Short-Term Effect of Drought and Salinity on Growth and Mineral Elements in Wheat Seedlings

Yuncai Hu a, Zoltan Burucs b, Urs Schmidhalter a

a Chair of Plant Nutrition, Technical University Munich, Freising-Weihenstephan, Germany
b Water Management Department, Georgicon Faculty, Pannon University of Agriculture, Keszthely, Hungary

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Yuncai Hu,1 Zoltan Burucs,2 and Urs Schmidhalter1

1Chair of Plant Nutrition, Technical University Munich, D-85350 Freising-Weihenstephan, Germany
2Water Management Department, Pannon University of Agriculture, Georgicon Faculty, 8361 Keszthely, Hungary

ABSTRACT

Both drought and salinity cause nutrient disturbance, albeit for different reasons: a decrease in the diffusion rate of nutrients in the soil and the restricted transpiration rates in plants for drought and extreme soil sodium (Na)/calcium (Ca), Na/potassium (K), and chloride (Cl)/nitrate (NO3) ratios for salinity. The objective of this study was to examine short-term effects of drought and salinity on nutrient disturbance in wheat seedlings. Wheat was grown in a greenhouse in soil under drought and saline conditions for 26 days after sowing. At harvest, shoot biomass and length, and fresh weight and dry weight of the blade and sheath in expanded leaves 3 and 4 and expanding leaf 5 were determined. Mineral elements (K, Ca, magnesium (Mg), phosphorus (P), nitrogen (N), Na, sulphur (S), iron (Fe), zinc (Zn), and manganese (Mn)) in leaf blades and sheaths were also analyzed. At harvest, the reduction in plant height, shoot biomass, and accumulative evapotranspiration under drought was similar to that under salinity as compared with control plants. However, drought decreased the accumulation of all ions in the blade of the youngest leaf 5 compared with the control, whereas there was either an increase or no difference in all ion concentrations under saline conditions. The change in concentration for most ions in the blade and sheath of expanded leaves 3 and 4 varied among control, drought, and salinity plants, which indicated a different competition for nutrients between the sheath and blade of expanded leaves under drought and saline conditions. It can be concluded from this study that ion deficiency might occur in expanding leaves under drought but not saline conditions.

Keywords: drought, expanding leaves, expanded leaves, mineral elements, salinity, wheat

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Address correspondence to Yuncai Hu, Chair of Plant Nutrition, Department of Plant Science, Technical University of Munich, Am Hochanger 2, D-85350 Freising-Weihenstephan, Germany. E-mail: hu@wzw.tum.de
INTRODUCTION

The increasing frequency of dry periods in many regions of the world and the problems associated with salinity in irrigation water frequently result in the consecutive occurrence of both drought and salinity on cultivated land, and pose serious problems limiting crop productivity worldwide. As such, a better understanding of physiological responses under each of these conditions is important to improve the tolerance of crops to both drought and salinity.

Because drought and salinity both lower the soil water potential, the major physiological mechanisms behind the similar reduction in plant growth might be considered the water deficit or osmotic effect. Therefore, numerous studies have focused on effect of drought and salinity on plant growth, which are caused by the lowered soil water potential (e.g., Shalhevet and Hsiao, 1986; Schmidhalter and Oertli, 1991; Munns, 2002). Surprisingly, there is still no information available on the responses of nutrient status in plants under each condition. Generally, drought reduces both nutrient uptake by the roots and transport from the roots to the shoots because of restricted transpiration rates and impaired active transport and membrane permeability. The overall result is a reduced root adsorbing power of crop plants (Hsiao, 1973; Kramer and Boyer, 1995). A decline in soil moisture also results in a decrease in the diffusion rate of nutrients (particularly phosphorus (P)) from the soil matrix to the absorbing root surface (Pinkerton and Simpson, 1986; Viets, 1972). Thus, nutrient availability under drought can also be a major limiting factor. By contrast, soils contain extreme ratios of sodium (Na)/calcium (Ca), Na/potassium (K), Ca/magnesium (Mg), and chloride (Cl)/nitrate (NO₃) under saline conditions, which cause reduced plant growth due to specific ion toxicities (e.g., Na and Cl) and ionic imbalance acting on biophysical and/or metabolic components of plant growth (Grattan and Grieve, 1999; Hu and Schmidhalter, 2005). Therefore, to further understand the physiological mechanisms of plants under both stresses, there is a need to study the effect of both drought and salinity on mineral nutrients in plants.

