Reduced cellular cross-sectional area in the leaf elongation zone of wheat causes a decrease in dry weight deposition under saline conditions

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Abstract. Expansion and dry weight (DW) of wheat leaves are spatially distributed along the axis and affected by salinity. The objective of this study was to evaluate the effect of salinity on the spatial distribution of cellular cross-sectional area and DW in the elongating and mature leaf zones of leaf 4 of the main stem of spring wheat (*Triticum aestivum* L. cv. Lona) during its linear growth phase. Plants were grown in illitic–chloritic silt loam with 0 and 120 mM NaCl in a growth chamber. Cellular cross-sectional area and DW contents of leaves were determined on the 5–20-mm scale along the leaf axis. Spatial distribution of cellular cross-sectional area changed slightly with distance within the elongation zone in both treatments. The cellular cross-sectional area of the leaf at 120 mM NaCl was reduced by 32% at 5 mm, as compared with about 36% averaged from the region between 5 and 30 mm from the leaf base, indicating that the reduction in the cellular cross-sectional area by salinity occurred mainly at the leaf base when the leaf initiates. A slight decrease in the DW per leaf length at a given location in the elongation zone may be due to the strongly decreased cellular cross-sectional area by salinity. This suggests that the limitation of leaf growth by salinity may be due mainly to the effect of salinity on leaf expansion, but not due to the effect on the synthesis of dry matter.

Keywords: leaf cellular cross-sectional area, leaf elongation, net deposition rate (NDR), saline soil, *Triticum aestivum* L.

Introduction

A visible leaf of grasses increases only in length, because the width remains unchanged once it has emerged from the sheath bundle (Dale 1988). Expansion of a growing grass leaf is restricted to a small region at the base of the blade enclosed by sheaths of older leaves, but is largely unidirectional as well (Kemp 1980). However, salinity reduces not only the leaf length, but also the leaf width. Our earlier study (Hu *et al.* 2000*a*) showed that the final length and width of wheat (*Triticum aestivum* L.) leaves on the main stem treated with 120 mM NaCl were reduced by about 20–30%, respectively, as compared with those under control conditions. Then, does the width of wheat leaves start to decrease in the growing zone under saline conditions, and how does salinity affect the leaf width? To make it clear how salinity affects the width in the growing zone of leaves, it is necessary to investigate the spatial change in width along the leaf axis, or even better in cellular cross-sectional area. Since most of the tissue water is cellular, and water is largely non-compressible, water content along the leaf axis can be used to describe the change in cellular cross-sectional area (i.e. cross-sectional area without air spaces) with distance from the leaf base.

Increase in the DW of grass leaves is one of the most important growth processes, due to a highly complex series of biochemical events. Salinity significantly decreases the leaf DW of grasses (Hu *et al.* 2000*a*). However, it is still unclear whether the decreased DW is due to the direct reduction in dry weight deposition rate or to the inhibition of cell expansion by salinity. To calculate the deposition rate of DW and water in a growing leaf, the continuity equation can be employed (Gandar 1980; Silk 1984; Schnyder and Nelson 1988). By analysing the spatial distribution of the net deposition rate (NDR) of water and of DW, it will be clarified whether the decreased DW is due to the direct reduction in DW deposition rate or to the inhibition of cell expansion by salinity. Furthermore, three components of water NDR, which can be calculated by using the continuity equation, can be also used to estimate the contribution of spatial leaf expansion to the lateral, vertical and longitudinal dimensions of leaf growth in the growing zone (Silk 1984; Schnyder and Nelson 1988).

Abbreviations used: DW, dry weight; FW, fresh weight, NDR, net deposition rate; R_s, relative elemental growth rate.

