Effects of short-term salinity on leaf gas exchange of the fig (*Ficus carica* L.)

S.D. GOLOMBEK and P. LÜDDERS
Institute of Crop Science, Technical University of Berlin, Albrecht-Thaer Weg 3, D-1000 Berlin 33, Germany

Abstract

The influence of short-term salinity (day 1–day 2: 50 mol m^{-3} NaCl, day 3–day 7: 100 mol m^{-3} NaCl in the nutrient solution) on leaf gas exchange characteristics were studied in two fig clones (*Ficus carica* L.), whose root mass had been varied in relation to the leaf area. The stomatal conductance was diminished by NaCl in the first week of treatment. NaCl slightly reduced the calculated intercellular partial pressure of CO_2. The net photosynthetic rate of plants with many roots was stimulated by NaCl on some days of the first week of treatment, whereas the net assimilation rate of the plants with few roots remained unaltered or decreased by NaCl. Only the assimilation of the salt-treated plants of one clone for some days during the first week of treatment seemed to be influenced by stomatal conductance. Nonstomatal factors were primarily responsible for the changes in CO_2 uptake in response to salt and/or root treatment. The water use efficiency increased during several days of the first week of NaCl treatment. Decreased stomatal conductance, increased water use efficiency and stimualtion of the net CO_2 assimilation rate appear to enhance salt tolerance during the first few days of salinity.

Introduction

The cultivation of the fig (*Ficus carica* L.), a moderately salt-tolerant species, is increasingly practised under irrigation. For this reason, and because the fig is often grown on already saline soils, salinity problems have become more important in fig cultivation. In the natural environment the salt concentration in the soil fluctuates over different time scales caused e.g. by rainfall or irrigation. Transplanting of young plants can also lead to a change in salinity in the root zone.

The ability of the plant to adapt to an increase of the salt concentration is of relevance for plant production. The reaction of the gas exchange parameters in response to salt treatment is sig-

nificant for the ability of the plant to adapt to salinity.

NaCl can influence the stomatal and the nonstomatal conductance to CO_2 (Long and Baker, 1986). Considering agricultural production it is important that the net CO_2 assimilation is reduced by salinity as little as possible. Salinity reduces the water availability of the external solution, which can effect the water status of the plant. Decreasing the transpiration rate in response to salinity is one of the mechanisms to enable the plant to improve the water conditions and to slow down the accumulation of sodium and chloride in the leaves (Munns and Termaat, 1986). A reduction of the stomatal conductance in response to salt treatment can cause a de-

crease of the net CO_2 uptake by reducing the intercellular partial pressure of CO_2 (Long and Baker, 1986).

A decrease of the stomatal conductance can also be the result of reduced nonstomatal conductance. Despite a marked reduction of the stomatal conductance the intercellular partial pressure of CO_2 may occasionally stay constant or rise (Farquhar and Sharkey, 1982). The fact that the intercellular partial pressure of CO_2 does not decrease indicates that the capacity of the nonstomatal conductance to CO_2 has been reduced and that the decrease in stomatal conductance compensates for this reduced capacity for CO_2-assimilation to optimise the efficiency of water use (Long and Baker, 1986).

There are only few studies on the short-term effects of NaCl on gas exchange characteristics of glycophytes. In greenash (*Fraxinus pennsylvanica* Marsh.) net CO_2 assimilation rate and stomatal conductance decreased from the first day of NaCl treatment (Pezeshki and Chambers, 1986); the net photosynthetic rate of soybean (*Glycine max* (L.) Merill) was diminished from the fourth day of treatment by 90 mol m^{-3} NaCl (Fritz, 1984). The photosynthetic gas exchange of rice (*Oryza sativa* L.) was not altered during the first day of treatment with 100 mol m^{-3} NaCl (Yeo et al., 1991). The net CO_2 uptake of old, but not of young leaves of the halophyte *Plantago maritima* L. and the net photosynthetic rate and stomatal conductance of the halophyte *Avicennia marina* (Forstk.) Vierh. declined when the NaCl concentration in the nutrient solution was increased in increments from 50 to 500 mol m^{-3} (Ball and Farquhar, 1984; Flanagan, 1987). An ecotype of *Agrostis stolonifera* L. from a non-saline environment reacted to 100 mol m^{-3} NaCl with a reduction of the net CO_2 assimila-

tion rate from the first day of treatment (Robertson and Wainwright, 1987).

