JOURNAL OF PLANT NUTRITION, 20(9), 1169–1182 (1997)

Interactive Effects of Salinity and Macronutrient Level on Wheat. II. Composition

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ABSTRACT

Results of several studies show interactive effects of salinity and macronutrients on the growth of wheat plants. These effects may be associated with the nutrient status in plant tissues. The objective of this study was to investigate interactive effects of salinity and macronutrients on mineral element concentrations in leaves, stems, and grain of spring wheat (*Triticum aestivum* L. cv. Lona), grown in hydroponics, and the relation of these effects to yield components. Eight salinity levels were established from 0 to 150 mM NaCl, and 1, 0.2, and 0.04 strength Hoagland macronutrient solution (x HS) were used as the macronutrient levels. Sodium (Na), potassium (K), calcium (Ca), magnesium (Mg), chlorine (Cl), and phosphorus (P) in leaves, stems, and grain, NO_3 in leaves and stems, and total nitrogen (N) in grain were determined. Supplemental Ca, Mg, K, and NO_3 added to 0.2 x HS increased mineral concentrations in leaves and stems, but did not improve growth or yield in salinized wheat plants except moderately at 100-150 mM NaCl. In contrast, growth or yield was improved significantly when the

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concentration of macronutrients was increased from 0.04 to 0.2 x HS. In contrast to leaves and stems, mineral concentrations in grain increased (Na, Cl) or decreased (Ca, Mg, K) only slightly or were not affected (K) by salinity except at high salinity and low macronutrient level. Nitrogen and P concentrations in grain were not affected by salinity. Sodium and Cl concentrations in leaves and stems increased significantly, whereas K and NO_3 decreased significantly, with an increase in salinity regardless of the macronutrient level. The latter was also observed for Ca and Mg in leaves. Extreme Na/Ca ratios in plant tissues negatively affected grain yield production at high salinity with medium or high macronutrient levels and at low macronutrient level together with medium salinity. Even though strong and significant correlations between mineral concentration at grain maturity in leaves, stems, and grain and various yield parameters were observed, our results are inconclusive as to whether toxicity, nutrient imbalance, nutrient deficiency, or all of these factors had a strong influence on grain yield.

INTRODUCTION

Activities of nutrients in the soil solution are affected by high concentrations of salt ions, usually Na and Cl, resulting in a nutritional disorder in plants (Grattan and Grieve, 1992). When nutrient deficiency limits plant growth more than salinity, an increase in the fertility level enhances plant tolerance. The results reported in a companion paper (Hu et al., 1997) showed that the increase in the macronutrient level from 0.2 to 1 strength Hoagland solution (x HS) did not markedly change the salt tolerance of wheat plants, whereas there was a significant increase in salt tolerance as macronutrients were increased from 0.04 to 0.2 x HS. Thus, interactive effects of salinity and nutrients on growth may be associated with changes in the nutrient status in plant tissues. However, there is little information available on the interactive effects of salinity and nutrient level on the mineral element concentration in plants. This study tried to identify limiting factors in salt-stressed wheat plants, subjected to different macronutrient levels, by analyzing mineral concentrations in various plant tissues and their association with yield parameters.

Accumulation of Na and Cl in leaves, through the transpiration flow, is a general, and a long-term process occurring in salt-stressed plants (Munns and Termaat, 1986). High internal concentrations of Na and Cl may provide a means of low energy osmotic adjustment for salt-tolerant plants, which at the same time must be capable of cellular compartmentation of toxic ions (Greenway and Munns, 1980). Plant growth is likely to be affected by the interactions of Na or Cl as well as by many mineral nutrients, causing imbalance in nutrient availability, uptake, or distribution within plants, and also increasing the plant requirements for essential elements (Grattan and Grieve, 1992). For example, high concentrations of Na in the external solution cause decreases in K and Ca concentrations in the tissue of many plant species (Greenway and Munns, 1980; Rathert, 1983). The decrease could be due to the antagonism of Na and K or Ca at sites of uptake in roots, to the effect of Na on the K and Ca transport into xylem (Lynch and Läuchli, 1984) or to the inhibition of uptake processes (Gronwald et al., 1990; Suhayda et al., 1990). Because Ca is essential for maintaining the selectivity and integrity of the cell membrane (Epstein, 1972), Ca deficiency could impair the selectivity and the integrity of the membrane and permit the passive accumulation of Na in plant tissues. Supplemental Ca in the growth medium increased the relative growth rate of barley under saline conditions (Cramer et al., 1990). Similarly, shoot and root growth of rice changed with the alteration of Na/Ca and Ca/K ratios in the external solution (Muhammed et al., 1987). Previous studies also demonstrated that increased NO_3 levels in the growth medium decreased Cl uptake and accumulation (Bernstein et al., 1974; Kafkafi et al., 1982; Feigin et al., 1987; Martinez and Cerda, 1989). However, most of the studies on the interactive effects of salinity and nutrients on the ionic relations in plants were concerned only with single or with two nutrients.