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Materials and methods

Growth conditions

Six seeds of spring wheat (*Triticum aestivum* L. cv. Lona), pre-germinated for 2 d on filter paper wetted by tap water at 20°C, were sown in 1.5-L pots (10 cm diameter and 20 cm height) containing an illitic–chloritic silty loam (fine mixed mesic Aquic Ustifluvent, from the Department of Crop Sciences, Charrat, ETH Zürich, Switzerland) (Schmidhalter *et al.* 1994). One week after sowing, seedlings were thinned to four plants per pot. There were about 150 pots available for each treatment. 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's solution for macronutrients, modified by increasing the phosphate concentration 10-fold to provide optimum phosphate concentration in the soil and by adding half-strength micronutrients as recommended by Epstein (1972). The composition of the modified Hoagland's nutrient solution was (in mol m^{-3}): 6.05 K^+, 15.0 NO_3^-, 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 thoroughly mixed and kept in tightly closed plastic boxes for 1 week to facilitate equilibration. Thereafter, the soil was sieved and put into pots. Soil moisture content was maintained at the initial content by watering with tap water. In order to minimize water loss by evaporation, the pots were covered with a perforated plastic film, where plants could grow through small holes. 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 photoperiod. The light intensity was approximately 550 µmol photon m^{-2} s^{-1} (PPFD). Air temperature was 20°C (day/night) and the relative humidity was maintained at 55–65%.

Tissue sampling and determination of fresh weight, dry weight and width

Because salinity delays the development of grass leaves (Hu *et al.* 2000*a*), plants in both treatments were harvested at the same developmental stage. Three d after leaf 4 emerged, sampling started at 3 h (0900 h) and 13 h (1900 h) into the 16-h photoperiod. Elongating leaves of length 12–14 cm were selected for sampling. Leaf elongation was approximately steady during this stage (Hu *et al.* 2000*a*). The elongation zone was carefully freed from surrounding leaf sheaths, then cut from the base of the leaf with a razor blade. Beginning at the base, about 20 leaves together were then sectioned into six 5-mm-long segments followed by three 10-mm and three 20-mm-long segments. In order to prevent disturbances in the water status of tissues, each sampling process was finished in less than 2–3 min and was conducted under low light intensity. In total, 120 leaf segments from the same position were combined into a sample. Two replicates were harvested successively and harvest time recorded. After fresh weight (FW) was determined, the samples were dried at 65°C for 48 h and DW was determined. Water content of samples was calculated as the difference between FW and DW.

After leaf 4 was freed from surrounding leaf sheaths, it was carefully unfolded and then a completely flat blade of leaf 4 was fixed on a piece of white paper with glue. Spatial distribution of width of leaf 4 at 5, 10, 20, 25, 30, 40, 50, 60, 80, 100 and 120 mm above the leaf base was measured by using a by using a Nikon stereoscopic zoom microscope (SMZ-2T, Nikon, Japan). Four replicate leaves were measured. Only one harvest time at 0900 hours was chosen for the spatial distribution of leaf width.

Numerical methods

Local NDR values (D, µg mm^{-1} h^{-1}) of water and DW were calculated according to the one-dimensional version of the continuity equation as described by Silk (1984):

$$D = (\partial P/\partial t) + V_d \cdot (\partial P/\partial x) + (R_s \cdot P)$$
$$\text{I} \qquad \text{II} \qquad \text{III},$$

where P is substance density (e.g. µg H_2O mm^{-1} leaf length); t is time (h); x is distance (mm) from the base of the leaf blade. R_s is the relative elemental growth rate (mm mm^{-1} h^{-1}) and V_d is the displacement velocity of a segment (mm h^{-1}) (integration of R_s). P in the terms of $V_d \cdot (\partial P/\partial x)$ and $R_s \cdot P$ was obtained from averaging the two harvest times. The calculation of the $(\partial P/\partial t$ (I), $V_d \cdot (\partial P/\partial x)$ (II), and $R_s \cdot P$ (III) on the right-hand side of the continuity equation was described in details in our previous study (Hu and Schmidhalter 1998*b*).

Statistical analysis

A randomized complete block design was used. Effects of salinity, harvest time (0900 h and 1900 h) and their interactions were evaluated by analysis of variance for each location along the leaf axis. Due to the larger 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 treatments did not differ except for a change among treatments, 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 parameters such as P, V_d and R_s in the equation were from the experiments with the different replicates, the variance for the NDRs of substances was in terms of a maximum standard error, which was estimated from a method described by Precht and Kraft (1992) and Precht *et al.* (1994). Terms were considered significant at $P \leq 0.05$.

