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Soil salinity effects on transpiration and net photosynthetic rates, stomatal conductance and Na^+ and Cl^- contents in durum wheat

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Abstract

Leaf gas exchange, plant growth and leaf ion content were measured in wheat (*Triticum durum* L. cv. HD 4502) exposed to steady-state salinities (1.6, 12.0 and 16.0 dS m^{-1}) for 8 weeks. Salinity reduced leaf area and number of tillers, and increased Na^+ and Cl^- concentrations in leaves. Leaf-to-leaf gradients of these ions were observed. The oldest leaf contained 6 to 8 times more Na^+ and Cl^- than the flag leaf. Net photosynthetic rate (P_N), transpiration rate (E) and stomatal conductance (g_s) were the highest in flag leaf, declined in the middle and fully expanded leaves, and were minimum in the oldest leaves. These processes were reduced by salinity with similar leaf-to-leaf gradients. Intercellular CO_2 concentrations in the older leaves were higher than in the flag leaf in non-saline plants, and increased similarly with salinity. Leaf age was the major factor in reducing P_N, and senescence processes were promoted by salinity.

Additional key words: growth rate, leaf age, senescence, *Triticum durum*.

Introduction

Soil salinity decreases the rates of photosynthesis and plant growth to various degrees in crop plants. When plants are exposed to saline media, gas exchange of their leaves is reduced. This reduction has been attributed to salt damage of the photosynthetic tissue, to stomatal effects and consequent restriction of the availability of CO_2 for carboxylation, or to acceleration of senescence (*e.g.* Pessarakli 1994). Besides, gas exchange pattern of any single leaf is responsive to ageing (for review see *e.g.* Čatský and Šesták 1996).

The aim of the present study was *(1)* to contribute to understanding the effects of salinity on plant growth, ion uptake and net photosynthetic rate (P_N), *(2)* to

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evaluate the role of stomatal *vs* non-stomatal responses to salinity, and *(3)* to determine the rate of osmotic *vs* ionic effects on P_N in wheat, a crop known to be moderately tolerant to salinity (Maas and Hoffman 1977).

These measurements were made in plants which had been exposed to long-term (8 weeks) steady-state salinities because short-term exposures to salinity and single-factor measurements of responses to salinity do not represent the crop functioning in field conditions.

Materials and methods

Durum wheat (*Triticum durum* L. salt sensitive cultivar HD 4502) (Sharma 1989), was grown in greenhouse at Central Soil Salinity Research Institute, Karnal (29°4' N, 76°58' E, 245 m above sea level) during the winter season with natural irradiance and temperature between 27 °C (maximum) and 4 °C (minimum). The plants were grown in porcelain pots with 20 kg thoroughly washed river sand. Plants were initially grown in half-strength Hoagland's nutrient solution (electrical conductivity 1.6 dS m^{-1}), and when 35-d old, gradually exposed to salinity of 12 and 16 dS m^{-1} and maintained around these salinities.

Salinity was created with a mixture of salts in ratios Na:Ca:Mg (5:2:3) and $Cl:SO_4$ (4.5:1) on milliequivalent basis. Initially, the salts were added in increments of 2 dS m^{-1} each day. Solutions were added in excess of the volumes required for saturation of sand in each pot. Pots were maintained around the desired salinities till maturity by flushing with respective salt solutions at weekly intervals. Pots were irrigated every 1 - 3 d, depending upon the irrigation requirement.

Leaves starting from the oldest one present near the base of the stem (leaf 1) toward the flag leaf were harvested during grain filling phase. Gas exchange was measured between 10.00 and 12.00 local time. Measurements of net photosynthetic rate (P_N), transpiration rate (E) and stomatal conductance (g_s) were carried out with *CIRAS-1* (*Combined Infrared Gas Analysis System*) portable photosynthesis system (*PP Systems*, Hitching, UK) using *PLC(N) Parkinson leaf cuvette*. CO_2 and H_2O exchange by leaf was detected by 4 IRGAs, 2 each for CO_2 and H_2O. One pair of CO_2 and H_2O IRGA have a common inlet/outlet and was referred to as the "reference", while another pair was referred to as the "analysis". Stomatal conductance was calculated for CO_2 transfer. The CO_2 readings were corrected for water vapour, temperature and atmospheric pressure.

