

Water relations and photosynthesis in *Cucumis sativus* L. leaves under salt stress

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Abstract

Hydroponically grown cucumber plants were exposed to 14-d period of salinity (0, 50, 100 mM NaCl). NaCl caused reduction in the relative water content in the leaves. The Na⁺ content increased and the K⁺ content decreased. The net photosynthetic rate, stomatal conductance and transpiration rate were markedly decreased by all of the salt treatments. Salinity decreased also the maximum quantum efficiency of photosystem 2 (PS 2) determined as the variable to maximum fluorescence ratio, the photochemical quantum yield of PS 2 and the photochemical fluorescence quenching, while the non-photochemical quenching increased. Above results indicate that NaCl affects photosynthesis through both stomata closure and non-stomatal factors.

Additional key words: chlorophyll fluorescence, NaCl, net photosynthetic rate, stomatal conductance, transpiration rate.

Introduction

At the present time about 20 % of the world's cultivated land and approximately half of all irrigated land is affected by salinity (Zhu 2001). Therefore, salinity is one of the most significant abiotic factor limiting crop productivity (Munns 2002). The reduction in growth under saline conditions is a consequence of several physiological responses, including modification of ion balance, water status, mineral nutrition, stomatal behaviour and photosynthetic efficiency (Munns 1993). High concentration of salt in the root zone reduces soil water potential and the availability of water (Lloyd *et al.* 1989). As a result reduction in the water content leading to dehydration at cellular level and osmotic stress is observed. Elevated Na⁺ and Cl⁻ content in environment affects many indispensable nutrients uptake through competitive interactions and by affecting the ion selectivity of membranes. For example, external Na⁺ negatively impacts intracellular K⁺ influx, attenuating

acquisition of this essential nutrient by cells. The Mg²⁺ and Ca²⁺ deficits in plant tissues induced by high salinity have also been noted (Grattan and Grieve 1992). The most important process that is affected in plants growing under saline conditions is photosynthesis. Reduced photosynthesis under salinity is not only attributed to stomatal closure leading to a reduction of intercellular CO₂ concentration, but also to non-stomatal factors. There is an increasing evidence that salt affects photosynthetic enzymes, chlorophylls and carotenoids (Misra *et al.* 1997).

For our experiment we chose cucumber (*Cucumis sativus* L.) that is an important crop for the agricultural production, limited by the quality of irrigation water. Previous researches have suggested that cucumber is a salt-sensitive plant (Jones *et al.* 1989). The aim of present study was to investigate the physiological reactions of cucumber to salinity.

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Abbreviations: Chl - chlorophyll; E - transpiration rate; ETC - electron transport chain; F₀- chlorophyll *a* fluorescence in dark-adapted plants when all PS 2 reaction centres are fully opened; F_m - maximum fluorescence; F_v - variable fluorescence; F_v/F_m - maximum (potential) quantum efficiency of PS 2; Φ_{PS2} - photochemical quantum efficiency (yield) of PS 2; g_s - stomatal conductance; P_N - net photosynthetic rate; PPFD - photosynthetic photon flux density; PS 2 - photosystem 2; q_N - non-photochemical quenching coefficient; q_P - photochemical quenching coefficient; RuBP - ribulose-1,5-biphosphate; RWC - relative water content; WUE - water use efficiency (P_N/E).

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Materials and methods

Cucumber seedlings (*Cucumis sativus* L. cv. Wisconsin) germinated for 48 h in darkness were grown hydroponically in Hoagland solution (pH 6.2 - 6.5) for 14 d under a 16-h photoperiod (PPFD 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$), temperature of 25 °C during the day and 22 °C in the night. The plants were then subjected to salt stress by adding NaCl (50 and 100 mM) to the Hoagland solution. Control plants were maintained in a NaCl-free solution.

Gas exchange was monitored using an infra-red gas analyser *CIRAS-1* (PPSystems, Hitchin, Hertfordshire, UK) provided with a *PLC-B Parkinson* leaf chamber (2.5 cm²). The net photosynthetic rate (P_N), stomatal conductance (g_s) and transpiration rate (E) were measured on intact leaves at PPFD of 300 $\mu\text{mol m}^{-2} \text{s}^{-1}$ after 10 - 15 min to achieve steady-state conditions. Leaf temperature within the chamber was controlled at 25 ± 1 °C and supplied CO₂ concentration was 365 $\mu\text{mol mol}^{-1}$. Measurements were conducted between 09:00 and 12:00. Water use efficiency (WUE) at the leaf level was calculated as the P_N/E ratio.