Results

Spatial distributions of water, DW and width

Spatial distributions of water and DW in the growing leaf 4 of the main stem of wheat plants, with and without 120 mM NaCl, sampled at 0900 and 1900 h on day 3 after the emergence of leaf 4, are shown in Fig. 1. During the period of sampling, the growth of leaf 4 occurred in the linear growth phase, and the length of the elongation zone was about 30 mm for plants in both treatments (Hu *et al.* 2000*a*). Leaf water content at 0 mM NaCl for both harvest times increased slightly from the leaf base up to the end of the elongation zone, and then slightly decreased or remained almost constant (Fig. 1*A*). At 120 mM NaCl, water content slightly increased from 10 to 50 mm above the leaf base. Beyond about 50 mm from the leaf base, water content markedly decreased in the two treatments at both harvest times.

Water content along the whole leaf axis was significantly decreased by 120 mM NaCl ($P < 0.01$). Salt effects on water content became greater at 1900 h beyond 60 mm from the leaf base. For example, 120 mM NaCl reduced the mean water content from the leaf base to 60 mm by 36 and 39.8% at 0900 and 1900 h, respectively, and from 60 to 120 mm by 47.8 and 55.9% at 0900 and 1900 h, respectively.

Time affected the water content in the control treatment. This became greater beyond the elongation zone. For example, mean water content was higher at 1900 h than at 0900 h by 8.5% in the region from 0 to 30 mm from the leaf base, 14% from 30 to 60 mm, and 16.4% from 60 to 120 mm. At 120 mM NaCl, the water content was about

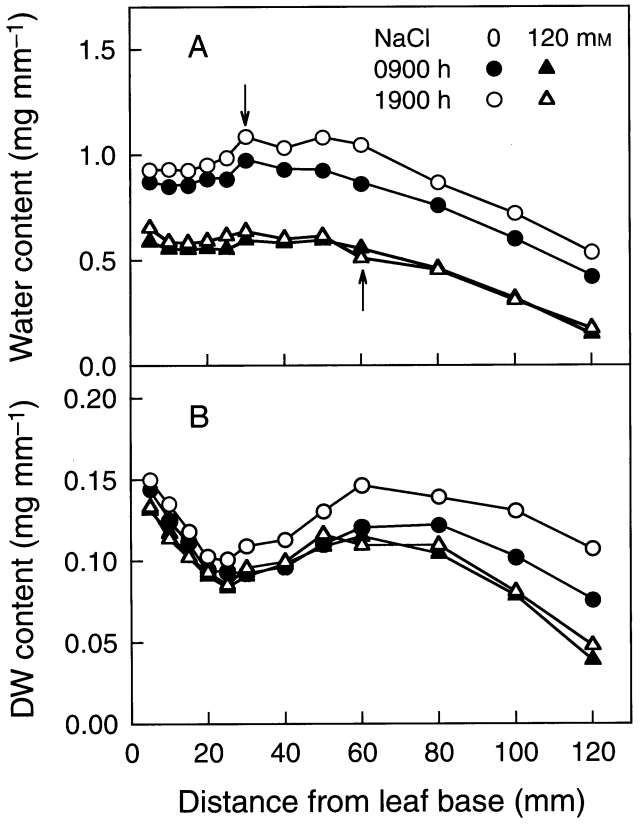

Fig. 1. Spatial distributions of water content (*A*) and dry weight (DW) content (*B*) in the growing leaf 4 of the main stem of wheat plants with 0 and 120 mM NaCl at two harvest times (0900 and 1900 h). The differences between two replications for each harvest time and treatment in the growing leaf 4 were within 20% for water content at 0900 and 1900 h at 0 mM NaCl and at 0900 h at 120 mM NaCl and for DW content at 0900 h at 0 mM NaCl; within 15% for water content at 1900 h at 120 mM and for DW content at 1900 h at 0 and 120 mM NaCl; within 10% for DW content at 0900 h at 120 mM NaCl. Arrows indicate the positions of the end of the leaf elongation zone and leaf sheath.

7% higher at 1900 h than at 0900 h in the elongation zone, whereas no effect of time on the water content was observed beyond the elongation zone (Fig. 1*A*).

