JOURNAL OF PLANT NUTRITION, 20(9), 1155–1167 (1997)

Interactive Effects of Salinity and Macronutrient Level on Wheat.
I. Growth

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ABSTRACT

Plant growth response to salinity is known to change under different fertility levels. The objective of this study was to investigate interactive effects of salinity and macronutrient level on growth and yield of spring wheat (*Triticum aestivum* L. cv. Lona), grown in hydroponic culture in growth chambers until grain maturity. Eight salinity levels, 0 to 150 mM NaCl, were established and 1, 0.2, and 0.04 strength Hoagland macronutrient solution (x HS) were designed as the levels of nutrient supply. Only small decreases in the grain yield of the main spike were found at 1 and 0.2 x HS with low and medium salinity (0 to 40 and 40 to 100 mM NaCl, respectively). Larger decreases in the grain yield of the main stem were found at either 0.04 x HS or at high levels of salinity (125-150 mM NaCl), being more marked at 0.2 than at 1 x HS. In contrast to the main spike grain yield, which was only slightly affected at 1 and 0.2 x HS with low and medium salinity, increasing salinity strongly

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decreased plant yield components except thousand grain weight. The salinity level associated with a 50% grain yield decrease was about 84, 72, and 31 mM NaCl for 1, 0.2, and 0.04 x HS, respectively. Salt tolerance was higher at high (full HS) macronutrient concentration. At all macronutrient levels, plant grain yield decreases were mainly and closely related to decreased leaf and tiller numbers. This result suggests that salinity exerts its main effects during the early growth stages. The most promising strategies for increasing wheat yields in saline soils will be (i) increasing nutrient supply in nutrient-poor soils, (ii) creating favorable conditions in the root zone during germination, seedling stage, and early tillering by salt elimination, and (iii) increasing main stem population density by increasing seeding density. The second and third measures will increase yields to a greater extent at moderate and sufficient nutrient levels than additional supplies of nutrients.

INTRODUCTION

Under saline conditions, characterized by low nutrient activities and high ratios of Na/Ca, Na/K, Ca/Mg, or Cl/NO_3 in the root medium, nutritional disorders and osmotic effects develop and plant growth may be hindered.

Numerous studies have confirmed that fertilization management of saline soils plays a vital role in agricultural economics (Ravikovitch and Yoles, 1971; Bernstein et al., 1974; Feigin, 1985; Kafkafi et al., 1982; Papadopoulos and Rendig, 1983). Addition of nutrients resulted in either enhancing, decreasing, or in no changes in plant salt tolerance, depending on the level of salt stress. In many cases, salinity-to-fertility relationships can be summarized as follows: 1) under low salt stress, nutrient deficiency limits plant growth more than salinity, and a positive interaction or increased salt-tolerance response occurs with additional nutrient supplies, 2) under moderate salinity, nutrient deficiency and salinity may equally limit plant growth, and no interaction may occur, and 3) under high salinity, salinity limits growth to a greater extent than nutrient deficiency (Grattan and Grieve, 1992). Plant response in relation to the concentration of an essential nutrient in the root medium has often been described, whereas studies on the interactive effects of salinity and nutrients have been concerned with only single or with two nutrients. It is anticipated that, under different nutrient status (concentration and composition), plant response to salt stress may change.

The objective of this study was to obtain information on the interactive effects of salinity and macronutrient level on spring wheat. The plants were grown in saline solution culture (0 to 150 mM NaCl) at three levels of major nutrients based on Hoagland's solution. Morphological parameters (plant height, leaf number, and tiller number), yield components (dry weight of leaves, stems, grain, and above-ground plant part) of spring wheat were investigated to identify effects of macronutrient concentration on salt tolerance.

MATERIALS AND METHODS

Plant Growth

Seeds of spring wheat (*Triticum aestivum* L. cv. Lona) were germinated on sand:soil (2:1 w:w) for 7 days, and then four seedlings were transplanted to polyethylene containers filled with 30 liters of nutrient solution. The experiment was conducted in growth chambers with a photoperiod of 16 h/day. The light intensity was approximately 450-500 μmol m^{-2} s^{-1} (PPFD) provided by a mixture of 160-watt cool white fluorescent and 60-watt standard tungsten lamps. The air temperature was 23/13°C (day/night), and the relative humidity was 55-65%.