The leaves on which gas exchange was measured were subsequently used for ion determination. Five replicates were made for all measurements. Leaves were weighed immediately, subsequently dried, weighed and extracted (in 100 mol m^{-3} acetic acid, for 2 h, 90 °C) and sodium and potassium were determined by flame photometry (*Corning*, *EEL*, Bethesda, UK). Tissue chloride was determined by silver ion titration with a *Buchler-Cotlove Chloridometer* (*Buchler*, Kenexa, Kansas, USA).

Results and discussion

Salinity caused significant reduction in the rate of plant dry matter accumulation. After 8-week exposure to salinity, plant growth was reduced by 56 and 82 % at 12 and 16 dS m^{-1}, respectively, which indicates the severity of stress. Reduction in live leaf area on these plants was even slightly higher. In addition, salinity had effects on the area of each leaf blade. It also restricted the number of leaves on other tillers besides limiting the number of tillers (Table 1).

Table 1. Total shoot dry mass, live leaf area and number of tillers of wheat plants grown at different salinity levels during grain filling stage. Values followed by different letters are significantly different at $P < 0.01$, $n = 10$.

Salinity [dS m^{-1}]	Dry mass [g $plant^{-1}$]	Leaf area [cm^2 $plant^{-1}$]	Tiller number
1.6	25.870 a	265.20 a	12.8 a
12.0	11.465 b	93.25 b	6.3 b
16.0	4.654 c	36.20 c	2.1 c

Salinity resulted in increased chloride and sodium concentrations in all the leaves. The increase was more marked in older leaves than in younger leaves, flag leaf showed the lowest concentrations of sodium and chloride (Fig. 1 *A,B*). There were increasing chloride and sodium content from young to old leaves. Chloride concentrations were 2 - 4 times higher than those of Na^+ so the net flux of Cl^- and Na^+ into flag and other younger leaves was lower than into older leaves under salinity.

When plants were exposed to salinity during their development, some leaves were usually already fully developed, while others were developing during exposure to salinity. Nevertheless, salinization caused a reduction in gas exchange rates in all leaves on the plant (Fig. 1*C*). The response of P_N and g_s to salinity may thus differ between leaves due to their age, adaptation to salinity, and differences in Na^+ and/or Cl^- concentration. Younger leaves had higher E which declined with leaf age; this pattern gradient from flag leaf to the oldest leaf in non-saline plants persisted even in salinized plants, and was paralleled by decreases in g_s. Salinity, therefore, affects the amount of photosynthates produced in two ways, firstly by restricting the development of leaf area and secondly by reducing P_N.

Regression equations for relationship between net P_N and leaf sodium and chloride contents were calculated to evaluate the importance of chloride and sodium concentrations in the leaves on leaf P_N (Fig. 2*A,B*). P_N in the leaves linearly decreased with increasing Cl^- and/or Na^+ concentrations. P_N in the leaves decreased.

A linear regression of P_N against g_s ($r^2 = 0.87$) clearly indicated the control of P_N by g_s (Fig. 3*A*). g_s also showed a strong correlation with E (Fig. 3*B*).

Intercellular CO_2 (c_i) increased from 214 μmol mol^{-1} in flag leaf to 351 μmol mol^{-1} in the oldest leaf of non-saline plants and these values ranged from 220 to 430 μmol mol^{-1} in salinized plants.