Wheat is a major food crop in most countries where drought and salinity problems exist or might develop. Although drought and salinity can affect all growth stages of wheat plants, the vegetative stage is the most sensitive to both stresses (Munns and Termaat, 1986; Maas and Poss, 1989; Hu, Camp, and Schmidhalter, 2000). The vegetative stage of wheat is characterized by tiller initiation, sequential leaf appearance, and leaf elongation on the tillers (Kirby and Jones, 1977). Thus, leaf growth in the early growth stages is potentially extremely sensitive to drought and salinity.

Leaves of wheat grow successively on the tiller, and a mature leaf in wheat consists of a leaf blade, and sheath. Under saline conditions, a non-uniform distribution of ions in the successive leaves within the shoots and between the leaf blade and sheath has been observed frequently (Flowers et al., 1977; Boursier and Läuchli, 1989; Jeschke and Wolf, 1988; Munns et al., 1988; Blits
Effect of Drought, Salinity on Wheat Seedling Growth, Mineral Elements

and Gallagher, 1990). For example, whereas Na concentrations were low in young and developing leaves, and high in mature leaves, the opposite was true for K. Higher concentrations of the toxic ion Na in the older leaves or sheath may show the protection of toxic ions into the growing tissues for an adaptation mechanism to salinity. Therefore, to fully document any differential effect of drought and salinity on the ion disturbance in wheat seedlings, it is necessary to investigate the distribution of ions in different leaves and organs under both stresses.

The objectives of the present article are 1) to investigate the effect of drought and salinity on the shoot and leaf growth of wheat seedlings and 2) to study the ion distribution in the successive leaves and in the different organs on the mainstem under both stresses.

MATERIALS AND METHODS

Plant Materials and Growth Conditions

Wheat seeds (Triticum aestivum cv. Star) were pre-germinated for one day, after which, 25 seeds were sown in 7 L pots filled with loamy soil. One week after sowing, the seedlings were thinned to 19 plants per pot. The air temperature ranged from 37°C (maximum at day) to 10°C (minimum at night). The daily average temperature was about 20°C. Relative humidity fluctuated between 30 and 85%, with the average value being 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 that contained the nitrogen with or without NaCl was added to the first five layers from the bottom. The final level of 100 mM NaCl was obtained by applying a solution of NaCl to the top soil layer ten days after sowing. 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 the previous tests.

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 losses after this time. During the drought period, soil matric potentials decreased from −0.2 bars at day 19 to −4 bars at day 23, and was about −10 bars at day 26 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, the physiological effect of these two stresses at harvest time was compared when the growth of plants showed a similar reduction as compared with control plants.

Analysis of Plant Growth

The rate of evapotranspiration was determined by daily weighing the pots with the plants, and evaporation was determined by weighing the pots without the plants. The height of the main stem (“plant height”) in each treatment was also recorded daily.

At harvest, the reduction in plant height and accumulative evapotranspiration under drought was similar to that under salinity as compared with control plants. At harvest, the shoot fresh weight was determined. The three leaves on the mainstem (leaves 3, 4, and 5) were carefully removed from the shoot, which was enclosed in the older leaf sheath. The blade and sheath were separated if present (e.g., leaf 5 did not have a sheath at harvest). The length and fresh weight of the leaf blade and of the sheath were measured. Plant material was dried at 60°C for two days and then the dry samples were weighed.