Eight salinity levels were established (0, 20, 40, 60, 80, 100, 125, and 150 mM NaCl). The levels of macronutrients were 1, 0.2, and 0.04 strength Hoagland macronutrients (x HS) (Table 1). Micronutrients were kept at 0.5-strength as recommended by Epstein (1972) for each of the treatment solutions. All treatments were replicated twice. In order to avoid an osmotic shock to plants, salinity was gradually increased in nutrient solutions except at the level of 20 mM NaCl. Daily increments were about 10 mM NaCl. A final NaCl concentration (150 mM) was reached 17 days after transplanting. Throughout the course of the experiment, the concentration of macroelements was analyzed and maintained by adding nutrients or by changing solutions. If necessary, adding nutrients and exchanging solutions were made daily.

The number of leaves and tillers and the height of the main stem were recorded weekly. The leaf water status was determined on days 35 and 70 after transplanting. Water and osmotic potentials from the middle of the second youngest fully developed leaf blades were measured with a pressure bomb (PMS Instrument Co., Model 1002, Corvalis Co., OR) (Scholander et al., 1965) and vapor pressure osmometer (Wescor 5100C, Wescor, Inc., Logan, UT), respectively. Two plants

TABLE 1. Strength of Modified Hoagland Macronutrient Solution (HS). Used to evaluate the effects of macronutrient levels and salinity on growth of spring wheat.

Elements	Macronutrient Level		
	1 x HS	0.2 x HS	0.04 x HS
	mM		
N	15.0	3.00	0.60
P	1.00	0.20	0.04
K	6.05	1.21	0.24
Ca	5.00	1.00	0.20
Mg	2.00	0.40	0.08
S	2.00	0.50	0.04

from each treatment were used for measuring the leaf water status. After measuring the water potential (Ψ), the same leaf was used for measuring the osmotic potential (Ψ_s). Turgor pressure (P) was calculated according to the equation: $P=\Psi-\Psi_s$.

Grain maturity was estimated visually according to the complete loss of green color from the glumes. At grain maturity, plants were harvested and separated into leaves, stems, roots, and ears. Main spikes were separated from the other spikes of plants, dissected, and examined in detail. Each fresh fraction was weighed and then dried at 105°C for 1 hour and then at 65°C for 48 hours. The dry samples were weighed. Ears were threshed, and the grain was redried at 65°C for 24 hours. The chaff weight and thousand grain weight were determined.

Statistical Analysis

Data were analyzed for the correlations between yield parameters of main spike and whole plants and salinity. Linear regression analysis was used to evaluate the