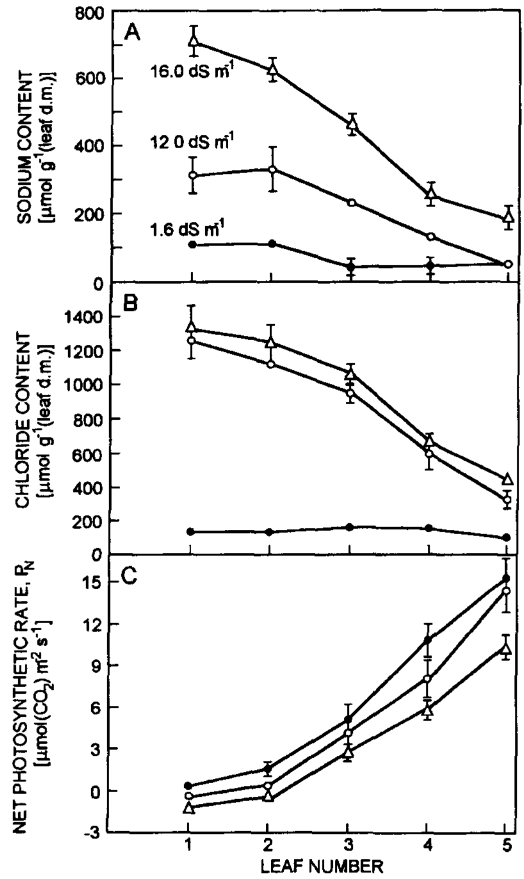

Fig. 1. Salinity effects (control, 1.6 dS m^{-1} - *closed circles*; salinity 12.0 dS m^{-1} - *open circles* and 16.0 dS m^{-1} - *open triangles*) on sodium (*A*) and chloride (*B*) content and on P_N (*C*) in different leaves of wheat. Leaf 1 represents the oldest and leaf 5 the youngest (flag) leaf. (Mean ± S.E.).

The slight effect of salinity on c_i refutes the simple dependence of P_N on g_s. This imply a possible direct effect of salinity on photosynthetic capacity. Brugnoli and Lauteri (1991) also found that bean plants grown under salinity showed a marked decline of P_N and g_s, but not c_i. However, the possible effect of stomatal patchiness on c_i calculation (for review see *e.g.* Pospíšilová and Šantrůček 1993) could not bee excluded. The rise in intercellular CO_2 with leaf age presumably reflected poorer stomatal control in old leaves.

The correlation matrix showed P_N to be significantly negatively correlated with leaf age ($P < 0.01$) and with each to the other variables considered ($P < 0.05$).

Considering the partial correlation coefficients, leaf age accounted for significantly more of the variation than did any other variable.

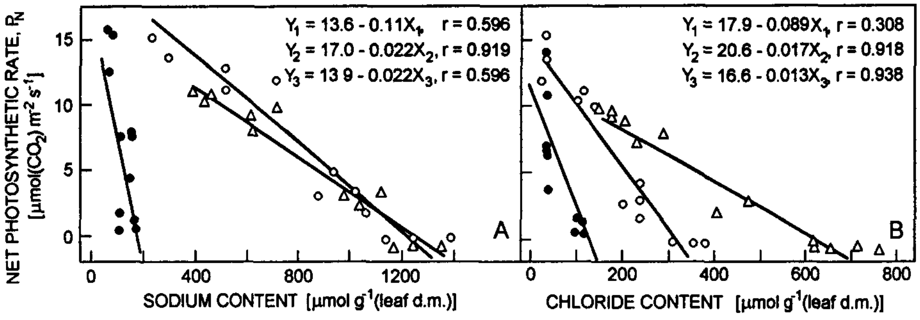

Fig. 2. The relationships between P_N and sodium (*A*) and chloride (*B*) ion contents in different leaves as affected by salinity (symbols as in Fig. 1)

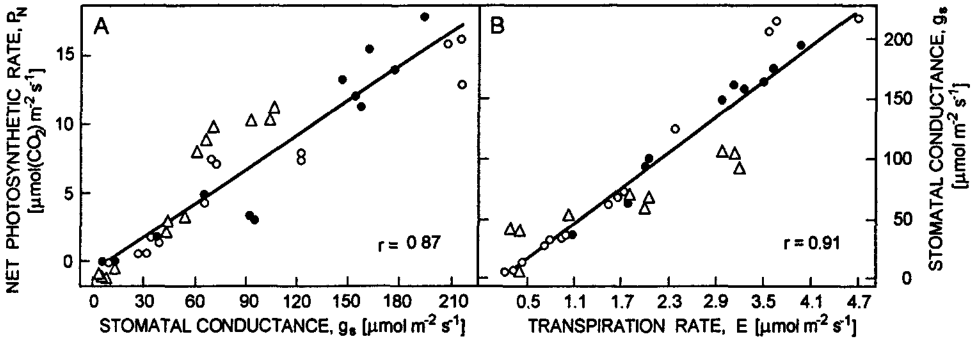

Fig. 3. The relationships between P_N and E (*A*) and E and g_s (*B*) in different leaves as affected by salinity (symbols as in Fig. 1).

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