The pattern of change in DW content (mg mm^{-1} leaf length) along the leaf axis was similar in both treatments at both harvest times, which may be characterized by three types along the leaf axis (Fig. 1*B*). DW content decreased linearly from the leaf base to reach a minimum at 25–30 mm from the leaf base, near the end of the elongation zone, and then increased from about 30 mm to reach a maximum at 60–80 mm. Beyond about 80 mm, DW content decreased again. In the first region (from the leaf base to 30 mm), the mean DW was consistently higher at 0 mM NaCl than at 120 mM NaCl at both harvest times. From 30 to 60 mm above the leaf base, mean DW content at 0 mM NaCl was the same as that at 120 mM NaCl at 0900 h, whereas at 1900 h, DW content was 16.4% greater at 0 mM NaCl than at 120 mM NaCl. Beyond 60 mm from the leaf base, mean DW content was reduced by 25.9 and 36.7% by 120 mM NaCl at 0900 and 1900 h, respectively (Fig. 1*B*).

DW content at 0 mM NaCl increased consistently at the second harvest, especially beyond the elongation zone. For example, mean DW content was 7.6% higher from 0 to 30 mm from the leaf base, 16% higher from 30 to 60 mm, and 20.6% higher from 60 to 120 mm at 1900 h than at 0900 h. At 120 mM NaCl, no time effect on the mean DW content was observed.

Width increased slightly with distance up to 50–60 mm above the leaf base for the two treatments, and then decreased with distance (Fig. 2). The reduction in width of leaf 4 by 120 mM NaCl at the leaf base was about around 20%, and there was a similar reduction along the leaf axis.

NDR of water and DW

The NDR of water and DW was obtained from the average of the two harvest times. NDR of water in both treatments increased from the leaf base to the most actively elongating zone at 15 mm and then decreased to near zero at the end of the elongation zone (about 30 mm from the leaf base) (Fig. 3). NDR of water at all locations along the elongation zone was greater at 0 mM NaCl than at 120 mM NaCl. Figure 3 shows that the difference in the NDR of water between 0 and 120 mM NaCl was greater within the elongation zone than in the relative elemental growth rate of leaves (R_s), due to the net rate of water deposition in terms of change in volume per unit leaf length per unit time. The cumulative rate of water deposited into the elongation zone at 0 mM NaCl, calculated by integrating the rate from 0 to 30 mm above the leaf base, was twice as high as at 120 mM

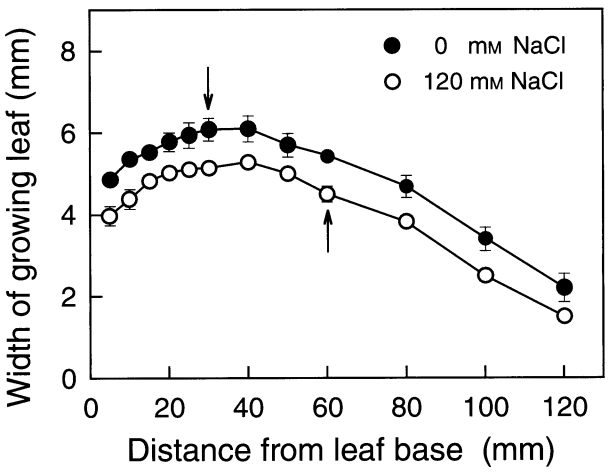

Fig. 2. Spatial distributions of width in the growing leaf 4 of the main stem of wheat plants with 0 and 120 mM NaCl at 0900 h. Error bars (n = 4) represent standard errors and fit within the plot symbol if not otherwise shown. Arrows indicate the positions of the end of the leaf elongation zone and leaf sheath.