Chlorophyll *a* fluorescence was measured with a pulse modulated portable fluorometer *FMS2* (*Hansatech Instruments Ltd.*, Pentney, Norfolk, UK) at 25 °C first in the leaves dark adapted for 30 min and next after 15 min of exposition at PPFD of 300 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (light-adapted leaves). Dark-adapted leaves were initially exposed to a fast modulating measuring beam of radiation at 594 nm to determine F_0 . Saturating (10 000 $\mu\text{mol m}^{-2} \text{s}^{-1}$) pulses of white light were supplied to obtain maximum fluorescence emission F_m and F_m' . Photochemical and non-photochemical quenching coefficients (qP , qN) were

calculated according to Havaux *et al.* (1991) as follows: $qP = (F_m' - F_s)/(F_m' - F_0)$, $qN = (F_m - F_m')/(F_m - F_0)$. Quantum efficiency of PS 2 was calculated according to Genty *et al.* (1989): $\Phi_{PS2} = (F_m' - F_s)/F_m'$.

Following gas exchange and chlorophyll fluorescence measurements, the plants were harvested, weighed fresh (FM) and incubated in distilled water for 4 h in dark to rehydrate. After the period, the mass of water-saturated leaves (TM) was measured. The leaf samples were subsequently dried at 105 °C for 1 h and at 60 °C for 48 h and next re-weighed for determination of dry mass (DM). The relative water content (RWC) was calculated as: $RWC = [(FM - DM)/(TM - DM)] \times 100$.

Lyophilised leaves were milled to powder for mineral nutrient analyses. Powdered samples (0.5 g) were put into the teflon tubes with addition of 5 cm³ of HNO₃ and next placed in the rotor of the microwave digestion system *MDS-2000* (*CEM*, Matthews, USA). The resulting solutions were diluted appropriately and analysed for Na⁺ and K⁺. Cation concentrations were determined with a *Perkin-Elmer M3300* atomic absorption spectrophotometer (Norwalk, USA).

After extraction with 80 % acetone, the chlorophyll content was analysed according to Arnon (1979) using spectrophotometer *Beckman DU 640* (Fullerton, USA).

All measurements were taken between 1 and 14 d after initiating salinity treatment. Data points in the figures represent the means \pm SE of three independent experiments with at least three replications per cultivar per treatment combination each.

Results

Salt stress reduced RWC in the leaves of cucumber seedlings grown at both salinity levels, however, the effect was greater at higher NaCl concentration (Fig. 1A). After 8 d of salinity the RWC decreased by 13 and 27 % in plants treated with 50 and 100 mM NaCl, respectively. Further the RWC values maintained relatively constant.

Both Chl *a* and Chl *b* content considerably decreased in the leaves of cucumber plants with increasing NaCl concentration. Chl *a* (Fig. 1B) was less affected by NaCl than Chl *b* (Fig. 1C). While the reduction in the Chl *b* content persisted during successive days, the Chl *a* content fell till the 8th d after the salt addition, and subsequently either rose to normal level (50 mM NaCl) or stabilised (100 mM NaCl). The resulting Chl *a+b* content and Chl *a/b* ratio (data not shown) dropped throughout the experiment.

The tissue concentration of Na⁺ increased significantly under salt stress (Fig. 2A). The maximum sodium contents were detected on the 4th day after initiation of salinity treatment for both 50 and 100 mM NaCl

concentrations (350 and 426 % of control, respectively). In the following days there was a noticeable fall in the leaf Na⁺ content in plants subjected to salt stress. A concomitant decrease in K⁺ content in the cucumber seedlings grown in saline conditions was detected (Fig. 2B). The reduction in K⁺ was more pronounced at higher NaCl concentration. After 4 d of salt treatment a slight increasing tendency in the K⁺ content was noted.

