

be as important to survival as stomatal or cuticular regulation of water loss.

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## Inhibition by NaCl of Net CO<sub>2</sub> Fixation and Yield of Cucumber

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**Abstract.** Cucumber (*Cucumis sativus* L. cv. Fidelio) grown in sand culture in the greenhouse was trickle-irrigated with nutrient solution containing 0, 10, or 50 mM NaCl. Gas exchange of individual leaves was measured by a portable infrared gas analyzer at saturating photosynthetic photon flux. Salt at 10 mM had no detectable effect on plant performance, but exposure to 50 mM NaCl caused net CO<sub>2</sub> fixation to decline by 33% and 48% in the eighth and ninth oldest leaves, respectively. Stomatal conductance and transpiration rate were also reduced (≈ 50%) in these leaves. These differences, as well as lower leaf water potentials, were associated with a 60% reduction in fruit fresh weight. The relationship between net CO<sub>2</sub> fixation and intercellular (substomatal) CO<sub>2</sub> concentrations was determined for individual, attached leaves of plants with roots exposed to various concentrations of NaCl in hydroponics. With 50 and 100 mM NaCl, a nonstomatal contribution to the inhibition of photosynthesis at the chloroplast level was indicated by strong inhibition of CO<sub>2</sub> fixation at a saturating CO<sub>2</sub> concentration. Salt-induced inhibition of CO<sub>2</sub> fixation was associated with accumulation of Na<sup>+</sup> and Cl<sup>-</sup>, and lower K<sup>+</sup> in the individual leaves examined.

High productivity of cucumbers in the greenhouse results from optimization of the aerial and rooting environments, with yields between 223 to 446 t·ha<sup>-1</sup>, compared with 10.7 t·ha<sup>-1</sup> under field conditions (Ware and McCollum, 1975). Such heavy yields, combined with higher market prices obtainable out of season, offer advantages to producers located in the southern and southwestern United States, where solar radiation is rarely limiting. However, the quality of water supply in the region is potentially limiting to the productivity of greenhouse cucumbers, a moderately salt-sensitive crop (Gornat et al., 1973; Maas and Hoffman, 1977; Sonneveld and Vogt, 1978; Drews, 1979). The threshold electrical conductivity of the rooting medium of cu-

cumbers, above which appreciable declines in growth and yield can be expected, is between 2.5 and 3.0 dS·m<sup>-1</sup> (reviewed by Maas and Hoffman, 1977; see also Kazim and Khaliel, 1983; Maas, 1985), and can be as low as 0.8 to 1.6 dS·m<sup>-1</sup> (Jones et al., 1989).

Although mechanisms of salt tolerance and salt injury have been examined in numerous crop species (Maas and Nieman, 1978; Wyn Jones, 1981), there is relatively little information available on cucumber. In general, the more-negative osmotic potential of saline irrigation water contributes adversely to plant water relations, and the excess accumulation of specific ions (especially Na<sup>+</sup> or Cl<sup>-</sup>) within the leaf mesophyll is a major factor associated with depression of plant, growth (Jennings, 1976; Greenway and Munns, 1980).

Many salt-sensitive species tolerate moderate exposure to salt by the roots' ability to exclude ions from the xylem sap and, hence, the leaves through energy-dependent processes (Läuchli, 1984; Drew and Läuchli, 1985). At higher concentrations of salt, the processes of exclusion are inadequate, and excess Na<sup>+</sup> and/or Cl<sup>-</sup> are transported via the xylem to the shoot (Drew and Dikumwin, 1985; Drew and Läuchli, 1985). Abnormal concentrations of these ions in the cytoplasm have been associated with

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loss of enzyme activity (Jennings, 1976), enhanced respiration rate (Schwartz and Gale, 1981; Bloom and Epstein, 1984; Rawson, 1986, inhibition of photosynthesis (Hasson et al., 1983; Downton et al., 1985; Seemann and Critchley, 1985; Rawson, 1986), and stomatal closure (Walker et al., 1981; Hasson et al., 1983; Rawson, 1986).