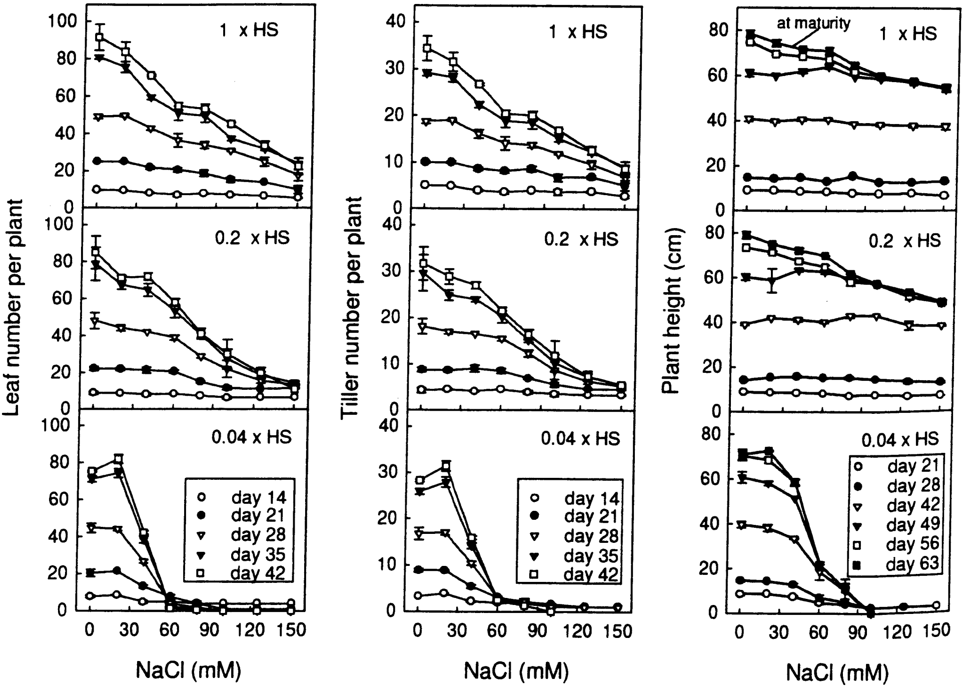

FIGURE 1. Interactive effects of salinity and macronutrient level on leaf number, tiller number, and height of main stem of wheat plants at various intervals after transplanting. Error bars represent standard deviations. Error bars fit within the plot symbol if not shown.

salt tolerance of wheat with 1, 0.2, and 0.04 x HS. Data were also analyzed by analysis of variance (ANOVA) to test for the significance of main effects and interactions. Terms were considered significant at $P \leq 0.05$.

RESULTS AND DISCUSSION

Morphology

Visual observations at early growth stages revealed signs of injury such as chlorosis, necrosis, and burning of the leaf margin, in all salt stressed plants; these injuries were severe at high salt concentrations. The injuries also appeared to be greater in salinized plants provided with low macronutrient concentrations. All plants receiving 100 mM NaCl or higher salt concentrations with 0.04 x HS died within 25 days after transplanting, indicating that an increase in the macronutrient level may increase the tolerance of plants to salinity.

For the early diagnosis of crop salt tolerance, easily assessible morphological parameters of plant growth, i.e., leaf number, tiller number, and main stem height of wheat plants, were chosen. The leaf number, tiller number, and height of the main stem of spring wheat were decreased as salt concentration increased (Figure 1). Increasing macronutrient concentration improved the growth of spring wheat. On day 7 after transplanting, leaf number and tiller number of plants provided with 0.04 x HS were affected by salinity; this occurred after only 21 days for plants with 1 and 0.2 x HS (data not shown). With time, numbers of leaves and tillers were more strongly decreased at high salinity levels for plants with 0.2 x HS than with 1 x HS. Results in Figure 1 show that the decrease in leaf number was closely related to the decrease in tiller number. Twenty-one days after transplanting, leaf number of plants with 150 mM NaCl was decreased by 61, 48, and 95% for 1, 0.2, and 0.04 x HS, respectively, compared with the nonsalinized treatments; tiller number of plants with 150 mM NaCl was decreased by 49%, 47%, and 83% for 1, 0.2, and 0.04 x HS, respectively (Figure 1). At the high and medium macronutrient levels, the numbers of leaves and tillers differed only slightly among salinity levels before 21 days, since the salt level of 150 mM NaCl was reached only at day 17 after transplanting. These observations suggest that salinity exerts significant effects during the early stages and that enhanced fertilization considerably inhibited the deleterious impact of salinity. Similarly, the height of plants with high salt concentrations and lower macronutrient concentrations decreased most (Figure 1), but the obvious changes in height appeared during the reproductive stages. One hundred fifty mM NaCl decreased the height of spring wheat at the final harvest from 79 to 55 cm in plants provided with 1 x HS, whereas the height of plants receiving 0.2 x HS and 0.04 x HS decreased from 79 to 49 cm and 71 to 1 cm, respectively, relative to the nonsalinized treatments.

Growth of Main Stem

Growth Stages

No effects of salinity on the growth stages of plants were observed until tillering which occurred on the fifth day after transplanting regardless of macronutrient concentrations (Table 2). Ear emergence was observed at 43 days and flowering stage was observed at 49 days after transplanting in the nonsalinized treatment with 1 x HS, whereas under 150 mM NaCl, ear emergence and flowering occurred 39 and 43 days after transplanting (Table 2). There were similar changes in the

TABLE 2. Interactive effects of salinity and macronutrient levels on the growth stages of spring wheat grown in hydroponics.

