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Spatial distributions of inorganic ions and sugars contributing to osmotic adjustment in the elongating wheat leaf under saline soil conditions

Yuncai Hu[A] and Urs Schmidhalter

Chair of Plant Nutrition, Technische Universität München, D-85350 Freising-Weihenstephan, Germany.
[A]*Corresponding author; email: huyuncai@edv.agrar.tu-muenchen.de*

Abstract. In this study, we quantified the spatial distributions of inorganic ions and sugars contributing to osmotic adjustment and their net deposition rates in the elongating and mature zones of leaf 4 of the main stem of spring wheat (*Triticum aestivum* L. cv. Lona) during its linear growth phase under saline soil conditions. Plants were grown in growth chambers in soil irrigated/treated with nutrient solution containing either no added or 120 mM NaCl. The sampling was conducted on the 3rd day after emergence of leaf 4 at 3 and 13 h into the 16 h photoperiod. The patterns of spatial distributions of total osmoticum, cation, anion and sugar contents (mmol kg^{-1} H_2O) were distinct and were affected by salinity. The total osmoticum content in the region between 0 and 60 mm above the leaf base differed between the two harvests at 120 mM NaCl. Net deposition rates of total osmotica, cations, anions, and sugars (mmol kg^{-1} H_2O h^{-1}) in both treatments increased from the base of the leaf to the most actively elongating location and then decreased near the end of the elongation zone. Contributions of cations, anions, and sugars to osmotic adjustment varied with distance from the leaf base, and were about 21–30, 15–21, and 13%, respectively, in the elongation zone. We suggest that the accumulation of solutes under saline conditions occurs both by increasing the net deposition rate of osmotica and by reducing growth.

Keywords: elongating leaf, net deposition rate, osmotic adjustment, salt stress, soil salinity, *Triticum*.

Introduction

An earlier study (Hu 1996) showed that the length and width of leaf 4 of the main stem of wheat plants treated with 120 mM NaCl were both reduced by 20% as compared with those in control conditions. The growth inhibition may be caused primarily by ionic components of salinity and/or the osmotic effects which can induce water deficit in plants (Thiel *et al.* 1988). Under saline condition, plants adjust osmotically by having higher tissue solute concentrations (Greenway and Munns 1980). Since the solutes in the elongation zone are greatly diluted by water uptake, growing cells must produce or import solutes to maintain the osmotic potential. In order to identify mechanisms of salt inhibition to leaf growth, it is, therefore, very important to answer the following questions: how do solutes build up along the leaf axis in growing leaves under saline conditions? How much do solutes contribute spatially to osmotic adjustment along the leaf axis?

The continuity equation is a statement of the law of mass conservation. This equation can be used to calculate the local net deposition rate of substances, which may be viewed as sink and source relationships (Gandar 1980; Silk 1984). Studies by Bernstein *et al.* (1995) and Hu and Schmidhalter (1998) showed that salinity affects the net deposition rates of nutrients in the elongation zone of sorghum and wheat. The relationship between the net deposition rates of solutes and water in the elongation zone can be used to analyse the mechanisms of the build-up of solutes for osmotic adjustment at low water potential (Sharp *et al.* 1990). However, there is no information available on the spatial distributions of osmotic adjustment in the elongating leaves of wheat plants at the morning and evening under saline conditions.

The objective of this study was to quantitatively evaluate the spatial distributions of inorganic ions and sugars contributing to osmotic adjustment and their net deposition rates in the elongating and mature zones of wheat leaf 4 of the main stem during its linear growth phase in soil with no added NaCl (control) and 120 mM NaCl.

Materials and methods

Growth conditions

Six seeds of spring wheat (*Triticum aestivum* L. cv. Lona), pregerminated for two days on filter paper moistened by tap water at 20°C, were sown in 1.5 L pots (10 cm in diameter and 20 cm high: soil bulk density 1 kg dm^{-3}) containing an illitic-chloritic silty loam (fine, mixed, mesic Aquic Ustifluvent) (Schmidhalter *et al.* 1994). The soil was initially watered to 0.25 g H_2O g^{-1} dry soil (soil matric potential: Ψ_m = –0.03 MPa, which allowed for an optimum aeration) with full strength Hoagland solution for macronutrients, modified by increasing the phosphate concentration 10-fold to provide optimum phosphate concentration in the soil, and by adding 0.5-strength micronutrients as recommended by Epstein

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(1972). The composition of the modified Hoagland nutrient solution was (in mM): 6.05 K^+, 15.0 N, 5.0 Ca^{2+}, 2.0 Mg^{2+}, 10.0 $H_2PO_4^-$, and 2.0 SO_4^{2-}. The salt level of 120 mM NaCl was obtained by adding NaCl to the nutrient solution. The soil was mixed thoroughly and kept in tightly closed plastic boxes for 1 week to facilitate equilibrium. Thereafter, the soil was sieved and put into pots. Soil moisture content was maintained at the initial water content by daily replacing the water loss. In order to avoid water loss by evaporation, the pots were covered with a perforated plastic film; plants grew through small holes in the film. One week after sowing, the seedlings were thinned to four plants per pot. The experiment was conducted in a growth chamber with a 16 h light period per day. The PPFD was approximately 550 µmol photon m^{-2} s^{-1}; air temperature was 20°C (day/night), and the relative humidity was maintained at 55–65%.

Tissue sampling

Three days after emergence of leaf 4, the sampling started at 3 h (0900 h) and 13 h (1900 h) into the 16 h photoperiod. Two replicates were harvested successively; all sampling was finished within 1 h. In order to ensure sampling in the linear growth phase, the leaf blades between 12 cm and 14 cm long were selected for sampling. The elongation zone was carefully freed from surrounding leaf sheaths and then cut with a razor blade from the stem at the leaf base. The excised leaf blade was cut, beginning at the leaf base, into six segments 5 mm long followed by three 10 mm and three 20 mm long.

About 120 leaf segments from the same position were combined into a sample for analysis of inorganic ion contents. After fresh weight (FW) was determined, the samples were dried at 65°C for 48 h and dry weight (DW) was determined. Dry plant material was stored for the analysis of ion contents.

For the analysis of sugar contents, segments from 20 blades of the control plants and from 30 blades of the salinized plants within one replication were combined according to position and quickly placed in preweighed 15 mL test tubes, capped tightly and placed on ice for less than 1 h.

