

## Differential leaf gas exchange responses to salinity and drought in the mangrove tree *Avicennia germinans* (Avicenniaceae)

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**Abstract.** Leaf gas exchange was assessed in *Avicennia germinans* L. grown under different NaCl concentrations (0-40‰), after salt-relief, and then during drought. Stomatal conductance ( $g_s$ ) and net photosynthetic rate ( $P_n$ ) decreased with increasing NaCl concentration, and intrinsic water use efficiency ( $P_n / g_s$ ) increased. Under desalinization  $P_n / g_s$  declined. Thus,  $g_s$  did not change in plants grown at low NaCl concentration (10‰), but increased up to 30-32% at higher NaCl concentration (20 - 40‰). However,  $P_n$  was only slightly enhanced (10-15%). Under drought,  $P_n$  decreased by as much as 46% in plants grown at low NaCl concentration (10‰) and by 22% at high NaCl concentration (40‰). Thus,  $P_n / g_s$  decreased and water use efficiency was lower during drought compared to estimates prior to salt-relief. Rev. Biol. Trop. 54(2): 371-375. Epub 2006 Jun 01.

**Key words:** *Avicennia germinans*, mangrove, NaCl, stomatal conductance, water use efficiency.

Salinity-dependent reduction in carbon assimilation is a function of stomatal limitation of CO<sub>2</sub> diffusion into leaves, of ion toxicity, and of the impairment of essential ion uptake (Flowers *et al.* 1977, Ball and Farquhar 1984a, b, Flowers and Yeo 1986, Munns 1993). One remarkable feature of the leaf gas exchange of mangrove species is their low transpiration and high water use efficiency (Ball and Farquhar 1984a, b). As NaCl concentration increases, mangrove water use characteristics become conservative (Ball 1988, Clough and Sim 1989, Medina and Francisco 1997). *Avicennia germinans* L. is a mangrove well known for its ability to thrive in areas with both high and fluctuating salinity. Drought enhances the salinity effect on mangrove species performance and distribution (Lugo and Snedaker 1974). Effect of drought on photosynthesis of *A. germinans* has been conducted under field conditions where interplay with NaCl

concentration was unavoidable (Smith *et al.* 1986, Sobrado 1999a). Here, leaf gas exchange was assessed in *A. germinans* grown under a variety of salinity conditions, after salt was removed, and finally when watering was withheld. Thus, soil NaCl concentration increases with drought progression were avoided.

### MATERIALS AND METHODS

Ten plants of *A. germinans* L. Stearn per treatment were grown in pots with sand at salinities of 0, 10, 20, 30 and 40‰ NaCl. Plants were kept in a glasshouse with natural sunlight and photoperiod for six months. Gas exchange measurement was taken prior to salt-relief in each plant group. Then plants were removed from salinity by washing the salt repeatedly, and pots were watered with full Hoagland solution (desalinization). After three days of salt

relief, gas exchange measurements were taken again in each plant group. Afterwards, watering was withheld for seven days (drought), and leaf gas exchange measurements were taken again. Five of the ten control plants grown without salt addition were maintained under irrigation and five plants were subjected to drought. Gas exchange measurements were taken at midday in two fully expanded sunny leaves per plant per treatment, by using a portable gas analyzer model *LCA-2* (*Analytical Development Co.*, Herts, UK). Average irradiation for measurements was  $1600 \mu\text{mol m}^{-2} \text{s}^{-1}$ , leaf temperature was between  $29\text{--}32 \text{ }^\circ\text{C}$  (prior to salt relief) and  $33\text{--}34 \text{ }^\circ\text{C}$  (drought), relative humidity was  $70\text{--}75\%$  and ambient  $\text{CO}_2$  concentration was  $350 \mu\text{mol mol}^{-1}$ . Leaf water potential ( $\Psi_w$ ) was also measured with a pressure chamber at the time of gas exchange measurements. Means obtained for each plant group, at the time of maximal salinity, salinity relief and drought, were analyzed by using an ANOVA test. The least statistically significant difference (LSD) at  $p < 0.05$  was determined.