There was an evident decrease in P_N in leaves of cucumber seedlings subjected to salinity (Fig. 3A). Prior to NaCl application P_N was 12.0 - 12.8 $\mu\text{mol}(\text{CO}_2) \text{m}^{-2} \text{s}^{-1}$ (Fig. 3A). On the 14th day of treatment (50 and 100 mM NaCl), P_N was reduced to 8.2 and 2.88 $\mu\text{mol}(\text{CO}_2) \text{m}^{-2} \text{s}^{-1}$, respectively. Salinity strongly decreased g_s (Fig. 3B) and the declined g_s resulted in reduced E (Fig. 3C). After 14 d of salt treatment, transpiration rate had fallen by 59 % for plants grown at 50 mM NaCl and by 74 % for those grown at 100 mM NaCl. The WUE was modified as a result of reported changes in P_N and E (Fig. 3D). While in the leaves of cucumber subjected to 50 mM NaCl the WUE was continuously increasing on successive days, in

the seedlings grown under 100 mM NaCl there was strong rise in this parameter until the 4th day and then a subsequent fall to the end of experiment.

The antennae efficiency was found to be affected by

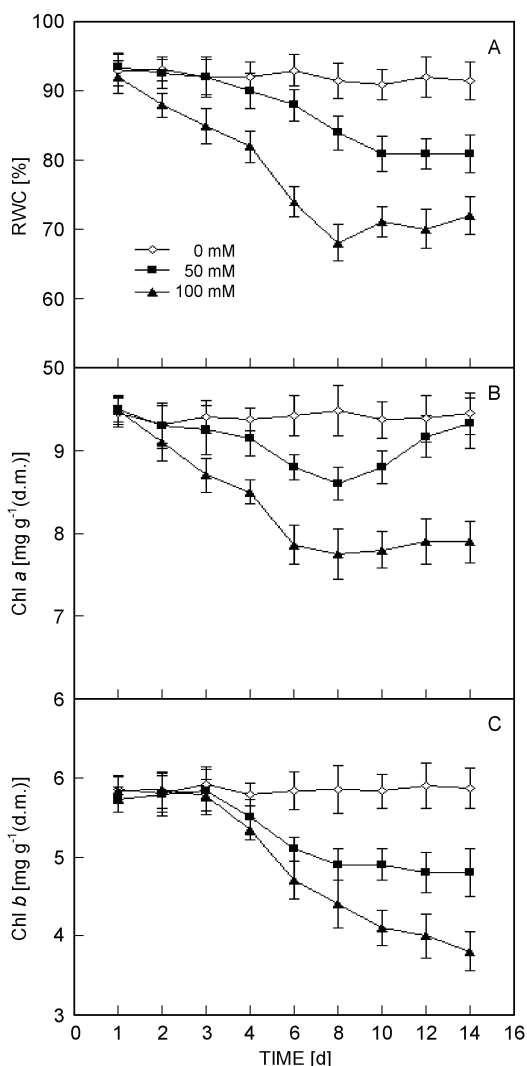


Fig. 1. Changes in relative water content (A), Chl a (B) and Chl b (C) content with time in leaves of cucumber seedlings grown under 0 (rhombs), 50 (squares), and 100 (triangles) mM NaCl. Data points in the figures represent the means \pm SE of three independent experiments with three replications per cultivar per treatment combination each.

Discussion

Water status is highly sensitive to salinity and therefore is dominant in determining the plant responses to stress (Yeo *et al.* 1985). Through the analysis of water relation characteristics in the cucumber leaves, we observed a common reaction to salinity similar to those reported for other species (Banuls and Primo-Milo 1992, Walker *et al.* 1993). The observed reduction in the RWC was a result of high salt concentration in the external solution, which

salt stress since a fall in F_0 was observed (Fig. 4A). Maximum quantum efficiency of PS 2 (F_v/F_m) did not change significantly with salinity (Fig. 4B). By the final day of experiment this had fallen by 4 and 12 % in plants treated with 50 and 100 mM NaCl, respectively. While the decrease in F_v/F_m was not as evident, the drop in the photochemical quantum efficiency (yield) of PS 2 (Φ_{PS2}) was well defined (Fig. 4C). At the end of experiment, the Φ_{PS2} decreased by 27 % for plants grown at 50 mM NaCl and by 49 % for plants grown at 100 mM NaCl. Salinity caused a fall in the qP (Fig. 4D). The decrease of qP was more significant in the seedlings subjected to a higher NaCl concentration. The accompanying rise in the qN was noted (Fig. 4E). The dissipation of energy in the non-photochemical processes was more intensive with increasing salinity.