Analyses of inorganic ion contents and total osmotica

Dried segment samples from different positions on leaf 4 of the main stem were ground by hand with a glass rod in test tubes. The ion content was measured using the following methods.

Sodium, K^+, Ca^+, Mg^{2+}, and $H_2PO_4^-$

Approximately 20 mg of ground sample were extracted with 15 mL distilled water at 100°C for 5 min, shaken for about 1 min, and then filtered by a cellulose nitrate filter (Sartorius AG, Göttingen, Germany). The ions were determined with an Inductively Coupled Plasma Emission Spectrometer (ICP model Liberty 200, Varian Australia Pty. Ltd., Mulgrave, Victoria, Australia).

Chloride, NO_3^-, and total osmotica

20 mg ground samples were extracted with 2 mL distilled water at 100°C for 5 min, shaken with a Vortex for about 1 min, and then filtered with a Millex-HV_{13} filter unit (Millipore Corporation, Bedford, MA, USA). Chloride was determined with a chloride-selective electrode (Chloride analyser 926, Corning Ltd., Halstead, Essex, England) and NO_3^- with an HPLC detector (LC 75, Perkin-Elmer Co., Norwalk, CT, USA). Total osmotica were determined with a micro-osmometer (Roebling, Medizinische Technik und Elektronik, Vogel, 6300 Giessen, Germany) in a water-extract of dry tissues of leaves, but not determined in expressed sap from leaves. Compared with a parallel experiment in which the osmotic potential was determined in expressed sap of non-growing leaf tissues, no difference between these methods were observed. To estimate osmotic adjustment, total osmotica determined at a fixed water content were converted to those of fully turgid plants based on a previous experiment (Hu 1996). Osmotic adjustment for fully turgid plants was then calculated as difference in the osmoticum content between control and stressed treatments at a given segmental location at the same time.

Analysis of sugar content

Sugars were extracted from the fresh tissue samples with 92% ethanol at 60°C for 20 min. Sucrose, glucose, and fructose were measured according to enzymatic methods from a kit from Boehringer Mannheim with a Kontron spectrophotometer (UVIKON 810, Tegimenta AG, Rotkreuz, Switzerland).

Thereafter, the sediment was extracted twice with water at 60°C for the determination of fructans. Fructans were hydrolysed with 0.5 mL 1 N H_2SO_4 into fructose and glucose at 100°C for 15 min, and then the sample was neutralized with 0.5 mL 1 N KOH. Fructose and glucose contents were determined using enzymatic methods and a kit from Boehringer Mannheim with a Kontron spectrophotometer.

Numerical methods

Local net deposition rates (D, mmol kg^{-1} H_2O or nmol mm^{-1} h^{-1}) of total osmotica, cations, anions, and sugars were calculated by the one-dimensional version of the continuity equation as described by Silk (1984):

$$D = (\partial P/\partial t) + V_d \cdot (\partial P/\partial x) + (R_s \cdot P), \quad (1)$$

where P is substance density (e.g., mmol kg^{-1} H_2O), t is time (h), and x is distance (mm) above the leaf base of the leaf blade. V_d and R_s are the displacement velocities of a segment (mm h^{-1}) and the segmental elongation rate (mm mm^{-1} h^{-1}).

On the right side of the continuity equation (1), the first term, $\partial P/\partial t$, represents the local rate of change (time rate change in substance content at a fixed distance from the leaf base). It was calculated from data obtained from the tissue sampled at the beginning (t_a) and end (t_b):

$$\partial P/\partial t = (P_b - P_a)/(t_b - t_a) \quad (2)$$

Thus, the local rate of change was assumed to occur at a linear rate between t_a and t_b.

The second term, $V_d \cdot (\partial P/\partial x)$, of equation (1) is called 'convective rate of change' which represents the change due to movement of cells away from the leaf base and can be considered as the deposition rate needed to maintain any spatial gradient in density (Silk *et al.* 1984). It was calculated according to the following equation (Schnyder and Nelson 1988):

$$\partial P_i/\partial x_i = 0.5 \cdot [(P_i - P_{i-1}) \cdot (x_i - x_{i-1})^{-1} + (P_{i+1} - P_i) \cdot (x_{i+1} - x_i)^{-1}], \quad (3)$$

where P_i is the substance content of the segment i and x_i is the distance (mm) above the base of the leaf. For the first or last segment, $\partial P_i/\partial x_i$ was calculated according to

$$(P_{i+1} - P_i) \cdot (x_{i+1} - x_i)^{-1} \text{ or } (P_i - P_{i-1}) \cdot (x_i - x_{i-1})^{-1}. \quad (4)$$

The third term on the right side of equation (1), $R_s \cdot P$, is the 'stretch rate' or the 'growth dilution term' which represents the deposition rate needed to maintain a constant local density to avoid dilution due to tissue expansion (Silk *et al.* 1986). V_d and R_s were taken from a study of growth analysis (Hu 1996).

Statistical analysis

A randomized complete block design was used. Effects of salinity, harvest time (0900 h and 1900 h) and their interaction were evaluated by analysis of variance for each location along the leaf axis. Due to the high number of plants and homogeneous growing conditions, the block effect was never significant. Hence, we assumed that the different batches of plants harvested within the different treatments did not differ except for treatment differences, and included the distance from the leaf base and the

interaction with salinity and harvest time as subhierarchical effects in the model of analysis of variance. Because the parameters such as P, V_d and R_s in equation (1) were obtained from different experiments with different numbers of replicates, the estimation of the maximum standard error was used to calculate variances for the net deposition rates according to the method described by Precht and Kraft (1992) and Precht *et al.* (1994). Terms were considered significant at $P \leq 0.05$.

Results and discussion

Spatial distribution of total osmoticum content

The total osmoticum content at 120 mM NaCl tended to increase slightly with distance, whereas in the control treatment it decreased from the leaf base to about 20 mm and then increased with distance at both harvests (Fig. 1). The difference in the total osmoticum content between the two treatments was significant. For instance, the mean osmoticum content at 120 mM NaCl was increased by 220 mmol kg^{-1} H_2O at 0900 h and 172 mmol kg^{-1} H_2O at 1900 h in the elongation zone (from 0 to 30 mm from the leaf base) and by 169 mmol kg^{-1} H_2O at 0900 h and 148 mmol kg^{-1} H_2O at 1900 h in the mature tissues. A time effect on the total osmoticum content was observed only for plants treated with 120 mM NaCl in the regions between 5 and 10 mm and between 0 and 60 mm above the leaf base (Fig. 1).