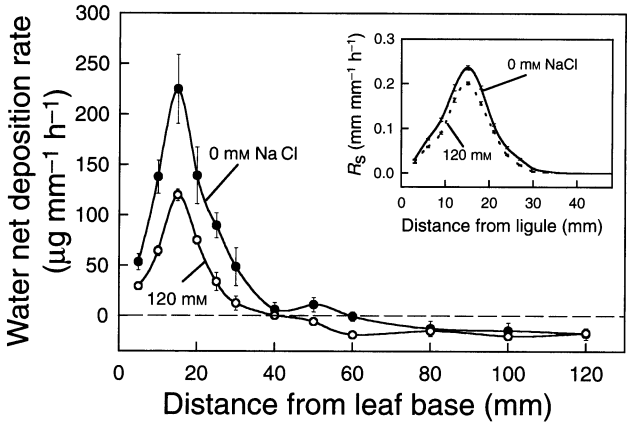

Fig. 3. Spatial distribution of net deposition rates of water in the growing leaf 4 of wheat plants with 0 and 120 mM NaCl. The inset shows the spatial distribution of the relative elemental growth rate of leaf 4 (R_s) during the linear phase of leaf elongation (Hu *et al. 2000a*). Error bars (n = 2–14) represent maximum standard errors and fit within the plot symbol if not otherwise shown.

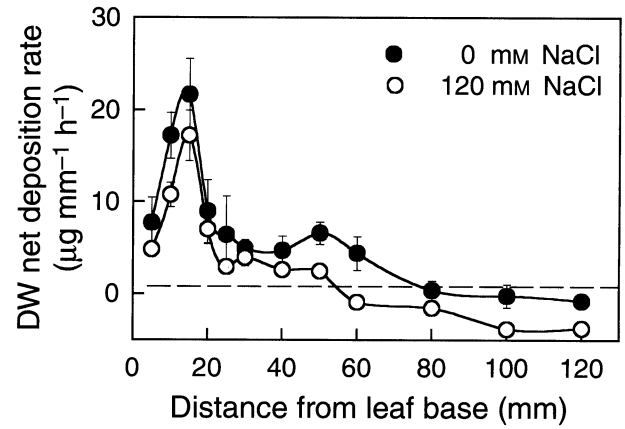

Fig. 4. Spatial distributions of dry weight net deposition rates in the growing leaf 4 of wheat plants with 0 and 120 mM NaCl. Error bars (n = 2–14) represent maximum standard errors and fit within the plot symbol if not otherwise shown.

NaCl (Table 1). NDR of water slightly decreased beyond the elongation zone in both treatments, but there was no difference in the rate of water deposition between the two treatments.

NDR of DW in both treatments increased from the base to the most actively elongating zone at 15 mm from the leaf base and then decreased in both treatments from 15 to 25 mm. Beyond the elongation zone, the net rate of DW deposition decreased slightly. The rate of deposition became negative at 80 and 60 mm from the leaf base for the plants with 0 and 120 mM NaCl, respectively (Fig. 4). With the exception of two locations, 20 and 30 mm from the leaf base, DW deposition rates were consistently higher at 0 mM NaCl than at 120 mM NaCl.

Discussion

Spatial distribution of leaf cellular cross-sectional area

Since most of the tissue water is cellular and non-compressible for the most part, the change in the water content along the leaf axis can be used to describe the spatial distribution of cellular volume per mm leaf length (i.e. cellular cross-sectional area). In general, the spatial distribution of cellular cross-sectional area slightly changed with distance within the elongation zone (Fig. 1*A*). The cellular cross-sectional area of the leaf at 120 mM NaCl was reduced by 32% at 5 mm as compared with about 36% averaged from the region between 5 and 30 mm from the leaf base. This implies that the salinity induced reduction in the cellular cross-sectional area occurred mainly at the leaf base where the leaf initiates. This is further supported by reduction in width, which mainly occurred at leaf base (Fig. 2). In addition, leaf cellular cross-sectional area increased with distance in the growth zone less for both treatments compared with leaf width. This may be due to smaller air spaces near the leaf base because of highly compacted cells there and air space may increase with distance. When leaves were harvested, the leaf segments at 5 mm, which may contain some ligule tissues, caused an overestimation of leaf cellular cross-sectional area at 5 mm for both treatments. However, the overestimation for two treatments at 5 mm was similar, because spatial distribution of the difference in leaf cellular cross-sectional area in the growth zone between two treatments was similar to that of leaf width (Figs 1*A* and 2).

Leaf expansion is the result of water uptake. The local NDR of water describes the expansion of leaves in the three dimensions with time, and is determined by three components of the right-hand side of the continuity equation (Fig. 5). These three components can be used to analyse how the leaf grows with time at a given location and expands in lateral and vertical and longitudinal directions (Silk 1984; Schnyder and Nelson 1988).