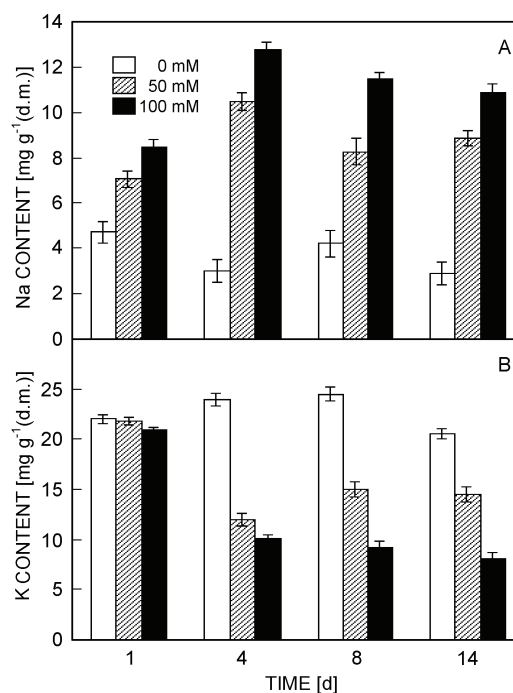


Fig. 2. Changes in sodium (A) and potassium (B) content with time in leaves of cucumber plants grown under 0, 50 and 100 mM NaCl. The means \pm SE of three independent experiments with three replications per cultivar per treatment combination each.

caused osmotic stress and dehydration at cellular level (Munns 1993). Dehydration symptoms were greater in the 100 mM NaCl treatment than in the 50 mM NaCl treatment because higher sodium chloride concentrations increased cellular water loss. However, there is substantial evidence that glycophytic as well as halophytic species adjust to high salt concentration by lowering tissue osmotic potentials with an increase of

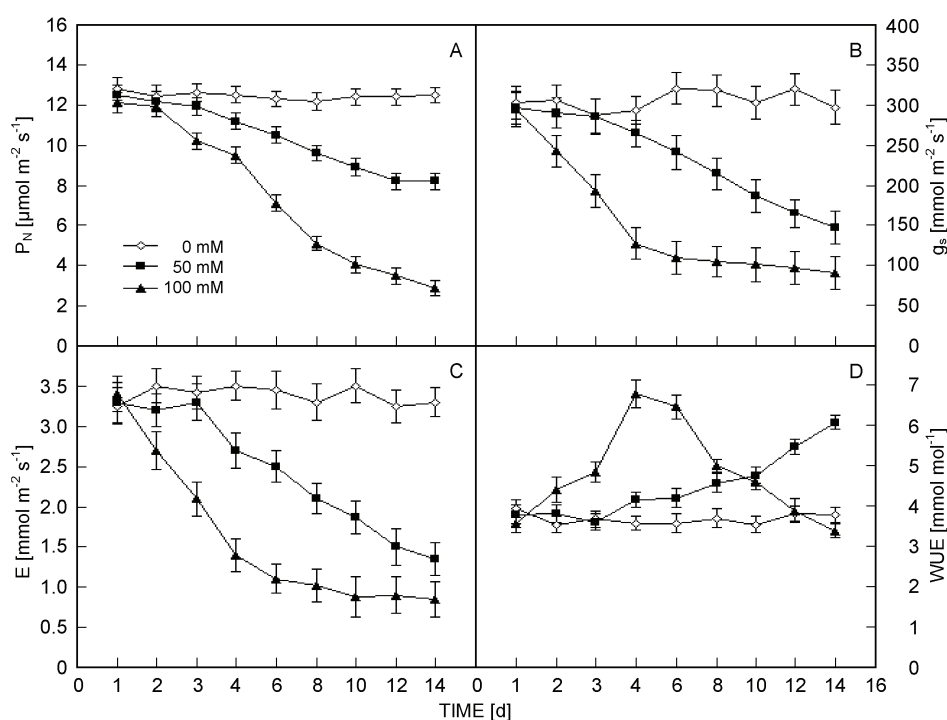


Fig. 3. Changes in net photosynthetic rate, P_N (A), stomatal conductance, g_s (B), transpiration rate, E (C), and water use efficiency, WUE (D) with time in leaves of cucumber seedlings grown under 0 (*rhombs*), 50 (*squares*), and 100 (*triangles*) mM NaCl. The means \pm SE of three independent experiments with five replications per cultivar per treatment combination each.