Materials and methods

Plants

Cuttings from clones of *Ficus carica* L. of the variety 'Bardajik' (Turkey) and the origin 'Faro' (Portugal) were heated from below (25°C) in a box with a high relative humidity. After rooting they were selected for uniformity and were transferred to 50 liter pots (eight plants per pot) in a climate chamber with nutrient solution. The climate chamber was maintained under the following conditions: 23°C, RH 60 to 80%, 14 h daylength, light intensity of 380 μmol m^{-2} s^{-1} (PAR) at canopy height provided by HQI-TS 400 W/D lamps (Osram). The nutrient solution contained in mol m^{-3}: 2 K_2SO_4, 3 $CaNO_3$, 2. 5KH_2PO_4, 3 $MgSO_4$, and in μM: 50 FeEDTA, 30 H_3BO_3, 2 $MnSO_4$, 1 $CuSO_4$, 1.4 $(NH_4)_6Mo_7$, 1 $ZnSO_4$. The pH was 6.5 and the pots were continuously aerated. The solutions were replaced weekly and were topped up daily with deionized H_2O. NaCl-treated plants received 50 mol m^{-3} NaCl in the first two days and 100 mol m^{-3} from the third day of treatment. Control plants were grown without additional NaCl.

To study the influence of root mass on photosynthesis in the presence of salinity, 'model plants' with one large leaf left on the shoot were used. The area of the leaf of the clone 'Bardajik' was larger than that of the clone 'Faro' (Table 1). One week before starting the experiment, all leaves except of the first fully expanded leaf from the apex of the shoot, which was horizontally

Table 1. Leaf area and root mass of the clones 'Bardajik' and 'Faro' with many (+) and few (−) roots after one week of NaCl treatment

Parameter	Clone 'Bardajik'				Clone 'Faro'			
	Control		100 mM NaCl		Control		100 mM NaCl	
	+	−	+	−	+	−	+	−
Leaf area (cm^2)	443a*	435a	441a	446a	246b	234b	238b	250b
Root mass (g)	9,5a	5,2b	10,1a	4,9b	9,1a	4,8b	8,7a	4,3b

* Means within a physiological parameter are significantly different at the $p < 0.05$ level if followed by different letters.

orientated to the light, were removed. Before this tretment there has been five leaves per plant. The roots were varied in size by cutting off a part of the root system one week before starting the experiment (Table 1).

A randomized block design with six replications per treatment was used.

Gas exchange

The measurements of the gas exchange were made by use of a portable open gas exchange system with differential infrared gas analysers for CO_2 and H_2O (H. Walz, Mess- und Regeltechnik, Effeltrich, FRG) described in detail by Schulze et al. (1982). A portion of an attached leaf was inserted into a cuvette; the measurements were carried out in steady state conditions and at the abaxial leaf surface because the stomata of the leaves were mainly located on this side. Leaf temperature, relative humidity and temperature inside the cuvette and of the flowmeter were recorded. The absolute CO_2 concentration in the gas stream entering the chamber was measured by an infrared gas analyser (WA 225 Mk3, Analytical Development Co. Ltd., Hoddesdon, England). The measurements were performed at a light intensity of 1000 μmol m^{-2} s^{-1} and 3–4.5 h after the beginning of the light period, the net assimilation rate remained constant after the first two hours of exposure to light (Golomek and Lüdders, 1990).

Photosynthesis, transpiration, stomatal conductance to CO_2 and the intercellular partial pressure of CO_2 were calculated as in von Caemmerer and Farquhar (1981), the nonstomatal conductance to CO_2 as in Jarvis (1971).

Results and discussion

The gas exchange measurements were conducted in the absence of any visible toxicity symptoms. The chlorophyll content was not altered by salinity (data not shown).

