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Short-term effects of drought and salinity on mineral nutrient distribution along growing leaves of maize seedlings

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Abstract

The objectives were to study the effect of drought and salinity on the spatial distribution of mineral nutrients along the growing leaves of maize. Maize plants were grown in a greenhouse in soil under drought and saline conditions for 23 days after sowing. At harvest, the spatial distribution of fresh weight and dry weight contents and mineral nutrient concentrations along growing leaves 4 and 5 of maize was determined. Drought and salinity reduced the fresh weight content regardless of leaf number and caused a similar reduction. However, they affected the dry weight content differently, resulting from the reduction in the relative water content by drought. The results showed that the change in ion concentration along the growing leaf axis for most ions is independent of treatments. Although both drought and salinity cause a low nutrient availability in soil and low nutrient transport in plants, this study showed that except for Na⁺, there was no difference in the concentrations of most ions at any given location between plants in the control and either of the drought or saline treatments. Thus, reduction in leaf growth under drought and saline conditions may be due to other causes rather than the limitation of nutrients in a short-term period of drought and salt stresses.

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Keywords: Drought; Growing leaves; Maize; Mineral nutrients; Salinity

1. Introduction

Maize is one of the major food crops in most of the countries where drought and salinity problems exist or may develop. In the early growth stages, leaf growth is one of the most sensitive processes to drought and salinity (e.g. Tardieu et al., 2000; Neves-Piestun and Bernstein, 2005). Because drought and salinity both lower the soil water potential, similar physiological mechanisms such as the water deficit or osmotic effect in plants might explain the reduction in plant growth. Therefore, considerable attention has been focused on comparing the differential responses of plant growth under drought and salinity that are mediated by the lowered soil water potential (e.g. Shalhevet and Hsiao, 1986; Schmidhalter and Oertli, 1991; Munns, 2002). Under drought stress, nutrient uptake by the roots is reduced, in part because the decline in soil moisture results in a decreased rate of diffusion of nutrients from the soil matrix to the absorbing root surface (Viets, 1972; Pinkerton and Simpson, 1986).

Moreover, nutrient transport from the roots to the shoots is also restricted by the reduced transpiration rates and impaired active transport and membrane permeability, altogether resulting in a reduced root adsorbing power of crop plants (Hsiao, 1973; Kramer and Boyer, 1995). Thus, the reduced nutrient availability is one of the most important factors limiting plant growth under drought. Under saline conditions, however, soils contain extreme ratios of Na⁺/Ca²⁺, Na⁺/K⁺, Ca²⁺/Mg²⁺, and Cl⁻/NO₃⁻, leading to specific ion toxicities (e.g. Na⁺ and Cl⁻) and ionic imbalance (Grattan and Grieve, 1999).

To better understand the physiological mechanisms involved in both stresses, it is important to examine both conditions. In grasses such as maize, the elongation of the growing leaves 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. Studies have shown that water-soluble carbohydrates, macronutrients (N, P, K⁺, Ca²⁺ and Mg²⁺) and micronutrients (Fe, Mn and Zn) are spatially distributed along the grass leaves (Schnyder and Nelson, 1987; Bernstein et al., 1995; Meiri et al., 1992; Hu and Schmidhalter, 1998a; Hu et al., 2000; De Lacerda et al., 2003;

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Neves-Piestun and Bernstein, 2005), and that the growing tissues are a strong sink for nutrients. Therefore, metabolic or nutritional changes associated with control and stress conditions should be much more closely linked with the most actively growing tissues than with the whole or non-growing tissues. Although previous studies reported the effect of salinity on macro- and micronutrient distribution along the growing leaves of sorghum (Bernstein et al., 1995; De Lacerda et al., 2003), wheat (Hu and Schmidhalter, 1998a; Hu et al., 2000) and maize (Neves-Piestun and Bernstein, 2005), there is no information available for the spatial distributions of these nutrients in the growing leaves of grasses under drought conditions and for the comparative responses of different species to drought and salinity stresses.

Therefore, to more fully understand the nutrient disturbance in plants under drought and salinity, the objectives of this study were to investigate the effect of these conditions on the spatial distribution of macro- and micronutrients along the growing leaves of maize and to compare the ion distribution in the growing leaves under drought and salinity.

2. Materials and methods

2.1. Plant materials and growth conditions

Maize (*Zea mays* L. cv. Rasant) seeds were pre-germinated for 1 day, after which 10 seeds of maize were sown in 7-l pots filled with loamy soil. One week after sowing, the seedlings were thinned to seven per pot. The experiment was carried out in a greenhouse. The daily air temperature ranged from 37 °C (maximum at day) to 10 °C (minimum at night), with the daily average temperature being about 20 °C. Relative humidity fluctuated between 30 and 85%; the average value was about 60%.