inorganic ions accumulation in tissues (Cachorro *et al.* 1995). Although osmotic adjustment was achieved by the uptake of inorganic ions, this could also lead to problems of ion compartmentation and a decline in leaf function. In particular, salinity alters uptake and absorption rates of all mineral nutrients resulting in deficiency symptoms. We found that the salt treatments decrease potassium distribution with increasing NaCl level. The reduction in K^+ uptake caused by Na^+ is likely to be the result of the competitive intracellular influx of both ions (Cerdea *et al.* 1995). It is well known that many K^+ transport systems have significant affinity for Na^+ (Blumwald *et al.* 2000, Schachtman and Liu 1999). An increase in the K^+/Na^+ ratio observed after the 4th day of salt treatment there suggests compensation over time, probably by the K^+ re-translocation from roots and stem to leaves (Romero *et al.* 1994).

Ion accumulation in leaves adversely affects Chl content (Yeo *et al.* 1985, Loggini *et al.* 1999, Meloni *et al.* 2003). The observed decrease in Chl content in the cucumber plants grown under saline conditions may be attributed to both an increased degradation and inhibited synthesis of that pigment (Sultana *et al.* 1999, Garcia-Sanchez *et al.* 2002). Interestingly, Chl *a* was less sensitive or better protected against salt stress than Chl *b*. The alterations in Chl *a* content were accompanied by changes in Chl fluorescence kinetics from the 8th experimental day. Since F_0 mainly originates from Chl *a* antennae, it can be inferred that salt stress damaged the

PS 2 antenna system (Rutten and Santarius 1992). The resulting high Chl *a/b* ratio indicates that the ratio of PS 2/PS 1 content was changed in stressed leaves (Anderson 1986). We observed a considerable decrease in the efficiency of PS 2 in the leaves of plants subjected to salt stress. The most sensitive parameter of fluorescence induction was found to be Φ_{PS2} . The reduction in Φ_{PS2} indicates that for both NaCl concentrations there was a fall in the photosynthetic energy conversion in PS 2. The fall in F_v/F_m was not as great. As shown by others (Jefferies 1994, Allakhverdiev 2000) the F_v/F_m was not significantly decreased under saline and drought conditions. Although the F_v/F_m reduction was not so well defined, this might suggest the existence of some inhibition in the reaction centre of PS 2 in salt treated plants (Schreiber and Bilger 1993). The fall in the qP corresponds to a drop in the amount of absorbed light energy dissipated in the photochemical pathway and consequently less utilised in the light phase of photosynthesis (Öquist *et al.* 1993, Holaday *et al.* 1991). This points to an increase in the amount of the reduced form of plastoquinon Q_A and less transfer effectiveness of the electron transport chain (ETC). The results reported by others also demonstrated that during leaf dehydration the whole electron transport chain was affected (Cornic and Massacci 1996). The concomitant increase in the qN confirmed a higher loss of energy resulting from more intensive dissipation as heat (Krause and Weis 1991). It was also reported that both salinity and drought caused a