The stretch rate, i.e. the change due to longitudinal elongation of the segment, contributes most to the net rate of water deposition, accounting for 82 and 88% of the water

Table 1. Contribution of growth components to the net water deposition rate (μg (growing zone)$^{-1}$ h^{-1}) in the elongation zone (0–30 mm from ligule) in control and salt treatments

Growth components	NaCl (mM) 0	120
Local rate change (I)	245.5	134.6
Convective rate of change (II)	366.6	75.0
Stretch rate (III)	2861.6	1469.4
Net rate of deposition (total)	3473.7	1679.0

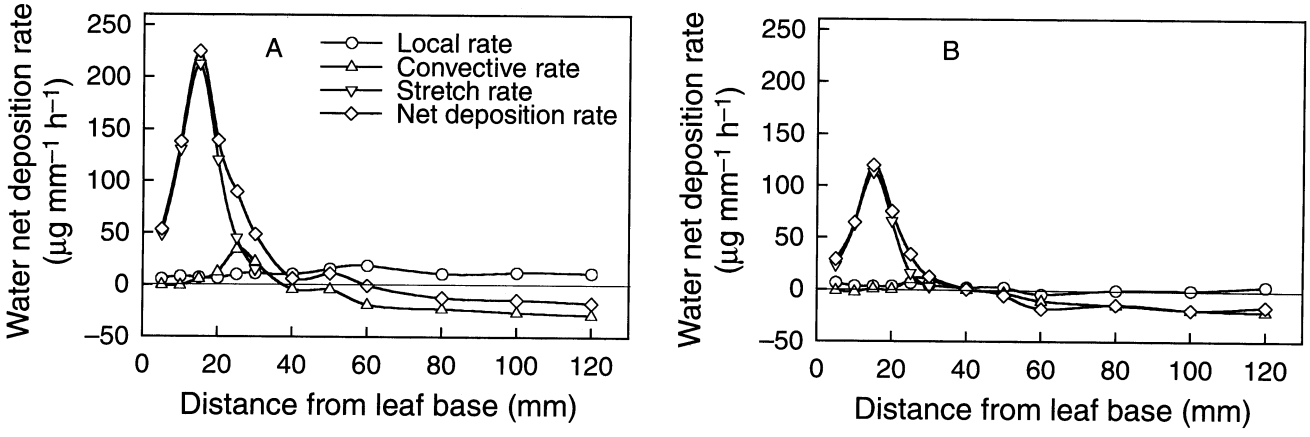

Fig. 5. Components (local rate of change, convective rate of change, and stretch rate) of the net rate of water deposition in the growing leaf 4 of wheat plants with 0 mM NaCl (*A*) and 120 mM NaCl (*B*).

deposition in the elongation zone at 0 and 120 mM NaCl, respectively (Table 1). This confirms that, after the leaf initiates from the leaf base, the expansion of the leaf mainly occurs in length. The local rate of change in water content contributed only about 7% to the total net rate of water deposition in the elongation zone for both treatments (Table 1). This indicates that the spatial distribution of water content within the elongation zone was relatively steady (time invariable). The convective rate of change term is the change due to the movement of cellular particles away from the leaf base, occurring by means of a spatial gradient in water content (Fig. 1*A*). Throughout the elongation zone, 10.6% of the net rate of water deposition was attributed to the convective rate of change in the control treatment, suggesting that expansion laterally and vertically contributed only a small proportion to the overall growth of cells in the elongating tissue (Schnyder and Nelson 1988). Since convective rate and local change rate represent only a small part of the local net deposition of water (Table 1), the reduction in leaf expansion by salinity due to the decreased relative elemental growth rate of leaves (R_s) occurred mainly after the leaf initiated. Thus, this study suggests that the effect of salinity on the leaf expansion occurred during two phases at the steady growth stage. Phase I describes the reduction in the leaf cellular cross-sectional area at the leaf base, and phase II describes the reduction in leaf elongation after the leaf initiates.

