical coastlines (Table 1). Mangroves tolerate a wide range of soil salinity (Lugo and Snedaker, 1974; Odum *et al.*, 1982; Hutchings and Saenger, 1987). While salinity has long been recognized as an important factor that limits mangrove growth and productivity (Clough and Sim, 1989; Lin and Sternberg, 1992; Ball, 2002) mangroves are nonetheless highly adapted to salt concentrations in soils that exceed concentrations tolerated by most other plant species (Ball, 1988). Saline habitats represent a physiological challenge for plants because of the highly negative water potentials of the soil pore water, making water acquisition more energetically unfavourable than in non-saline soils. The ability to maintain water uptake in saline conditions is key to salt tolerance. Another physiological challenge is ion toxicity, as high concentrations of salt are potentially cytotoxic to all plants, including mangroves. The high water use efficiency of mangroves under saline conditions suggests that regulation of water transport, in conjunction with managing ions, is a crucial component of their salinity tolerance.

SALT EXCLUSION MEASURES

Mangroves exert tight control over salt concentrations in their tissue by decoupling water uptake from ion uptake. Xylem sap in all mangrove species tested has relatively low salt concentrations (Table 2), with up to 99 % of the salts in the soil solution prevented from entering the xylem stream (Waisel *et al.*, 1986;

Werner and Stelzer, 1990; Melcher *et al.*, 2001; Stuart *et al.*, 2007) regardless of soil salinity (Table 2). Such efficient filtration at the root is achieved by the prevention of non-selective apoplastic water uptake (Krishnamurthy *et al.*, 2014).

Mangrove root epidermal cells are highly suberized (Krishnamurthy *et al.*, 2014). Suberin is a hydrophobic polyphenol-based compound that is deposited between the cell wall and the plasma membrane, providing an efficient barrier to water movement into the cell (Kolattukudy, 1984). Additionally, the endodermal layer of mangroves has a highly developed Casparian strip, starting very close to the root cap (Lawton *et al.*, 1981). In *Avicennia marina* this suberization significantly limits passive ion and water transport into the stele and blocks almost all apoplastic water (Moon *et al.*, 1986; Krishnamurthy *et al.*, 2014). Therefore, water must enter the stele through membranes (Steudle and Peterson, 1998). This transcellular transport relies on the high permeability of these membranes to water.

Most of the hydraulic conductivity of plant cell membranes, and subsequently the cell-to-cell pathway for water uptake, is attributed to the presence of water channel proteins known as aquaporins (Chrispeels and Maurel, 1994; Maurel, 1997; Tyerman *et al.*, 1999; Maurel *et al.*, 2008). Aquaporins are 27-kDa proteins belonging to the major intrinsic protein (MIP) family. The presence of aquaporins in membranes increases the water permeability along the cell-to-cell pathway. Using the aquaporin blocker 0.1 mM $HgCl_2$, applied to the roots of mangrove seedlings, we established a significant role for aquaporins in water uptake in two mangrove species, *A. marina* and *Rhizophora stylosa*, as evidenced by significant reductions in stomatal conductance and an

TABLE 1. *Occurrence of salt glands, leaf pubescence and relative salinity tolerance of mangrove tree species. Salt glands occur in four genera. Leaf pubescence has been noted in seven genera. Where leaf pubescence has been assessed in multiple species within a genus (e.g.* Avicennia *and* Bruguiera*), species within the genus appear to have similar leaf pubescence. High levels of salinity tolerance occur in species with and without salt glands and in species with and without leaf pubescence. The global distribution is from Duke (1992). High salinity tolerance indicates growth is observed in soil salinities that exceed those of seawater. Salinity tolerance data are based on Johnstone and Frodin (1982), Jimenez (1984), Jimenez and Soto (1985), Clough (1992), Allen* et al. *(2003) and Duke (2010). Pubescence is based on Stace (1965), Tomlinson (1986), Das (2002) and Wilson (2011). Taxonomy is based on the APGII system of flowering plant classification (APG, 1998)*