The objective of this study was to investigate the interactive effect of salinity and macronutrients on the mineral element concentrations in leaves, stems, and grain of spring wheat.

MATERIALS AND METHODS

Plant Growth

Growth conditions were as described in the companion paper (Hu et al., 1997). Briefly, spring wheat (*Triticum aestivum* L. cv. Lona) was grown in hydroponics in growth chambers until maturity. Eight levels of salinity between 0 to 150 mM NaCl were established and 1, 02, and 0.04 strength Hoagland macronutrient solution (HS) were used as the level of nutrient supply. At grain maturity, plants were harvested and separated into leaves, stems, roots, and ears. Samples were dried at 105°C for one hour and at 65°C for 48 hours. Dried ears were threshed and then the grain was redried at 65°C for 24 hours. Dried samples were stored for ion analysis.

Analysis of Ion Concentration

Dried flag and second leaves from the top of plant, stems, and grain of each plant were ground with a centrifugal mill (Cyclotec, Sampling mill 1093, Instrumenten-Gesellschaft AG, Zürich, Switzerland) to pass a 0.5-mm diameter sieve. The concentrations of mineral elements in leaves, stems, and grain of spring wheat were measured as follows.

Sodium, Potassium, Calcium, Magnesium, and Phosphorus

Plant samples (250 mg) were ashed at 560°C for 6 h and were digested with 2 mL of 20% HCl at 60°C for five minutes. The concentrations of Na, K, Ca, Mg, and P were determined with an inductively coupled plasma emission spectrometer (ICP model Liberty 200, Varian Australia Pty. Ltd., Mulgrave Victoria, Australia).

Chloride and Nitrate

Fifty mg ground plant samples were extracted with 10 mL distilled water for 15 minutes at 20°C. Within 15 minutes they were shaken twice with a Vortex (Vortex-Genie, K-550-GE, Bender & Hobein AG, Zürich, Switzerland) and then filtered. Chloride was determined using a chloride-selective electrode (Chloride analyzer 926, Corning Ltd., Halstead, Essex, England). Nitrate was analyzed with a HPLC detector (LC 75, Perkin-Elmer Co., Norwalk, CT).

Total Nitrogen

Six mg plant samples were weighed with a supermicro-balance (Sartorius, GMBH, Goettingen, Germany). Nitrogen was analyzed with a nitrogen analyzer (Carlo ERBA Strumentazione, Nitrogen analyzer 1500, Cable Erbadas, Milan, Italy).

Statistical Analysis

Data were analyzed for the correlations between the mineral element concentrations in various tissues and the yield parameters of the main spike and whole plants. Data were also analyzed by using analysis of variance (ANOVA) to test for significance of main effects and interactions. Terms were considered significant at $P \leq 0.05$.

RESULTS

Sodium and Potassium

Salinity increased the concentration of Na in leaves, stems, and grain (Figure 1). Sodium concentration in leaves increased about 50-fold at 150 mM NaCl for plants with 1 and 0.2 x HS and about 90-fold at 60 mM NaCl for the plants with 0.04 x HS as compared with the nonsalinized treatments. The increase in Na concentration in stems was smaller than in leaves and much lower in grain than in leaves and stems, regardless of the macronutrient level. Sodium concentration in grain did not differ significantly ($P>0.05$) up to 125 mM NaCl at 1 and 0.2 x HS and up to 40 mM NaCl at 0.04 x HS. For any given salinity higher than 20 mM NaCl, decreasing the macronutrient concentration in the root medium from 0.2 to 0.04 x HS significantly increased Na accumulation in leaves, stems, and grain, whereas increasing the macronutrient level from 0.2 to 1 x HS did not or only slightly affect Na concentration in leaves, stems, and grain.

