BIOLOGIA PLANTARUM 44 (3): 435-438, 2001

BRIEF COMMUNICATION

# Hydraulic properties of a mangrove *Avicennia germinans* as affected by NaCl

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## Abstract

Water transport was assessed in seedlings of the mangrove *Avicennia germinans* L. grown at 171 and 684 mol m$^{-3}$ NaCl. Leaf specific conductivity declined by 25 % at high salinity. This was related to low specific conductivity, because Huber values remained similar. Leaves of *A. germinans* featured low internal conductance to water transport. This was lowered further under high salinity. Water transport constrains imposed by whole shoot and leaf blade at high salinity were balanced by stomatal regulation of water loss, which possibly maintain stem water potentials above embolisms levels.

*Additional key words*: hydraulic conductance, leaf conductance, salinity, water relations.

Mangrove species with higher water use efficiency, derived from gas exchange analysis, seemed less efficient in water transport at the shoot level (Sobrado 2000). Indeed, stomatal responses to soil water availability may be constrained by insufficient water transport (Jones and Sutherland 1991). Despite the fact that the mangrove *A. germinans* maintains a large leaf-soil water potential gradient as soil salinity increases (Smith *et al.* 1989, Suárez *et al.* 1998, Suárez and Sobrado 2000), stomatal conductance decreases (Smith *et al.* 1989, Sobrado 1999a,b). Relationship between whole shoot conductance and leaf water loss control under salinity may have important implications for canopy water relations (Meinzer and Grantz 1990, Sperry *et al.* 1993, Saliendra *et al.* 1995, Lu *et al.* 1996, Cochard *et al.* 1997). Thus, it may be hypothesised that conservative water use observed in *A. germinans* as salinity increase could be related to decreased plant water transport capacity. Therefore, hydraulic and water relations properties were assessed in seedlings of this species grown at two different salinities.

Seedlings of *Avicennia germinans* (L.) L. were planted in pots with sand and a nutrient solution in a glasshouse under natural sunlight and 12-h photoperiod. Temperatures ranged from 25 to 35 °C during the day and 15 to 20 °C at night. NaCl was dissolved in 50 % Hoagland solution to obtain 171 and 684 mol m$^{-3}$ concentration, and the plants were maintained under these salinities for 6 months. At the end of experiment, seedlings were transported to the laboratory early in the morning kept in wet plastic bags to avoid dehydration until all measurements were completed. Twenty terminal shoots of similar diameters were chosen from 10 plants for each salinity treatment. Shoots were attached to a high-pressure flowmeter (HPFM, *Dynamax Inc.* Houston, USA) to determine leaf and stem hydraulic conductances (Tyree *et al.* 1993, 1995, 1999, Yang and Tyree 1994, Cochard *et al.* 1997, Zotz *et al.* 1998, Sobrado 1998,

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*Received* 6 June 2000, *accepted* 20 October 2000.

*Abbreviations*: $A_b$ - leaf area, $A_w$ - wood cross section area, E - transpiration rates, $g_s$ - stomatal conductance, HPFM - high pressure flowmeter, HV - Huber value, $K_l$ - leaf specific conductivity; $K_s$ - specific conductivity; $R_{+b}$ - resistance of shoots bearing leaves; $R_{-b}$ - resistance of shoot without leaves, $R_b$ - leaf conductance, $K_{ws}$ - whole shoot conductance, $\Psi_w$ - leaf water potential, $\Delta\Psi_w$ - water potential drop from petiole to evaporative surface.

*Acknowledgements*: To DID-USB for providing financial support for this project (Fondo de Trabajo 1999).