Treatment		Growth Stage			Time of
HS[1]	NaCl	Tillering	Ear Emergence	Flowering	Harvesting
	mM	Days after Transplanting			
1.0	0	5	43	49	123
	20	5	42	47	119
	40	5	40	46	123
	60	5	40	46	117
	80	5	39	45	106
	100	5	39	45	106
	125	5	39	44	100
	150	5	39	43	91
0.2	0	5	43	49	117
	20	5	41	46	116
	40	5	40	45	117
	60	5	39	44	112
	80	5	38	43	106
	100	5	38	43	106
	125	5	38	43	95
	150	5	38	43	85
0.04	0	5	43	49	115
	20	5	42	48	123
	40	5	41	47	108
	60	5	53	--[2]	61
	80	5	--	--	44
	100	5	--	--	29
	125	5	--	--	29
	150	5	--	--	29

[1] Strength of Hoagland macronutrient solution (HS).

[2] Plants died.

growth stages of spring wheat at low and medium salinity levels with 0.2 x HS and 1 x HS, but at 0.04 x HS the growth stages were accelerated with increasing salinity (Table 2). A shorter growth period under stress conditions may be one of the reasons for the decrease in the plant yield. Francois et al. (1986) found that, under optimum macronutrient conditions, flowering of wheat occurred approximately 10 days earlier in a high salt treatment than in the nonsalinized treatment. Cerda and Bingham (1978) also reported that ear emergence and grain maturity were accelerated at high salinity and low phosphorus level. The results of the work presented here support the findings that salinity and low macronutrient levels accelerate ear emergence, flowering, and grain maturity.

Leaf Water Relations

Figure 2 shows the results of the interactive effects of salinity and macronutrients on Ψ and Ψ_s 35 and 70 days after transplanting. At all three macronutrient levels, Ψ and Ψ_s were highest in plants grown in lower salt concentrations. Increasing salt concentration decreased both the water potential and the osmotic potential of the leaf. Although in the root medium was lower with 1 x HS than with 0.2 and 0.04 x HS, there were no great differences in Ψ and Ψ_s among 1, 0.2, and 0.04 x HS 35 days after transplanting. Hoffman and Rawlins (1971) reported that plant age could significantly affect Ψ and Ψ_s in root crops. In this study, Ψ and Ψ_s were measured at the vegetative and reproductive stages. The results show that Ψ_s and Ψ decreased as plants aged (Figure 2).

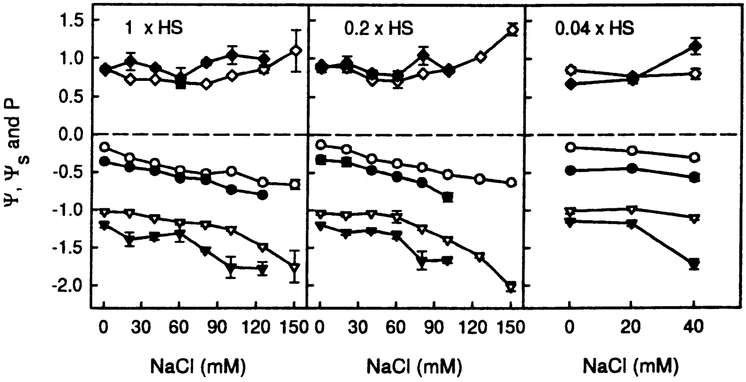

FIGURE 2. Interactive effects of salinity and macronutrient level on leaf water potential (Ψ=circles), osmotic potential (Ψ_s=triangles), and turgor pressure (P=diamonds) 35 days (open symbols) and 70 days (filled symbols) after transplanting. Error bars represent standard deviations. Error bars fit within the plot symbol if not shown.