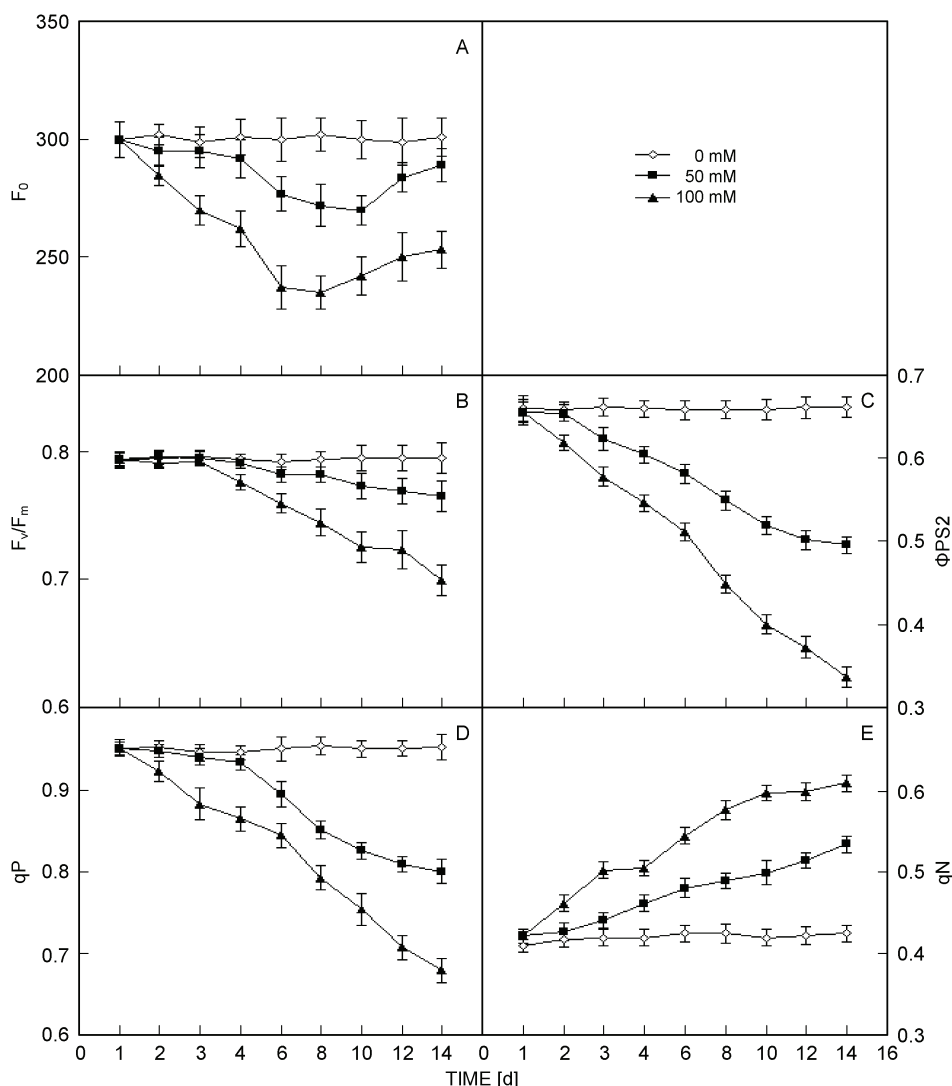


Fig. 4. Changes in chlorophyll fluorescence parameters: initial fluorescence, F_0 (A), maximum quantum efficiency of PS 2, F_v/F_m (B), photochemical yield of PS 2, ϕ_{PS2} , (C), photochemical quenching, q_P (D) and non-photochemical quenching, q_N (E) with time in leaves of cucumber seedlings grown under 0 (rhombus), 50 (squares), and 100 (triangles) mM NaCl. The means \pm SE of three independent experiments with five replications per cultivar per treatment combination each.

reversible increase in the thermal dissipation of energy trapped by PS 2, thus contributing to protection against the deleterious effect of excessive light during reduced CO_2 assimilation (Cornic 2000).

Salt stress in cucumber promoted significant differences in gas exchange parameters. Increasing salinity level progressively decreased P_N , g_s and E . Stomatal closure is known to be an effective mechanism for economical water utilisation under salt stress and limitation of the harmful salt ions uptake (Hasegawa *et al.* 2000). Unfortunately, the decrease in g_s caused a simultaneous decrease in P_N . The water use efficiency (WUE), was significantly modified as a result of reported changes in the net photosynthetic rate and transpiration rate. In the cucumber seedlings grown at 50 mM NaCl P_N/E increase until the end of experiment. For plants subjected to higher salinity (100 mM NaCl) the same

tendency was observed till the 4th day after salt addition. This could imply a higher inhibition of photosynthesis by stomatal closure than by biochemical activity. After the 4th day of 100 mM NaCl treatment there was the subsequent fall in P_N/E to the end of experiment. Similar results have been reported by Hsiao (1993) and Garcia-Sanchez *et al.* (2002). This trend in the water use efficiency observed in the leaves of cucumber suggests that the non-stomatal factors, in addition to the stomatal ones, affected photosynthesis. The reduced CO_2 assimilation rate at high salinity could be attributed, in part, to increased Na^+ concentration resulting in the reduced content of K^+ ions which are indispensable in maintaining the steady-state photosynthetic rate and contribute to better regulation of stomata opening. It was also shown (Cornic 1994) that oxygenase activity of Rubisco may increase during dehydration. Since we

noticed a considerable changes in Chl fluorescence the leaves of plants subjected to salt stress, inhibition of photosynthesis by non-stomatal factors could also result from decreased capacity of the electron transport chain

(ETC). It is also suggested that declined P_N may be an effect of inhibited RuBP synthesis, related to lower ATP content resulting from loss of ATP synthase activity (Tezera 1999).

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