Order	Family	Genus	Species	World distribution	Salt glands	Leaf pubescence	Salinity tolerance
Arecaceae	Palmae	*Nypa*	*fruicans*	WP*	–	–	Low
		Phoenix	*paludosa*	IM	–	–	Mid
Caryophyllales	Plumbaginaceae	*Aegialitis*	*annulata*	WP	+	+	High
			rotundifolia	IM	+	+	High
Ericales	Myrsinaceae	*Aegiceras*	*corniculatum*	WP	+	+	Mid
			floridum	IM	+	NA	NA
	Pellicieraceae	*Pelliciera*	*rhizophorae*	Americas	–	–	Low
Lamiales	Acanthaceae	*Acanthus*	*ebracteatus*	WP	+	NA	NA
			ilicifolius	WP	+	+	Low
	Avicenniaceae	*Avicennia*	*alba*	WP	+	+	Mid
			bicolor	W. America	+	+	High
			germinans	AEP	+	+	High
			integra	Australasia	+	+	Mid
			marina	IWP	+	+	High
			officinalis	WP	+	+	High
			rumphiana	WP	+	+	Mid
			schaueriana	E. America	+	+	NA
Malpighiales	Euphorbiaceae	*Excoecaria*	*agallocha*	IWP	–	–	Low
			indica	IM	–	NA	NA
	Rhizophoraceae	*Bruguiera*	*cylindrica*	WP	–	–	Low
			exaristata	Australasia	–	–	High
			gymnorrhiza	IWP	–	–	Mid
			hainesii	WP	–	–	NA
			parviflora	WP	–	–	Mid
			sexangula	WP	–	–	Low
		Ceriops	*australis*	Australasia	–	–	High
			decandra	WP	–	–	Low
			tagal	IWP	–	–	Mid
		Kandelia	*candel*	IM	–	–	Mid
		Rhizophora	*apiculata*	WP	–	–	Mid
			mangle	AEP	–	–	High
			mucronata	IWP	–	–	Low
			racemosa	AEP	–	–	Low
			samoensis	W. America	–	–	Mid
			stylosa	WP	–	–	High
Malvaceae	Sterculiaceae	*Heritiera*	*fomes*	IM	–	+	Low
			globosa	IM	–	NA	NA
			littoralis	IWP	–	+	Mid
Myrtales	Combretaceae	*Conocarpus*	*erectus*	AEP	–	+	Mid
		Laguncularia	*racemosa*	AEP	–	+	Mid
		Lumnitzera	*littorea*	WP	–	+	High
			racemosa	IWP	–	+	High
	Lythraceae	*Sonneratia*	*alba*	IWP	–	–	Mid
			apetala	IM	–	–	Low
			caseolaris	WP	–	–	Low
			griffithii	IM	–	–	NA
			lanceolata	WP	–	–	Low
			ovata	WP	–	–	NA
	Myrtaceae	*Osbornia*	*octodonta*	WP	–	–	High
Sapindales	Meliaceae	*Xylocarpus*	*granatum*	IWP	–	–	Low
			mekongensis	WP	–	–	Mid

IWP, Indo-West Pacific; WP, Western Pacific; IM, Indomelasia; AEP, Atlantic East Pacific; NA, data were not available for the species.
*Naturalized at other locations throughout the tropics.

increase in xylem absisic acid (ABA) concentrations (Figs 1 and 2) following HgCl$_2$ application. The HgCl$_2$ was applied in low concentration and did not lead to damage to the photosynthetic apparatus based on fluorescence measurements [PSII maximum efficiency (F_v/F_m) was not lower in seedlings that received HgCl$_2$ treatment]. Addition of the aquaporin blocker to the soil

resulted in a significant reduction in stomatal conductance in both species within 60 min (Fig. 1). *Avicennia marina* showed a 65 % reduction in stomatal conductance within 200 min (3·3 h) and *R. stylosa* stomatal conductance was lower by 40 % in seedlings receiving HgCl$_2$ than in seedlings that did not, although full recovery was recorded within 3·5 h. This is within the highest range of sensitivity measured for plants (Wan and Zwiazek, 1999; Martre *et al.*, 2002; Martinez-Ballesta *et al.*, 2006). We also detected a significant increase in ABA concentration in xylem sap in HgCl$_2$-treated plants in both species (Fig. 2).

The rapid and strong reduction in stomatal conductance and the increase in xylem sap ABA concentrations indicates that when the cell-to-cell water transport pathway was inhibited, a drought response developed in the mangrove seedlings, which indicates that very little apoplastic transport occurs in these species. This provides further support for previous work that showed that in order to maintain a relatively salt-free xylem, mangroves avoid apoplastic water transport through suberization and highly developed Casparian strips.

In addition to tight control over water and ion uptake, 14 of the 51 species in Table 1, from the families Plumbaginaceae, Myrsinaceae, Acanthaceae and Avicenniaceae, have salt glands that excrete salt on the leaf surface. While six of these species are known to have a high level of salinity tolerance, the other eight species have moderate and even low (*Acanthus*) salinity tolerance. Additionally, high levels of salinity tolerance can be achieved in species without salt glands (Table 1). Therefore, salt excretion (the salt gland trait) is not sufficient or necessary to confer high levels of salinity tolerance. The presence of salt glands (Table 1) is also not linked to levels of salt exclusion (Table 2). Although salt glands are important for excreting some of the salt that enters the plant in the species in which they occur, below we suggest that a benefit of the presence of salt on the leaf surface may be a reduction in leaf vapour pressure deficit.

Mangroves are not only exposed to variation in salinity at the root zone but also to variation in the level of root zone anoxia because of fluctuating water levels during tidal inundation, as well as variability in sediment characteristics and the capacity of root systems to transport air (McKee, 1996). Aquaporins are sensitive to levels of anoxia (Tournaire-Roux *et al.*, 2003), which may indicate that anoxic conditions in soils and variation in inundation tolerance among species may interact with salinity to influence water uptake in mangroves (Ye *et al.*, 2010).

