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

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Received 20-IX-2001. Corrected 02-X-2005. Accepted 23-II-2006.

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_2 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 germinas* 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 µmol m^{-2} s^{-1}, leaf temperature was between 29-32 ºC (prior to salt relief) and 33-34 ºC (drought), relative humidity was 70-75% and ambient CO_2 concentration was 350 µmol mol^{-1}. Leaf water potential (Ψ_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 ± 0.5 µmol m^{-2} s^{-1}, g_s of 365.5 ± 20.4 mmol m^{-2} s^{-1} and C_i/C_a of 0.597± 0.022. Similarly, leaf water potential (Ψ_w) was kept constant at -2.0 ± 0.1 MPa. Under salinity , Ψ_w (MPa) declined to about -2.6 ± 0.2 (10‰), -3.0 ± 0.2 (20‰), -3.2 ± 0.3 (30‰) and -3.5± 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 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 efficency with salinity (Fig. 1). Three days after salt-relief, Ψ_w. was about -2.0 to -2.2 MPa in treatments. Desalinization 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 desalinization 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 Ψ_w drop to about -3.3 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 µmol $mol^{-1}$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

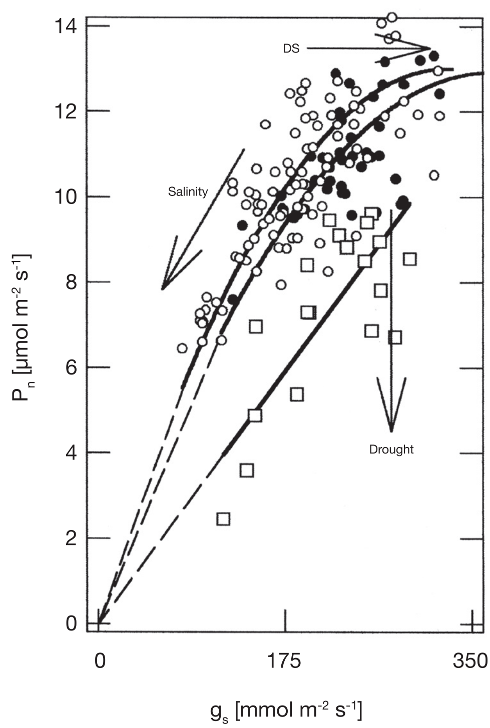

Fig. 1. Net photosynthetic rate (P_n) as a function of stomatal conductance (g_s) in *A. germinans* as affected by NaCl concentration (O), desalinization (•, DS) and drought (□). Tendency of the changes for each treatment are pointed out by arrows.

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

Parameter	Salinity (‰)			
	10	20	30	40
P_n (μmol m^{-2} 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 (mmol m^{-2} 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 (μmol 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 (mol mo l^{-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 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 Ψ_w (Suárez and Sobrado 2000). This may alleviated 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.

ACKNOWLEDGMENTS

Financial support was provided by DID-USB.

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 concentaciones (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 evalolres stimados previos a la desalinización.

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

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