Loamy soil was collected from the soil surface (0–15 cm), air-dried, ground, passed through a 5-mm mesh screen, and thoroughly mixed. The soil consisted of 23% clay, 48% silt and 29% sand, and the organic matter content was 1.66%. The pH (CaCl₂) was 5.7. The air-dried soil, with a gravimetric water content of 8%, was filled layer-wise in six layers in 7-l pots. To obtain the final value of 20% soil gravimetric water content, the nutrient solution with or without NaCl was added to each layer. Nitrogen was applied as 0.2 g NH₄NO₃ per pot. Both the water content and amount of nutrient was optimal for plant growth according to our previous tests. For the salinized treatment, the final concentration of 100 mM NaCl was obtained by adding NaCl to the nutrient solution and applying it to the top soil layer 10 days after sowing. To reduce evaporation, 400 g of coarse sand (2 mm in diameter) was placed on the soil surface for all treatments. For the control and salinized treatments, the pots were weighed daily and the water loss was replaced by adding tap water during the experiment as necessary. The drought stress was started at day 18 after sowing by replacing only 1/4 of water loss after this time. During drought period, the soil matric potentials decreased from –0.2 bars at day 19 to –4 bars at day 23 after sowing. Salinity treatment at 100 mM NaCl caused a soil osmotic potential of about –4 bars. Ideally, to compare drought and salinity effects, similar soil water potentials for the two treatments should be

imposed. Practically, it was difficult to achieve this. Thus, we compared the physiological effect of these two stresses at harvest time when the growth of plants showed a similar reduction as compared with control plants.

2.2. Analysis of plant growth and tissue sampling of growing leaves

The accumulation of evapotranspiration and evaporation were determined by respectively weighing the pots with and without the plants daily. Maize plants were harvested at day 23 after sowing. Shoot fresh weight (FW) was determined. At the final harvest, leaves 4 and 5 were still expanding. These two youngest leaves were carefully removed from the shoot, which was enclosed in the older leaf sheath.

The growing leaves of the maize plants were cut into different segments along the leaf axis to study the effect of drought and salinity on the mineral elements present in the different tissues. A growing grass plant consists of several functional zones as defined by characteristics of tissues. According to the age of a growing leaf, these zones include the growth, secondary deposition (enclosed mature tissues in the old leaf sheath), and photosynthetic zones (exposed mature tissues) (Evequoz, 1993). Thus, decisions regarding the lengths and positions of the leaf segments must be based on the tissue age and functions in the growing leaf. Leaves 4 and 5 were cut at the ligule with a razor blade and divided into four additional segments: (1) the growth zone (3 cm above the ligule; seg1), (2) the remaining part of the leaf enclosed by sheath (seg2), (3) the first 6 cm of the exposed part of the leaf (seg3), and (4) the remainder of the exposed leaf (leaf distal; seg4). To ensure that sufficient material was available for ion analysis, six segments at the same position were combined into one sample. The length of the growth zone for maize (about 3 cm) was determined following studies by Evequoz (1993). After FW of the segments were determined, samples were dried at 60 °C for 2 days. Dry weights (DW) were determined and the materials were stored for the analysis of ion concentrations. Relative water content (RWC) (%) was calculated from: $RWC = 100 \times (FW - DW)/FW$.

Besides the separated youngest leaves 4 and 5, other plant material was also oven-dried at 60 °C for 2 days and the dried samples were weighed. The shoot DW was calculated by the total DW of leaves 4 and 5 plus the DW of other plant materials.

2.3. Analysis of ion concentrations

Oven-dried samples of leaves and sheathes at harvest were ground to pass through a 1-mm diameter sieve. The concentrations of Na⁺, K⁺, Ca²⁺, Mg²⁺, Mn, Fe, Zn, and S were determined using an Inductively Coupled Plasma Emission Spectrometer (ICP model Liberty 200, Varian Australia Pty. Ltd., Mulgrave Victoria, Australia). Before the analysis, 50 mg of ground dry material was digested by adding 2 ml concentrated HNO₃ (65%) and 1 ml H₂O₂ (30%) for 30 min at 2600 kPa (80 psi) in a MDS-2100 microwave oven (CEM Corp., Matthews, NC). After digestion, each sample was brought up to the final volume of 25 ml with deionized water.

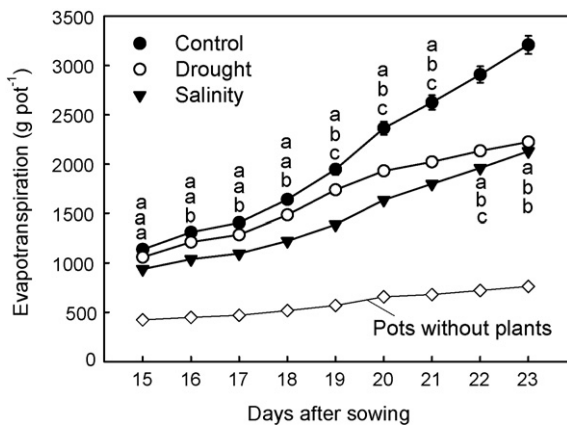


Fig. 1. Accumulative evapotranspiration (g pot^{-1}) with time under control, drought and saline conditions. Error bars ($n=4$) represent standard errors and fit within the plot symbol if not visible. Within measuring dates, means accompanied by different letters are significantly different ($P < 0.05$).