Analysis of Ion Concentration

Oven-dried samples of leaf and sheath samples at harvest were ground to pass through a 1-mm diameter sieve. The concentrations of Na, K, Ca, Mg, phosphorus (P), sulphur (S), manganese (Mn), iron (Fe), and zinc (Zn) were determined by Inductively Coupled Plasma Emission Spectrophotometry (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 25 mL final volume with deionized water.

The total nitrogen was analysed with an IRMS combined with a preparation unit (ANCA SL 20-20 Europe Scientific, Crewe, UK). Two milligram samples were weighed with a supermicro-balance (Sartorius AG, Gottingen, Germany).

Statistical Analysis

A completely randomized design was used with five replications for all treatments. Data were analyzed using an analysis of variance (ANOVA) to test the significance of the main effects using JMP 4.02 (SAS 2000).
RESULTS

Cumulative Evapotranspiration

Figure 1 shows that the cumulative evapotranspiration was significantly decreased by drought from day 20 after sowing and by salinity from day 17 after sowing. At day 23 after sowing, the evapotranspiration of the plants under either the drought or saline conditions was reduced by about 32% compared to the control plants.

Plant Growth

The measurements of plant height started one day after drought conditions were initiated. Results in Figure 2 illustrate that plant height responded to drought quickly and that the differences between the drought and control treatments were obvious after only one day. Reduction in plant height under drought (14%) was almost the same as that under salinity from day 4 after drought conditions began.

To compare the effects of salinity and drought on the wheat seedling growth, all plants were harvested at a similar developmental stage of the wheat leaves. Shoot fresh weight (FW) and dry weight (DW) of plants under either stress at final harvest were significantly reduced compared with those of plants in the control treatment (Figure 3).
There was a significant reduction in the length and the FW of the blades of leaves 3, 4, and 5 under both drought and saline conditions, and the reduction was larger with increasing leaf number (Figure 4). However, the only significant difference between the two treatments in blade length and FW occurred for leaf 4 (Figure 4). By contrast, the length of the sheath in leaves 3 and 4 was reduced by both drought and salinity compared to the control treatment, although the length of the sheath was greater under salinity than under drought (Figure 4). The relative water content in leaves from plants under drought stress was 5–10% lower than that in the control and salinized plants (data not shown). Thus, there...
was no difference in the blade dry weight (DW) for leaves 3 and 5 between control and drought treatments. The blade DW of leaves 3 and 5 was higher under drought conditions than under saline ones. Although salinity resulted in a decrease in the sheath DW of leaves 3 and 4 compared with control treatment, drought led to an increase (Figure 4).

**Mineral Nutrient Accumulation in Leaves of Wheat**

The concentrations of mineral elements (K, Ca, Mg, P, N, Na, S, Fe, Zn, and Mn) in leaves 3, 4, and 5 (mmol kg\(^{-1}\) DW or \(\mu\)mol kg\(^{-1}\) DW) are presented in Figures 5, 6, and 7. Salinity significantly increased the Na concentration in the blade and sheath of all three leaves (Figure 5). The Na concentration in the sheaths was only slightly higher than that in the blades.
Figure 5. Sodium, K, Ca and Mg concentration (mmol kg\(^{-1}\) DW) in the blade and sheath in leaves 3, 4, and 5 of wheat seedlings at harvest under control, and drought and saline conditions. Error bars \((n = 5)\) represent standard errors and fit within the plot symbol if not visible.