TABLE 2. *Published concentrations of sodium ions measured in the xylem sap of mangroves grown at a range of salinities, and means and range of sodium ions measured in the xylem sap of mangroves, other halophytes and glycophyte species grown at a range of salinities. Exclusion percentages were calculated from the ratio between the sodium concentrations in the xylem and that in the soil. The complete table can be accessed in Supplementary Data Table S1*

| Vegetation type	[Na+]$_{soil}$ (mM)	[Na+]$_{xylem\ sap}$ (mM)	Exclusion (%)	References
Mangroves				
Aegiceras corniculatum	75	5·2	92·9	Popp *et al.*, 1993
Aegiceras corniculatum	360	6·9	98·1	Popp *et al.*, 1993
Avicennia alba	140	4·4	96·9	Paliyavuth *et al.*, 2004
Avicennia alba	285	17·8	93·8	Paliyavuth *et al.*, 2004
Avicennia alba	430	42	90·2	Paliyavuth *et al.*, 2004
Avicennia alba	560	115	79·5	Paliyavuth *et al.*, 2004
Avicennia marina	110	6·7 (6·4)	93·9	Moon *et al.*, 1986
Avicennia marina	900	130 (60)	85·6	Waisel *et al.*, 1986
Bruguiera gymnorrhiza	140	1	99·3	Paliyavuth *et al.*, 2004
Bruguiera gymnorrhiza	285	1	99·6	Paliyavuth *et al.*, 2004
Bruguiera gymnorrhiza	430	3	99·3	Paliyavuth *et al.*, 2004
Bruguiera gymnorrhiza	560	5	99·1	Paliyavuth *et al.*, 2004
Conocarpus erectus	75	0·9	98·8	Popp *et al.*, 1993
Conocarpus erectus	360	7·5	97·9	Popp *et al.*, 1993
Laguncularia racemosa	0	2 (0·4)	-	Sobrado, 2004
Laguncularia racemosa	215	4·3 (0·7)	98	Sobrado, 2004
Laguncularia racemosa	240	8·7 (0·3)	96·4	Sobrado, 2004
Laguncularia racemosa	400	11·6 (0·9)	97·1	Sobrado, 2004
Laguncularia racemosa	430	8·9 (0·7)	98	Sobrado, 2004
Rhizophora mangle	0	11·1 (5·4)	–	Werner and Stelzer, 1990
Rhizophora mangle	200	20·1 (8·7)	90	Werner and Stelzer, 1990
Range	0–900	0·9–130	90–99·6	
Mean ± s.d.		20 ± 35	95 ± 6·6	
Other halophytes				
Range	0–530	0·5–46·6	76·7–98·6	Flowers, 1985; Arndt *et al.*, 2004; Kant *et al.*, 2006
Mean ± s.d.		13 ± 12	93 ± 7·5	
Glycophytes				
Range	0–430	0–31·5	71–97·6	Munns, 1985, 1988; Gouia *et al.*, 1994; Seel and Jeschke, 1999; Chen *et al.*, 2001; Sunarpi *et al.*, 2005; Kant *et al.*, 2006
Mean ± s.d.		7 ± 0·7	90·4 ± 6·6	
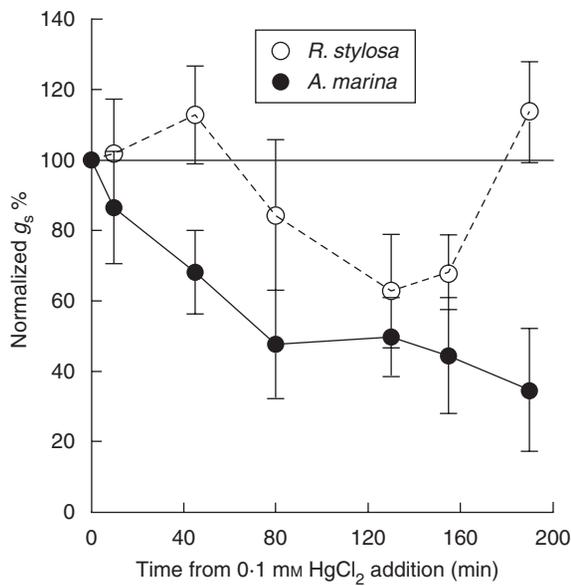
FIG. 1. Temporal changes in mean stomatal conductance (g_s) of 0·1 mM HgCl$_2$-treated plants normalized against the mean stomatal conductance of control plants at each time point for *Avicennia marina* and *Rhizophora stylosa* seedlings (as indicated in the key). Repeated measures ANOVA: $F_{(5,131)} = 17·08$, $P < 0·001$ for *A. marina* and $F_{(1,131)} = 16·197$, $P = 0·0008$ for *R. stylosa*. Error bars are s.e.m. ($n = 5$). Representative seedlings of both species are shown to indicate size and developmental stage.
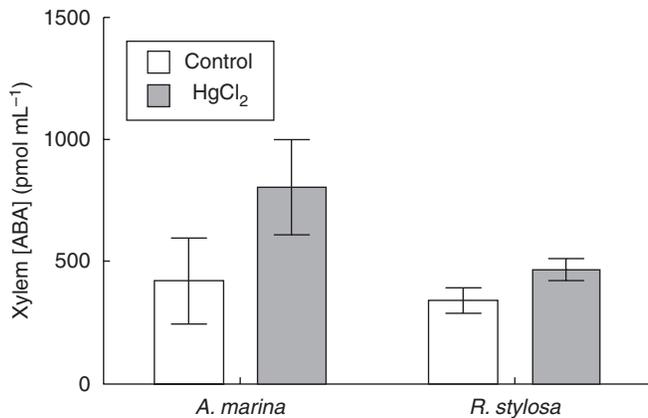

