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Spatial distributions and net deposition rates of Fe, Mn and Zn in the elongating leaves of wheat under saline soil conditions

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Abstract. In this study, we quantified the spatial distributions of Fe, Mn and Zn and their net deposition rates in the elongating and mature zones of leaf 4 on the main stem of spring wheat (*Triticum aestivum* L.) on a millimetre scale during its linear growth phase under saline soil conditions. Plants were grown in an illitic-chloritic silty loam with 0 and 120 mM NaCl in growth chambers. The sampling was conducted on the 3rd day after leaf 4 emerged during the photoperiod. The patterns of spatial distributions of Fe, Mn and Zn concentrations (mmol kg^{-1} FW) in the growing leaves were distinct. Salinity affected the distribution pattern of Fe concentration on the FW basis, whereas it did not affect those of the Zn and Mn. The distribution patterns of Fe and Mn differed from those for N, P, K, Ca and Mg found in a previous study, whereas the distribution pattern of Zn was similar to those of Mg, P and N. The spatial distribution of the net deposition rates (mmol kg^{-1} FW h^{-1}) in both treatments demonstrated the strongest sink for the micronutrients in the elongation zone, and their net deposition rates were enhanced by 120 mM NaCl at the middle of the elongation zone. From the results, we conclude that the inhibition of leaf growth of wheat is probably not due to the effect of salinity on Fe, Mn and Zn in leaves.

Keywords: elongating leaf, micronutrients, net deposition rate, saline soil, *Triticum*.

Introduction

The vegetative stage, which establishes the final yield potential in wheat plants, is most sensitive to salinity (Munns and Termaat 1986; Maas and Poss 1989; Arif and Tomos 1993; Hu *et al.* 1997). In the vegetative stage, leaf development largely determines the rate of wheat growth. Our earlier study (Hu 1996) showed that the final length and the averaged width of leaves on the main stem of wheat plants treated with 120 mM NaCl were both reduced by more than 20% as compared with those in control conditions.

The elongation of a growing leaf of grasses is restricted to a small region at the base of the blade enclosed by sheaths of older leaves (Kemp 1980). Along the leaf elongation zone, there is a gradient of cell development, which causes spatial distributions of nutrients along the leaf axis. The studies have shown that water-soluble carbohydrates (sucrose, glucose, fructose and fructan) and macronutrients (N, P, K, Ca and Mg) are spatially distributed along the grass leaves (Schnyder and Nelson 1987; Meiri *et al.* 1992; Bernstein *et al.* 1995; Hu and Schmidhalter 1998*a*). They also show that the elongation zone is a strong sink for nutrients. Therefore, the leaf growth of grasses under control and stress conditions should be much more closely associated with metabolic / nutritional changes within the most actively growing tissues than the whole or non-growing tissues. Although previous studies reported the effect of salinity on macronutrients along the elongation zone of sorghum leaves (Bernstein *et al.* 1995) and along the growing leaves of wheat (Hu and Schmidhalter 1998*a*), there is no information available for the spatial distributions of micronutrient in the growing leaves of grasses under saline conditions.

Many studies have reported micronutrients and their uptake rates within plants, but most studies have only focused on whole plants or non-growing tissues. Moreover, the results from previous reports were not always in agreement. For example, salinity increased Fe concentration in the shoots of pea (Dahiya and Singh 1976), tomato (Maas *et al.* 1972), and rice (Verma and Neue 1984), but decreased its concentration in the shoots of barley and corn (Hassan *et al.* 1970*a*, *b*). Salinity also increased the Mn and Zn concentrations in the shoots of barley (Hassan *et al.* 1970*a*), tomato (Maas *et al.* 1972) and rice (Verma and Neue 1984), but decreased them in corn (Hassan *et al.* 1970*b*). Interestingly, only a few studies dealt with the micronutrients in the leaves of grasses affected by salinity, but in the non-growing regions of leaves at seedling stages or at final harvest (corn, Hassan *et al.* 1970*b*; Sorghum, Francois *et al.* 1984; wheat, Y. Hu and U. Schmidhalter, unpublished data).

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 in growing leaves of grasses, and thus to investigate sink and source relationships (Gandar 1980; Silk 1984). This type of analysis was used to study the effects of salinity on the net deposition rates of macronutrients in the elongation zone of sorghum and wheat (Meiri *et al.* 1992; Bernstein *et al.* 1995; Hu and Schmidhalters 1998*a*). However, there is no information

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available on the net deposition rates of micronutrients in the growing leaves of wheat plants under saline conditions.

The objective of this study was to quantitatively evaluate the spatial distribution of micronutrients, e.g. Fe, Mn and Zn, 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 treated with 0 or 120 mM NaCl.