Total nitrogen was analysed using an IRMS combined with a preparation unit (ANCA SL 20-20 Europe Scientific Crewe UK). Two milligram samples were weighed with a supermicrobalance (Sartorius AG, Gotingen, Germany).

2.4. Statistical analysis

A randomized complete block design was used. All treatments were replicated four times. Data were analysed by an analysis of variance (ANOVA) using JMP 4.02 (SAS, 2000) to test the significance of the main effects. Means separation on data was conducted using LSD multiple range tests. Terms were considered significant at $P < 0.05$.

3. Results

3.1. Accumulative evapotranspiration and shoot FW and DW

Fig. 1 shows that the accumulative evapotranspiration was significantly affected by drought at day 1 after the treatment began (or day 19 after sowing) and by salinity at day 16 after sowing ($P < 0.05$). At day 23 after sowing, the evapotranspiration of the plants under drought stress was reduced by about 31%, which was not different to the values of the salinized plants. The shoot FW under drought and salinity were both reduced by about 50% compared with the control plants (Table 1). Similarly,

Table 1
Shoot fresh weight (FW) and dry weight (DW) (g plant^{-1}) of maize seedlings at harvest under control, drought and saline conditions

Treatments	FW (g plant^{-1})	DW (g plant^{-1})
Control	13.4 a	2.2 a
Drought	6.5 b	1.4 b
Salinity	6.6 b	1.1 b

Means ($n=4$) followed by the same letters in columns are not statistically different at $P < 0.05$.

shoot DW was significantly reduced by both drought and salinity ($P < 0.05$) (Table 1).

3.2. Short-term effects of drought and salinity on FW, DW and mineral nutrient distribution along growing maize leaves

Spatial distributions of FW and DW contents (mg per mm), and RWC (%) for leaves 4 and 5 are presented in Fig. 2. In general, FW and DW contents increased with distance, reached a maximum and then decreased regardless of treatments and leaf number. Drought and salinity significantly reduced FW content in both leaves 4 and 5 at any location ($P < 0.05$). Compared to FW content of leaf 4 under drought, FW content was parallelly higher along leaf 4 under salinity, while there was no significant difference between drought and salinity treatments. However, the difference in the FW content of leaf 5 between drought and salinity treatments was only observed for segment 3, i.e. the first 6 cm of the exposed part of leaf 5. In contrast to FW content, in leaf 4 there was no difference in DW content between drought and control treatments for the first three segments, whereas DW content in those segments under saline conditions was lower than that under control and drought conditions. For segment 4, however, DW content was significantly lower under both drought and salinity conditions than that under control conditions ($P < 0.05$). There was no difference in DW content of leaf 5 for the first 2 segments among the three treatments, while the DW content of leaf 5 for segments 3 and 4 was significantly higher under control than that under drought and salinity ($P < 0.05$). The relative water content slightly decreased along the leaf axis for leaf 4 regardless of treatments, whereas for leaf 5 it slightly increased up to the end of the sheath, and then decreased along the leaf axis. In contrast to no reduction in the RWC by salinity, drought significantly reduced the RWC in all segments for leaf 4 and in the first three segments for leaf 5 ($P < 0.05$).

Fig. 3 shows that the Na^+ concentration increased under salinity regardless of the leaf number or location along the leaf axis. Under saline conditions, Na^+ concentrations in leaves 4 and 5 were higher in growing tissues ($22\text{--}28 \text{ mmol kg}^{-1} \text{ DW}$) than in mature ones (about $18 \text{ mmol kg}^{-1} \text{ DW}$).

Along the axis of leaves 4 and 5, K^+ concentrations increased with distance up to the secondary cell wall deposition zone (seg2 in Fig. 3) and decreased thereafter. However, a continuous decrease in K^+ concentration with distance was observed in leaf 4 under control and saline conditions. Except for the segment 4 in leaf 4, there was no significant difference in K^+ concentrations in leaves 4 and 5 among all three treatments ($P < 0.05$).

The distribution patterns of Ca^{2+} concentration were similar to those of Mg^{2+} in all leaves and treatments (Fig. 3). The concentrations of both ions decreased with distance from the leaf base to the middle of the leaf and then remained unchanged or increased slightly to the distal part of the leaf. At any given location, the Ca^{2+} and Mg^{2+} concentrations were lower in leaf 5 than in leaf 4. Salinity increased the Ca^{2+} concentration in the base and distal part of leaf 4, whereas drought increased it only in distal portion. There was no significant difference among treatments for leaf 5 ($P < 0.05$). In leaf 4, however, salinity increased