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2000). The HPFM is a device designed (Tyree *et al.* 1993) to perfuse water into the base of branches while controlling the pressure ($\Delta P$, MPa) and simultaneously measuring flow (F, kg $s^{-1}$). All hydraulic measurements were made with distilled water filtered through a 0.1 μm filtration membrane. Once shoots were connected to the HPFM, leaves were infiltrated by perfusing water at a pressure of 0.5 MPa for 30 min in order to assure zero leaf water potential. Subsequently, F was measured at 4 s intervals while P was changed at a constant rate of 3 to 5 kPa $s^{-1}$. Measurements were made both in shoots with leaves and after leaf removal in order to obtain the two resistances: $R_{+b}$ (with leaves) and $R_{-b}$ (without leaves). Whole shoot leaf specific hydraulic conductance ($K_{ws}$) was calculated as $1/(R_{+b} \times A_b)$ where $A_b$ = leaf area. The following characteristics were also determined: shoot length, diameter and leaf area. The leaf blade resistance ($R_b$) was calculated as $R_b = R_{+b} - R_{-b}$, and conductance ($K_b$) per unit of leaf area as $K_b = 1/(R_b \times A_b)$. Specific conductivity was computed as $K_s = l/(R_{-b} \times A_w)$ where l = segment length and $A_w$ = cross section of wood, and leaf specific conductivity entering the leaf as $K_l = l/(R_{-b} \times A_b)$. Huber values (HV) were also calculated for each sample as cross section area of wood per unit of leaf blade area ($HV = A_w/A_b$).

Predawn and midday water potentials ($\Psi_w$) were measured with a pressure chamber in the glasshouse. Transpiration rates (E) and stomatal conductances ($g_s$) were measured with a portable gas exchange system (*LCA-2, ADC*, Hoddesdon, England). $\Delta\Psi_w$ was calculated for each species by using the averages of E and $K_l$ ($\Delta\Psi_w = E/K_l$).

Table 1. Leaf characteristics, water relations and hydraulic parameters measured in *A. germinans* grown at 171 and 684 mol $m^{-3}$ NaCl. Values for each salinity are means ± SE of 20 samples for leaf water content, stomatal conductance ($g_s$), transpiration rates (E), Huber value (HV), specific conductivity ($K_s$), leaf specific conductivity ($K_l$), whole shoot leaf specific hydraulic conductance ($K_{ws}$) and leaf blade conductance ($K_b$), and of 4 samples for water potential ($\Psi_w$) measurements. Statistical significance of differences between different salinities are indicated by * ($P \leq 0.05$), ** ($P \leq 0.01$) and *** ($P \leq 0.001$).

| Parameter | 171 mol(NaCl) $m^{-3}$ | | 674 mol(NaCl) $m^{-3}$ |
|---|---|---|---|
| Water content per area [g $m^{-2}$] | 274.00 ± 8.00 | ** | 255.00 ± 3.00 |
| Water content per dry mass [g $g^{-1}$] | 2.73 ± 0.06 | * | 2.20 ± 0.02 |
| Fresh to dry mass ratio [g $g^{-1}$] | 3.72 ± 0.06 | * | 3.20 ± 0.02 |
| Predawn $\Psi_w$ [MPa] | -1.62 ± 0.14 | *** | -3.53 ± 0.07 |
| Midday $\Psi_w$ [MPa] | -2.85 ± 0.02 | *** | -4.67 ± 0.04 |
| $g_s$ [mmol $m^{-2}$ $s^{-1}$] | 253.00 ± 17.00 | *** | 148.00 ± 14.00 |
| E [mmol $m^{-2}$ $s^{-1}$] | 7.40 ± 0.30 | ** | 5.10 ± 0.30 |
| HV [× $10^{-4}$ m $m^{-2}$] | 6.17 ± 0.98 | ns | 6.64 ± 0.63 |
| $K_s$ [× $10^{-2}$ kg $m^{-1}$ $s^{-1}$ $MPa^{-1}$] | 14.94 ± 2.89 | * | 10.42 ± 2.26 |
| $K_l$ [× $10^{-5}$ kg $m^{-1}$ $s^{-1}$ $MPa^{-1}$] | 8.59 ± 1.39 | * | 6.32 ± 1.03 |
| $K_{ws}$ [× $10^{-5}$ kg $m^{-2}$ $s^{-1}$ $MPa^{-1}$] | 15.26 ± 0.20 | * | 11.26 ± 0.12 |
| $K_b$ [× $10^{-4}$ kg $m^{-2}$ $s^{-1}$ $MPa^{-1}$] | 2.15 ± 0.38 | * | 1.19 ± 0.24 |