FIG. 2. Mean ± s.e.m. ($n = 5$) ABA concentration (pmol ml^{-1} xylem) in xylem sap of *Avicennia marina* and *Rhizophora stylosa* in HgCl$_2$-treated seedlings and control seedlings (see key) 200 min (3·5 h) following HgCl$_2$ addition. Xyem sap was collected by low-speed centrifugation of stem segments and ABA concentrations were determined by competitive ELISA (Phytodetek PDK 09347/0096 Agdia Inc. Elkhart, IN, USA). Differences in ABA concentration were significant for the HgCl$_2$ treatment. Factorial ANOVA, $F_{(1,15)} = 5·35$, $P = 0·0391$.

MAINTAINING LOW WATER POTENTIALS

In order to take up water through the root filtration system, mangroves need to maintain water in their tissues against a strong osmotic gradient. Furthermore, if the water potential of the soil is lower than that of the plant, water could potentially be lost from the plant to the soil. Dephosphorylation of root aquaporins can significantly reduce root hydraulic conductivity and minimize water loss under hyperosmotic conditions (Horie *et al.*, 2011), and the strong dependence of water uptake in mangroves on

cell-to-cell pathways can provide strong regulation of water loss to the environment during periods of hyperosmotic conditions. However, in order to maintain water uptake, mangroves need to maintain water potentials that are lower than those of the soil. The leaf water potential of *Avicennia germinans* in Belize and Florida was between 0·1 and 1 MPa lower than the water potential of the soil pore water, and that for *Rhizophora mangle* was 0·6−0·8 MPa lower (Melcher *et al.*, 2001; Lovelock *et al.*, 2006a). In order to exceed the osmotic pressure of seawater, mangroves need to maintain a water potential (the combination of osmotic and hydrostatic xylem sap pressure) of at least −3·5 MPa. Beginning with the pioneering work of Scholander *et al.* (1962), numerous publications have reported particularly negative water potential values for mangrove sap. In a high-resolution diel analysis of water potential in *A. marina*, hydrostatic potentials as low as −5 MPa were recorded at midday and −3 MPa at night, when the plant was not transpiring (Waisel *et al.*, 1986). Similar maximal daytime values were measured for *A. germinans* (Lovelock *et al.*, 2006a). Vandegehuchte *et al.* (2014) measured values between −2·5 and −4 MPa for *A. marina* and between −2 and −3·5 MPa for *R. stylosa* during the night and day respectively. The two species from the same location differed in their water potential, indicating interspecific differences in gradients driving water uptake, which may also relate to differences among species in salinity tolerance.

Organic and inorganic osmotica

Mangroves, like many other halophytes, use ions as solutes to decrease osmotic potential in cells (Scholander *et al.*, 1962). As ambient salinity increases, so do ion concentrations in all mangrove tissue (roots, leaves and stems) (e.g. *R. mangle*; Werner

and Stelzer, 1990). To a certain level, leaf sap osmolality, determined mainly by the concentration of Na$^+$ and Cl$^-$ ions in the cells, is positively correlated with soil salinity (Medina and Francisco, 1997). However, the capacity to sequester ions within the vacuoles is not limitless. Summaries of the few studies that have measured cellular ionic concentrations can be found in Supplementary Data Tables S1 and S2 and illustrate the difference between external and internal sodium concentrations over a range of salinities. In mangroves growing at high salinities, the predicted osmotic potential of the shoot, calculated from cellular ion concentrations, is higher than the observed osmotic potential and is not low enough to counter the low water potential of the soil. Thus, above a salinity threshold other osmotica are necessary to reduce water potential; these are organic solutes such as mannitol, proline, glycinebetaine and triterpenoids (Popp *et al.*, 1985). These compatible solutes are also used to adjust the osmotic potential in the cytoplasm, which must maintain much lower Na$^+$ and Cl$^-$ concentrations than the vacuole to allow enzyme function. Since the cytoplasm makes up <10 % of the cell volume (Mallery and Teas, 1984), readily available inorganic ions are the main osmotica used by mangroves to decrease leaf water potentials.

Cavitation-resistant hydraulic anatomy

Operating at low xylem water potentials puts mangroves at a high risk of cavitation (the formation of gas bubbles), because the pressurized water may vaporize in vulnerable areas such as xylem pit membranes (Tyree *et al.*, 1994; Melcher *et al.*, 2001; Hacke *et al.*, 2006). These gas bubbles can then block the ascent of water through the embolized xylem vessel and thus reduce overall hydraulic conductivity. Cavitation events can be repaired by refilling, although the exact mechanism by which this process occurs is still debated (Woodruff *et al.*, 2007; Zwieniecki and Holbrook, 2009; Wheeler *et al.*, 2013). However, evidence suggests that vessels can only be repaired a limited number of times before cavitation becomes permanent (cavitation fatigue). Cavitation fatigue varies among tree species, with some species able to withstand repeated cavitation and repair cycles better than others (Hacke *et al.*, 2001). Cavitation fatigue has not been studied in mangroves, so it is unknown whether they are better adapted than other species to withstand repeated cavitation. However, mangrove species are better than their rainforest family counterparts at avoiding cavitation (Sperry *et al.*, 1988). Mangroves (especially at high salinities) use less water than similar sized freshwater wetland trees and thus have lower rates of sap flow (Krauss *et al.*, 2007), which in turn lowers the xylem tension and the associated risk of cavitation. By adopting a cavitation-resilient anatomy, mangroves can safely operate at higher xylem tensions and thus colonize areas with higher soil salinities.