In seeking the mechanism of inhibition by salt of photosynthesis and growth, an important consideration is whether stomatal closure alone can account for the observed slowing of gas exchange. In pea (*Pisum sativum* L.), salinity resulted in increased stomatal resistance and parallel inhibitions of net photosynthesis and dry weight gain (Hasson et al., 1983). Stomatal resistance in bean (*Phaseolus vulgaris*) increased greatly with additions of NaCl to the rooting medium (Seemann and Critchley, 1985). However, when stomatal conductance was no longer limiting at high, saturating concentrations of CO<sub>2</sub> within the leaf, net CO<sub>2</sub> fixation remained inhibited, providing evidence for inhibition of chloroplast function.

The following experiments were designed to determine the principal mechanism of inhibition of photosynthesis in greenhouse-grown 'Fidelio' cucumbers when exposed to excess salt. Changes in gas exchange were compared with leaf concentrations of Na<sup>+</sup>, Cl<sup>-</sup>, and K<sup>+</sup>, and related to yield. The relative importance of stomatal and nonstomatal factors in slowing net CO<sub>2</sub> fixation were estimated from gas exchange at various concentrations of intercellular (substomatal) CO<sub>2</sub>.

### Materials and Methods

*Plants grown in sand with trickle irrigation (Expt. 1).* 'Fidelio' cucumber, a European type, was used. This cultivar is gynocercous, parthenocarpic, resistant to powdery mildew, and produces fruit with edible skin and no seeds. Seed was sown 5 cm deep in 8-liter plastic pots containing 15 kg of coarse sand and trickle-irrigated. Plants were grown at College Station, Texas, between September and November in a free-standing greenhouse where temperatures ranged between 15 to 38C. Emergence occurred at 4 days, and plants, spaced 20 cm apart in double rows, 'were supported by nylon string attached to the stem base and by horizontal supports at 1.5 m above the pots. Lateral shoots and flowers were removed at the first five nodes to minimize crowding (Ware and McCollum, 1975).

Plants were trickle-irrigated six to nine times daily (15 to 22.5 mm-day<sup>-1</sup>) with a nutrient solution prepared with distilled water in 190-liter, covered plastic drums. No differences in flow rate were found between emitters (two per pot) located at different distances from the pump. The composition of the nutrient solution was (mM): KNO<sub>3</sub>, 1.7; Ca(NO<sub>3</sub>)<sub>2</sub>, 5.8; MgSO<sub>4</sub>, 2.0; K<sub>2</sub>SO<sub>4</sub>, 4.0; and H<sub>3</sub>PO<sub>4</sub>, 1.6 with 54 μM Fe as Fe EDTA. Micronutrients were (μM): MnSO<sub>4</sub>, 9.0; H<sub>3</sub>BO<sub>3</sub>, 46; ZnSO<sub>4</sub>, 3.0; CuSO<sub>4</sub>, 3.0; and MoO<sub>3</sub>, 1.0.

Additions of NaCl were made to the nutrient solution beginning 35 days after sowing when fully expanded leaves had developed at eight nodes and flowering had begun at the lowest nodes. NaCl was added at 0, 10, and 50 mM to the nutrient solution. The respective electrical conductivities (EC) of the solutions were 1.8, 2.7, and 6.1 dS·m<sup>-1</sup>, and the solute potentials were -0.06, -0.12, and -0.24 MPa. Treatments were arranged in a randomized block design with four blocks, each containing one plant per treatment.