Materials and methods

Growth conditions

Six seeds of spring wheat (*Triticum aestivum* L. cv. Lona) in each pot, pre-germinated for two days on filter paper moistened by tap water at 20°C, were sown in a 1.5 L pot (10 cm diameter × 20 cm height; 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 and by adding 0.5-strength micronutrients as recommended by Epstein (1972). Because the soil has a very high affinity for absorption of P, especially for the calcareous soil used in this study, the Hoagland solution for macronutrients was modified by increasing the phosphate concentration 10-fold to provide optimum phosphate concentration based on the study by Studer (1993). The composition of the modified Hoagland nutrient solution was (in mM): 6.05 K, 15.0 N, 5.0 Ca, 2.0 Mg, 10.0 H_2PO_4 and 2.0 SO_4. 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 one 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 the growth chambers with a 16-h light period per day. The photosynthetic photon flux density (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 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 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. 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 concentration.

Analysis of Fe, Mn and Zn concentrations

Dry samples from different positions in the leaf 4 of the main stem were ground by hand with a glass rod into test tubes. The total and water-soluble concentrations of ions were measured by the following methods:

Total concentrations of Fe, Mn, and Zn: approximately 25-mg plant samples were ashed at 560°C for 6 h and digested with 1 mL 20% HCl at 65°C for 5 min and then diluted to 25 mL. Water-soluble concentrations of Fe, Mn, and Zn: 20-mg ground samples were extracted with 2 mL distilled water at 100°C for 5 min, shaken for about 1 min and then filtered with a Millex-HV_{13} filter unit.

The concentrations of Fe, Mn, and Zn were determined with an inductively coupled plasma emission spectrometer (ICP model Liberty 200; Varian Australia Pty. Ltd., Mulgrave Victoria, Australia).

Numerical methods

Local net deposition rates (D, mmol kg^{-1} FW h^{-1}) of micronutrients like Fe, Mn and Zn were calculated according to the one-dimensional version of the continuity equation as described by Silk (1984):

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

where P is substance density (e.g. mmol kg^{-1} FW); t is time (h); x is distance (mm) from the base of the leaf blade, R_s is the relative segmental 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 harvests. The calculation of the $\partial P/\partial t$, $V_d \cdot (\partial P/\partial x)$, and $R_s \cdot P$ 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 randomised complete block design was used. Effects of salinity, harvest time (0900 h and 1900 h) and their interactions were evaluated by analysis of the 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 the variance. Because parameters such as P, V_d and R_s in the equation were from the experiments with different replicates, the variance for the net deposition rates of substances was in terms of a maximum standard error. This was estimated from a method described by Precht and Kraft (1992) and Precht *et al.* (1994). For example, if y is a function of x_1, x_2, ..., x_n, i.e. $y = f(x_1, x_2, ..., x_n)$, and x_i (i=1, 2, ..., n) has a standard error Δx_i (i=1, 2, ..., n), then the maximum standard error for y is:

$$\Delta y = \left|\frac{\partial y}{\partial x_1}\right| \Delta x_1 + \left|\frac{\partial y}{\partial x_2}\right| \Delta x_2 + ... + \left|\frac{\partial y}{\partial x_n}\right| \Delta x_n = \sum_{i=1}^{n} \left|\frac{\partial y}{\partial x_n}\right| \Delta x_n$$

Because the partial differentiation ($\partial y/\partial x_i$, i=1, 2, ..., n) can be negative, absolute values must be applied. Terms were considered significant at $P \leq 0.05$.

Results

Spatial distributions of total Fe, Mn and Zn concentrations

Iron concentration (mmol kg^{-1} FW) at 0 mM NaCl slightly decreased with distance to reach a minimum at the end of the elongation zone and then increased with distance (Fig. 1*A*). On the other hand, at 120 mM NaCl this remained unchanged from the leaf base up to the end of the elongation zone and then increased with distance again. In general, the Fe concentration within the whole leaf was higher at 120 mM NaCl than at 0 mM NaCl. Time did not affect the Fe concentration along the leaf axis regardless of the treatments.

The spatial distribution of Mn concentration along the leaf axis and the effect of salinity on the pattern of the distribution was similar to those for Fe (Fig. 1*B*). There was no time effect on those patterns in the two treatments.

Zinc concentration decreased with distance from the leaf base to reach a minimum at the end of the elongation zone

and then slightly increased or remained unchanged in both treatments (Fig. 1*C*). Zn concentration was consistently higher at 120 mM NaCl than at 0 mM NaCl.

Because the width of leaf 4 varied with leaf distance, and the averaged width was reduced by about 20% due to 120 mM NaCl (Hu 1996), Figs 1*D–F* show that there were different patterns of micronutrient distributions in the growing leaf 4 on a millimetre basis from those on the FW basis. On the DW basis, the patterns of spatial distribution for all three micronutrients were generally similar to those on the FW basis in both treatments at two harvests (data not shown). The concentration of Mn was consistently higher at 120 mM NaCl than at 0 mM NaCl on the DW basis. However, there was no difference in the concentrations of Fe and Zn (mmol kg^{-1} DW) between the control and salinised treatments.