The K concentration in the blade of leaf 3 was higher under drought conditions and lower under salinity as compared with the control (Figure 5). In leaf 4, the K concentration in the blade was slightly higher in plants under drought stress compared with salinized and control plants (which were not significantly different from one another). In leaf 5, however, the K concentration in the blade was lower under drought than under salinity or the control. The K concentration in the leaf blades from plants under drought stress decreased with increasing leaf number, whereas there was no difference among leaves in the control treatment. In the salinized treatment, the K concentration was highest in leaf blade
Effect of Drought, Salinity on Wheat Seedling Growth, Mineral Elements

4 and lowest in leaf 3. In the sheaths, the K concentration in leaf 3 was lower under salinity compared with the drought and control treatments, whereas it was higher in leaf 4 under salinity (and similar to control) than under drought. Similar to the blades of leaves 3 and 4, the K concentration in the sheaths under drought decreased with increasing leaf number, whereas it increased under salinity. There was no difference between leaves 3 and 4 in the control plants. The K concentration in the leaf sheath for the control and salinized treatments were higher than that for the blades of leaves 3 and 4.

The Ca concentration in the leaf blade significantly decreased with increasing leaf number for all three treatments (Figure 5). Salinity slightly increased the Ca concentration in the blades of leaves 4 and 5 compared with the control and drought treatments. Drought decreased the Ca concentration in the blades of only leaves 3 and 5 compared with control treatment. There was no difference in the Ca concentration between the sheaths of leaves 3 and 4 for the control and salinized treatments. By contrast, the Ca concentration in the sheath decreased progressively with increasing leaf number under drought. For all three treatments, the Ca concentrations in the blade of leaf 3 were higher than in sheath for all three treatments, whereas the opposite was true for leaf 4.

Compared to the control plants, the Mg concentration in the blades of leaves 3 and 4 increased under salinity and decreased under drought, whereas it decreased in leaf 5 under drought and remained unchanged under salinity (Figure 5). Under control conditions, the Mg concentration in the blade decreased from leaf 3 to 4 and increased again from leaf 4 to 5. Under drought conditions, the Mg concentration in the blades decreased with increasing leaf number. Under saline conditions, however, the Mg concentration decreased from leaf 3 to 4 and remained unchanged between leaves 4 and 5. Salinity increased the Mg concentration in the sheaths of leaves 3 and 4 compared with control plants, whereas drought decreased the Mg concentration. There was no difference between leaves 3 and 4 for the control and salinized treatments. The Mg concentration in the sheath of leaf 3 was lower than in blade in control plants, whereas it was higher in sheath of leaf 4 compared to the blade under salinity.

Compared to the control, total N content in the blades was increased under salinity and decreased under drought regardless of leaf number (Figure 6). The N content for the control and salinized treatments was higher in the blade of leaf 5 than that in leaves 3 and 4, whereas the reverse was true under drought. Differences in N content in the sheaths among treatments were observed in leaf 4 only. Nitrogen content was clearly lower in the sheaths than in blades for all treatments. The P concentration in the leaf blade and sheath increased with increasing leaf number in all treatments (Figure 6). Salinity increased the P concentration in both the blade and sheath regardless leaf number. By contrast, drought decreased the P concentration in both the blade and sheath except for the sheath of leaf 3. The P concentration in the sheath of leaf 3 was lower than that in the blade, whereas there was no difference between the blade and sheath of leaf 4.
Figure 6. Nitrogen content (g kg\(^{-1}\) DW) and P concentration (mmol kg\(^{-1}\) DW) in the blade and sheath in leaves 3, 4, and 5 of wheat seedlings at harvest under control, and drought and saline conditions. Error bars (\(n = 5\)) represent standard errors and fit within the plot symbol if not visible.

The S concentration in the blades of leaves 3 and 5 was lower under salinity than that under control, whereas it was lower in the blade of leaves 4 and 5 under drought than under control. The S concentration in the blades of plants under drought decreased with increasing leaf number. Salinity also decreased the S concentration in sheaths of leaves 3 and 4, but drought did not. The S concentration was lower in the sheath than in the blade regardless of leaf number and treatments.

The Fe concentration in the blade was lower in the drought and saline treatments than in control treatment regardless of leaf number. However, the Fe concentration under drought was even lower than under salinity. Drought significantly decreased the Fe concentration in the leaf sheath compared with the control and salinity treatments.