Turgor pressure increased slightly with increasing salinity regardless of the macronutrient level (Figure 2). On the whole, turgor pressure increased with time under salt stress, whereas in the nonsalinized treatments, turgor pressure remained similar at 1 and 0.2 x HS and decreased at 0.04 x HS. Greenway and Munns (1980) proposed that the decrease in plant growth is due to the decline in turgor pressure with increasing salt stress. In contrast, Munns (1988) reported no relationship between turgor pressure and plant growth under salinity. In this study, the decrease in plant growth under saline conditions is probably not due to the limitation of turgor.

Main Spike Yield Parameters

The main spike of wheat develops through an orderly series of morphogenic events. These events determine the number of spikelets, the number of kernels

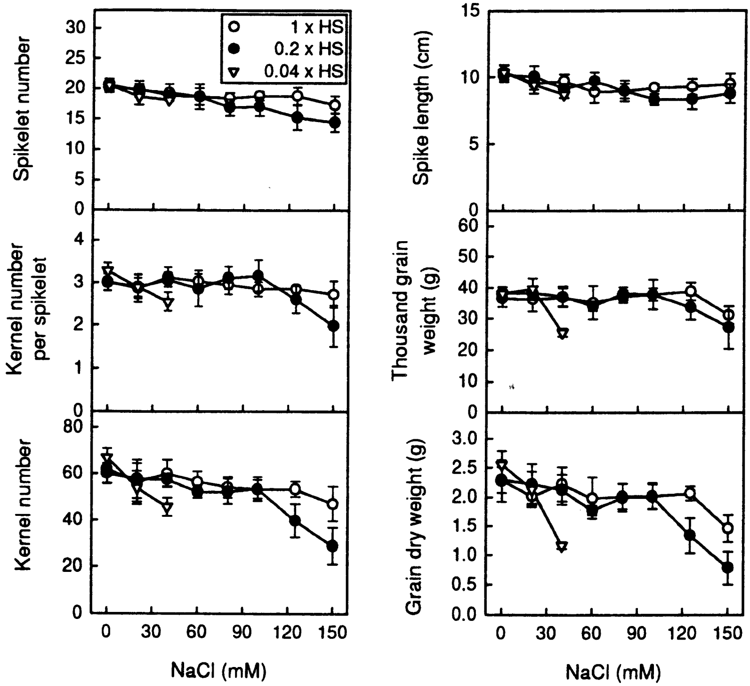

FIGURE 3. Interactive effects of salinity and macronutrient level on the main spike parameters (spikelet number, kernel number per spikelet, kernel numbers, spike length, thousand grain weight, and grain dry weight) of wheat plants. Error bars represent standard deviations. Error bars fit within the plot symbol if not shown.

per spikelet, and the dry weight of individual kernels of the main spike. Spikelet number is determined prior to differentiation of the terminal spikelet. Kernel number is determined during the period of spike emergence to anthesis and maturity (Bingham, 1969). Data in Figure 3 show that the effect of salinity on the components of the yield of the main spike was stronger at 0.2 and 0.04 x HS than at 1 x HS. At all three macronutrient levels, spikelet number, kernel number, and total kernel weight per spike responded more strongly to salinity than did spike length and individual kernel weight (Figure 3). Spike length was 10.4 cm at 0 mM NaCl and 9.5 cm at 150 mM NaCl with 1 x HS; and 10 and 8.7 cm with 0.2 x HS. At 150 mM NaCl, the spikelet number of the main spike was decreased by 16, 28, and 100% for plants provided with 1, 0.2, and 0.04 x HS, respectively. The decrease in kernel number per spike was consistent and significant ($P \leq 0.05$) as salt stress increased from 125 to 150, 100 to 150, and 20 to 60 mM NaCl for plants grown at 1, 0.2, and 0.04 x HS, respectively. Total kernel dry weight of plants grown at 150 mM NaCl with 1, 0.2, and 0.04 x HS was decreased by 36, 66, and 100% as compared with the nonsalinized treatments, whereas the thousand kernel weight was decreased by 16, 28, and 100%, respectively.