Spatial distributions of solute contents

Cation, anion, and sugar contents were calculated by summing Na^+, K^+, Ca^{2+} and Mg^{2+}, Cl^-, NO_3^- and $H_2PO_4^-$, and sucrose, glucose, fructose and fructan (assuming the average degree of polymerization is 5) (Fig. 2). The pattern of spatial distribution of cation content (Fig. 2*A*) was similar to that of the total osmoticum content. Salinity significantly increased the cation content beyond 5 mm above the leaf base at 0900 h and beyond 15 mm above the leaf base at 1900 h.

Different patterns of spatial distribution of the anion content between the two treatments are observed in Fig. 2*B*. In the control treatment, anion content slightly increased with distance, ranging from about 70 to 95 mmol kg^{-1} H_2O in both harvests. In contrast, a sharp increase in the anion content at 120 mM NaCl occurred from 0 to 30–40 mm above the leaf base; beyond this location, the anion content

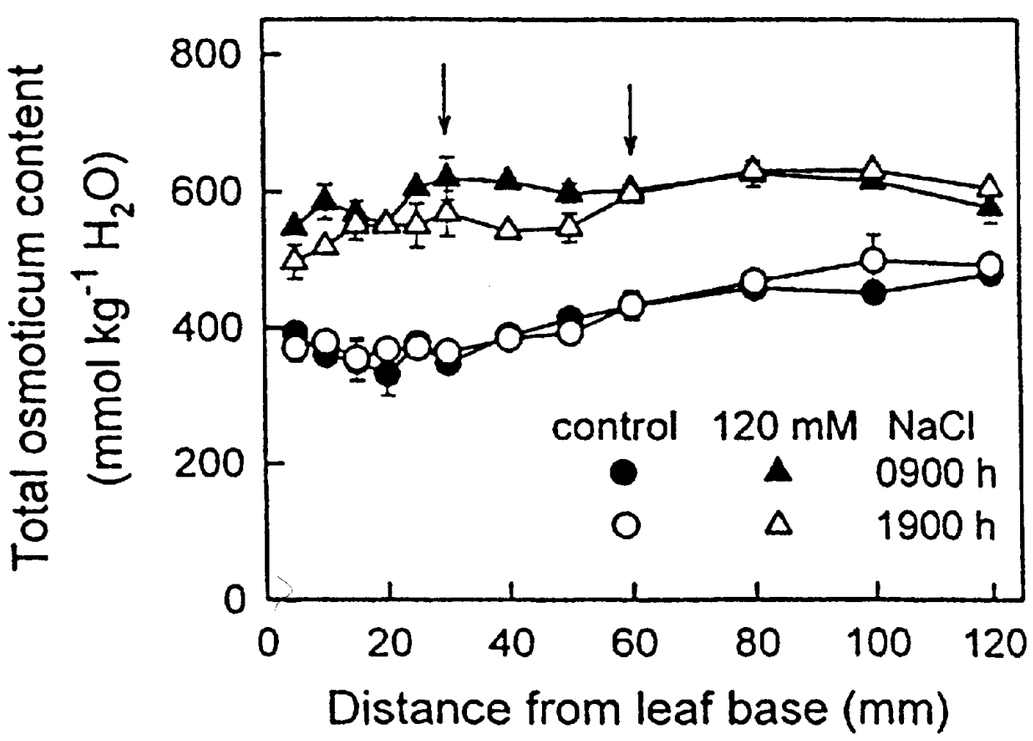


Fig. 1. Spatial distribution of total osmoticum content (mmol kg^{-1} H_2O or mOsm kg^{-1}) in the growing leaf 4 of the main stem of wheat plants grown in soil with no added NaCl (control) and 120 mM NaCl at two harvest times (at 0900 and 1900 h). Error bars ($n = 2$) represent standard errors and fit within the plot symbol if not otherwise shown. Arrows indicate the length of the elongation zone and the position of the end of the leaf sheath.