The Zn concentration in the blades was higher in leaf 5 than in leaves 3 and 4, but it was not affected by either drought or salinity (Figure 7). By contrast, salinity increased the Zn concentration in the sheaths of leaves 3 and 4, whereas drought decreased it. Under saline conditions, the Zn concentration in the sheaths was much higher than in the blades of leaves 3 and 4. Similar to the Zn concentration in the leaf sheath, salinity increased the Mn concentration in both the blades and sheaths, whereas drought decreased it. Figure 7 also shows that, under control and saline conditions, the Mn concentration in the sheath was greater than that in the blade regardless of the leaf number.
DISCUSSION

Although the reductions at harvest in evapotranspiration, plant height, and FW per plant under drought were similar to that under salinity (Figures 1–3), it is obvious that the two stresses had different effects on the mineral nutrient concentration of a given leaf and a given organ (Figures 5–7). The concentrations of most mineral elements in expanded and expanding leaves, except for K, N, and S in some leaf blades and sheaths, were consistently lower in plants under drought than that in those under salinized conditions. Notably,
the concentrations of all ions in the expanding leaf 5 were much lower under drought than under salinity compared to the expanded leaves 3 and 4.

Mineral Nutrient Concentrations in Expanding Leaves

The results here show that drought decreased the accumulation of all mineral elements in the blade of the youngest leaf 5 relative to the control plants, whereas there was either an increase or no difference in the concentrations of all mineral nutrients under salinity (Figures 5–7). The differences in the ion accumulation in leaves under drought and salinity might be caused either by the rate of supply to and the rate of uptake by the cell, or by different mechanisms of osmotic adjustment in growing tissues.

Generally, drought reduces nutrient uptake by roots and transport from roots to shoots because of restricted transpiration rates and impaired active transport and membrane permeability, resulting in a reduced root adsorbing power of crop plants (Hsiao, 1973; Kramer and Boyer, 1995). A decline in soil moisture also results in a decrease in the diffusion rate of nutrients from the soil matrix to the absorbing root surface (Pinkerton and Simpson, 1986; Viets, 1972). As such, the overall lowered rate of ion supply from the roots and expanded leaves might be a major cause of the low ion concentrations observed in the youngest leaves of the wheat seedlings.

By contrast, the unchanged or increased ion concentrations in expanding leaves under salinity could be mediated by the roots, which select ions, and by expanded leaves, which regulate ion storage and partitioning (Greenway and Munns, 1980; Marschner, 1995). Under saline conditions, Na in the growth medium might compete with other cations such as K, Ca, and Mg, among others, resulting in the low absorption of the latter by the roots. It is generally recognized that K and Ca uptake to the plant and their deposition in both expanding and expanded tissues are reduced under saline conditions (Lazof and Bernstein, 1999). For example, Bernstein, Silk, and Läuchli (1995) observed low concentrations of K and Ca in the expanding leaf of sorghum.

However, it was observed in this study that the K concentration in leaf 5 under salinity was slightly lower than in the control plants, whereas Ca concentration was higher. Hu and Schmidhalter (1998) found that the K and Ca concentrations in expanding and expanded tissues of leaves in wheat were increased under saline conditions, which is in agreement with the results here. Furthermore, although the Na concentration was significantly higher under saline conditions compared with control treatment, it was only 25 mmol kg\(^{-1}\) DW, which was much lower from the concentration in the mature plants (Hu and Schmidhalter, 1997). This is in agreement with the findings from Na concentration in the expanding leaves of wheat (Hu and Schmidhalter, 1998), barley (Munns et al., 1988), sorghum (Bernstein et al., 1995; de Lacerda et al., 2003). These may suggest that Na concentrations probably would not cause ion toxicity.
The special characters of the growing leaves of grasses could also be a factor that explains the observed difference in the ion accumulation in the expanding leaf 5 between wheat seedlings under drought and salinity. At harvest, leaf 5 was still expanding, and its ligule had not yet appeared. The majority of leaf 5, including its growth zone, is enclosed inside a whorl of older leaf sheaths and does not transpire. Thus, cell expansion itself might possibly lower water potential and drive water flux (Nonami and Boyer, 1989; Nonami, Wu, and Boyer, 1997), because water uptake and/or biosynthetic production are the forces driving the ion accumulation in the growing tissues. Despite the similarities of lowered water potential in soils under drought and salinity, a frequent observation is the lack of wilting under salt stress at water potentials that cause wilting under water stress (Shalhevet and Hsiao, 1986).