## RESULTS

In control plants (0‰), the mean values of measurements in the three stages were net photosynthetic rate ( $P_n$ ) of  $14.9 \pm 0.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ ,  $g_s$  of  $365.5 \pm 20.4 \text{ mmol m}^{-2} \text{s}^{-1}$  and  $C_i/C_a$  of  $0.597 \pm 0.022$ . Similarly, leaf water potential ( $\Psi_w$ ) was kept constant at  $-2.0 \pm 0.1 \text{ MPa}$ . Under salinity,  $\Psi_w$  (MPa) declined to about  $-2.6 \pm 0.2$  (10‰),  $-3.0 \pm 0.2$  (20‰),  $-3.2 \pm 0.3$  (30‰) and  $-3.5 \pm 0.3$  (40‰). Leaf gas exchange showed a significant effect by NaCl concentration on  $P_n$  and  $g_s$ , as well as on  $P_n/g_s$  ratio and intercellular to ambient  $\text{CO}_2$  concentration ratio ( $C_i/C_a$ ; Table 1). The tendency of the relationship between  $P_n$  and  $g_s$ , under salinity, was exponential in consistency increased water use efficiency with salinity (Fig. 1). Three days after salt-relief,  $\Psi_w$  was about  $-2.0$  to  $-2.2 \text{ MPa}$  in treatments. Desalination also had a strong positive effect on  $g_s$ , and to a lesser degree on  $P_n$  (Fig. 1, Table 1). Thus  $g_s$  did not change in

plants grown at 10‰, but increased up to 30–32% at higher NaCl concentration (20–40‰). However,  $P_n$  was slightly enhanced (10–15%) after salt relief in plants grown at high NaCl concentration. Thus,  $P_n/g_s$  was lowered during desalination of plants grown at high NaCl concentration and also  $C_i/C_a$  (Table 1). However, plants grown at the higher NaCl concentration were the most efficient in water use.

The 7-d drought caused a comparable  $\Psi_w$  drop to about  $-3.3 \text{ MPa}$  in all plant groups. In control plants (0‰), drought resulted in concomitant decline of  $P_n$  by 49% and  $g_s$  by 53% as compared to those in unstressed plants. Thus,  $P_n/g_s$  remained about  $44.5 \mu\text{mol mol}^{-1}$  and  $C_i/C_a$  about 0.602 suggesting that water use efficiency was comparable to that in non-stressed control plants. By contrast, plants grown under NaCl concentration showed that  $P_n$  was more

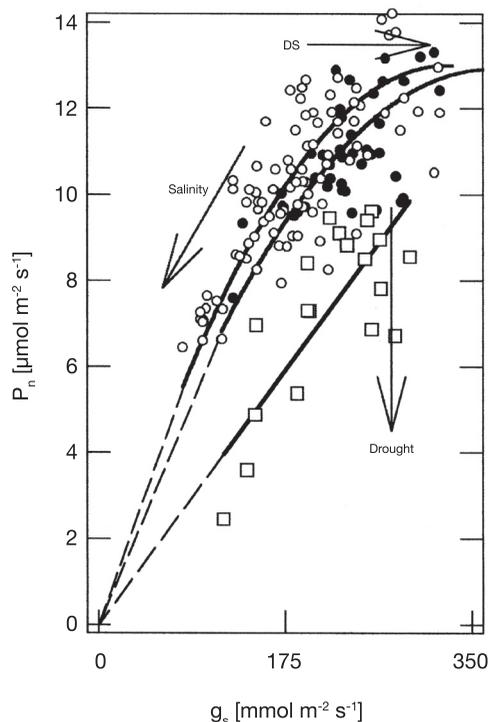


Fig. 1. Net photosynthetic rate ( $P_n$ ) as a function of stomatal conductance ( $g_s$ ) in *A. germinans* as affected by NaCl concentration (O), desalination ( $\bullet$ , DS) and drought ( $\square$ ). Tendency of the changes for each treatment are pointed out by arrows.

TABLE 1  
*Leaf gas exchange parameters measured in A. germinans seedlings*

Parameter	Salinity (‰)			
	10	20	30	40
$P_n$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )				
S	11.79 (0.45) a	10.31 (0.32) a	9.43 (0.27) a	8.97 (0.36)a
DS	11.89 (0.54) a	11.38 (0.28) b	10.60 (0.44) b	10.33 (0.33) b
D	6.38 (1.02) b	6.66 (0.80) c	7.03 (1.02) c	8.01 (0.90)a
$g_s$ ( $\text{mmol m}^{-2} \text{s}^{-1}$ )				
S	257 (11) a	191(8) a	163 (10) a	153 (11) a
DS	281 (13) a	249 (6) b	215 (12) b	198 (11) b
D	198 (30) b	237 (24) b	228 (20) b	208 (11) b
$P_n / g_s$ ( $\mu\text{mol mol}^{-1}$ )				
S	46.7 (1.4) a	54.8 (2.4) a	58.7 (2.9) a	61.3 (2.4) a
DS	42.6 (1.4) a	46.1 (1.3) b	50.1 (1.4) b	53.2 (2.5) b
D	32.6 (4.6) b	32.6 (2.2) c	30.7 (3.3) c	38.2 (3.3) c
$C_i / C_a$ ( $\text{mol mol}^{-1}$ )				
S	0.588 (0.008) a	0.598 (0.009) a	0.559 (0.007) a	0.550(0.009) a
DS	0.615 (0.010) b	0.598 (0.008) a	0.596 (0.010) b	0.587(0.006) b
D	0.709 (0.028) c	0.699 (0.017) b	0.716 (0.029) c	0.665 (0.020)c