Potassium concentration decreased in leaves and very markedly in stems with increasing salinity (Figure 1). Raising the macronutrient level from 0.04 to 0.2 x HS significantly increased K concentration in leaves and stems under saline

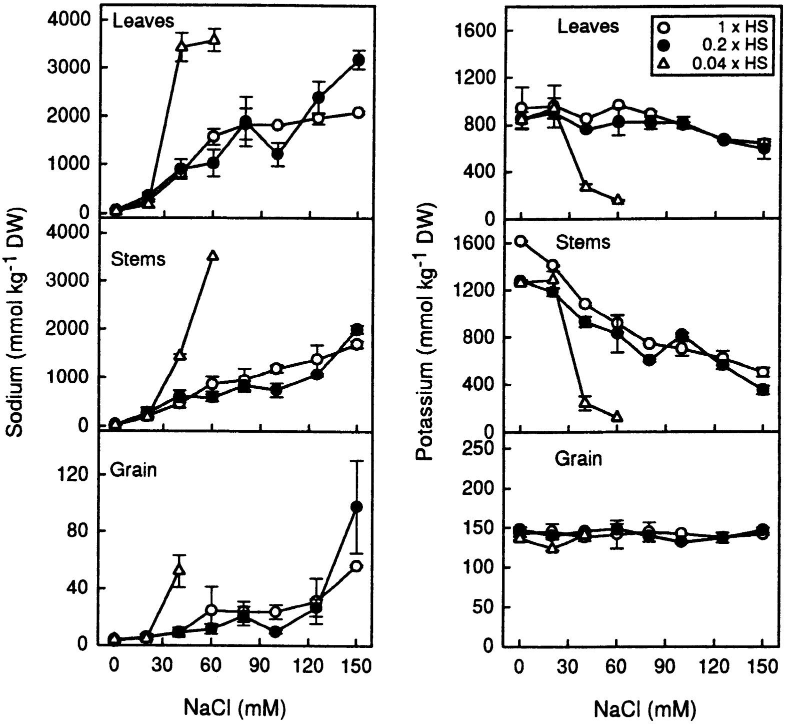

FIGURE 1. Interactive effects of salinity and macronutrients on the sodium and potassium concentrations in leaves, stems, and grain of wheat plants. Error bars represent standard deviations. Error bars fit within the plot symbol if not shown.

conditions. Potassium concentrations in leaves and stems were slightly increased at 1 x HS as compared with 0.2 x HS. No effect of salinity and macronutrient level on K concentration in grain was observed (Figure 1). Sodium/K ratios increased between 0 and 150 mM NaCl in plants provided with 1 and 0.2 x HS from 0.05 to 3-5, 0.02 to 3-6, and 0.02 to 0.5 in leaves, stems, and grain, respectively. This increase was even more pronounced at 0.04 x HS between 0 and 40 mM NaCl.

Calcium and Magnesium

Calcium concentration in leaves decreased with increasing salinity and decreasing macronutrient level (Figure 2). Calcium concentration in stems was enhanced or unaffected by salinity at 1 x HS and decreased with 0.2 and 0.04 x HS. Calcium concentration was higher in leaves than in stems. The decrease in