Shoots used for hydraulic measurements were 0.12 ± 0.03 m long and 9.1 ± 1.6 × $10^{-6}$ $m^2$ of transverse area. In previous experiments, leaves of *A. germinans* were succulent with large hypodermal and parenchyma cells at moderate salinity, but leaf cells become smaller and tightly packed at high salinity (Sobrado 1999b). At 171 mol $m^{-3}$ leaves also seemed more succulent than at 684 mol $m^{-3}$ NaCl. This was suggested by their significantly higher water content per area, water content to dry mass ratio, as well as fresh to dry mass ratio (Table 1).

Changes in leaf water potentials ($\Psi_w$) from predawn to midday were similar at both salinities (Table 1). However, midday stomatal conductance ($g_s$) and transpiration rate (E) were severely reduced at high salinity. Decline in water loss as salinity increases is related to the high water use efficiency found in *Avicennia* species by measurements of gas exchange or carbon isotope composition (Ball and Farquhar 1984, Clough and Sim 1989, Lin and Sternberg 1992, Medina and Francisco 1997, Sobrado 1999 a,b).

Leaf specific conductivity ($K_l$) declined significantly at high salinity. This was related to lowered specific conductivity ($K_s$), because Huber values (HV) remained unchanged (Table 1). Thus, $A_w/A_b$ at high salinity is similar to that at low salinity. However, xylem was slightly less efficient and in consequence, water supply to leaves is limited by both low soil $\Psi_w$, and by low efficiency of the xylem. At both salinities, the parameters were in the range reported for tropical trees (Patiño *et al.* 1995). Whole shoot hydraulic conductance ($K_{ws}$) was 26 % lower at high salinity. Leaves of *A. germinans* also featured low internal conductance ($K_b$) to water transport. This was lowered further under high salinity. Within the leaf, resistance to water flow is mainly determined by non-vascular pathway (Tyree and Cheung 1977). $\Psi_w$ drop from petiole to evaporative surface ($\Delta\Psi_w = E/K_l$ ) was $0.87 \pm 0.21$ MPa at both salinities. Therefore, low $K_b$ and E under salinity caused little change in $\Delta\Psi_w$. Low internal conductance to $CO_2$ has also been detected in *Avicennia marina* leaves under high salinity (Sobrado and Ball 1999, Ball and Sobrado 1999). Thus, leaf internal conductance for water and $CO_2$ in *Avicennia* leaves seems variable with salinity.

In conclusion, the ability of *A. germinans* to vary slightly in hydraulic capacity reveals the existence of other possible adaptations to saline environments. In mangrove forest, the selection pressure for mangroves to be able use low amount of water in relation to carbon gain seems high (Ball 1996). Indeed, mangrove species show low water transport capacity and high water use efficiency (Sobrado 2000). However, low hydraulic capability may further limit water supply and gas exchange of leaves under high salinity, if an excessively low $\Psi_w$ develops within the leaves. The leaf osmotic and elasticity adjustments with salinity enable the large water potential gradients for water uptake and maintenance of leaf pressure potential (Suárez and Sobrado 2000). Nevertheless, E and $g_s$ must be balanced with the water transport constraints to reduce water loss, which possible maintain stem water potentials ($\Psi_w$) above embolisms levels. There are observations of reduced $g_s$ in response to reduced hydraulic conductance for safety of the xylem (Sperry *et al.* 1993, Cochard *et al.* 1997). Despite the fact that embolism need not have entirely negative consequences in some species (Alder *et al.* 1996), embolism reversal in saline soils with very low $\Psi_w$ may be improbable. Thus, there is compelling evidence that catastrophic embolisms in mangrove species may be avoided by stomatal control of water loss (Sperry *et al.* 1988).

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