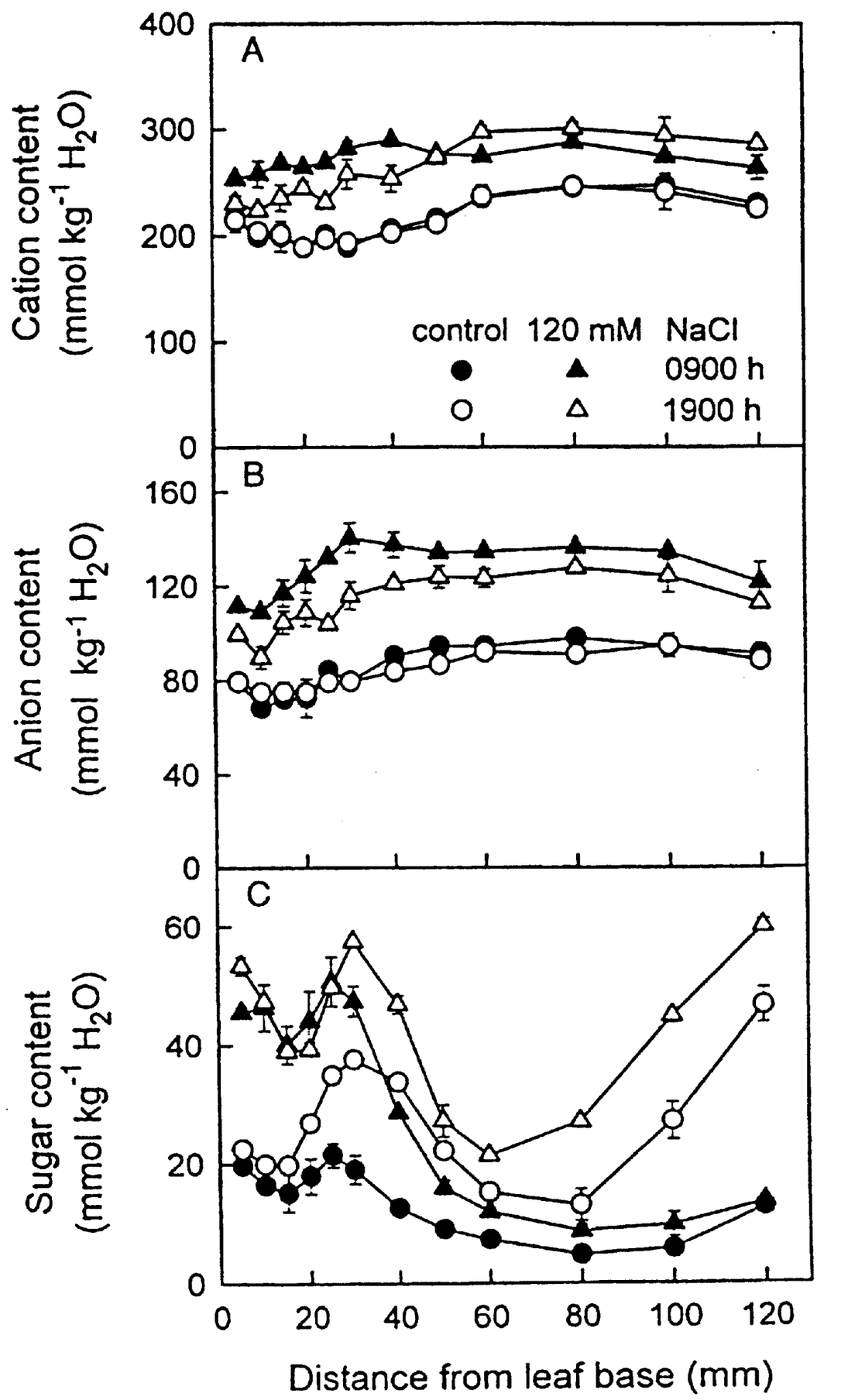


Fig. 2. Spatial distribution of cation *(A)*, anion *(B)* and sugar *(C)* contents (mmol kg^{-1} H_2O) in the growing leaf 4 of the main stem of wheat plants grown in soil with no added NaCl and 120 mM NaCl at two harvest times (at 0900 and 1900 h). Error bars ($n = 2$) represent standard errors and fit within the plot symbol if not otherwise shown.

remained almost constant. The mean anion content at 120 mM NaCl was increased by 61% at 0900 h and 35% at 1900 h, respectively, in the elongation zone, whereas these values were increased by 42% at 0900 h and 37% at 1900 h, respectively, in the mature tissue. Time did not affect the anion content in the control treatment, whereas in the salinized treatment, the anion content was higher at 0900 h than at 1900 h from the leaf base to about 80 mm.

A marked increase in the sugar content with distance in both treatments at 1900 h was observed between 15–20 and 30 mm and beyond 60 mm from the leaf base as compared with that at 0900 h (Fig. 2*C*). Sugar content was significantly increased by 120 mM NaCl between 5 and 100 mm above the leaf base at 0900 h and at all locations except at 50 mm at 1900 h. Time significantly affected sugar content beyond 15 mm in the control treatment and beyond 25 mm in the salinized treatment.

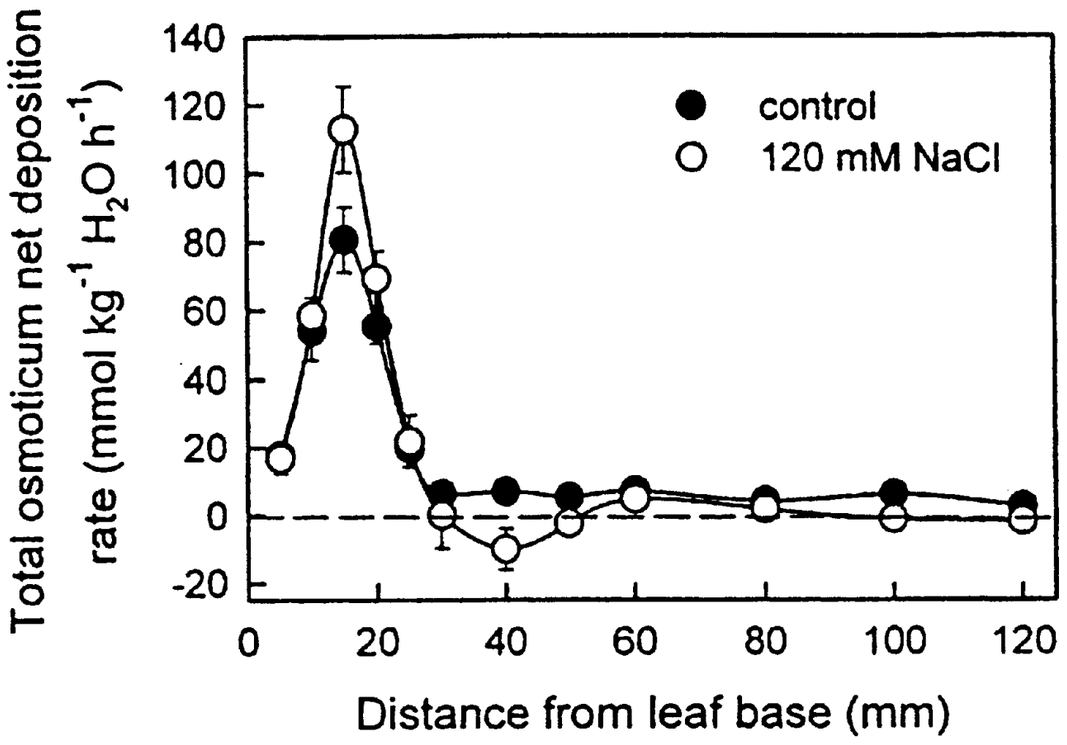


Fig. 3. Spatial distribution of total osmoticum deposition rate (mmol kg^{-1} H_2O h^{-1} or mOsm kg^{-1} h^{-1}) in the growing leaf 4 of wheat plants grown in soil with no added NaCl and 120 mM NaCl. Error bars (n = 2 to 14) represent maximum standard errors and fit within the plot symbol if not otherwise shown.

Net deposition rates of total osmotica, cations, anions, and sugars

Net deposition rates of total osmotica, cations, anions, and sugars (mmol kg^{-1} H_2O h^{-1}), as shown in Figs 3 to 5, were obtained from the average data of both harvests. Net deposition rates of total osmotica, cations, and anions increased in both treatments from the base of the leaf to the most actively elongating location at 15 mm, and then decreased to near zero at the end of the elongation zone (about 30 mm from the leaf base) (Figs 3, 4*A*, *B*). Total osmoticum deposition rates were greater at 120 mM NaCl than in the control treatment in the region from 10 to 20 mm above the leaf base, whereas in the region between 30 and 50 mm above the leaf base, they were lower at 120 mM NaCl. Salinity decreased cation net deposition rate at 40 mm above the leaf base, and increased the anion net deposition rate at the middle of the elongation zone.