Mangroves have a range of anatomical adaptations to maintain hydraulic conductivity under the very low xylem water potentials needed to extract water under saline conditions (Sobrado, 2000, 2001; Melcher *et al.*, 2001; Ewers *et al.*, 2004). One such adaptation is a high degree of plasticity in vessel size and density. Xylem vessels become narrower and form at higher densities as salinity increases (Melcher *et al.*, 2001; Yáñez-Espinosa *et al.*, 2004; Lovelock *et al.*, 2006*b*; Schmitz *et al.*, 2006; Hao *et al.*, 2009), thus reducing the risk of cavitation [possibly by

reducing the pit area (Hacke *et al.*, 2006)] and providing alternative routes for water transport when bubbles do form (Schmitz *et al.*, 2006). However, smaller vessels, while safer in terms of embolism development under low water potentials, significantly reduce hydraulic conductivity (Hacke *et al.*, 2006; Lovelock *et al.* 2006*c*) and may impose constraints on photosynthetic carbon assimilation rates and growth (Lovelock *et al.*, 2006*c*). A high degree of plasticity in the anatomical response to the salinity environment is advantageous, allowing plants to modify their vulnerability to embolisms as well as their photosynthetic carbon gain over time and space. Differences in the ability to avoid embolisms contribute to interspecific differences in mangrove salinity tolerance (Ewers *et al.*, 2004; Robert *et al.*, 2009). Under high salinity, xylem vessels also become more circular (Robert *et al.*, 2009). The advantage for the change in eccentricity is unclear; however, we hypothesize that it could provide an advantage as the area over which two vessels touch becomes smaller, thereby reducing the risk of air aspiration into functional vessels from embolized ones.

Some mangrove species also have a high sugar and water storage capacity in the stem and leaves, which may allow the rapid repair of embolisms when they occur. Some of the most salt-tolerant species and drought-tolerant species have successive cambia, where phloem and parenchyma cells are in close proximity to xylem, arranged in concentric bands (Carlquist, 2007; Robert *et al.*, 2011). Over gradients of increasing salinity, the number of parenchyma cells and fibres in the mangrove genus *Avicennia*, which has successive cambia, increased (Schmitz *et al.*, 2008; Santini *et al.*, 2012). In *Laguncularia racemosa*, higher salinities resulted in a more confluent parenchyma (Yáñez-Espinosa *et al.*, 2004). Confluent parenchyma, like successive cambia, may allow the storage of water and sugars near the xylem vessels, which could facilitate the rapid repair of embolisms (Carlquist, 2007).

WATER-SAVING ADAPTATIONS

Since water acquisition is more energetically costly in saline than in non-saline soils, mangroves have evolved a range of adaptations that facilitate efficient water use during photosynthetic carbon gain during the day and reduce losses of water to saline soils at night. Mangroves have a number of properties, from the scale of the arrangement of leaves in the canopy to microscopic structures within leaves, that contribute to high photosynthetic water use efficiencies.

Leaf temperature regulation

In most mangrove species, stomata are present only on the abaxial leaf surface and are usually located in crypts (slightly sunken within the epidermis) (Tomlinson, 1986). Both of these anatomical characteristics function to reduce transpiration, while not affecting CO$_2$ uptake, by significantly increasing the humidity (reducing the leaf-to-air vapour pressure deficit) around the stomatal pore (Roth-Nebelsick, 2007). Mangrove leaves are held at almost vertical orientations when exposed to full sunlight (up to 75° from horizontal), which corresponds to a projected area that can be as low as 10 % of that of horizontal leaves (Ball *et al.*, 1988; Lovelock and Clough, 1992). The leaf angle of sun-exposed leaves differs among mangrove species (Lovelock and Clough, 1992), which, in addition to leaf

anatomical traits, could be a contributory factor influencing the distribution of species over salinity gradients. A lower leaf display area results in a reduction in direct radiation, allowing the leaf to remain at temperatures that are favourable for photosynthesis whilst requiring minimal evaporative cooling (Ball *et al.*, 1988).

Another water-saving adaptation is reduction in leaf size; mangroves growing in high salinity conditions develop smaller leaves. Smaller leaves result in higher conductance across the leaf boundary layer, allowing the leaf temperature to equilibrate with the atmosphere more effectively. This too minimizes the need for evaporative cooling while enabling photosynthesis rates to remain high (Ball *et al.*, 1988). Correspondingly, a negative correlation between leaf size and leaf sap osmolality was found in many mangrove species (Medina and Francisco, 1997). Mangrove leaves have a high water content per unit area (salt succulence), which increases with salinity (Camilleri and Ribi, 1983). High water content increases leaf heat capacity, thus reducing the need for evaporative cooling.