An ADC portable system (Analytical Development Corp., Hoddesdon, Herts, U.K.) was used to measure net photosynthesis (carbon exchange rate) and stomatal conductance. Relevant calculations used to obtain net photosynthesis (A), stomatal

conductance (g<sub>s</sub>), substomatal CO<sub>2</sub> concentration (C<sub>i</sub>), and transpiration (E) are described by von Caemmerer and Farquar (1981) and Parkinson (1985). The equipment was calibrated using an ADC gas diluter for CO<sub>2</sub> and an ADC water vapor generator for humidity sensing. This open, steady state system allowed for continuous measurements in a leaf cuvette inserted over a leaf attached to the plant. The leaf area inside the cuvette was 620 mm<sup>2</sup>. A photo incandescent flood lamp provided supplementary light, when necessary, giving a photosynthetic photon flux density saturating to the rate of photosynthesis (>650 μmol·s<sup>-1</sup>·m<sup>-2</sup>). All measurements were made between 1000 and 1600 HR on unshaded leaves. Air supplied to the leaf cuvette was drawn from outside the greenhouse and at least 5 min was allowed, after insertion of the leaf in the cuvette, for the rate of photosynthesis to stabilize before recording data. Air temperatures at the time of measurement were between 26.5 and 32.8C. The greatest differences between leaf and air temperature were ± 1.9C and differences usually were no more than +0.5C. The leaves studied, eighth and ninth oldest (the first oldest being at the base of the plant), were chosen because they were almost fully expanded by the time the NaCl treatments began and were already photosynthesizing rapidly. Measurements were made on the same leaves on several occasions during the growth of the crop during 28 days. Leaf water potential (ψ<sub>l</sub>) was obtained at final harvest at 35 days from the start of salt treatments and between 1200 and 1700 HR using a pressure chamber (Soil Moisture Corp., Santa Barbara, Calif.). Measurement was on young leaves, 50 to 100 mm across, to allow insertion in the pressure chamber.

### Plants grown in nutrient solution (Expt. 2).

*Salinization and measurement of gas exchange.* The relationship between salinity and gas exchange was examined in greater detail with plants grown in aerated nutrient solution. Seeds were germinated at 25C on moist filter paper in the dark. At 4 days, germinated plants maintained in the dark were suspended on stainless steel mesh over an aerated nutrient solution comprising a 1 : 9 dilution of the following (mM): KNO<sub>3</sub>, 1.0; Ca(NO<sub>3</sub>)<sub>2</sub>, 4.0; NH<sub>4</sub>H<sub>2</sub>PO<sub>4</sub>, 1.0; and MgSO<sub>4</sub>, 0.5 together with iron (100 μM) supplied as Fe EDTA and FeSO<sub>4</sub>·(NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub> and micronutrients as described in Expt. 1. Two days later, plants were exposed to daylight in a water-cooled, ventilated greenhouse, and, after a further 10 days, each plant was transferred to 2-liter volumes of the full-strength (i.e., undiluted) nutrient solution. Nutrient solutions were replenished at 6- to 7-day intervals. Additions of NaCl were made to the nutrient solution on day 25 to produce final concentrations of 25, 50, or 100 mM; controls received no additions of NaCl. The concentration of NaCl was raised in increments of 25 mM per day to avoid salt shock. Because gas exchange measurements (see below) were limited to only two plants per day, germination and treatment with NaCl were staggered during June and July.

Gas exchange measurements were made on plants that were transferred (within ≈ 3 min) from the greenhouse to an adjoining laboratory. The laboratory air temperature was 25C, and the concentration of CO<sub>2</sub> supplied to the leaf cuvette was controlled using an ADC gas diluter so that net photosynthesis could be determined on the same leaf as a function of the substomatal CO<sub>2</sub> concentration (von Caemmerer and Farquar, 1981). The external CO<sub>2</sub> concentration applied to the leaf was in the range of 150 to 2000 μbar (beginning with the lowest concentration), with O<sub>2</sub> at normal ambient concentration (20.6%). Leaves chosen for study were exposed to saturating light for at least 1 hr

before data were recorded. Data on gas exchange was recorded continuously, and we found that 20 to 30 min was more than sufficient for adjustment of a leaf to each CO<sub>2</sub> concentration. Almost fully expanded leaves were chosen for study, since we expected that these would have the highest rates of net CO<sub>2</sub> fixation. Infrared radiation from the incandescent light source (1-kW flood lamp) was intercepted by an infrared mirror. Leaf temperature did not depart from the ambient air by more than 0.5°C. Measurements of gas exchange, as a function of the CO<sub>2</sub> concentration, were made on attached leaves, each leaf on a separate plant, with three plants for each salt treatment.