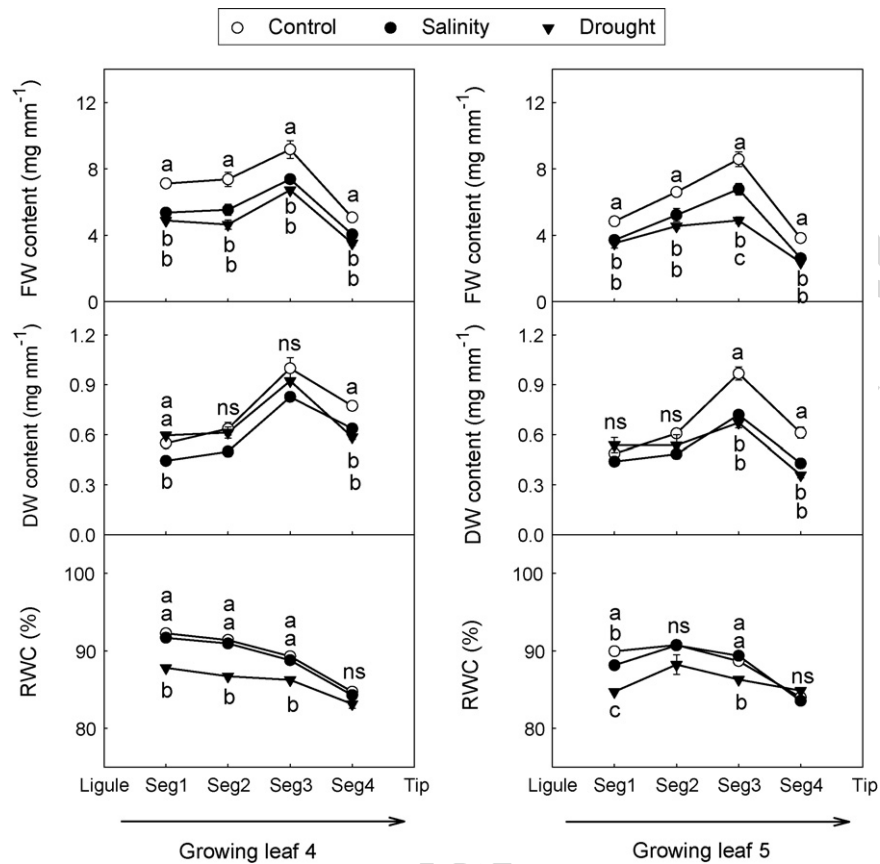


Fig. 2. Spatial distributions of fresh weight (FW) and dry weight (DW) content (mg/mm^{-1}) and relative water content (RWC) (%) along the growing leaves 4 and 5 of maize seedlings at day 23 after sowing. Seg1 and seg2 indicate the growing zone (3 cm above the ligule) and the remaining part of the leaf enclosed by sheath, respectively. Seg3 indicates the first 6 cm of the exposed part for maize leaves 4 and 5. Seg4 indicates the remainder of the exposed portion of maize leaves 4 and 5 (leaf tip). Error bars ($n=4$) represent standard errors and fit within the plot symbol if not visible. Within measuring segments, means accompanied by different letters are significantly different ($P<0.05$); ns, not significantly different.

the Mg^{2+} concentration in the growing tissues, whereas drought reduced it in the growth zone.

Similarly, the N concentrations were high in the growing tissues and low in the mature ones. The N concentration at the leaf base was higher in leaf 4 than in leaf 5. Salinity and drought did not significantly affect the N concentration in leaf 4 ($P<0.05$).

The distribution of and the effect of drought and salinity on the S concentration along the leaf axis and was similar to those of N (Fig. 3). The Fe concentration tended to increase with distance from the leaf base for leaf 4 under drought or control conditions (Fig. 4). Under saline conditions, the changes in the Fe concentration in leaf 4 fluctuated with distance. In leaf 5, the Fe concentration decreased slightly in moving from the base to the mature tissues and then increased again with to the distal tip of the leaf. In the proximal half of leaves 4 and 5, the Fe concentration was higher under drought and salinity than in the control plants. The Mn concentration remained almost unchanged in the proximal half of leaves, but then increased to the leaf tip. At any given location, the Mn concentration was lower in leaf 5 than in leaf 4. However, it was higher under drought compared to the control plants in the exposed parts of leaves, whereas it was higher under salinity than in the control plants along the whole leaf axis for leaf 4 and in the mature tissues of leaf 5. For all

treatments, the Zn concentration decreased with distance from the leaf base to the end of enclosed tissues (at seg3 in Fig. 4) and then remained unchanged in leaves 4 and 5. Compared with the control and saline treatments, higher Zn concentrations were found in mature tissues of leaf 4 and in growing tissues of leaf 5 under drought.