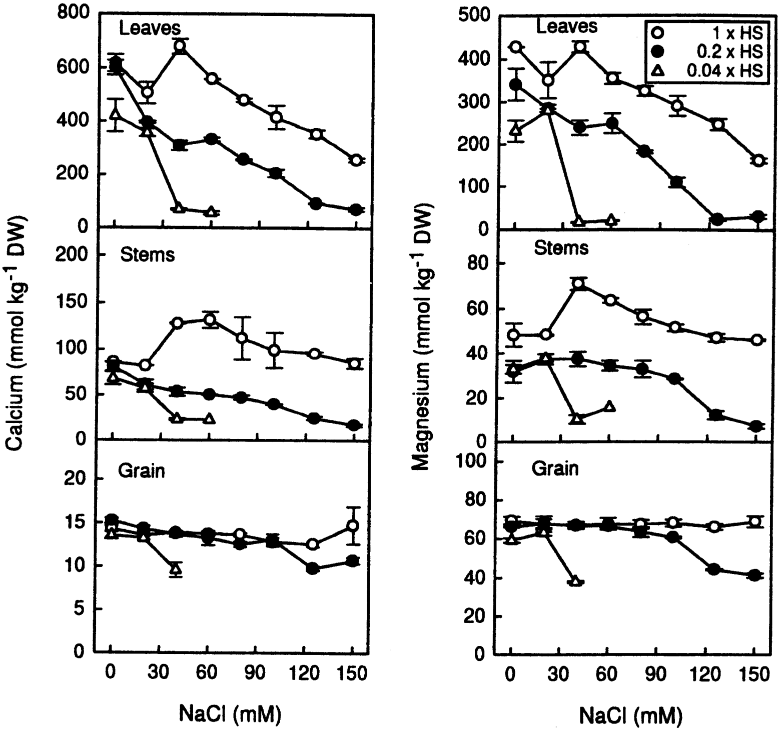

FIGURE 2. Interactive effects of salinity and macronutrients on the calcium and magnesium concentrations in leaves, stems, and grain of wheat plants. Error bars represent standard deviations. Error bars fit within the plot symbol if not shown.

Ca concentration at 0.2 and 0.04 x HS was less pronounced in stems than in leaves. Calcium concentrations in grain with 1 and 0.2 x HS were hardly affected by salinity up to 100 mM NaCl. Strong increases in the Na/Ca ratio in leaves, stems, and grain were observed only at salt levels higher than 100 mM NaCl at 0.2 x HS and with 20 mM NaCl at 0.04 x HS. Magnesium concentration in leaves decreased with increasing salinity and decreasing macronutrient level (Figure 2). The behavior of Mg was very similar to Ca in leaves, stems, and grain.

Chloride and Nitrate

Salinity increased Cl concentrations in leaves, stems, and grain (Figure 3). Chloride accumulation was higher in leaves than in stems and grain. Unlike Na, Cl concentration was not significantly enhanced at 0.04 x HS at a given salt level as compared with higher macronutrient levels. Nitrate concentrations in leaves

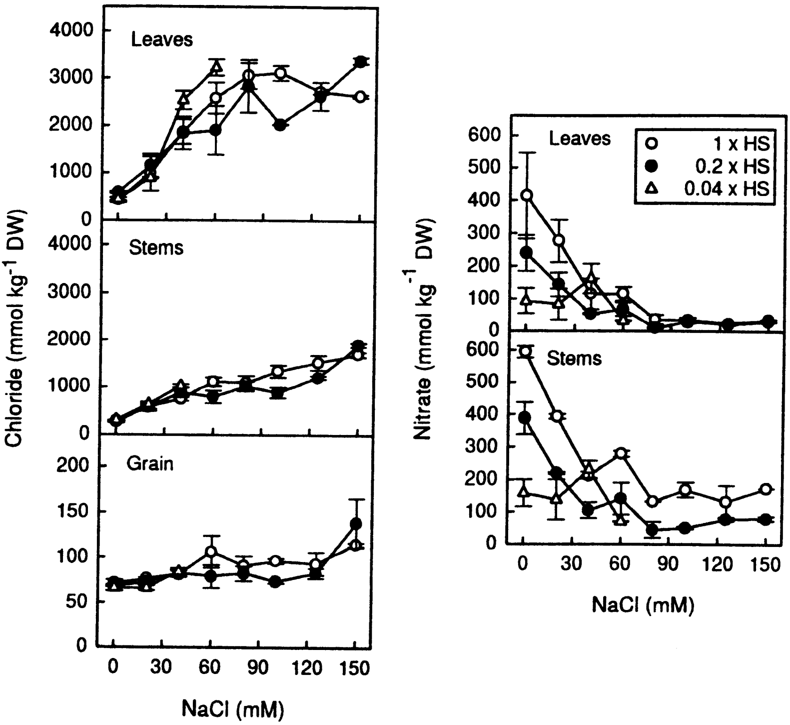

FIGURE 3. Interactive effects of salinity and macronutrients on the chloride and nitrate concentrations in leaves, stems, and grain of wheat plants. Error bars represent standard deviations. Error bars fit within the plot symbol if not shown.

and stems of plants provided with 1 and 0.2 x HS declined significantly with an increase in salinity between 0 and 40 mM NaCl (Figure 3). Beyond 40 mM NaCl, NO_3 concentration decreased slightly or remained constant with increasing salinity at 1 and 0.2 x HS. At 0.04 x HS, however, NO_3 concentration in leaves and stems was unaffected by salinity except at 60 mM NaCl. Raising the macronutrient level from 0.2 to 1 x HS increased NO_3 concentrations in leaves and stems in the range from 0 to 80 mM NaCl and from 0 to 150 mM NaCl, respectively.