Generally, conditions such as high temperature, long days, and water deficit that decrease spikelet number also decrease floret number and grain set per spikelet. Salinity, in common with other stress factors, decreases spikelet number (Grieve et al., 1992). However, the difference in spikelet number depends on the level of stress and nutrients. The small decrease in grain yield of the main spike (Figure 3) under high and medium (1 and 0.2 x HS) nutrient supply at low and medium salinity (0-40 and 40-100 mM NaCl) was due mainly to the effect of salinity on spikelet number. In contrast, stronger decreases in grain yield, found at the low macronutrient level (0.04 x HS) and at high salinity (100-150 mM NaCl), were primarily caused by decreased kernel number per spikelet and decreased thousand grain weight. Therefore, in the latter case, the development of the main spike was also affected from spike emergence to anthesis and maturity.

Plant Growth

The average dry weights of leaves, stems, grain, and above-ground plant parts and spikes per plant are presented in Figure 4. Above-ground dry weight is defined as the sum of leaf, stem, chaff, and grain dry weight. The analysis of regression between yield parameters and salinity demonstrated a consistent decrease in all yield components with increasing salinity. This decrease was partly counteracted in plants provided with high macronutrient levels. Analysis of variance showed that there were no significant differences in the yield components between 1 and 0.2 x HS under low and moderate salinity (Figure 4). At 150 mM NaCl, leaf dry weight decreased by 89, 90, and 92% with 1, 0.2, and 0.04 x HS, respectively; stem dry weight was decreased by 88, 92, and 99%, grain dry weight was decreased by 89, 97, and 100%, and above-ground plant dry weight was decreased by 89, 95, and 100%. The salinity level associated with a decrease of 50% grain yield

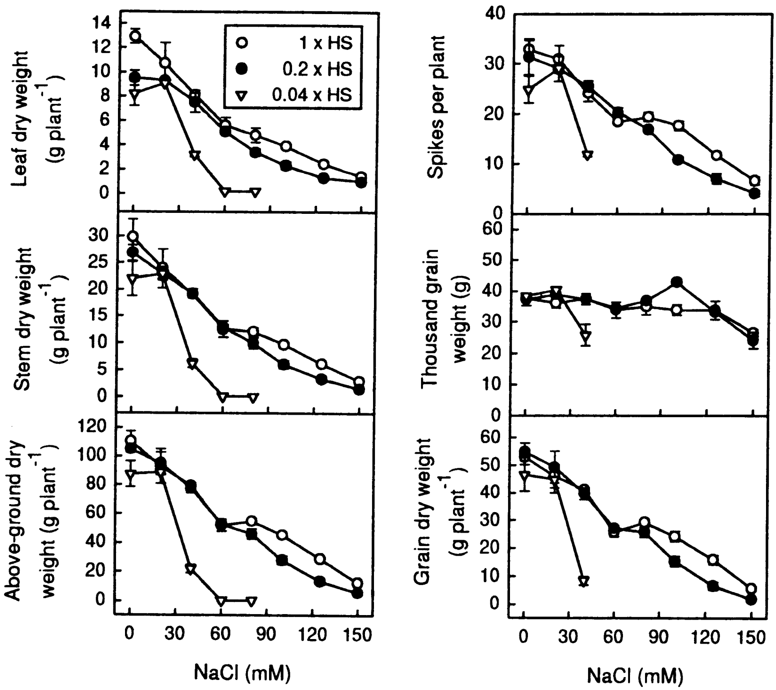

FIGURE 4. Interactive effects of salinity and macronutrient level on plant yield parameters (leaf dry weight, stem dry weight, above-ground part dry weight, spikes per plant, thousand grain weight, and grain dry weight). Error bars represent standard deviations. Error bars fit within the plot symbol if not shown.