Spatial distributions of water-soluble Fe, Mn and Zn concentrations

The concentration of water-soluble Fe started to increase with distance except that at 5 mm above the leaf base at 120 mM NaCl (Fig. 2*A*). The water-soluble Fe concentration between the two treatments differed only at the locations of about 5 mm and at 120 mm above the leaf base. The water-soluble Mn concentration increased with distance in the two treatments. Salinity affected the water-soluble Mn concentration from 15 mm to the leaf tip (Fig. 2*B*). No time effects on the water-soluble Fe and Mn concentration were observed in both treatments.

The water-soluble Zn concentration decreased with distance from the leaf base to about 15 mm and then increased with distance up to the end of the leaf elongation zone in the non-salinised treatment and up to 50 mm above the leaf base at 120 mM NaCl (Fig. 2*C*). Beyond the elongation zone at 0 mM NaCl and beyond 50 mm above the leaf base at 120 mM NaCl, the water-soluble Zn concentration decreased slightly with distance except that at 0 mM NaCl at 0900 h.

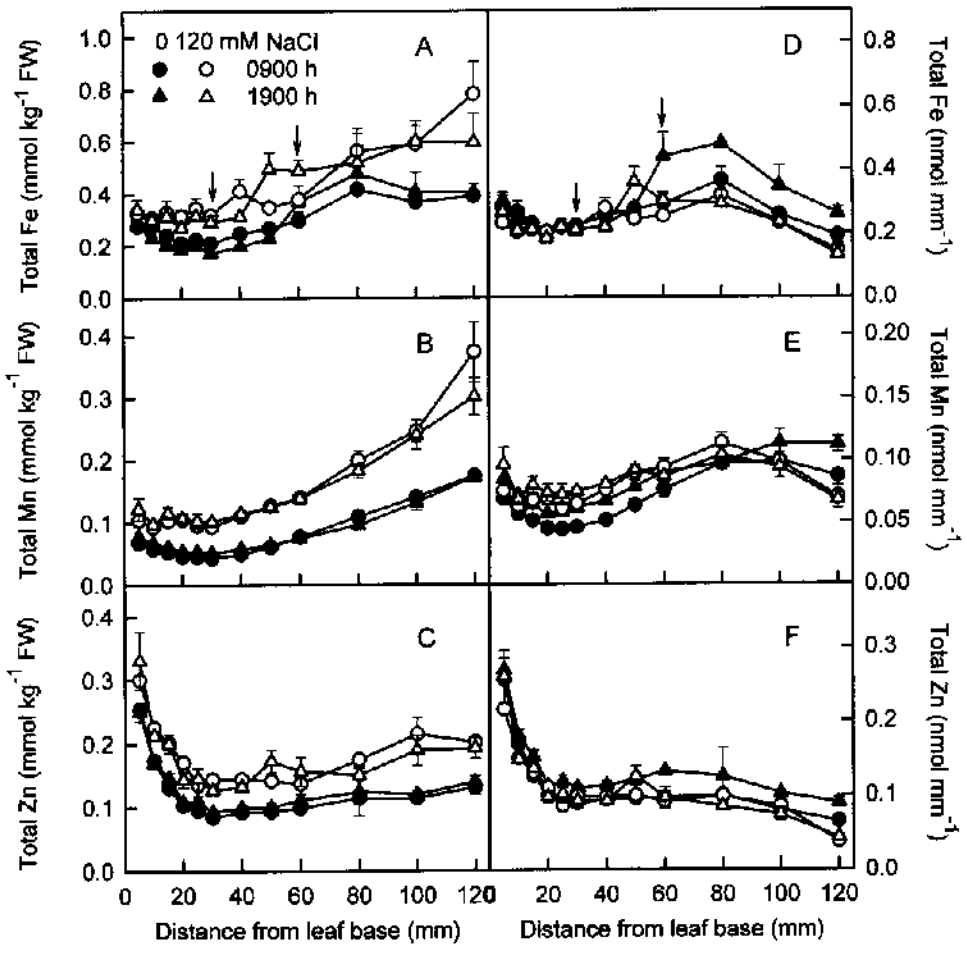

Fig. 1. Spatial distributions of total iron (*A*), manganese (*B*) and zinc (*C*) concentrations on the FW basis (mmol kg^{-1} FW) and total iron (*D*), manganese (*E*) and zinc (*F*) contents on a millimetre basis in the growing leaf 4 of the main stem of wheat plants grown in soil with 0 and 120 mM NaCl at two harvest times (0900 and 1900 h). Error bars represent standard errors. Error bars ($n = 2$; each replicate consisted of 120 subsamples from different plants) fit within the plot symbol if not otherwise shown. The first arrow indicates the end of the elongation zone and the second shows the end of the leaf sheath.