**Chemical analysis.** The same leaves that had been used for gas exchange measurements reported above on plants grown in nutrient solution were excised, dried at 70°C, and ground. Samples of the ground tissue were ashed overnight in a muffle furnace at 575°C, then dissolved in a mixture containing 1 M nitric acid and 3.5 M acetic acid and analyzed for Na<sup>+</sup> and K<sup>+</sup> by flame emission spectrophotometry. Chloride in the above acid solution was analyzed coulombimetrically with a Haake-Buchler chloridometer (Haake Buchler Instruments; Saddle Brook, N.J.).

**Statistical analysis.** Data from Expt. 1 were subject to analysis of variance. Dunnett's test was also used to compare treatment means with the control.

## Results

**Effect of salinity on yield of cucumber fruit and on leaf gas exchange (Expt. 1).** Trickle irrigation gave a total yield per plant of 3.9 kg fresh weight (Table 1). Addition of 10 mM NaCl had no appreciable effect on yield, but, at 50 mM NaCl, there was a 60% reduction compared with unsalinized controls. This reduction was not due to fewer fruits per plant, but to smaller fruit. Application of 10 mM NaCl also reduced mean fresh weight per fruit.

Preliminary experiments showed no detectable effect of 10 mM NaCl on gas exchange; therefore, effort was limited to 0 and 50 mM. An initial set of gas exchange measurements was made immediately before NaCl was introduced into the irrigation system (Table 2). Exposure to 50 mM NaCl (7 to 11 days of salinization) significantly inhibited net carbon exchange rates by 33% in leaf 8 and by 48% in leaf 9. Reductions of leaf conductance and transpiration rate were also recorded, indicating partial stomatal closure. Leaves used for gas exchange measurements were green and healthy in appearance, although the salinized plants were clearly slowed in their growth. By the 28th day, net carbon fixation of leaves 8 and 9 had declined and was more variable, and the inhibitory effect of NaCl was no longer statistically significant.

Leaves excised at the end of the experiment exhibited lower  $\psi_L$  with increasing salinization, decreasing from  $-0.53 \pm 0.02$  MPa in controls to  $-0.74 \pm 0.01$  MPa at 10 mM NaCl and  $-1.28 \pm 0.02$  MPa at 50 mM NaCl.

*Leaf gas exchange characteristics of plants grown in nutrient*

Table 1. Effect of NaCl on fruit yield of 'Fidelio' cucumber in a greenhouse with trickle irrigation.

Fruit yield	NaCl concn (mM)		
	0	10	50
Total fresh wt (kg/plant)	3.9 <sup>a</sup>	3.5	1.6 <sup>**</sup>
No. of fruits/plant	7.7	9.3	6.5
Mean fresh wt (g/fruit)	508	375 <sup>*</sup>	240 <sup>**</sup>

<sup>a</sup>Mean separation in rows between control (0 mM) and treatment by Dunnett's test,  $P = 0.05$  (\*) or  $0.01$  (\*\*),  $n = 4$ .

Table 2. Effect of NaCl concentration on gas exchange in leaves of 'Fidelio' cucumber in a greenhouse with trickle irrigation.

Time from start of salinization (days)	Leaf no. <sup>a</sup>	Variable measured <sup>b</sup>	NaCl concn (mM)	
			0	50
0	8	A	16.0	---
		g <sub>s</sub>	0.61	---
		E	7.8	---
	9	A	12.7	---
		g <sub>s</sub>	0.34	---
		E	6.5	---
7-11	8	A	10.7	7.2 <sup>**</sup>
		g <sub>s</sub>	0.44	0.16 <sup>**</sup>
		E	6.2	3.5 <sup>**</sup>
	9	A	11.5	6.0 <sup>**</sup>
		g <sub>s</sub>	0.43	0.11 <sup>**</sup>
		E	6.0	2.9 <sup>**</sup>
28	8	A	8.9	5.5
		g <sub>s</sub>	0.25	0.12
		E	3.8	3.8
	9	A	6.0	3.0
		g <sub>s</sub>	0.09	0.05
		E	2.2	2.0

<sup>a</sup>Measurements were made on the eighth and ninth oldest leaves.