Uptake of non-stomatally derived CO_2

Another water-saving feature is the use of CO_2 for photosynthesis acquired through non-leaf tissues, and thus acquired at lower water costs. Fixation of CO_2 can occur through stem photosynthesis, whereby respired, non-stomatally derived CO_2 is fixed by chloroplasts within the bark and pith of mangrove trees (Teskey *et al.*, 2008). While this phenomenon is not unique to mangroves, it occurs in a number of mangrove species to a significant extent, contributing up to 5 % of the CO_2 fixed by the plant (Schmitz *et al.*, 2012). Uptake of CO_2 by roots, while not yet studied in mangroves, has been shown in other submerged and wetland plants (Raven *et al.*, 1988; Brix, 1990; Rich *et al.*, 2008). Many wetland plants, including mangroves, have continuous gas spaces extending from the stomata to the roots. This aerenchyma, which is not limited to roots but is formed in most parts of the plant (Raven, 1996), can hold significant amounts of CO_2 (Constable *et al.*, 1992). Utilization of this aerenchyma CO_2 for photosynthesis has been shown in a number of wetland plants, such as *Typha latifolia* (Constable and Longstreth, 1994) and *Phragmites australis* (Brix, 1990). Mangroves have highly developed aerenchyma, an adaptation to their anoxic environment (Pi *et al.*, 2009), and occupy soils with high concentrations of organic carbon (Donato *et al.*, 2011). In non-flooded terrestrial plants, where there is little or no aerenchyma, such soil-derived CO_2 can contribute 1–3 % of total C fixed by the plant (Ford *et al.*, 2007); it may make a significantly higher contribution in mangroves, although this is yet to be established.

USE OF NON-SALINE WATER SOURCES AND INCREASING HUMIDITY

Uptake of less saline water sources within the rhizosphere

High-salinity soils are often characterized by high levels of spatial and temporal heterogeneity in salinity (Silvestri *et al.*, 2005; Hao *et al.*, 2009). The ability of some halophytes to tolerate high salinity has been linked to an ability to utilize those less saline patches in the rhizosphere (Semeniuk, 1983; Yakir and

Yechielie, 1995). Mangroves can be relatively large trees that have expansive root systems (Comley and McGuinness, 2005). With such a large below-ground biomass, roots are exposed to heterogeneous salinities throughout the rhizosphere. Moreover, due to their location in the intertidal zone, mangroves may be exposed to both terrestrial and marine water sources, which vary greatly in salinity, from 0 to >160 p.p.t., where evaporation is high (Ball, 1998). Thus, while salinity might be high in part of the rhizosphere, some roots are often in contact with less saline water sources [e.g. groundwater, rainwater or riverine water (Ewe *et al.*, 2007)].

When less-saline water sources are available, they can become the main source of water in the xylem of mangroves, as has been documented for some species (Sternberg and Swart, 1987; Lin and Sternberg, 1992; Ewe *et al.*, 2007; Lambs *et al.*, 2008; Wei *et al.*, 2013). Successful utilization of less-saline water sources, when available, can increase halophyte survivorship, growth and productivity under conditions in which salinity limits growth rates (Yakir and Yechielie, 1995). In other halophytes, long-term responses to heterogeneity in salinity that is spatially or temporally stable leads to a proliferation of root growth into areas of lower salinity, and this can contribute to the preferential uptake of freshwater in some cases (Mensforth and Walker, 1996; Bazihizina *et al.*, 2012). For mangroves, this has not yet been tested.

Uptake of atmospheric water and decreasing leaf-to-air vapour pressure deficit

Using atmospheric water sources is another way of reducing the utilization of saline water. A number of plant species can take up water that condenses on their leaves (Slayter, 1956; Munné-Bosch and Alegre, 1999; Martin and von Willert, 2000), most likely through their stomatal pores (Eichert *et al.*, 2008). This is especially common in cloud forests (Johnson
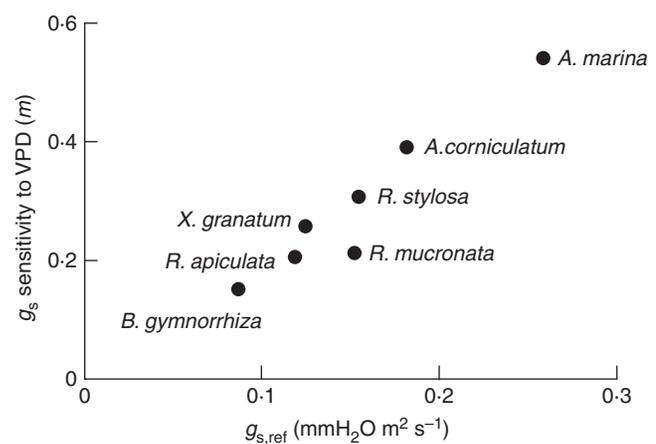

FIG. 3. Relationship between the sensitivity of stomatal conductance to VPD (*sensu* '*m*'; Oren *et al.*, 1999, calculated as the slope of the regression line describing the relationship between g_s and VPD) and stomatal conductance rates at a low reference VPD (interpolated form the relationship between g_s and VPD, at VPD = 1) for a number of Australian mangrove species (data from Clough and Sim, 1989). Species plotted are *Avicennia marina*, *Aegiceras corniculatum*, *Rhizophora stylosa*, *Rhizophora mucronata*, *Rhizophora apiculata*, *Xylocarpus granatum* and *Bruguiera gymnorrhiza*.