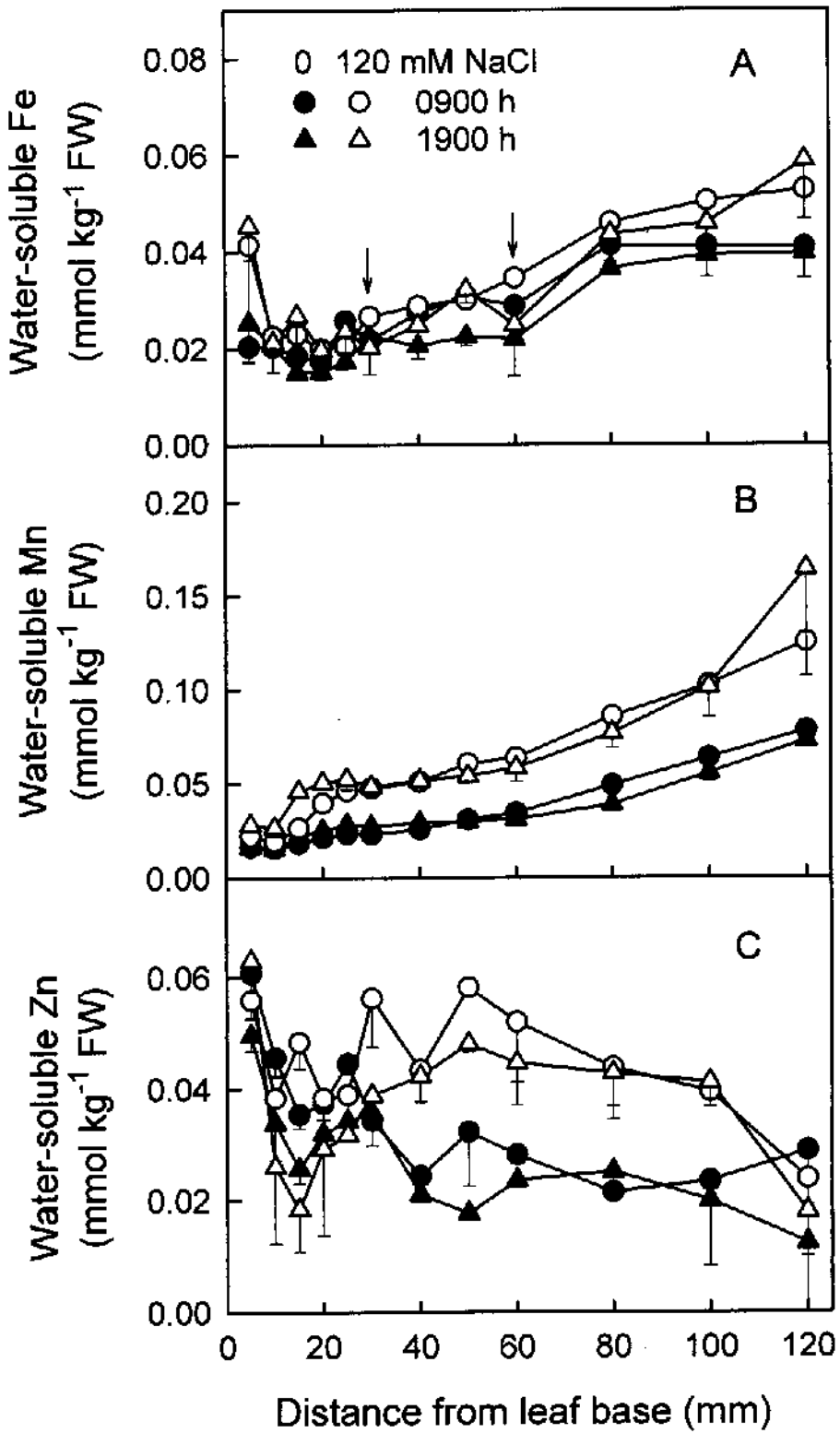

Fig. 2. Spatial distribution of water-soluble iron (*A*), manganese (*B*), and zinc (*C*) concentrations (mmol kg^{-1} FW) in the growing leaf 4 of the main stem of wheat plants grown in soil with 0 and 120 mM NaCl at two harvest times (0900 and 1900 h). Error bars represent standard errors. Error bars ($n = 2$; each replicate consisted of 120 subsamples from different plants) fit within the plot symbol if not otherwise shown. The first arrow indicates the end of the elongation zone and the second shows the position of the end of the leaf sheath.