<sup>b</sup>Values are for net CO<sub>2</sub> assimilation (A,  $\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ ), stomatal conductance (g<sub>s</sub>,  $\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ ) and transpiration (E,  $\text{mmol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ ). The ambient pCO<sub>2</sub> was 349  $\mu\text{bar}$ .

\*\*Significant differences between treatments based on LSD at  $P = 0.05$ ,  $n = 4$ .

*solution at various NaCl levels (Expt. 2).* Additions of 25 and 50 mM NaCl to the nutrient solution resulted in a partial depression of, net photosynthesis, compared with unsalinized plants. (Table 3), and, at 100 mM NaCl, there was a very marked depression. There were only small differences between plants treated with 25 and 50 mM NaCl, with 25 mM apparently the more damaging. Similar reversals of response to NaCl concentration have been found by others (see Discussion). Inhibitions of photosynthesis were associated with reduction in stomatal conductance. However, partial stomatal closure in these experiments did not result in greater water use efficiency, which, on the contrary, became very low with 100 mM NaCl in the solution.

The effect of salt on photosynthetic capacity was determined by measuring net assimilation (A) at various (calculated) intercellular CO<sub>2</sub> concentrations (C<sub>i</sub>). Results in Fig. 1 for individual representative leaves show that the presence of 25 and 50 mM salt caused similar depressions of net assimilation at saturating C<sub>i</sub>, compared with unsalinized controls. At 100 mM NaCl, there was a very marked inhibition, with virtually no response to increased CO<sub>2</sub> concentration.

Analysis of the same individual leaves used for gas exchange measurements described in Fig. 1 showed marked increases in Na<sup>+</sup> and Cl<sup>-</sup> concentration with increasing concentrations of NaCl in the nutrient solution (Table 4). Chloride and Na<sup>+</sup> increased  $\approx 74$  fold and 20 fold, respectively, over the 0- to 100-mM range of NaCl concentration. However, there was little difference between values at 25 and 50 mM NaCl. The foliar concentration of K<sup>+</sup> showed a gradual decline (32% at 100 mM) with additions of NaCl to the medium.

## Discussion

Fruit size, but not total yield per plant, was depressed by the presence of 10 mM NaCl (2.7 dS·m<sup>-1</sup> electrical conductivity)

Table 3. Mean leaf gas exchange characteristics at ambient CO<sub>2</sub> of 'Fidelio' cucumber grown in nutrient solutions at various NaCl concentrations.

Variable measured <sup>a</sup>	NaCl concn (mM)			
	0	25	50	100
A	10.4 ± 1.45	4.0 ± 1.53	7.5 ± 0.7	0.48 ± 0.07
C <sub>i</sub>	272 ± 20	261 ± 6	256 ± 6	302 ± 0.1
g <sub>s</sub>	0.276 ± 0.069	0.122 ± 0.041	0.243 ± 0.058	0.046 ± 0.009
A/E	2.3 ± 0.44	1.12 ± 0.18	1.43 ± 0.04	0.34 ± 0.01

<sup>a</sup>Values are for net CO<sub>2</sub> assimilation (A; μmol·s<sup>-1</sup>·m<sup>-2</sup>), intercellular CO<sub>2</sub> concentration (C<sub>i</sub>, μbar), stomatal conductance (g<sub>s</sub>, mol H<sub>2</sub>O/m<sup>2</sup> per sec) and water use efficiency (A/E, mmol CO<sub>2</sub>/mol H<sub>2</sub>O). Measurements on the third to fifth oldest leaves, 6 days after NaCl additions. Conditions were 350 μbar CO<sub>2</sub>, 21% (v/v) O<sub>2</sub>, light saturation (800 μmol·s<sup>-1</sup>·m<sup>-2</sup> air 25C. Values are means ± SE.