The net rate of sugar deposition (mmol kg^{-1} H_2O h^{-1}) increased from the leaf base to the most actively elongating location at 15–20 mm, then sharply decreased to reach a minimum at about 40–50 mm and increased again beyond 50 mm above the leaf base. Between 5 and 10 mm above the leaf base, the sugar deposition rate was higher at 120 mM NaCl than in the control treatment. Between 30 and 50 mm, however, the rate of sugar deposition was lower at 120 mM NaCl. The sugar net deposition rate beyond 60 mm was greater at 120 mM NaCl.

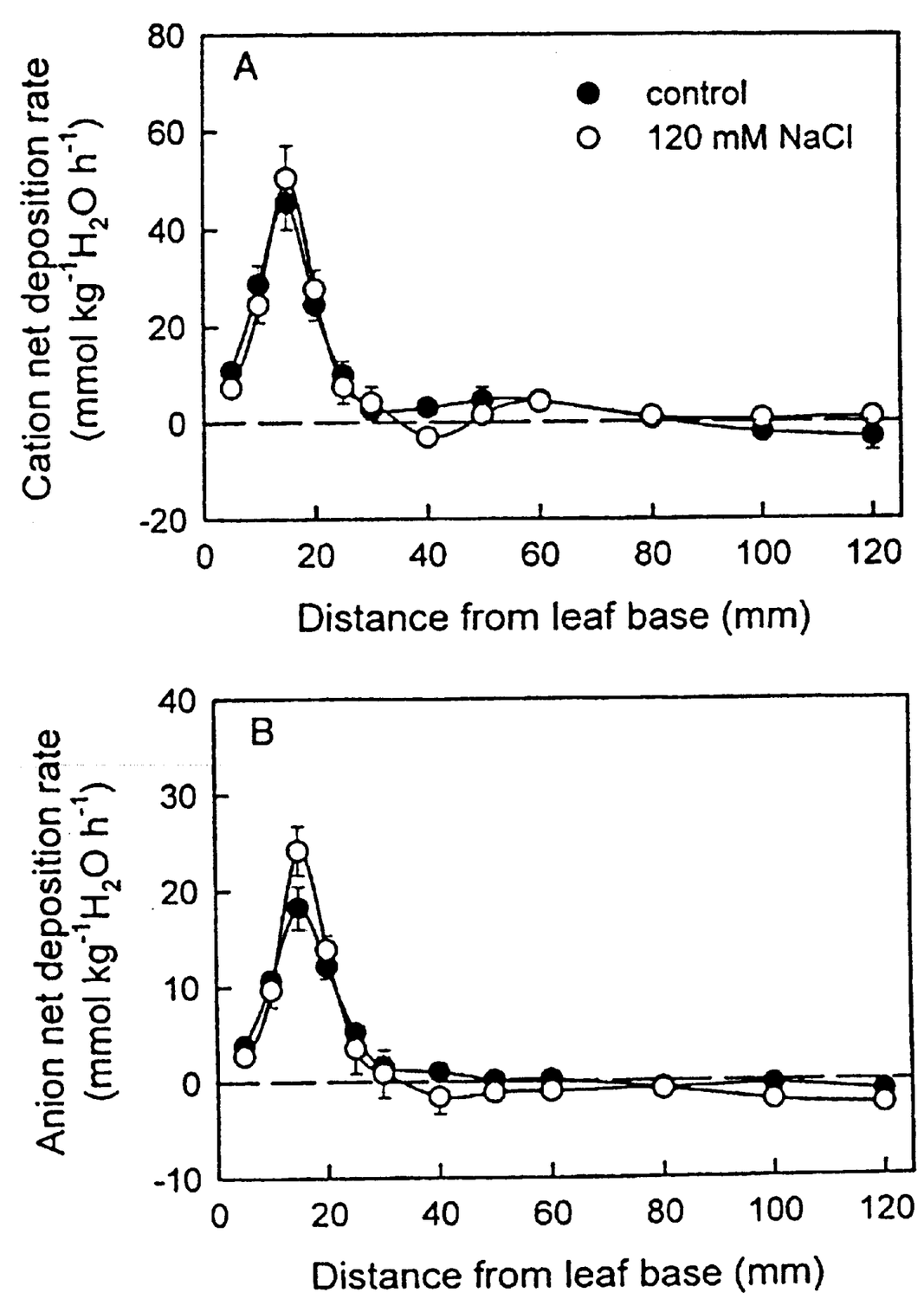


Fig. 4. Spatial distribution of cation *(A)* and anion *(B)* net deposition rates (mmol kg^{-1} H_2O h^{-1}) in the growing leaf 4 of wheat plants grown in soil with no added NaCl and 120 mM NaCl. Error bars (n = 2 to 14) represent maximum standard errors and fit within the plot symbol if not otherwise shown.

Spatial distribution of cations, anions, and sugars contributing to osmotic adjustment

Osmotic adjustment rapidly increased in the region from 5 to 10 mm from the leaf base and was greater in the elongation zone than in the maturation zone for both harvests (Fig. 6). Osmotic adjustment was smaller at 1900 h than at 0900 h.

To determine the inorganic ions contributing to osmotic adjustment, the ionization of solutes (i.e. cations and anions) and other deviations from perfect solutions were not considered in this study. The contributions of different solutes contributing to osmotic adjustment were expressed as the percentage of $\Delta \psi_s^{i}$ (i = cations, anions or sugars) to $\Delta \psi_s^{total}$ (total = total osmotica). At 0900 h, the contributions of cations, anions, and sugars to osmotic adjustment were about 30, 21, and 13%, respectively, in the elongation zone and about 28, 24, and 3%, respectively, in the mature tissue (Fig. 7*A*, *B*); at 1900 h, these values were about 21, 15, and 13%, respectively, in the elongation zone and about 39, 22, and 8%, respectively, in the mature leaf tissues. The total ions (cations and anions) accounted for 51% at 0900 h and 36% at 1900 h in the elongation zone and for 52% at 0900 h and 62% at 1900 h in the mature leaf tissue. Thus, ions accounted for the major contribution to osmotic adjustment as compared with 3–13% from sugars at both harvests. The contribution of ions to osmotic adjustment was mainly due to the net accumulation of K^+, Na^+, and Cl^-. For instance, K^+ and Cl^- in the elongation zone accounted for 47 and 34% of the total ions, respectively, at 0900 h and for 36 and 43% at 1900 h, whereas these values were 32 and 44% at 0900 h and 52 and 39% at 1900 h in the mature tissues. Sodium accounted for 8% of the total ions at 0900 h and 15% at 1900 h in the elongation zone and for 17% of the total ions at 0900 h and 8% at 1900 h in the mature tissues. The low proportion of Na^+ in the leaf tissues may be due to the characteristics of Na^+ exclusion by roots (Marschner 1995).