Stomatal conductance of fig leaves were diminished by NaCl in the first week of treatment (Fig. 1). A decline of stomatal conductance from the first day of NaCl treatment was observed with green ash (*Fraxinus pennsylvanica* Marsh.)

by Pezeshki and Chambers, 1986. The osmotic potential of the nutrient solution was substantially reduced by an increase of the NaCl concentration, about 50 or 100 mol m^{-3} from −0,06 MPa to −0,28 MPa or −0,49 MPa. The decline of the stomatal conductance of fig leaves in the first days of salt treatment could be one of the causes of the responses of the plant water status, which was not measured, or a reaction to chemical messages from the roots to the decreased osmotic potential of the nutrient solution (Neuman and Smit, 1991).

NaCl enhanced the calculated nonstomatal conductance significantly only in the case of plants with many roots – of 'Bardajik' during the first week, and of 'Faro' at the 3rd and 4th day of treatment (Fig. 1). On the other hand, the calculated nonstomatal conductance of plants with few roots was not significantly influenced by NaCl. It has been shown that stomata can behave nonhomogeneously (Downton et al., 1988; Terashima et al., 1988); the calculated nonstomatal conductance of a leaf area with nonuniform behaviour of stomata might be underestimated (Raschke, 1989). Furthermore, if the decrease of the stomatal conductance in response to the first days of NaCl treatment was caused by nonuniform stomatal changes, the real stomatal conductance of the NaCl treated plants may be higher in relation to the controls than the calculated nonstomatal conductance.

The decrease of stomatal conductance and the partial increase of the calculated nonstomatal conductance in response to short-term salinity resulted in a slight salinity-induced decrease of the calculated intercellular partial pressure of CO_2 (Fig. 1). Because of the possibility that stomata can close nonhomogeneously, the calculated intercellular partial pressure of CO_2 of the NaCl-treated plants may be overestimated (Downton et al., 1988; Terashima et al., 1988). The extent of the reduction of the calculated intercellular partial pressure of CO_2 in response to salt treatment was not influenced by the root treatment.