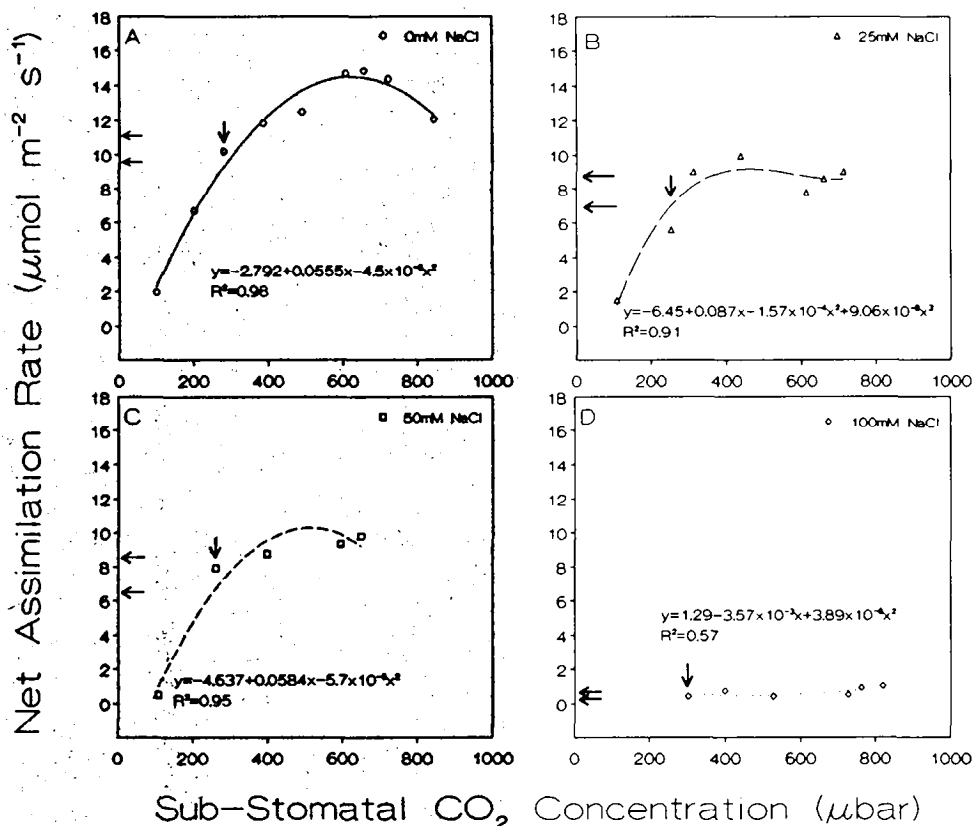


Fig. 1. Relationship between sub-stomatal CO<sub>2</sub> concentration (C<sub>i</sub>) and net CO<sub>2</sub> assimilation rate (A) in single attached leaves of 'Fidelio' cucumber plants exposed to various concentrations of NaCl for 6 days. The vertical arrow indicates the relationship when the external CO<sub>2</sub> concentration was that in ambient air (pCO<sub>2</sub> = 347 μbar). Paired horizontal arrows indicate the slowing of photosynthetic rate imposed by a reduction of C<sub>i</sub> below 347 μbar as a result of stomatal resistance (see Discussion for further explanation).