4. Discussion

This study clearly showed that the difference in the FW content between drought and salinity stresses is mainly due to the effect of drought on the relative water content (Fig. 2), especially for leaf 4. When stress conditions like salinity do not affect the relative leaf water content, the reduction in the FW content (mg/mm^{-1}) of grass leaves reflects their effect on the cross-section area of grass leaves (Hu and Schmidhalter, 2001). Therefore, the lower FW content of leaves 4 and 5 under saline conditions indicates that there is a reduction in the cross-sectional area of maize leaves. Salinity reduced the DW content of leaves 4 and 5 (Fig. 2). However, drought only reduced the DW content for leaf 5, but not for leaf 4. This may be due to the drought stress that started after leaf 4 emerged. The growing grass leaves contain different ages of tissues. Growing

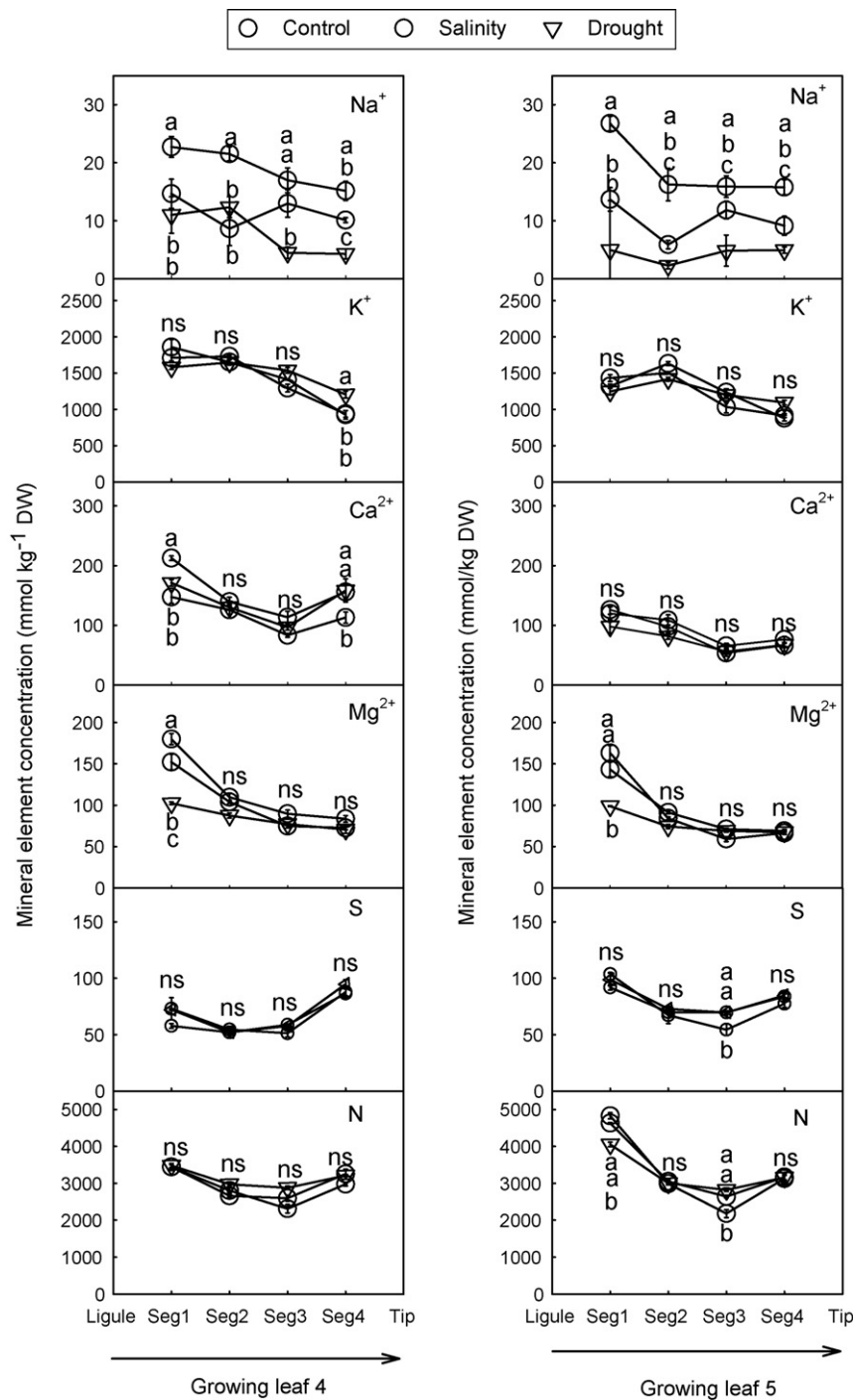


Fig. 3. Spatial distributions of Na^+ , K^+ , Ca^{2+} , Mg^{2+} , S and N concentrations (mmol kg^{-1} DW) along the growing leaves 4 and 5 of maize seedlings at day 23 after sowing and leaf. Seg1 to seg4 are defined as in Fig. 2. Error bars ($n=4$) represent standard errors and fit within the plot symbol if not visible. Within measuring segments, means accompanied by different letters are significantly different ($P < 0.05$); ns, not significantly different.

tissues at the leaf base are most active in metabolism and strong sinks for nutrients, the leaf growth of grasses under control or stress conditions should be much more closely associated with metabolic/nutritional changes within the most actively growing tissues than the whole plant. By comparing the spatial distribution of leaf growth of grasses with that of mineral elements in the different tissues of grasses under drought and salinity, it is possible to determine the direct causes of the different

effects of drought and salinity on leaf growth in the different zones.