At present, it is not clear why the reduction in the cellular cross-sectional area due to salinity occurs mainly near the leaf base. The zone of cell division in grass leaves is located at the leaf base. For tall fescue, epidermal cell division is restricted to the basal 1.5–2 mm (MacAdam *et al.* 1989; Skinner and Nelson 1994). The elongation of grass leaves is always unidirectional and occurs mainly after the cell division zone. Munns and Termaat (1986) reported that cell numbers in grass leaves were significantly reduced by salinity. In this study, the data of the spatial effect of salinity on leaf cellular cross-sectional area do not allow to see how salinity affects the cell division; nevertheless, they give an indication that the reduced cellular cross-sectional area may be due to the effects of salinity on cell division and cell expansion. Salinity delays leaf emergence, indicating the primordia formation is also delayed under saline conditions, which most likely represent effects on cell division. In and near the meristem, cells are not vacuolated. There is vascular discontinuity between stem and leaf vessels in the cell division zone of the leaf base, requiring that transport through the leaf division zone and into the developing vascular systems of the expanding zone rely either on symplastic transport or transport through thin cell walls (Lazof and Bernstein 1999). The requirement for continuous nutrient supply to maintain the mineral status within rapidly expanding tissue renders the meristematic region highly susceptible to nutrient disturbances. Some additional likely mechanisms are that salinity causes ionic imbalance and disturbance of carbon metabolism in the elongation zone of grass leaves under saline conditions (Munns *et al.* 1982; Bernstein *et al.* 1995; Hu *et al.* 2000*b*; Hu and Schmidhalter 1998*a*) and by water deficit. Besides possible causes of ion toxicity and ion imbalance due to salinity; however, the causes for the reduction in the longitudinal elongation of leaves under saline conditions (i.e. Phase II) may be directly due to either decreases in the turgor pressure and cell wall extensibility or increase in yield threshold. Recent studies revealed that no decrease in turgor pressure (measured with a pressure probe) occurred in the elongating cells for wheat under saline conditions (Arif and Tomos 1993). Our previous study of osmotic adjustment in the elongating tissue of wheat leaves showed that turgor pressure of elongating tissues was maintained under saline conditions in the steady growth phase (Hu and Schmidhalter 1998*b*). However, reports in the literature demonstrated that under saline conditions, decreases in the cell wall extensibility of maize leaves (Cramer and Bowman 1992; Neumann 1993) and

increases in the yield threshold of maize leaves (Cramer and Bowman 1992) may be responsible for the reduction in leaf elongation.

Spatial distribution of DW

DW content (mg per mm leaf length) is relatively high at the base in both treatments (Fig. 1*B*), where cells are closely packed and divide actively (MacAdam and Nelson 1987). During the period of most active elongation, the growing leaf of wheat presents three functionally distinct zones, i.e. the elongation (0–30 mm above the leaf base), the secondary cell wall deposition (30–60 mm), and the exposed photosynthetically active zone (> 60 mm) (Hu *et al.* 2000*b*). The zones of elongation and secondary cell wall deposition are the regions of the highest biosynthetic activity, and are strong sinks for carbon photosynthate (Allard and Nelson 1991). The DW content decreased from the leaf base up to 25 mm for both treatments, due to dilution with water (Figs 1*A*, *B*). Beyond 25 mm from the leaf base, an increase in DW content up to 50–60 mm is probably due to an increase in secondary cell wall deposition (MacAdam and Nelson 1987; Schnyder and Nelson 1988). However, the decrease in DW content beyond 60 mm from the leaf base is mainly due to the decrease in the cellular cross-sectional area along the leaf axis (Fig. 1*A*).

The DW (mg mm^{-1}) was slightly higher at 0 mM NaCl than 120 mM NaCl (Fig. 1*B*). High ratios of the NDR of DW to the NDR of water under saline conditions imply that the reduction in cell expansion rate was greater than in the NDR of DW. The study by Hu *et al.* (2000*b*) showed that salinity did not affect the sucrose import rate in the sink (the elongation and secondary cell wall deposition zone), and only changed the partitioning of imported sucrose to water soluble carbon and structural carbon. Thus, the slight decrease in the DW per leaf length at a given location in the elongation zone may be due to the strongly decreased cellular cross-sectional area by salinity. This suggests that the limitation of leaf growth by salinity may be due mainly to the effect of salinity on the leaf expansion, but not due to the effect on the deposition (i.e. synthase) of dry matter.

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