Phosphorus and Total Nitrogen

Phosphorus concentrations in leaves were higher at 0.2 x HS than at 1 x HS regardless of the salinity level and were also higher in stems at salt levels higher than 80 mM NaCl (Figure 4). At these two macronutrient levels, P concentrations decreased between 0 and 80 mM NaCl in leaves and stems. Beyond 80 mM

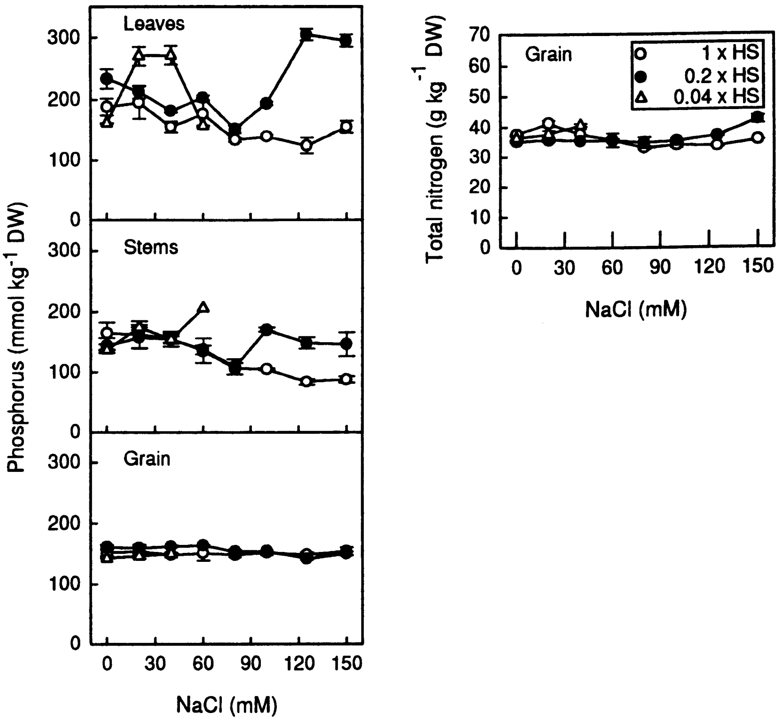

FIGURE 4. Interactive effects of salinity and macronutrients on the phosphorus concentrations in grain of wheat plants. Error bars represent standard deviations. Error bars fit within the plot symbol if not shown.

NaCl, however, P concentrations either increased at 0.2 x HS or remained steady at 1 x HS. P concentrations in grain did not differ, regardless of the salinity and the macronutrient levels. Total nitrogen concentration in grain was not influenced by the salinity or macronutrient level (Figure 4).

DISCUSSION

Increasing salinity linearly reduced yield components of spring wheat such as dry weight of leaves, stems, and grain, regardless of the macronutrient level (Hu et al., 1997). Dry weight of leaves, stems, straw, and grain and spike number were positively correlated with each other (r>0.97***) at all macronutrient levels.

The correlation analysis between yield parameters and mineral concentrations in different organs showed that yield parameters (main spike and whole plant) were more closely correlated to the mineral element concentrations in leaves and stems than in grain. Yield parameters (leaf, stem, grain, straw, above-ground dry weight, and spike number per plant) were significantly correlated with Na ($r<-0.82$), Cl ($r<-0.79$), and K ($r>0.62$) in leaves and stems regardless of the macronutrient level. These parameters were significantly correlated with NO_3 ($r>0.73$) concentrations in leaves and stems at 0.2 and 1 x HS, and not significantly correlated with Ca and Mg concentrations in stems and grain at 1 x HS. However, Ca ($r>0.76$) and Mg ($r>0.75$) concentrations of leaves at 1, 0.2, and 0.04 x HS and of stems at 0.2 and 0.04 x HS were found to be highly significantly correlated to yield parameters. No significant correlations were found between yield parameters and P concentrations in leaves at 0.2 and 0.04 x HS, P concentrations in grain at 1 and 0.04 x HS and K concentration in grain, regardless of the macronutrient level. Correlations between yield parameters of the main spike and mineral concentrations in different organs of plants were similar to those of yield parameters in the whole plant.