Under saline conditions, sugars + ions together contributed 64% at 0900 h and 49% at 1900 h to osmotic adjustment in the elongation zone and 55% at 0900 h and

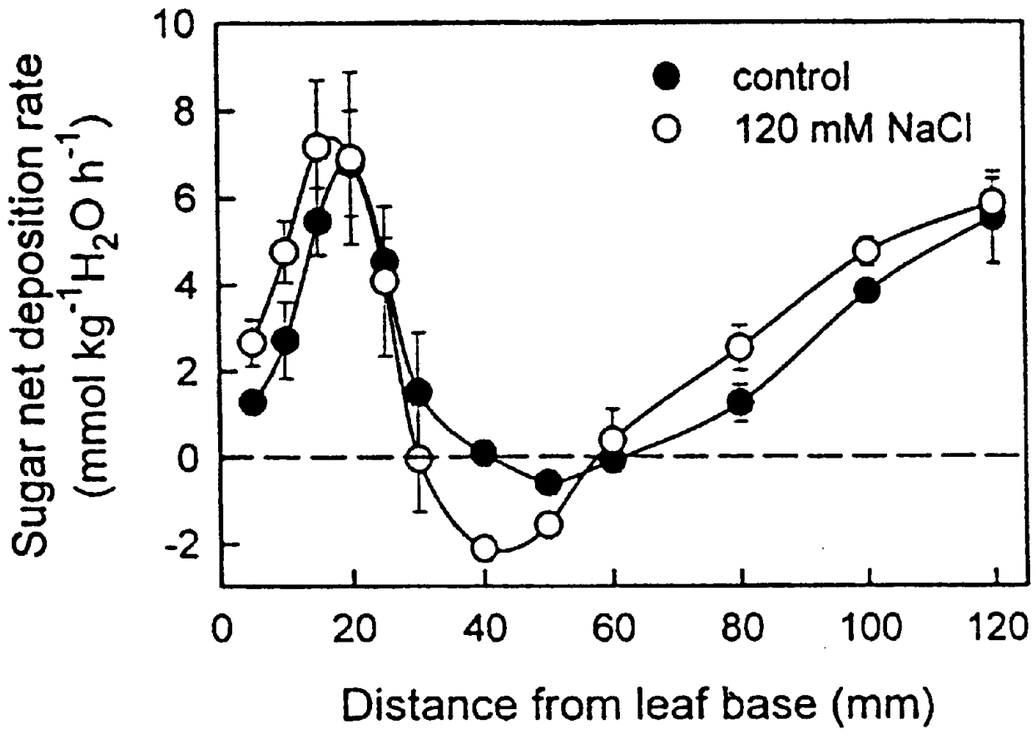


Fig. 5. Spatial distribution of sugar deposition rate (mmol kg^{-1} H_2O h^{-1}) in the growing leaf 4 of wheat plants grown in soil with no added NaCl and 120 mM NaCl. Error bars (n = 2 to 14) represent maximum standard errors and fit within the plot symbol if not otherwise shown.

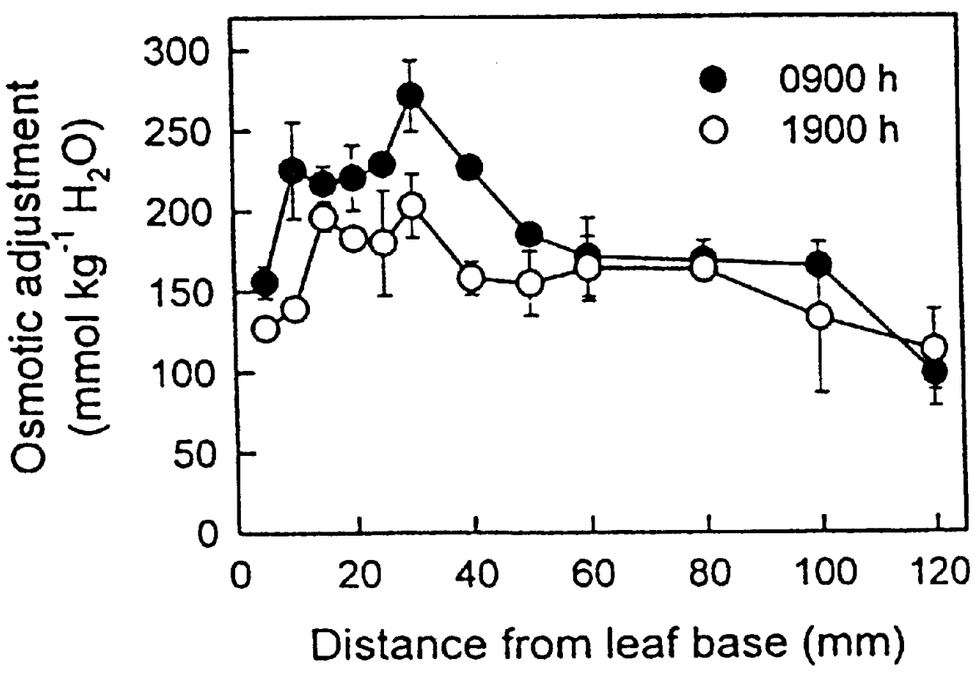
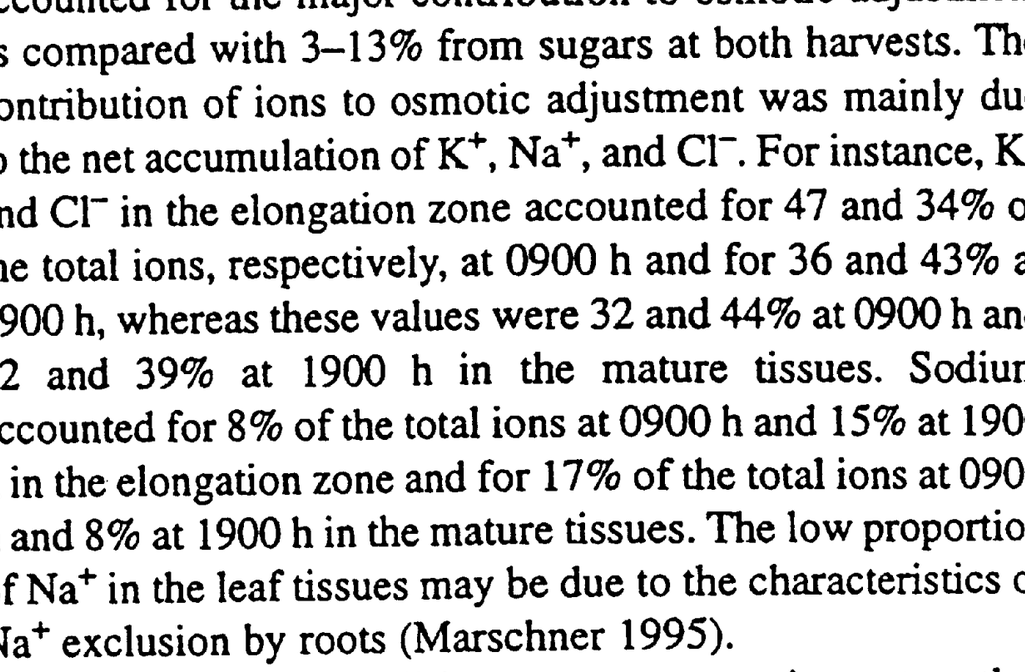