Measurements were taken under saline conditions (S), three days after salt relief (DS) and seven days after watering was withheld (D). Values are the means (SE). Comparison are among treatments for each plant group and means followed by different letter are statistically different at  $p < 0.05$ .

sensitive than  $g_s$  under drought (Fig. 1, Table 1). This resulted in an up to 46% decline of  $P_n$  in plants grown at low NaCl concentration (10‰) and a 22% decline in those grown at the highest NaCl concentration (40‰).  $g_s$  was only negatively affected in plants grown at low NaCl concentration (10‰). Drought resulted in lower water use efficiency as shown by higher  $C_i/C_a$  and lower  $P_n/g_s$  (Table 1, Fig. 1), and linearity between  $P_n$  and  $g_s$ , was consistent with similar water use efficiency among salinity treatments (Fig. 1).

## DISCUSSION

In this study, leaf gas exchange parameters, under salinity or after salinity relief, pointed to increasing water use efficiency as NaCl concentration became higher, as has been previously found (Smith *et al.* 1989, Medina and Francisco 1997, Sobrado 1999b). However, non-stomatal limitations overrode effect of drought on  $P_n$  and water use efficiency was lowered. Leaf ion concentration of *A. germinans* can remain high up to 10 days after salt is eliminated from the

soil (Suárez *et al.* 1998, Suárez and Sobrado 2000). Thus, plants grown under higher NaCl concentration are osmotically adjusted and have high leaf turgor and leaf water content for a given  $\Psi_w$  (Suárez and Sobrado 2000). This may alleviate effect of drought  $g_s$ . Our results could also reflect insensitivity to ABA by stomata of plants grown under high sodium (Jarvis and Mansfield 1980).  $P_n$  could be affected by the synergistic influence of drought and ion concentration without concomitant changes in  $g_s$ . Under field conditions,  $g_s$  under drought has either been unaffected by drought (at high relative air humidity; Sobrado 1999a) or has been decreased (at low relative air humidity; Naidoo and von Willert 1994, Smith *et al.* 1986

In conclusion, there were differences in the response of  $P_n$  and  $g_s$  to NaCl concentration and drought. Stomatal functioning appears to be consistent with maximizing carbon gain by water loss under salinity. However, the reverse trend occurs during desalinization and drought. Declining water use efficiency as consequence of drought in the field overrides the opposite effect as result of salinity (Sobrado 1999a) Thus, the interaction of drought with salinity, as found in the field, may modulate the overall ecophysiological performance of *A. germinans* in drought-prone areas. In *A. germinans*, an accurate control of water loss to salt secretion capacity is required to maintain the balance of salt influx-efflux at leaf level (Sobrado 2001). Failure in water loss control may lead to salt build-up in leaves and to enhancement of leaf senescence.

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#### RESUMEN

Se estudió el intercambio de gases en las hojas de *Avicennia germinans* L. en varias concentraciones de NaCl (0-40‰), después de la desalinización y durante la desecación. La conductancia de los estomas ( $g_s$ ) y la tasa de fotosíntesis ( $P_n$ ) decrecieron con el incremento en la concentración de NaCl, y se incrementó la eficiencia en el uso intrínseco de agua ( $P_n / g_s$ ). Bajo desalinización  $P_n / g_s$  declinó. Así,  $g_s$  no cambia en el crecimiento de las plantas a bajas concentraciones de NaCl (10‰), pero se incrementó hasta 30-32% a las concentraciones de NaCl más altas (20 - 40‰). Sin embargo,  $P_n$  aumentó ligeramente (10-15%). En desecación  $P_n$  fue reducido hasta un 46% a bajas concentraciones (10‰) de NaCl, y a un 22% a altas concentraciones (40‰) de NaCl. Así,  $P_n / g_s$  decrecieron y la eficiencia en el uso de agua fue menor durante desecación en comparación con los valores estimados previos a la desalinización.

**Palabras clave:** *Avicennia germinans*, manglar, NaCl, conductancia, estomas, eficiencia de uso de agua.

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