In contrast to leaves and stems, mineral concentrations in grain were increased (Na, Cl) or decreased (Ca, Mg, K) only slightly or did not change (K) as a result of increasing salinity. Nitrogen and P concentrations in grain were not affected by salinity. Therefore, mineral concentrations in grain, although sometimes strongly and significantly correlated with yield parameters, do not reflect a serious growth limitation except at very high salinity and low macronutrient level. However, Na, K, Ca, Mg, Cl, and NO_3 concentrations in leaves and/or stems may be associated or even related to yield decreases.

Grain yield of the main spike was only slightly affected by salinity, except at a high level (>120 mM NaCl) with 1 and 0.2 x HS (Hu et al., 1997). This result suggests that, at least with regard to the grain yield of the main spike, none of factors of the toxicity, deficiency, and inoic imbalance limited yield to a great extent. We found that chloride decreased the availability of NO_3 in the leaf growth zone of the main stem (Hu and Schmidhalter, 1997). This restriction may affect leaf and tiller formation and development. Furthermore, tillers which develop later are at greater risk because salts continue to accumulate in the already developed organs and these tillers depend initially on their subtending tillers. A higher risk may be caused by toxic compounds which are derived from source tillers, by nutrient antagonism due to, for example, non-optimal Na/K, Na/Ca, K/Ca supply, or by a deficiency caused by insufficient Ca or NO_3 supply. Another possibility may be disturbances in the hormonal balance (Jennings, 1976; Munns and Termaat, 1986). Thus, wheat yield decreases caused by salinity probably cannot be explained based on mineral concentrations measured at grain maturity in leaves, stems or grain. However, it could be argued that the final mineral concentrations not only accidentally correlate with yield. Nutrient imbalances, deficiencies or toxicities observed at grain maturity might also indicate the likelihood of their occurrence at earlier growing stages.

Sodium and Potassium

It is generally accepted that Na disturbs the nutrient balance and causes specific toxicity. In this study, salinity significantly increased sodium concentrations in leaves and stems (Figure 1). This increase was accompanied by a decline in the K concentration, especially in the stem (Figure 1), indicating an apparent antagonism between K and Na. This antagonism may be due to the direct competition between K and Na at a site of ion uptake in the plasmalemma (Epstein, 1966). Sodium may also enhance the efflux of K into the growth medium, because of disturbed membrane integrity (Cramer et al., 1985).

At any given salinity level, the Na concentration in leaves and stems did not differ at 1 and 0.2 x HS, whereas the K concentration was slightly lower with 0.2 x HS at 0-90 mM NaCl than at 1 x HS (Figure 1). Na/K ratios in plant tissues increased with salinity, markedly only at 0.04 x HS. Difference in Na/K ratios in plant tissues between 1 and 0.2 x HS was not associated with the change in external Na/K ratios. The small differences in plant grain yield which were observed at >100 mM NaCl between 0.2 and 1 x HS could not be accounted for by the Na/K ratio in plant tissues.

Calcium and Magnesium

There was no relationship between Ca concentration in stems and final grain yield at 1 x HS. Calcium concentration in leaves declined with increasing salinity (Figure 2). High Na levels in the external medium may have greatly reduced the activity of Ca in the solution and may have resulted in a decrease in the amount of Ca available for uptake by the plants (Alam, 1994; Grattan and Grieve, 1992). Root growth and function may be inhibited by a high Na/Ca ratio (Kent and Läuchli, 1985), and processes whereby Ca is transported from the root to the shoot may be impaired. The Ca disorder was eliminated when external Na/Ca was reduced to 18 (Grieve and Fujiyama, 1987). Numerous studies have shown that the K concentration in plant tissues is reduced as the Na/Ca ratio in the root medium increases (Okusanya and Ungar, 1984; Cramer et al., 1985; Janzen and Chang, 1987; Subbarao et al., 1990). In this study, however, a five-fold increase in Ca and K concentrations in the nutrient solution (1 x HS as compared with 0.2 x HS) did not influence Na concentrations in leaves and stems. Although Na/Ca ratios in leaves and stems steadily increased with increasing salinity in all treatments, they hardly influenced main spike grain yield, and probably, most likely also not plant grain yield except at very high salinity (>120 mM NaCl) and in the treatment with 0.04 x HS.