Fig. 6. Spatial distribution of osmotic adjustment (mOsm kg^{-1}) at two harvest times (0900 and 1900 h) in the growing leaf 4 of wheat plants grown in soil with 120 mM NaCl. Error bars (n = 2) represent standard errors and fit within the plot symbol if not otherwise shown.



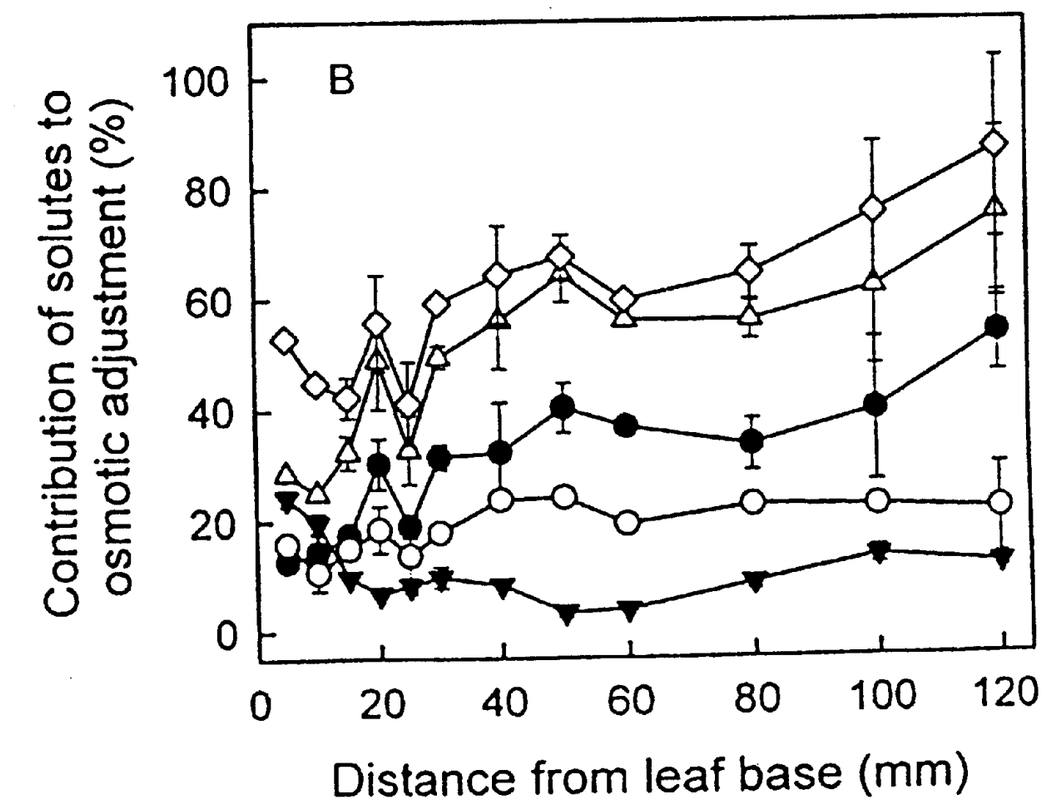


Fig. 7. Spatial distribution of the solutes contributing to osmotic adjustment (%) at 0900 *(A)* and at 1900 h *(B)* in the growing leaf 4 of wheat plants grown in soil with 120 mM NaCl. Error bars (n = 2) represent standard errors and fit within the plot symbol if not otherwise shown.

70% at 1900 h in the mature leaf tissues. About 30–50% of solutes contributing to the remaining osmotic adjustment are unknown. The sugar alcohols, organic acids and amino acids, such as proline, betaine, etc., may be responsible for the remaining osmotic adjustment (Greenway and Munns 1980; Delane *et al.* 1982; Bachmann 1990).

The role of osmotic adjustment

Osmotic adjustment is regarded as an important adaptation of plants to salinity, because it helps to maintain turgor and cell volume. According to the biphasic model of growth responses to salinity proposed by Munns (1993), osmotic adjustment might be an adaptation for surviving stress. The osmotic effect may cause a greater reduction in wheat growth during the first phase, or in the short term, in salt stress (Munns *et al.* 1995). Later, the reduction in leaf growth may be due to ion toxicity, ion deficiency, ion imbalance, growth regulators, and/or other processes such as hardening of cell walls, that limit cell expansion (Neumann *et al.* 1994; Nabil and Coudret 1995). In contrast, Neumann (1997) reported that early growth reduction by moderate salinity is also independent of turgor pressure in root and leaf growth zones. Nevertheless, it is difficult to determine when the first phase ends and the second phase starts. Our study (Hu 1996) showed that, at the same growth stage, turgor in the mature tissue of leaf 4 was not affected by 120 mM NaCl. Maintenance of turgor in non-growing zones makes it highly likely that turgor was maintained in growing zones as well (Schmidhalter *et al.* 1998). Arif and Tomos (1993) reported that no decrease in turgor pressure (measured with a pressure probe) occurred in the elongating cells despite the decrease in the growth of plants with 25–150 mM NaCl. In this study, data cannot be interpreted in terms of turgor pressure within the elongation zone, because the leaf water potential was not measured in this zone. However, the increase in total osmolality between control and 120 mM NaCl was higher in the elongating tissues than in the growth media. This may indicate that plants probably did not suffer from water deficit in the elongation zone at this stage. In addition, other studies showed that turgor pressure (measured with a pressure probe) remained unchanged within the elongation zone for barley (Fricke *et al.* 1997) and for wheat (Arif and Tomos 1993) though the segmental elongation rate of leaves significantly changed with distance. This probably also indicates that reduction in leaf elongation might be related to other major factors such as the mechanical properties of cell walls which may be affected by salinity.