The results show that the change in concentration for most ions along the growing leaf axis is independent of treatments (Figs. 3 and 4). The distribution patterns of the mineral elements along the leaf axis here was also in agreement with reports from the literature, which has identified two major patterns of spatial distributions of mineral nutrients in the growing leaves

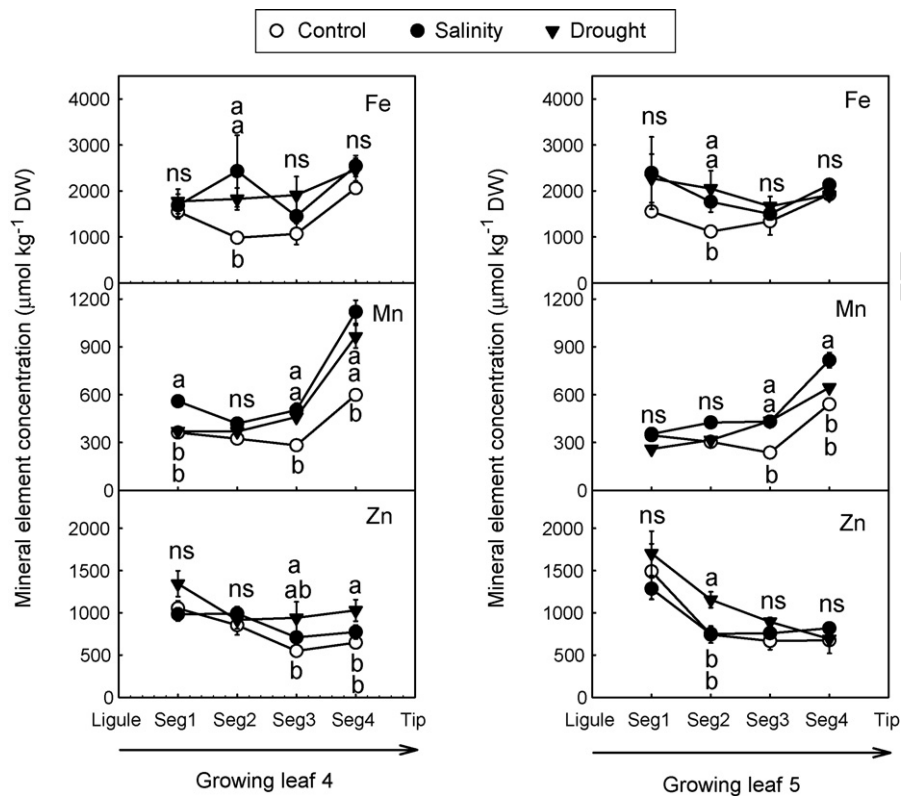


Fig. 4. Spatial distributions of Fe, Mn and Zn concentrations ($\mu\text{mol kg}^{-1}$ DW) along the growing leaves 4 and 5 of maize seedling at day 23 after sowing. Seg1 to seg4 are defined as in Fig. 2. Error bars ($n=4$) represent standard errors and fit within the plot symbol if not visible. Within measuring segments, means accompanied by different letters are significantly different ($P<0.05$); ns, not significantly different.

of grasses. First, ion concentrations are highest at the leaf base, reach their minimum at the end of the elongation zone, and then remained virtually unchanged to the tip of the leaf (e.g. Mg^{2+} , P, Zn, S and total N) (Meiri et al., 1992; Gastal and Nelson, 1994; Bernstein et al., 1995; Hu and Schmidhalter, 1998a; Hu et al., 2000, 2005). This pattern might derive from the small cells at the leaf base, which contain a larger proportion of proteins and nucleic acids compared to more distal cells. Second, ion concentrations decrease slightly or remain unchanged in the elongation zone and then increase consistently moving distally beyond the elongation zone (e.g. Fe and Mn) (Hu et al., 2000). This pattern is probably associated with the function of these ions in the chloroplasts. Although chloroplasts develop progressively along the entire leaf axis of grasses, they increase markedly after the end of the growth zone (Nakamura and Hashimoto, 1988), which is coincident with the changes in the Fe and Mn concentrations in the growing leaves (Hu et al., 2000).

Although under drought conditions, nutrient uptake is reduced by the roots and nutrient transport from the roots to the shoots is also restricted by the reduced transpiration rates and impaired active transport (Viets, 1972; Hsiao, 1973; Kramer and Boyer, 1995), the reduction in the ion concentration for most of macro- and micronutrients was not observed in this study (Figs. 3 and 4). Because of a great reduction in the relative water content, the mineral element concentrations in all locations of growing leaves 4 and 5 on a FW base

should be even higher in the draughted treatment than those in salinized and control treatments. No effect of drought on the ion concentration may indicate that reduction in water uptake or leaf growth under drought conditions is greater than ion uptake and/or transport. The recent studies have shown that hydraulic and chemical signals may control leaf growth under drought conditions (Dodd and Davies, 1996; Bahrin et al., 2002; Liu et al., 2003). Schmidhalter et al. (1998) have studied the sequence of response of maize seedlings to drought and demonstrated that reduction in leaf elongation can occur before significant changes in the transpiration, stomatal conductance, photosynthesis and the water relations in non-growing leaves of maize plants.