The response of the rate of net assimilation to salinity was similar to the reaction of the calculated nonstomatal conductance (Fig. 1). The net photosynthetic rate of plants with many roots was stimulated by NaCl in the early stages of
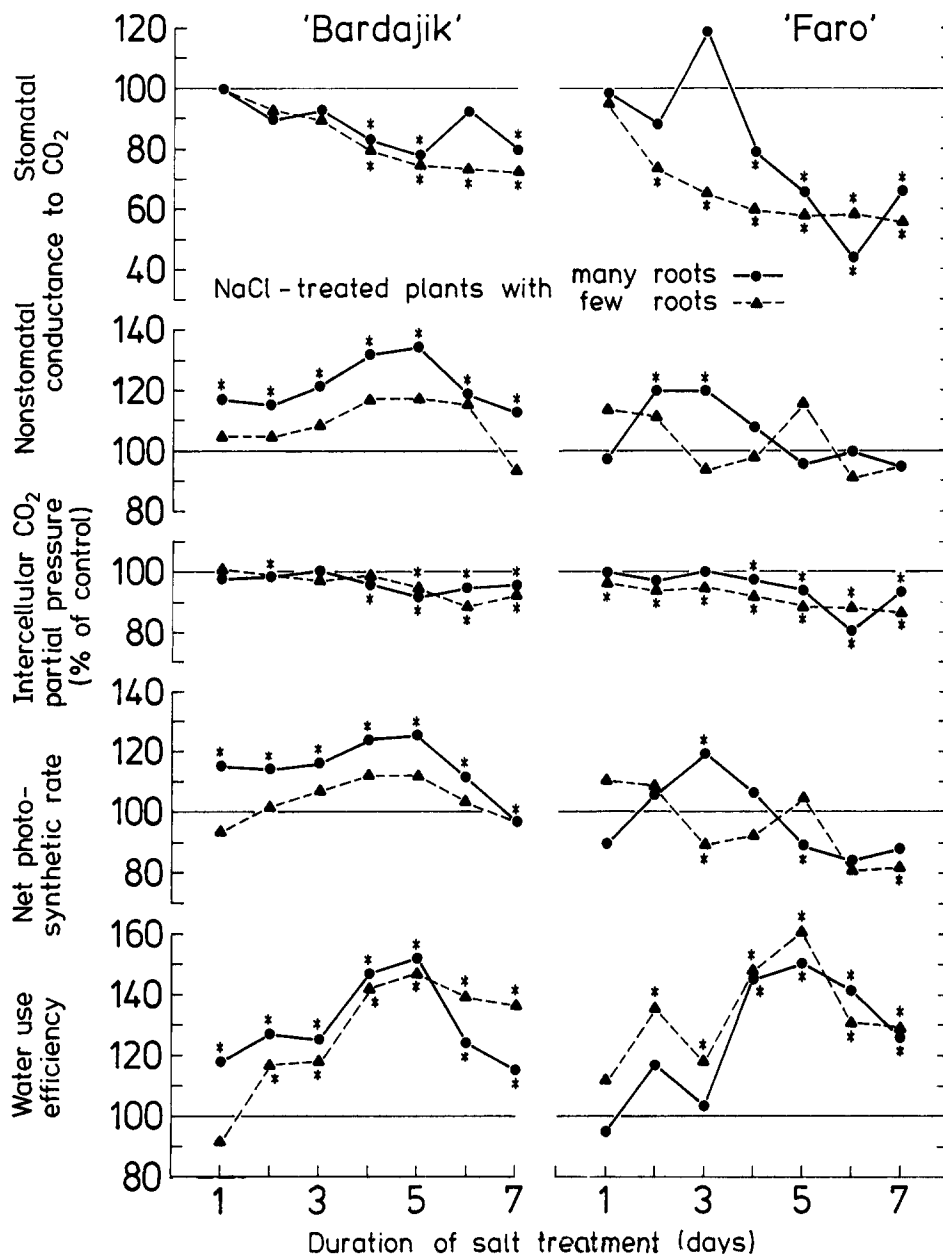
Fig. 1. Gas exchange characteristics of the fig clones 'Bardajik' and 'Faro' under control and salinized ($100\,\mathrm{mol\,m^{-3}}$) conditions, the results of salinized plants presented as percentage of the mean of the control. Asterisks denote significant difference from controls ($p < 0.05$).

salinization, of 'Bardajik' from the 1st to the 6th, and of 'Faro' on the 3rd day of salinity. The net assimilation rate of the plants with few roots remained unaltered ('Bardajik') or decreased ('Faro') by NaCl. Thus, the relation of leaf area to root mass can influence the reaction of net CO_2 uptake of these two fig clones in the first

few days of salinity. A long-term treatment with $100\,\mathrm{mol\,m^{-3}}$ NaCl led to a reduction of the net CO_2 assimilation rate by NaCl (Golombek, 1991).

A positive relation between net assimilation rate and stomatal conductance appeared mainly with the salt-treated 'Faro' (Table 1). If a de-

creased stomatal conducance in response to salinity results in a reduced intercellular partial pressure of CO_2, stomata can impose a limitation to assimilation. A positive relation between net assimilation and intercellular partial pressure of CO_2 occurred only occasionally with the salt-treated 'Faro' (Table 2). This relation indicates the dependence of the assimilation on the stomatal conductance of the NaCl-treated 'Faro' on some days during the first week of treatment. A decrease of the stomatal conductance without an effect on the assimilation optimizes the water use efficiency.

A strong positive correlation existed between

Table 2. Correlation coefficients[a] (linear regression) between net photosynthetic rate and calculated nonstomatal conductance to CO_2, stomatal conductance or intercellular partial pressure of CO_2 in the first week of NaCl treatment of plants with many (+) and few roots (−)