and Smith, 2008; Eller *et al.*, 2013) and foggy coastal areas (Burgess and Dawson, 2004). Fog uptake by leaf surfaces of the cloud forest tree *Drimys brasiliensis* can contribute more than 40 % of the leaf's water content, leading to the reverse flow of sap from the leaf down to the roots. Some evidence for reverse flow has been reported in mangroves at night (Rada *et al.*, 1989; Hao *et al.*, 2009) and during rainfall events (K. Steppe, University of Ghent, unpublished results) and could potentially be associated with the uptake of atmospheric water sources (top-down rehydration). However, the contribution of atmospheric water sources to leaf water is yet to be determined for mangroves.

Salt secretion in mangroves could be important for improving the leaf water balance. The capacity to absorb water from the air may be assisted by salt crystals on the surface of leaves, which both attract liquid to the leaf surface by lowering the dew point and enable liquid penetration into the stomata, by making the surface of the leaf less hydrophobic and reducing the water surface tension (Burkhardt *et al.*, 2012). Salt secretion exists only in some mangrove species (Table 1) but salt also accumulates on the leaves of non-salt-secreting species due to salts transported in air. The direct uptake of water from the leaf surface, with its high salt concentrations, is unlikely because of the low water potential of water on the surface of mangrove leaves. Furthermore, uptake of salty water through the stomata would introduce high concentrations of salt into the leaf. However, the generation of a humid environment surrounding the leaf
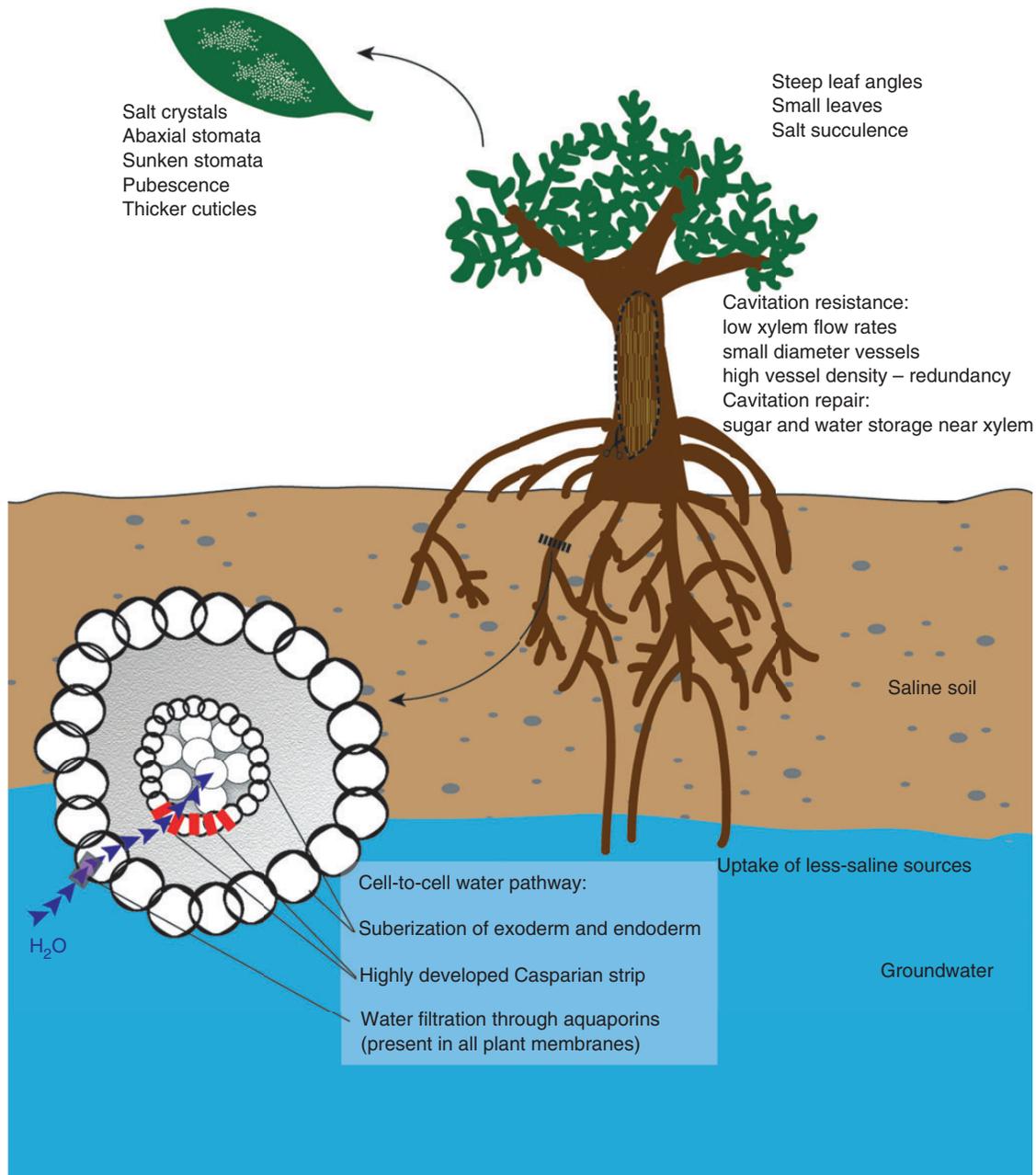