Since there was no significant difference between the two harvest times (Fig. 2), the percentages of water-soluble Fe, Mn and Zn to their total concentrations in leaf tissue along the leaf axis were calculated from the averaged results of both harvests, and are presented in Fig. 3. Except the fraction of water-soluble Fe at 0 mM NaCl at the base and at 120 mM NaCl in the region between 20 and 60 mm, the fraction remained nearly unchanged in the growing leaf. The percentages of water-soluble Mn and Zn generally increased with distance in the elongation zone, whereas they did not change or decreased with distance beyond the elongation zone. In this study, salinity decreased the fractions of water-soluble Fe and Mn in the region between 20 and 60 mm above the base and the fraction of water-soluble Zn in the elongation zone.

Net deposition rates of total Fe, Mn and Zn

The spatial distribution of the net deposition rates for all three elements in leaf 4 of the main stem in both treatments had a similar pattern in the elongation zone that demonstrated the strongest sink for the micronutrients, while the distribution patterns varied among three elements in the more mature region of the leaf (Fig. 4).

The maximum net deposition rates of Fe, Mn and Zn (mmol kg^{-1} FW h^{-1}) occurred at about 15 mm above the leaf base and reached a minimum at about the end of the leaf elongation zone (Fig. 4). Net deposition rate of Fe increased again from 30 to about 50–60 mm above the leaf base and then decreased up to the leaf tip with distance, whereas net

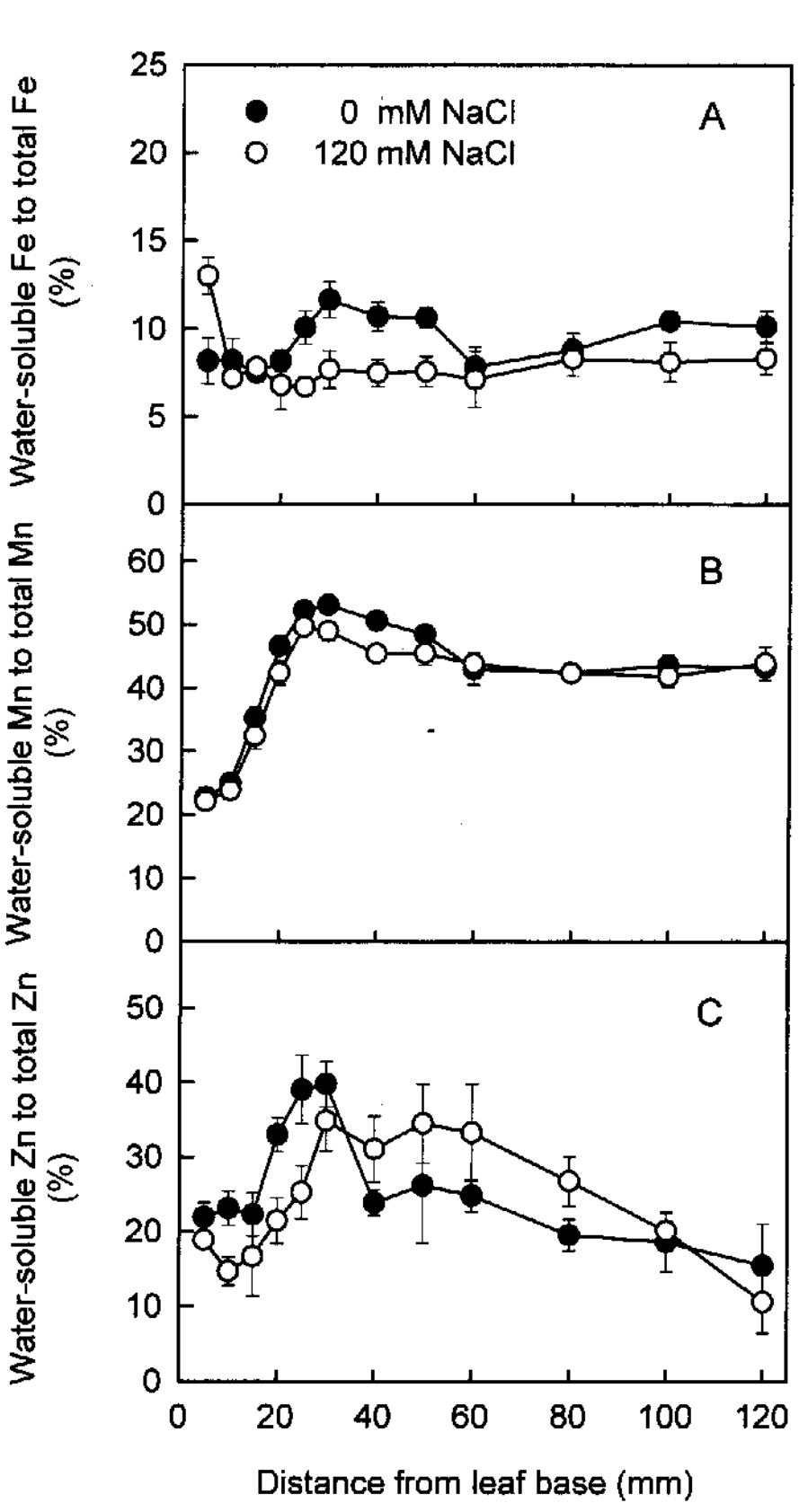

Fig. 3. The fractions of the water-soluble to total iron (*A*), manganese (*B*), and zinc (*C*) concentrations in the growing leaf 4 of wheat. Error bars ($n = 2$) represent maximum standard errors and fit within the plot symbol if not otherwise shown.