Parameter Clone Treatment Root mass		Days of NaCl treatment						
		1	2	3	4	5	6	7
Nonstomatal conductance to CO_2								
'Bardajik'								
Control	+	0,99***	1,00***	1,00***	0,98***	0,99***	0,97***	0,98***
	−	1,00***	1,00***	0,99***	0,99***	0,98***	0,99***	1,00***
100 mM NaCl	+	0,95***	0,97***	0,96***	0,97***	0,94***	0,72**	0,84***
	−	0,99***	0,99***	0,98***	0,99***	1,00***	0,85***	0,98***
'Faro'								
Control	+	0,99***	0,95***	0,99***	0,98***	0,94***	0,98***	0,78**
	−	0,99***	1,00***	0,99***	1,00***	0,99***	0,98***	0,98***
100 mM NaCl	+	0,98***	0,97***	0,98***	0,95***	0,90***	0,76**	0,85***
	−	0,93***	0,98***	0,99***	0,98***	0,97***	0,96***	0,77**
Stomatal conductance to CO_2								
'Bardajik'								
Control	+	0,15	0,39	0,13	0,18	−0,13	−0,22	0,24
	−	0,87***	0,36	−0,48	0,38	0,54	0,60*	0,24
100 mM NaCl	+	−0,18	0,23	0,35	0,32	0,62*	0,41	0,63*
	−	0,46	−0,17	0,56*	0,49	0,39	0,77**	0,65*
'Faro'								
Control	+	0,72**	−0,01	0,50	0,41	0,53	0,82***	0,13
	−	−0,01	−0,25	0,23	0,28	0,08	0,36	0,79**
100 mM NaCl	+	0,49	0,68**	0,59*	0,75**	0,86***	0,73**	0,72**
	−	0,47	0,58*	0,81***	0,78**	0,85***	0,91***	0,85***
Intercellular partial pressure of CO_2								
'Bardajik'								
Control	+	−0,61	−0,34	−0,56	−0,38	−0,67	−0,75	−0,25
	−	0,35	−0,68	−0,79	0,43	0,38	0,10	−0,81
100 mM NaCl	+	−0,52	−0,32	0,10	0,15	0,02	−0,08	0,24
	−	−0,35	−0,21	0,02	0,29	−0,63	0,58	−0,01
'Faro'								
Control	+	−0,23	−0,05	0,15	0,21	0,12	0,35	0,10
	−	−0,74	−0,66	0,32	0,49	0,54	0,38	0,21
100 mM NaCl	+	−0,09	0,63*	−0,25	0,43	0,54	0,38	0,21
	−	0,18	0,34	0,67*	0,52	0,61*	0,27	0,61*

[a] Positive correlation coefficients are significant at $*p < 0.05$, $**p < 0.01$ and $***p < 0.001$.

net photosynthesis and calculated nonstomatal conductance, both in control plants and NaCl-treated plants with many for with few roots during the entire treatment (Fig. 2, Table 2). This indicates that nonstomatal factors were primarily responsible or the changes in CO_2 uptake in response to salt and/or root treatment, providing that nonhomogeneous closure of stomata did not lead to an incorrect calculation of nonstomatal conductance. The stimulation or the lack of response of the net CO_2 uptake of 'Bardajik', despite a decrease of the stomatal conductance by NaCl, was caused by the reaction of the nonstomatal conductance.

The stimulation of the rate of net CO_2 assimilation by NaCl demonstrated that the unsalinized plants did not achieve their full assimilatory capacity. An increased maintenance component of respiration is often found under salt stress, probably because of the additional metabolic cost of osmotic adjustment, excluding or compartmentalizing the salt etc. (McCree, 1986). An increase of the net CO_2 assimilation rate in response to increased photosynthate demand has been reported in the literature (Herold, 1980;

Ho et al., 1983; von Caemmerer and Farquhar, 1984). The initial increase of the net CO_2 uptake in response to NaCl could be caused among other reasons by an enhanced assimilate demand by the plant.

To our knowledge a statistically significant increase of the net assimilation rate, relative to the control plants of the same day, in the first few days of salinity has not previously been reported for plant species other than the fig. With green ash (*Fraxinus pennsylvanica* Marsh.) a decrease of net CO_2 uptake of the leaves caused by NaCl has been observed from the first day of treatment (Pezeshki and Chambers, 1986) and with soybean (*Glycine mas* (L.) Merill) from the fourth day (Fritz, 1984).