in the irrigation nutrient solution. A large decline in fruit size and total yield was observed between 10 and 50 mM NaCl (Table 1). These results confirm other reports as to the moderately high salt-sensitivity of cucumber (Maas and Hoffman, 1977; Kazim and Khaliel, 1983; Maas, 1985; Jones et al., 1989). However, in five other cucumber cultivars (Jones et al., 1989), yield decreases with salinity resulted 'from a smaller number of fruits per plant without decreased fruit size. The differences may arise from the concentrations of salts used, timing of salinization in relation to growth stage and flowering; and the cucumber cultivar. The total salt concentration used by Jones et al. (1989) (4.0 dS·m<sup>-1</sup> electrical conductivity) was less than that of our 50 mM NaCl concentration (6.1 dS·m<sup>-1</sup>). Additions of NaCl were started by Jones et al. (1989) as soon as the first true leaf began to expand, and the flowers were subsequently hand-pol-

inated. In our experiment, NaCl was first added 35 days after sowing when flowering had begun, and the fruits developed parthenocarpically. It is a common observation that there is a reciprocal relationship between fruit number and fruit size.

Inhibition of yield and vegetative growth in cucumber with increasing salinity is associated with a marked inhibition of photosynthesis. Gas exchange characteristics of individual leaves in the greenhouse showed nearly a 50% inhibition of net CO<sub>2</sub> exchange rate in plants exposed to 50 mM NaCl (Table 2). Parallel decreases in stomatal conductivity and photosynthesis upon salinization have been reported (Hasson et al., 1983; Seemann and Critchley, 1985). The inhibition may have resulted from partial stomatal closure, since leaf conductivity to water and transpiration were appreciably smaller in salinized leaves. However, inhibition of chloroplast activities could also have

contributed to inhibition of photosynthesis, and smaller stomatal conductance may not necessarily have limited the entry of CO<sub>2</sub>.

To resolve the question of the relative importance of stomatal closure and chloroplast injury in the observed inhibition of net assimilation in cucumber, net assimilation was determined as a function of the substomatal CO<sub>2</sub> concentration. Minor veins in cucumber leaves do not have bundle sheath extensions, so that the leaves are essentially homobaric (Larcher, 1980). We assume that the influence of any heterogeneity in stomatal closure across the leaf will have only a small effect on estimates of C<sub>i</sub> by gas exchange measurements, in contrast to the behavior of heterobaric leaves (Downton et al., 1988; Robinson et al., 1988; Terashima et al., 1988). Our data indicate that stomatal closure played a relatively minor role in the restriction of net assimilation under our conditions (Fig. 1). The position on each curve at ambient CO<sub>2</sub> concentration (350 μbar), marked by a vertical arrow, gives a measure of the extent to which A was lowered by the limiting effect of stomatal conductance on C<sub>i</sub> (Matthews and Bayer, 1984). If stomata conducted with extreme efficiency (i.e., resistance was negligible), the arrow would be located at 350 μbar. The limitation imposed by stomatal conductance is small and no greater for NaCl-treated plants than for the unsalinized controls (Table 5).

The net assimilation rates at saturating concentrations of CO<sub>2</sub> provide a measure of the maximum rate of CO<sub>2</sub> fixation that the chloroplasts can attain. Fixation was inhibited when plants

Table 4. Foliar mineral analysis of individual leaves of 'Fidelio' cucumber used for gas exchange measurements during exposure of plants to nutrient solution supplemented with NaCl.

Concn of NaCl in nutrient solution* (mm)	Tissue concn (μmol·g <sup>-1</sup> dry wt)		
	K <sup>+</sup>	Na <sup>+</sup>	Cl <sup>-</sup>
0	274	74	12
25	244	900	256
50	205	767	458
100	185	1460	885

\*Plants were treated in stirred, aerated nutrient solution and exposed to salinity for 6 days before chemical analysis. Values are for the same four leaves shown in Fig. 1 and are the means of duplicate determinations.

Table 5. Components to photosynthesis in individual, salinized leaves of 'Fidelio' cucumber grown in nutrient solution supplemented with NaCl.