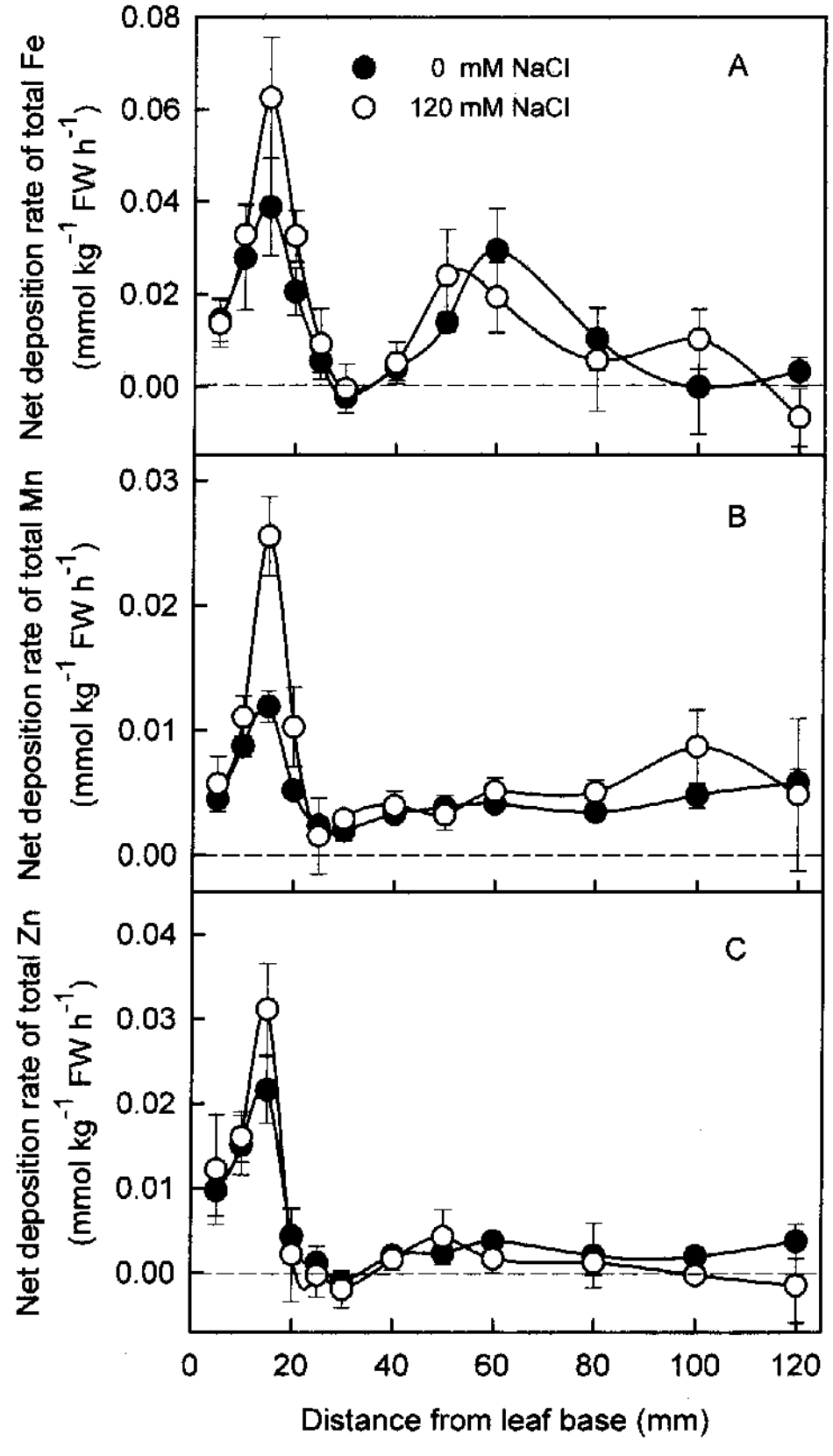

Fig. 4. Spatial distributions of net deposition rates of iron (*A*), manganese (*B*) and zinc (*C*) (mmol kg^{-1} FW h^{-1}) in the growing leaf 4 of wheat plants grown in the soil with 0 and 120 mM NaCl. Error bars ($n = 2$ to 14) represent maximum standard errors and fit within the plot symbol if not otherwise shown.

deposition rates of Mn and Zn in the mature zone slightly increased or remained unchanged.