A decrease of the stomatal conductance without an equivalent reduction of the net CO_2 uptake rate resulted in an enhancement of the water use efficiency during several days in the first week of NaCl treatment of plants with many and with few roots (Fig. 1). The decrease of transpiration per unit of carbon fixed under saline conditions could be an adaptation to the NaCl content and the diminished osmotic poten-
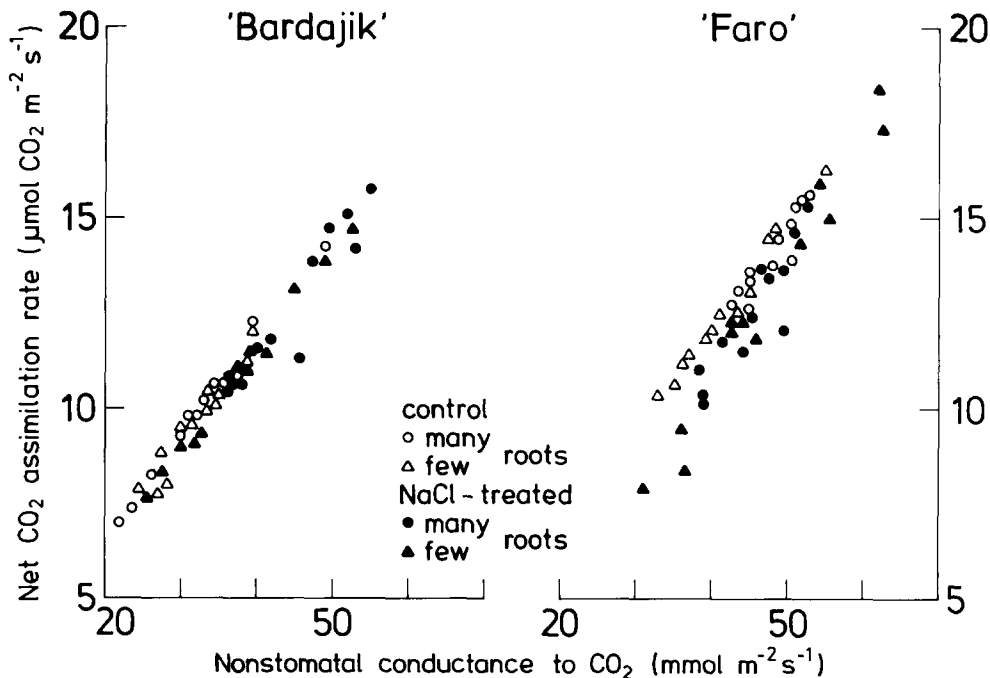

Fig. 2. Relationship between the net assimilation rate and the nonstomatal conductance to CO_2 of the fig clones 'Bardajik' and 'Faro' at the fifth day of NaCl treatment.

tial of the nutrient solution. The rate of accumulation of sodium- or chloride-ions in the leaves depends, among other processes, on the volume flux of the transpiration stream in relation to the growth rate of the leaves (Munns and Termaat, 1986).

In conclusion, the reaction of leaf gas exchange of the fig to the first few days of salinity up to $100 \, mol \, m^{-3}$ NaCl appeared to enhance salt tolerance. The decrease of stomatal conductance in response to salinity favours the improvement of the water conditions. The reduction of stomatal conductance only slightly influenced the net CO_2 uptake. The net photosynthetic rate remained unaltered or increased in response to NaCl as a consequence of the reaction of non-stomatal conductance and the water use efficiency increased. The maintenance or increase of the net CO_2 assimilation rate after an increase of the salt concentration may be of relevance for the ability of the plant to cope with salinity.

Acknowledgement

References

Ball C M and Farquhar G D 1984 Photosynthetic and stomatal responses of the grey mangrove, *Avicennia marina*, to transient salinity conditions. Plant Physiol. 74, 7–11.

Downton W J S, Loveys B R and Grant W J R 1988 Stomatal closure fully accounts for the inhibition of photosynthesis by abscisic acid. New Phytol. 108, 263–266.