Interestingly, except for Na^+ , there was almost no difference in the concentrations of most ions at a given location between the control and salinized treatments and between plants under drought and those in the control or saline treatments. Because the level of salinity in soil was achieved by adding NaCl, salinity increased the Na^+ concentration in the leaves regardless of the number of the leaves. Although Na^+ toxicity is one of the major factors limiting plant growth (rev. Greenway and Munns, 1980), the Na^+ concentrations observed here in the saline treatments were 20–25 mmol kg^{-1} DW in the growing leaves, which is lower than that in growing leaves of maize grown in hydroponics from Neves-Piestun and Bernstein (2005). This may be due to the buffering effect on soil salinity compared with hydroponics that was also found for wheat leaves by Hu and Schmidhalter

(1997, 1998a) or different genotypes of maize. Although Cl^- concentration in growing leaves of maize is not available, our preliminary study under a similar condition showed that Cl^- concentration can be 3–4 times higher than Na^+ concentration of maize leaves.

Under saline conditions, Na^+ in the growth medium might interact with other cations such as K^+ , Ca^{2+} , Mg^{2+} , resulting in the low absorption of the latter ions by the roots. It is generally recognized that K^+ and Ca^{2+} uptake by the plant, and their accumulation in both expanding and expanded tissues are reduced under saline conditions (Lazof and Bernstein, 1999). For example, lowered concentrations of both K^+ and Ca^{2+} were found in the expanding leaf of sorghum under saline conditions (Bernstein et al., 1995). However, in agreement with the current observations, Hu and Schmidhalter (1998a) found that the K^+ and Ca^{2+} concentrations in the expanding and expanded tissues of leaves of wheat were increased under saline conditions, which may be due to the used soils having a high Ca^{2+} content (Hu et al., 2005). Under saline conditions, ion accumulation either increased or was unchanged, which could be a result of osmotic regulation. In general, osmoregulation under saline conditions might utilize ions from the soil, and analyses show that osmotic adjustment via ion uptake is more energy efficient than adjustment through the production of organic solutes (Wyn-Jones, 1981). The study of Hu and Schmidhalter (1998b) further showed that, sugars accounted for about 13% of osmotic adjustment in the expanding zone of wheat leaves under saline conditions, whereas cations and anions accounted for about 21–30 and 15–21%, respectively. These findings were confirmed by De Lacerda et al. (2003). However, the solutes necessary for osmoregulation under drought in the absence of salinity (such as sugars) might have to be produced within the plant (Hsiao et al., 1976).

In conclusion, drought and salinity reduced the FW content regardless of leaf number and caused a similar reduction. However, they affected the DW content differently, resulting from the reduction in the relative water content by drought. Although both drought and salinity cause a low nutrient availability in soil and lower nutrient transport in plants, this study showed that except for Na^+ , there was no difference in the concentrations of most ions at any given location between plants in the control and either of the drought or saline treatments. Thus, reduction in leaf growth under drought and saline conditions may be due to other causes rather than the limitation of nutrients in a short-term period of drought and salt stresses.