In this study, the relative water content in leaf 5 was not affected by salinity, whereas it was reduced by about 10% under drought. This suggests that the water flux and biosynthetic activity in the growing tissues might be more inhibited by drought than by salinity. Furthermore, another important difference in the effect of plant growth between drought and salinity is that wilted leaves can recover quickly after re-watering. Thus, the limited ion uptake by cells in plants under drought might be temporary only.

The thin primary cell wall near the base of the growing leaf of monocots (Lazof and Bernstein, 1999) implies that apoplastic flow must be more restricted in these tissues than throughout much of the shoot (Esau, 1977; Bernstein et al., 1995; Hu, Fricke, and Schmidhalter, 2005). Although monocots have developed vascular elements traversing the expanding zone, cross-linking lateral veins might not be functional within this zone (Barlow, 1986) such that the longitudinal veins might need to supply a much larger area than within the mature leaf zones (Bernstein et al., 1995). Furthermore, cells are not vacuolated in and very near to the meristem. There is vascular discontinuity between the stem and the leaf vessels in the zone of cell division of the leaf base, requiring that transport through the zone of leaf division and into the developing vascular systems of the expanding zone rely either on symplastic transport or transport through the thin cell walls (Hanson, 1984). Thus, the dryer leaf tissue under drought compared with salinity could make nutrient transport through the meristem region more difficult.

The observed accumulation of all ions in leaf 5 under saline conditions could also result from the different contribution of ions to osmotic adjustment under drought and salinity. In general, osmoregulation under saline conditions appears to use ions from the soil, whereas under drought, solutes such as sugars that have to be produced within the plant are used instead (Hsiao et al., 1976). For example, a study on the contribution of sugars to osmotic adjustment in elongating and expanded zones of wheat leaves in drought (Munns and Weir, 1981) showed that sugars accounted for 55–88% of osmotic adjustment. Under saline conditions, however, sugars accounted for only about 13% in the expanding zone of wheat leaves, whereas cations and anions accounted
for about 21–30% and 15 to 21%, respectively (Hu and Schmidhalter, 1998). Analyses also show that osmotic adjustment through ion uptake is more energy efficient than adjustment through the production of organic solutes (Wyn-Jones, 1981).

**Ion Partitioning in Expanding and Expanded Leaves and in Blade and Sheath**

For all three treatments, the Ca concentration was higher in the expanded leaves than in the expanding ones (leaf 5), whereas the P concentration was lower in expanded leaves (leaves 3 and 4) (Figures 5–7). This could be due to the differential mobility of the two ions. Although there are no general patterns of ion distribution among the leaves for the other elements, a lower concentration for most ions under drought as compared with the control was found in the blade (except for K, Ca, S, and Zn) and sheath (except for S) of leaf 4. This reduced ion concentration might be due to either the reduced rate of ion uptake by the roots discussed above or retranslocation into expanding leaves. For example, the higher P concentration in younger leaves under drought might indicate a higher rate of retranslocation of P to the expanding leaves, whereas the lower mobility of Ca contributes to its lower rate of retranslocation to the young leaves. However, most ion concentrations in the salinized plants remained unchanged or were even higher than those in control treatment. This could be due to the required higher ion concentration in salinized plants to enable osmotic adjustment. Interestingly, although K is a mobile ion, results from all three treatments showed that K concentrations were not increased in young and developing leaves and reduced in mature leaves, which contradicts the results found by Blits and Gallagher (1990).