Farquhar D G and Sharkey T D 1982 Stomatal conductance and photosynthesis. Annu. Rev. Plant Physiol. 33, 317–345.

Flanagan L B 1987 Effects of long-term and transient changes in salinity on photosynthesis, leaf demography and growth in *Plantago maritima* L. *In* Progress in Photosynthesis Research 4. Ed. J Biggins. pp 197–200. Martinus Nijhoff Publishers, Dordrecht, The Netherlands.

Fritz R 1984 Veränderungen im Translokationsverhalten von Photosyntheseprodukten bei salzgestreßten Sojabohnen-Varietäten: Einsatz der Nuklide ^{11}C und ^{14}C. Ph.D. Thesis, Kernforschungsanlage Jülich GmbH.

Golombek S D and Lüdders P 1990 Gas exchange of *Ficus carica* in response to salinity. *In* Plant Nutrition – Physi-

ology and Applications. Ed. M L van Beusichem. pp 487–493. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Golombek S D 1991 Einfluß von NaCl auf Gaswechsel und Kohlenhydratmetabolismus von *Ficus carica* L. Ph.D. Thesis, Technical University of Berlin.

Herold A 1980 Regulation of photosynthesis by sink activity – the missing link. New Phytol. 86, 131–144.

Ho L C, Shaw A F, Hammond, J B W and Burton K S 1983 Source-sink relationships and carbon metabolism in tomato leaves. 1. ^{14}C Assimilate compartmentation. Ann. Bot. 52, 365–372.

Jarvis P G 1971 The estimation of resistances to carbon dioxide transfer. *In* Plant Photosynthetic Production. Manual of Methods. Eds. Z Sestak, J Catsky and P G Jarvis. pp 556–631. Dr. W. Junk, The Hague, The Netherlands.

Long S P and Baker N R 1986 Saline terrestrial environments. *In* Photosynthesis in Contrasting Environments. Eds. N R Baker and S P Long. pp 63–102. Elsevier, Amsterdam, New York, Oxford.

Munns R and Termaat A 1986 Whole-plant responses to salinity. Aust. J. Plant Physiol. 13, 143–160.

McCree K J 1986 Whole-plant carbon balance during osmotic adjustment to drought and salinity stress. Aust. J. Plant Physiol. 13, 33–43.

Neumann D S and Smit B A 1991 The influence of leaf water status and ABA on leaf growth and stomata of Phaseolus seedlings with hypoxic roots. J. Exp. Bot. 42, 1499–1506.

Pezeshki S R and Chambers J L 1986 Effect of soil salinity on stomatal conductance and photosynthesis of green ash (*Fraxinus pennsylvanica*). Can. J. For. Res. 16, 569–573.

Raschke K 1989 How abscisic acid causes depressions of the photosynthetic capacity of leaves. *In* Plant Growth Substances 1988, Proceedings of the 13th International Conference on Plant Growth Substances, Calgary, Alberta, Canada. Ed. R P Pharis, pp 383–390. Springer-Verlag, Berlin.

Robertson K P and Wainwright S J 1987 Photosynthetic responses to salinity in two cones of *Agrostis stolonifera*. Plant Cell Environ. 10, 45–52.

Schulze E-D, Hall A D, Lange O L and Walz H 1982 A portable steady-state porometer for measuring the carbon dioxide and water vapour exchanges of leaves under natural conditions. Oecologia 53, 141–145.

Terashima I, Wong S-C, Osmond C B and Farquhar G D 1988 Characterization of nonuniform photosynthesis induced by abscisic acid in leaves having different mesophyll anatomies. Plant Cell Physiol. 29, 385–394.

Von Caemmerer S and Farquhar G D 1984 Effects of partial defoliation, changes of irradiance during growth, short-term water stress and growth at enhanced $p(CO_2)$ on the photosynthetic capacity of leaves of *Phaseolus vulgaris* L. Planta 160, 320–329.

Yeo A R, Lee K-S, Izard P, Boursier P J and Flowers T J 1991 Short- and long-term effects of salinity on leaf growth in rice (*Oryza sativa* L.). J. Exp. Bot. 42, 881–889.

Section editor: H Lambers