References

- Bahrn, A., Jensen, C.R., Asch, F., Mogensen, V.O., 2002. Drought-induced changes in xylem pH, ionic composition, and ABA concentration act as early signals in field-grown maize (*Zea mays* L.). *J. Exp. Bot.* 53, 251–263.
- Bernstein, N., Silk, W.K., Läuchli, A., 1995. Growth and development of sorghum leaves under conditions of NaCl stress: possible role of some mineral elements in growth inhibition. *Planta* 196, 699–705.
- De Lacerda, C.F., Cambraia, J., Oliva, M.A., Ruiz, H.A., Prisco, J.T., 2003. Solute accumulation and distribution during shoot and leaf development in two sorghum genotypes under salt stress. *Environ. Exp. Bot.* 49, 107–120.
- Dodd, I.C., Davies, W.J., 1996. The relationship between leaf growth and ABA accumulation in the grass leaf elongation zone. *Plant Cell Environ.* 19, 1047–1056.
- Evequoz, M., 1993. Adaptation osmotique et proprietes rheologiques des parois cellulaires critères pour la selection du maïs à la Secheresse? PhD thesis Nr. 10234. Swiss Federal Institute of Technology at Zurich.
- Gastal, F., Nelson, C.J., 1994. Nitrogen use within the growing leaf blade of tall fescue. *Plant Physiol.* 105, 191–197.
- Grattan, S.R., Grieve, C.M., 1999. Salinity mineral nutrient relations in horticultural crops. *Sci. Hortic.* 78, 127–157.
- Greenway, H., Munns, R., 1980. Mechanisms of salt tolerance in nonhalophytes. *Ann. Rev. Plant Physiol. Mol. Biol.* 31, 149–190.
- Hsiao, T.C., 1973. Plant responses to water stress. *Ann. Rev. Plant Physiol. Mol. Biol.* 24, 519–570.
- Hsiao, T.C., Acevedo, E., Fereres, E., Henderson, D.W., 1976. Stress metabolism—water stress, growth, and osmotic adjustment. *Philos. Trans. R. Soc. Lond. Ser. B: Biol. Sci.* 273, 479–500.
- Hu, Y., Schmidhalter, U., 2001. Reduced cellular cross-sectional area in the leaf elongation zone of wheat causes a decrease in dry weight deposition under saline conditions. *Aust. J. Plant Physiol.* 28, 165–170.
- Hu, Y., Schmidhalter, U., 1998a. Spatial distributions and net deposition rates of mineral elements in the elongating wheat (*Triticum aestivum* L.) leaf under saline soil conditions. *Planta* 204, 212–219.
- Hu, Y., Schmidhalter, U., 1998b. Spatial distributions of inorganic ions and sugars contributing to osmotic adjustment in the elongating wheat leaf under saline soil conditions. *Aust. J. Plant Physiol.* 25, 591–597.
- Hu, Y., Schmidhalter, U., 1997. Interactive effects of salinity and macro nutrient level on wheat. 2. Composition. *J. Plant Nutr.* 20, 1169–1182.
- Hu, Y., Fricke, W., Schmidhalter, U., 2005. Salinity and the growth of non-halophytic grass leaves: the role of mineral nutrient distribution. *Funct. Plant Biol.* 32, 973–985.
- Hu, Y., von Tucher, S., Schmidhalter, U., 2000. Spatial distributions and net deposition rates of Fe, Mn and Zn in the elongating leaves of wheat under saline soil conditions. *Aust. J. Plant Physiol.* 27, 53–59.
- Kemp, D.R., 1980. The growth rate of successive leaves of wheat plants in relation to sugar and protein concentrations in the extension zone. *New Phytol.* 84, 1399–1411.
- Kramer, P.J., Boyer, J.S., 1995. *Water Relations of Plants and Soils*. Academic Press Inc., San Diego.
- Lazof, D.B., Bernstein, N., 1999. Effects of salinization on nutrient transport to lettuce leaves: consideration of leaf developmental stage. *New Phytol.* 144, 85–94.
- Liu, F.L., Andersen, M.N., Jensen, C.R., 2003. Loss of pod set caused by drought stress is associated with water status and ABA content of reproductive structures in soybean. *Funct. Plant Biol.* 30, 271–280.
- Meiri, A., Silk, W.K., Läuchli, A., 1992. Growth and deposition of inorganic nutrient elements in developing leaves of *Zea mays* L. *Plant Physiol.* 99, 972–978.
- Munns, R., 2002. Comparative physiology of salt and water stress. *Plant Cell Environ.* 25, 239–250.
- Nakamura, Y., Hashimoto, H., 1988. Characteristics of photosynthate partitioning during chloroplast development in *Avena* leaves. *Plant Physiol.* 87, 458–462.
- Neves-Piestun, B.G., Bernstein, N., 2005. Salinity-induced changes in the nutritional status of expanding cells may impact leaf growth inhibition in maize. *Funct. Plant Biol.* 32, 141–152.
- Pinkerton, A., Simpson, J.R., 1986. Interactions of surface drying and subsurface nutrients affecting plant-growth on acidic soil profiles from an old pasture. *Aust. J. Exp. Agric.* 26, 681–689.
- SAS Institute. SAS User's Guide, Version 4.0.2. SAS Inst, Cary, NC, 2000.
- Schmidhalter, U., Evequoz, M., Camp, K.H., Studer, C., 1998. Sequence of drought response of maize seedlings in drying soil. *Physiol. Plant* 104, 159–168.
- Schmidhalter, U., Oertli, J.J., 1991. Transpiration biomass ratio for carrots as affected by salinity, nutrient supply and soil aeration. *Plant Soil* 135, 125–132.
- Schnyder, H., Nelson, C.J., 1987. Growth-rates and carbohydrate fluxes within the elongation zone of tall fescue leaf blades. *Plant Physiol.* 85, 548–553.

- Shalhevet, L., Hsiao, T.C., 1986. Salinity and drought—a comparison of their effects on osmotic adjustment, assimilation, transpiration and growth. *Irrig. Sci.* 7, 249–264.
- Tardieu, F., Reymond, M., Hamard, P., Granier, C., Muller, B., 2000. Spatial distributions of expansion rate, cell division rate and cell size in maize leaves: a synthesis of the effects of soil water status, evaporative demand and temperature. *J. Exp. Bot.* 51, 1505–1514.
- Viets Jr., F., 1972. Water deficits and nutrient availability. In: Kozlowski, T. (Ed.), *Water Deficits and Plant Growth*. Academic Press, New York.
- Wyn-Jones, R., 1981. Salt tolerance. In: Johnson, C. (Ed.), *Physiological Processes Limiting Plant Productivity*. Butterworths, London, pp. 271–292.

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