Component	NaCl concn (mm)			
	0	25	50	100
<b>Maximum chloroplast activity at saturating pCO<sub>2</sub></b>				
μmol·s <sup>-1</sup> ·m <sup>-2</sup>	14.5	9.5	10.5	1.4
Percent of control	100	66	72	9.7
<b>Chloroplast activity at C<sub>i</sub> = 347 μbar</b>				
μmol·s <sup>-1</sup> ·m <sup>-2</sup>	11.3	9.0	9.0	0.8
Percent of control	100	80	80	7
<b>Reduction in photosynthetic rate attributable to stomatal conductance (%)<sup>†</sup></b>	16	23	28	25

<sup>†</sup>Calculated from the fractional reduction in A, as indicated by arrows on the y axis, Fig. 1 (see also Discussion for explanation). The ambient pCO<sub>2</sub> averaged 347 μbar (range 345-350 μbar).

were exposed to 25, 50, and 100 mM NaCl, especially at the highest concentration, where chloroplasts virtually ceased to respond to additional CO<sub>2</sub>. Leaf analysis (Table 4) indicated that an increasing Na<sup>+</sup>, as well as Cl<sup>-</sup>, content and a declining K<sup>+</sup> content were associated with loss of photosynthetic capacity. Little is known at present about the ability of the roots of this species to exclude excess Na<sup>+</sup> and Cl<sup>-</sup>.

The decrease in water use efficiency by leaves of salinized plants (Table 3) we found contrasts with earlier observations on field crop species (Richardson and McCree, 1985; McCree and Richardson, 1987). Based on theoretical considerations, partial stomatal closure will tend to conserve water more than it limits entry of CO<sub>2</sub> (Nobel, 1983) and thereby improve water use efficiency. In our plants, it appears that injury at the chloroplast level had a predominant effect in limiting CO<sub>2</sub> fixation. Because of boundary layer differences, rates of gas exchange for single leaves may not be an accurate quantitative estimate of those operating in an undisturbed greenhouse or field situation. However, such estimates should represent trends.

Net photosynthesis of plants treated with 25 mM NaCl was somewhat more inhibited than with 50 mM NaCl in experiments with cucumber in hydroponics (Expt. 2). Similar reversals of response have been recorded in salinity research by others (Munns et al., 1988). The explanation may be that, at the higher concentration, transpiration is inhibited by partial stomatal closure and by the lower osmotic potential of the nutrient solution. Less Na<sup>+</sup> and/or Cl<sup>-</sup> would then be carried to the leaves with the transpiration stream that at the lower concentration, where transpiration was uninhibited. This explanation is borne out by the Na<sup>+</sup> concentrations in leaves (Table 4), which were greater at 25 mM than 50 mM NaCl. At concentrations of NaCl that are highly injurious to salt-sensitive cucumber (100 mM), damaging amounts of Na<sup>+</sup> and Cl<sup>-</sup> accumulate in leaves whatever the transpiration rate may be.

The response of *Cucumis sativus* to salinity has several features in common with that of salt-sensitive *Phaseolus vulgaris*. In leaves of *Phaseolus* plants exposed to 100 mM NaCl for 10 to 14 days, the capacity to fix CO<sub>2</sub> at saturating concentrations was about two-thirds that of the unsalinized leaves (Seemann and Critchley, 1985); the inhibition in *Cucumis* leaves in our study was much more extreme. By contrast, stomatal closure of salinized leaves approximately halved photosynthesis in *Phaseolus* at ambient pCO<sub>2</sub>, while in *Cucumis*, stomatal conductivity had only a minor role in restricting photosynthesis (Table 5). This difference in the importance of stomatal conductance in our study can be explained by the slower rate of photosynthesis in control, as well as salinized cucumber plants, compared with *Phaseolus*.

In conclusion, low concentrations of NaCl (25 to 100 mM) in the rooting medium of cucumber in the greenhouse resulted in marked depression of photosynthesis and fruit yield. Rates of photosynthesis decreased with increasing levels of leaf Na<sup>+</sup> and Cl<sup>-</sup> and declining K<sup>+</sup>. The decrease in photosynthesis resulted more from inhibition of chloroplast activity than from concomitant closure of stomates.

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