The greatest effect of salinity on the net deposition rate of Mn occurred in the region between 10 and 25 mm above the leaf base (Fig. 4*B*). The differences in the net deposition rates of Fe and Zn in the elongation zone between the two treatments were not significant. The net deposition rates of these three elements from the end of the elongation zone to the distal of the leaf were not affected by 120 mM NaCl (Fig. 4).

Discussion

The vegetative stage, which establishes the final yield potential in wheat plants, is the most sensitive to salinity (Munns and Termaat 1986; Maas and Poss 1989; Arif and Tomos 1993; Hu *et al.* 1997). In the vegetative stage, leaf development largely determines the rate of plant growth of wheat. As a gramineous leaf, the leaf elongation of wheat is restricted to a small region near the base and enclosed by sheath (Kemp 1980). Our early study (Hu 1996) showed that the elongation rate of wheat leaves on the main stem was reduced by about 20–30% at 120 mM NaCl. The elongation rate of gramineous leaves is related to their length of the elongation zone and relative elemental growth rate (REGR). The REGR of wheat leaves was reduced by salinity, but the length of the growth zone was not affected (Hu 1996). Salinity did not only reduce the leaf length, but it also reduced the width of wheat leaves. For leaf 4 of wheat, for example, the averaged width was reduced by also about 20% at 120 mM NaCl, and 90% of the reduction in the leaf width occurred at the base (Hu 1996). Because the growth reduction of leaves occurs in the elongation zone, the effects of salinity or other stresses on growth of wheat should be much more closely associated with metabolic / nutritional changes within the growing tissues of leaves than in whole or non-growing leaf tissues. Moreover, the REGR of grass leaves is spatially distributed within the elongation zone (Kemp 1980). For example, our study (Hu 1996) showed that the REGR of wheat leaves was maximum at the middle of the elongation zone and minimum at the base and at the end of the elongation zone. Thus, the study of spatial distribution of nutrients in the growing leaves will contribute to our understanding of the physiological roles in gramineous leaf growth. To our knowledge, this is the first report about the spatial distributions of micronutrients in the elongating and maturation regions of the growing leaves.

Although a few studies dealt with the micronutrients in gramineous leaves under saline conditions (corn, Hassan *et al.* 1970b; sorghum, Francois *et al.* 1984; wheat, Y. Hu and U. Schmidhalter, unpublished data), there are no reports about the effect of salinity on micronutrients in the growing region of leaves. Although these studies demonstrated that there were consistently significant decreases in the leaf growth, Fe, Mn and Zn concentrations in leaves were increased, decreased or not changed by salinity. For example, salinity decreased Fe, Mn and Zn in mature leaves of corn (Hassan *et al.* 1970*b*), whereas salinity increased the concentration of those ions in wheat leaves at final harvest (Y. Hu and U. Schmidhalter, unpublished data). Francois *et al.* (1984) reported that salinity increased Mn and Zn concentrations in the non-growing tissues of sorghum leaves, but did not affect the Fe concentration.

In this study, the results show spatial distribution of Fe, Mn and Zn concentrations along the leaf axis. Salinity did not affect the pattern of distribution of Mn and Zn concentrations on the FW basis, whereas it altered that of Fe (Fig. 1). Because there was no difference between the two treatments in the elongation zone on the DW basis (data not shown), the increased Fe and Zn concentrations in the elongation zone may be due to the lowered relative water content (RWC) under saline conditions. However, the increased Mn concentration in the elongation zone at 120 mM NaCl may result from the high net deposition rate of Mn in the elongation zone (Fig. 4*B*). According to the optimal ranges of Mn concentration (0.4–5.5 mmol kg^{-1} DW) in the leaves generalised for various plant species (Jones 1991; Bennett 1993), however, the level of Mn in the leaf at 120 mM NaCl, e.g. about 0.6 mmol kg^{-1} DW at the leaf base and 1.5 mmol kg^{-1} DW at the leaf tip, did probably not reach toxic levels. Furthermore, as compared with the effect of salinity on NO_3, Cl, and K in the growing leaves of wheat in our early study (Hu and Schmidhalter 1998*a*), the Fe, Mn and Zn concentrations in leaves were less affected by salinity. Therefore, we conclude that limitation of leaf expansion is probably not due to the effect of salinity on the micronutrients in the elongation zone and mature regions.