Salinity affected Mg accumulation in leaves and stems similar to Ca (Figure 2). The decrease in the Mg concentration seems to be due mainly to ion competition between Na and Mg. Calcium is strongly competitive with Mg. The binding sites on the root plasma membranes appear to have less affinity for the highly hydrated Mg than for Ca (Marschner, 1995). Competition between Ca and Mg may have occurred in this study too. However, Ca/Mg ratios in leaves showed significant changes only at 40-60 mM NaCl in 0.04 x HS and at 125 and 150 mM NaCl in plants with 0.2 x HS, whereas the ratio did not change in the treatment with 1 x HS.

Chloride and Nitrate

Chloride is a more sensitive indicator of salt damage than Na, since, generally, more Cl than Na is stored in plants (Alam, 1994). In general, higher Cl than Na concentrations were found in leaves but not in stems. Macronutrient levels of 0.2 and 1 x HS did not affect Cl accumulation differently in leaves and stems. Chloride concentrations in leaves and stems increased with higher salinity (Figure 3). This increase may result from the reduction in the availability of Ca causing an increase in root permeability (Grattan and Grieve, 1992). Accumulated Cl may cause leaf injury, thereby decreasing photosynthesis and productivity (Greenway and Munns, 1980). Although Cl concentrations in leaves and stems strongly increased with increasing salinity main spike yield was hardly affected. Therefore, it is unlikely that a relation existed between plant grain yield and Cl concentrations in leaves and stems, even though highly significant strong correlations were observed.

Nitrate concentrations at 1 and 0.2 x HS were reduced by decreasing the macronutrient level and by increasing salinity up to 90 mM NaCl. Nitrate concentrations in leaves and stems strongly decreased at 0 mM NaCl with decreasing macronutrient level. Results from the companion paper (Hu et al., 1997) showed that increasing the external NO_3 concentration five-fold from 0.2 x HS to 1 x HS did not influence plant grain yield at low and medium salinity (0-90 mM NaCl). Only a few studies showed an increase in crop yield under saline conditions where N was applied above a level considered optimal under non-saline conditions (Ravikovitch and Yoles, 1971). Decreased NO_3 concentration may be associated with an increase in Cl concentration. Chloride had an antagonistic effect on NO_3 accumulation resulting in a suppression of NO_3 with increasing salinity (Greenway and Munns, 1980; Torres and Bingham, 1973). The decrease in the NO_3 concentration in leaves may also be attributable to the accelerated reduction of NO_3 to NH_4 under salt stress. This conclusion is supported by Munns and Termaat (1986) and Oertli (1991). In contrast, Abdul-Kadir and Paulsen (1982) attributed the decrease in NO_3 reductase activity in salt stressed wheat plants to inhibition of NO_3 uptake by Cl, which is in agreement with the reports of Imsande and Touraine (1994) and Wilkinson and Crawford (1993).

CONCLUSIONS

The grain yield is closely related with the effect of salinity on tiller number in the treatments with 1 and 0.2 x HS from low to moderate salinity levels (0 to 100 mM NaCl) during early growth stages (Hu et al., 1997). After tillers had been

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formed in these treatments, therefore, our results are inconclusive as to whether toxicity, nutrient imbalance, nutrient deficiency, or all of these factors had a strong influence on grain yield. Further work should focus on the relationship between plant growth and mineral concentration in early vegetative stages such as the tiller formation. We expect that these investigations will elucidate whether toxicity, nutrient imbalance, nutrient deficiency, or all of these factors limit grain yield in salinized wheat plants. In contrast, mineral concentrations measured at grain maturity at salinity levels higher than 120 mM NaCl with 1 and 0.2 x HS as well as with 0.04 x HS and >20 mM NaCl most likely reflect more than mere correlations to grain yield. In the latter case, increased Na concentrations and decreased Ca concentrations in the leaves, stems, and grain suggest that grain yield might be limited by Na/Ca disturbance, but not due to lowering the osmotic potential by increasing salinity.

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