was about 84, 72, and 31 mM NaCl for 1, 0.2, and 0.04 x HS, respectively. These results suggest that improved fertilization management can alleviate growth inhibition due to salinity. Stronger decreases in dry weight of leaves, stems, and grain as well as in the spike number were observed at high salinity levels (100-150 mM NaCl) at the medium macronutrient level (0.2 x HS) as compared with the high macronutrient level (1 x HS) (Figure 4). These decreases were closely related to those in leaf and tiller number (Figure 1). Tillering is closely related to leaf expansion during early growth and is the main determinant of the number of ears, i.e. the component most closely correlated with yield (Roy and Gallagher, 1985). Salinity decreases yield in wheat plants mainly by decreasing the tiller number independent of the nutrient supply. In contrast, the yield of the main stem is only slightly affected, even at high salinity levels. Tillers that are formed later may be subjected for a longer period to increased levels of toxic elements in plants, or non-compatible solutes are preferentially allocated to primary or secondary tillers. The main stem may thus avoid the build-up of harmful concentrations of toxic compounds.

Thousand grain weight (TGW) decreased only at the highest salinity level regardless of the macronutrient level (Figure 4). There were no significant differences in TGW of spring wheat under low and medium salinity except in TGW at 0.04 x HS. Because kernel number per spike of plants was not markedly decreased by low or medium levels of salinity, this indicates that grain yield was decreased mainly by the spike number (Maas and Poss, 1989).

Relative yield (% of the nonsalinized treatment) can be used to assess the sensitivity of plants to salt stress. Coefficients of determination of linear regression equations between relative yields for grain and for straw (sum of leaves, stems, and chaffs) and salinity levels were $\geq$0.95*** at 0.2 and 1 x HS and $\geq$0.86 at 0.04 x HS. An increase in each mM NaCl decreased the relative grain yield (%) in plants provided with 1, 0.2, and 0.04 x HS by 0.56, 0.68, and 1.89%. The increase in each mM NaCl concentration decreased the relative straw yield (%) in plants with 1, 0.2, and 0.04 x HS by 0.56, 0.67, and 1.86%, respectively. The values for grain were about the same as that of straw at the same macronutrient level, indicating a close relationship between grain yield and straw yield.

Several studies showed only a slight improvement in yield in saline soils as a result of increasing the nutrient level (Feigin, 1985; Grattan and Grieve, 1992). Data in Figure 4 indicate that the salt tolerance of spring wheat was greatly enhanced at low macronutrient levels by increasing the macronutrient concentration, whereas it increased only slightly when the macronutrient level was increased from 0.2 x HS to 1 x HS. Growth and yield in salinized wheat plants were probably not limited by nutrients at 0.2 and 1 x HS.

Successful management in saline areas must consider the local conditions and the availability of resources. Optimized strategies would relieve the most severe growth-limiting stress. At nearly sufficient nutrient levels in soils, increased macronutrient supply to saline soils will not improve yields and is not desirable from an economic and environmental point of view. With low fertility, nutrient supply causes a strong increase in yield. Improved yields due to higher macronutrient supply can also be expected in moderately and highly saline soils with below-optimum nutrient levels. However, relieving salinity stress during the early stages of development will be more successful than increasing nutrient supply. If feasible, salt elimination from the root zone at germination, at the seedling stage, and at early tillering will dramatically increase yields of wheat. If this measure is not applicable, increasing seeding densities, to achieve a higher total plant population per area to replace lost tillers with main stems, seems promising (Grieve et al., 1992).

CONCLUSIONS

This study suggests that the salt tolerance of wheat was significantly increased by increasing the macronutrient concentration under the conditions of below-optimum nutrient levels. Turgor did not limit growth. Growth stages were accelerated by salinity, especially at the low macronutrient level. Salinity exerted significant effects during the early growth stages. At later growth stages higher salt levels in the root zone can be tolerated by wheat plants (Maas and Poss, 1989). The grain yield of the main spike decreased much less than the vegetative growth parameters. Under high nutrient supply and low and medium salinity, the decrease in the final grain yield was mainly due to the effect of salinity on the spike number per plant. At low macronutrient level or high salinity, the grain yield was decreased by a decrease in the spike number and by the effect on the differentiation of spikelet and the development of the spike from spike emergence to anthesis and maturity.

Surprisingly, little efforts have been made to understand the mechanisms controlling the effect of salinity on the tiller number. Detailed studies of the effects of salinity on leaf emergence and tiller primordia initiation and development will improve substantially our understanding of these processes.

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