The distributions of micronutrients in the growing gramineous leaves present distinctive patterns, which are probably related to their biochemical and physiological functions in the different regions of a growing leaf. The two major patterns of spatial distributions of nutrient concentrations in the elongating gramineous leaves have been found: i) ionic concentrations were lower at the leaf base and reached their maximum at the end of the elongation zone and then decreased with distance (Cl and NO_3) and ii) ionic concentrations were higher at the leaf base and reached the minimum at the end of the elongation zone and then remained nearly unchanged with distance (Mg, P and total N) (Meiri *et al.* 1992; Evéquoz 1993; Gastal and Nelson 1994; Bernstein *et al.* 1995; Hu and Schmidhalter 1998*a*). The first pattern of spatial distribution may be due to these ions that are preferentially localised in the vacuoles, because vacuoles are relatively small at the leaf base compared with the larger volume of vacuoles at the end of the elongation zone; the decrease beyond the elongation zone might be due to the increase in the retranslocation rate of Cl and in the reduction of NO_3 (Hu and Schmidhalter 1998*a*). The second pattern of spatial distributions may be due to the small cells at the leaf base that contain a large proportion of proteins and nucleic

acids in contrast to more distal cells. In this study, the spatial distributions of Fe and Mn concentrations showed the different pattern from those for the elements reported in previous studies (Meiri *et al.* 1992; Evéquoz 1993; Gastal and Nelson 1994; Bernstein *et al.* 1995; Hu and Schmidhalter 1998*a*) (Figs 1*A* and *B*). Iron and Mn concentrations slightly decreased or remained unchanged in the elongation zone and increased consistently with distance beyond the elongation zone. However, the pattern of the spatial distribution of Zn concentrations showed a similar pattern to the second one (Fig. 1*C*), which is related to the large proportions of proteins and nucleic acids.

The spatial distributions of Fe and Mn concentrations are probably associated with their function in the chloroplasts. The growing gramineous leaves contain a complete age sequence of cells from the base to the tip and within these tissues all stages of chloroplasts could be developed. Although chloroplasts develop progressively along the leaf axis, a marked increase in number of thylakoids per granum, in chloroplast volume, and in chlorophyll concentration started beyond the end of the elongation zone of *Avena* leaves before the leaf emerges above the sheath (Nakamura and Hashimoto 1988). This is coincident with the change in Fe and Mn concentrations with distance. It has been reported that 80% of Fe is located in the chloroplasts (Marschner 1995). A pool of tightly bound Mn is found in the chloroplasts where amounts of 6 atoms per 400 molecules of chlorophyll are required (Burnell 1988). Thus, the increase in the chlorophyll content with distance is probably a main reason why the Fe and Mn concentrations increased sharply with distance beyond the elongation zone. The increase in the concentrations of Fe and Mn continued beyond the end of the leaf sheath. The highest concentration of Fe and Mn in the leaf tip may suggest that within the leaf Mn and Fe are not readily retranslocated against the transpiration stream.

Since the small cells at the base contain a large proportion of the protein, RNA, and nucleic acid, the high Zn concentration near the leaf base indicates that Zn like N, P and Mg may be related to the compounds of protein, RNA and nucleic acids (Fig. 1*C*). A remarkably high concentration of Zn is required in meristematic tissues of rice leaves where cell division as well as synthesis of nucleic acids and proteins occurs (Kitagishi and Obata 1986). The sharp decline in the Zn concentration with distance within the elongation zone may be due to taking up water more rapidly than Zn to the tissues.

Because a proportion of Fe, Mn and Zn in leaves is not physiologically available, e.g. due to the precipitations (van Goor and Wiersma 1974; Cakmak and Marschner 1987; Mengel and Geurtzen 1988), the total concentration of these ions may actually not reflect their active ions in leaves. It has been reported that the fractions of Fe in leaves extracted with dilute acids or chelators (Mengel and Bübl 1983) and of the water-soluble Mn and Zn (Horst and Marschner 1978; Cakmak and Marschner 1987) could be considered to be a better indicator for the physiologically active part compared with their total concentrations. In this study, the water-soluble Fe, Mn and Zn concentrations were determined. Although data of the extraction of Fe content with diluted acid and chelators is not available in this study, the greatest fraction of water-soluble Zn and the lowest fraction of water-soluble Fe in the growing leaves may reflect their different mobility, i.e. Zn may have higher mobility than Mn and Fe in leaves (Fig. 3). However, further study may be required on what causes the different patterns of spatial distributions of the fractions of water-soluble Fe, Mn and Zn in the growing leaves of grasses.

In conclusion, the patterns of spatial distributions of Fe and Mn and Zn concentrations in growing leaves present two different patterns that are probably related to their physiological functions in wheat leaves. The patterns of spatial distributions of Fe, Mn and Zn concentration (mmol kg^{-1} FW) in the growing leaves were distinct. Salinity affected the distribution pattern of Fe concentration on the FW basis, whereas it did not affect those of the Zn and Mn. The elongation zone was the strongest sink for micronutrients in the leaf tissues. Net deposition rate of Mn (mmol kg^{-1} FW h^{-1}) in the most actively elongating zone was significantly enhanced by 120 mM NaCl. Although salinity increased the Fe, Mn and Zn concentrations in wheat leaves, the decreased leaf growth is probably not due to the effect of salinity on these micronutrients in the growing leaves of wheat.

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