How did solutes build up for osmotic adjustment under saline conditions?

Under saline conditions, osmotic adjustment generally results from the increase in either the rate of solute supply to and uptake by the cells, or from the decrease in the utilization of organic substances. Furthermore, it has been observed that a higher osmotic adjustment occurred in the elongation zone as compared with the maturation zone of the leaf (Fig. 6). The most active cell elongation takes place in the zone of leaf growth (Schnyder and Nelson 1988; Hu and Schmidhalter 1998). Therefore, the elongation zone should be considered first as the zone where osmotic adjustment occurs. In the elongation zone, osmotic adjustment could occur by two basic mechanisms: reduction in the rate of tissue volume expansion and/or increase in the net rate of osmoticum deposition (Sharp *et al.* 1990). In this study, we suggest that osmotic adjustment is probably due to both the reduction in growth under saline conditions and the increase in the net rate of osmoticum deposition. Net deposition rate of total osmotica per unit water deposition rate was consistently higher in salinized treatment than in control treatment all along the elongation zone and also varied with distance (Fig. 8). This indicates that the reduction in cell elongation may be greater than the reduction in net deposition rate of total osmotica under saline conditions, because the net deposition rate of water was closely related to cell elongation (Hu 1996).

The production of sufficient osmotica is metabolically expensive and potentially limiting the plant growth by consuming significant quantities of carbon that could otherwise be used for growth (Greenway and Munns 1980). An alternative to producing organic osmotica is to accumulate a sufficiently high content of ions from the external medium. The energetic cost of osmotic adjustment using inorganic ions is much lower than that using organic molecules synthesised in the cell (Wyn Jones 1981; Yeo 1983). Fig. 7 shows that ion accumulation accounted for a

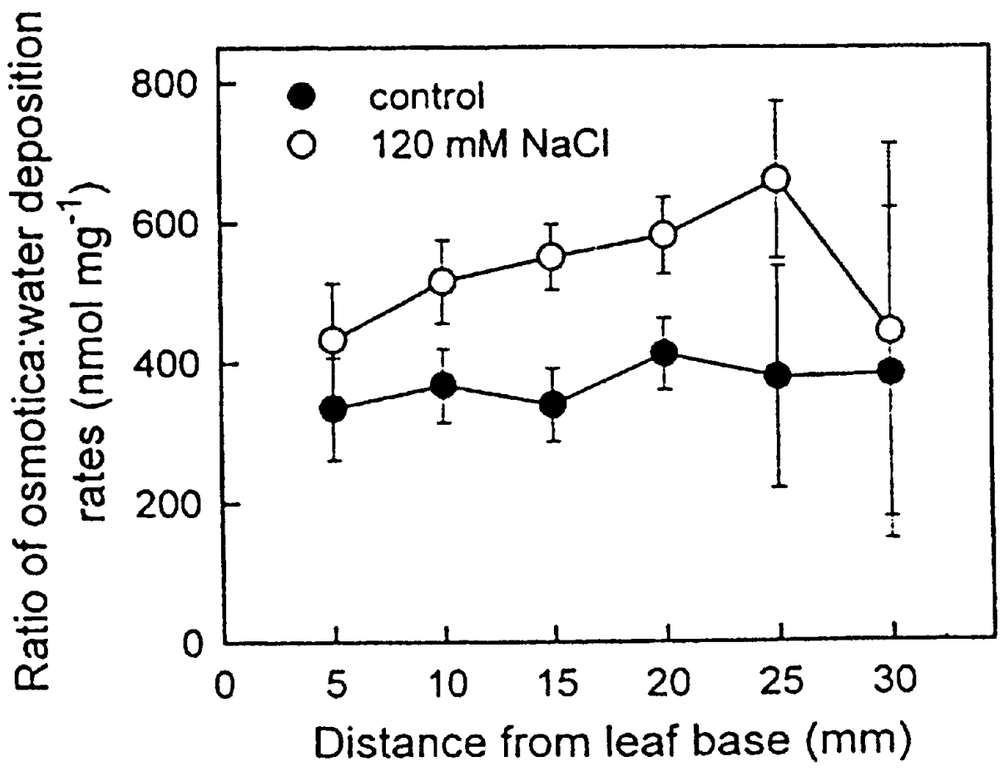


Fig. 8. Spatial distribution of the ratio of net deposition rate of total osmotica to water in the elongation zone in the leaf 4 of wheat plants grown in soil with no added NaCl and 120 mM NaCl. Data were calculated by dividing solute deposition rate per unit length through water deposition rate per unit length. Error bars (n = 2 to 14) represent maximum standard errors and fit within the plot symbol if not otherwise shown.

major contribution to the osmotic adjustment. K^+ and Cl^- in the elongation zone accounted for 34–47% of the total inorganic ions. However, this causes another problem that such high contents of Cl^- may interfere with normal biochemical activity within the cell (Poljakoff-Mayber 1975). A study of spatial distribution of ions (Hu and Schmidhalter 1998) has shown that NO_3^- deficiency may exist in the elongation zone due to the higher Cl^- content. Although a higher content of tissue Na^+ in the elongation zone did not lead to ion toxicity, it may cause ion imbalance.

Conclusions

Greater osmotic adjustment occurs in the elongation zone in the morning. Inorganic ions accounted for the major contribution to osmotic adjustment. Contributions of cations, anions, and sugars to osmotic adjustment were about 21–30, 15–21, and 13%, respectively, in the elongation zone and about 28–39, 22–24, and 3–8%, respectively, in the mature tissue. The contribution of inorganic ions to osmotic adjustment was mainly due to the net accumulation of K^+ and Cl^- which accounted for 36–47 and 34–43% of the total ions in the elongation zone. Solutes built up by increasing the net rate of osmoticum deposition and by reduction in growth under saline conditions.

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