Salt crystals
Abaxial stomata
Sunken stomata
Pubescence
Thicker cuticles

Steep leaf angles
Small leaves
Salt succulence

Cavitation resistance:
low xylem flow rates
small diameter vessels
high vessel density – redundancy
Cavitation repair:
sugar and water storage near xylem

Saline soil

Uptake of less-saline sources

Groundwater

Cell-to-cell water pathway:

Suberization of exoderm and endoderm

Highly developed Casparian strip

Water filtration through aquaporins
(present in all plant membranes)

H_2O

F IG . 4. Schematic representation of the different strategies employed by mangroves to regulate water balance in saline environments.

surface would significantly reduce loss of water through the stomata during carbon acquisition by significantly decreasing the leaf-to-air vapour pressure deficit (VPD).

Leaf cuticles can provide an important hydrophobic barrier to water loss and the composition of epicuticular lipids could also affect leaf wettability (Ahmad and Wainwright, 1976). In the mangrove *A. marina*, cuticle thickness increases with salinity (Naidoo *et al.*, 2011), but data on the relationship between salinity and mangrove leaf cuticle composition are not available. Leaf pubescence could be another water-conserving feature found in some mangrove plants, mainly from the genus *Avicennia* but also from *Acanthus*, *Heritiera*, *Excoecaria* and *Conocarpus* (Table 1). Leaf hairs at lower densities can introduce turbulence into the flow boundary layer of the leaf surface and thus enhance heat and water transfer from the leaf to the atmosphere (Benz and Martin, 2006); at higher densities they can increase surface roughness, create a thicker boundary layer and thus reduce gas diffusion and consequently water loss (Schuepp, 1993). However, increases and decreases in the boundary layer both have negligible effects on diffusion rates when conditions are even slightly windy (Roth-Nebelsick, 2001), and thus the contribution of leaf hairs to water conservation through changes to the boundary layer are likely to be very small under field conditions. A positive effect of pubescence on water conservation is more likely to be due to increased capacity to take up water through leaf surfaces, possibly by retaining rain or dew water on the leaf surface for longer (Grammatikopoulos and Manetas, 1994) or through direct uptake by the epidermal cells forming the hair.

Many mangrove adaptations attributed to salinity tolerance contribute to decreased VPD around their leaves. Such adaptations include small leaf size, leaf hairs, salt crystals and sunken stomata as well as adaptations for lowering leaf temperature, such as steep leaf angles and succulence. The VPD is perhaps the strongest environmental determinant of water loss through transpiration (Oren *et al.*, 1999) and is an important factor in plant growth and development (Leuschner, 2002). High VPD leads to stomatal closure, lower photosynthetic rates, higher rates of xylem cavitation and reduction in leaf area, among other effects. In mangroves, in which water use efficiency is central to their ability to survive in saline environments, a lower VPD environment can reduce the cost of carbon gain. A number of studies have indicated that mangroves are highly responsive to changes in VPD (Clough and Sim, 1989; Ball *et al.*, 1997). Plant species show large differences in the sensitivity of stomata to changes in VPD, but a general positive relationship exists between the sensitivity to increasing VPD and the stomatal conductance at low VPD (Oren *et al.*, 1999; Leuschner, 2002). A reanalysis of the data in Clough and Sim (1989) reveals a similar relationship among mangrove species (Fig. 3). It also reveals that the more salt-tolerant species (e.g. *A. marina*) are more sensitive to changes in VPD. The high sensitivity of salt-tolerant mangrove stomata to VPD corroborates previous findings that suggest that lower VPD can significantly improve mangrove salinity tolerance (Ball and Farquhar, 1984). Leaf-to-air VPD is thus likely to be an important component in how mangroves have adapted to tolerate saline environments and could be one of the drivers of regional and global mangrove species distributions and patterns in primary productivity.

CONCLUSIONS

In mangrove species, adaptations that influence water uptake, transport and loss while maintaining photosynthetic carbon gain are important for salinity tolerance (Fig. 4). The complexity of the suite of characteristics required for salinity tolerance may be linked to the wide variation in salinity tolerance evolved among different mangrove taxa. The variation in adaptations in water conducting pathways among mangrove taxa likely contributes to the maintenance of high levels of productivity in heterogeneous saline environments that occur in mangrove habitats.

SUPPLEMENTARY DATA

Supplementary data are available online at www.aob.oxford journals and consist of the following. Table S1: Published concentrations of sodium ions in the xylem sap of mangrove, other halophytes and glycophyte species growing at a variety of salinities. Exclusion percentages were calculated from the ratio between the sodium concentrations in the xylem and in the soil. Table S2: Published concentrations of sodium ions in the leaf tissues of mangroves grown at a range of salinities and the sodium concentrations in the growing medium.

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