Within a leaf, the blade is more metabolically active than the sheath (i.e., the blade is a stronger sink for inorganic nutrients than is the sheath). Thus, when nutrients are limited, they might flow into the blade from the sheath. The ratios of ions in the blade compared to the sheath under drought (Table 1) showed that in leaf 4, the ratios of all ions was not only higher than those under salinity and control treatments, but also that most of them were greater than one, indicating higher translocation of ions to the blade. This suggests that under drought conditions, a deficiency or imbalance of nutrients might occur in the leaf blade. For leaf 3, however, the ratios of most ions (except for K, Fe, and Mn) under drought were more similar to those under salinity or in the control plants.

Furthermore, in the expanded leaf 3, variation in the concentrations of most of the ions in blade and sheath between the drought and control treatments was much smaller than that between the saline and control treatments, while this was opposite in leaf 4. The reason for this could be that saline stress began earlier and was longer than was the drought stress.
Effect of Drought, Salinity on Wheat Seedling Growth, Mineral Elements

Table 1
Ratios of mineral ions in blade to sheath of leaves 3 and 4 in wheat seedlings under control, and drought and saline conditions

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Ca</th>
<th>K</th>
<th>Mg</th>
<th>Na</th>
<th>P</th>
<th>N</th>
<th>Fe</th>
<th>Mn</th>
<th>Zn</th>
<th>S</th>
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<tbody>
<tr>
<td>Leaf 3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>1.7</td>
<td>0.8</td>
<td>1.4</td>
<td>0.6</td>
<td>1.5</td>
<td>1.6</td>
<td>1.0</td>
<td>0.7</td>
<td>0.9</td>
<td>1.7</td>
</tr>
<tr>
<td>Drought</td>
<td>1.5</td>
<td>1.1</td>
<td>1.4</td>
<td>0.8</td>
<td>1.3</td>
<td>1.6</td>
<td>1.6</td>
<td>1.0</td>
<td>1.0</td>
<td>1.6</td>
</tr>
<tr>
<td>Salinity</td>
<td>1.1</td>
<td>0.7</td>
<td>1.0</td>
<td>0.9</td>
<td>1.2</td>
<td>1.8</td>
<td>1.2</td>
<td>0.8</td>
<td>0.5</td>
<td>1.6</td>
</tr>
<tr>
<td>Leaf 4</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>0.8</td>
<td>0.7</td>
<td>0.8</td>
<td>0.4</td>
<td>0.9</td>
<td>1.2</td>
<td>1.0</td>
<td>0.7</td>
<td>0.7</td>
<td>1.8</td>
</tr>
<tr>
<td>Drought</td>
<td>0.9</td>
<td>1.2</td>
<td>1.1</td>
<td>1.1</td>
<td>1.1</td>
<td>1.6</td>
<td>1.5</td>
<td>1.0</td>
<td>1.2</td>
<td>1.3</td>
</tr>
<tr>
<td>Salinity</td>
<td>0.6</td>
<td>0.8</td>
<td>0.7</td>
<td>0.7</td>
<td>0.9</td>
<td>1.2</td>
<td>0.8</td>
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</tr>
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</table>

CONCLUSIONS

In conclusion, the major differences in ion concentrations between drought and salinity in a given leaf and a given organ occur in the youngest leaf blade. The decreased accumulation of all macro- and micronutrients in the blade of the youngest leaf 5 under drought but not salinity suggests that an ion deficiency in expanding leaves might occur only under the former stress. The variation in the concentrations of most of the ions in the blades and sheaths of the expanded leaves 3 and 4 under drought and saline conditions was different, indicating a different competition for nutrients between the sheath and blade of expanded leaves under drought and saline conditions.

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Effect of Drought, Salinity on Wheat Seedling Growth, Mineral Elements


