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ORIGINAL ARTICLE

Differential effect of moderate salinity on growth and ion contents in the mainstem and subtillers of two wheat genotypes

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Abstract

To understand the differential effect of moderate salinity on the growth and ion contents in mainstem and subtillers of wheat plants, two spring wheat (*Triticum aestivum* L.) genotypes (Sakha 8 and Thasos) were grown in a greenhouse in soil with or without salinity. Both the above-ground dry weight and the leaf area at day 55 after sowing, as well as the grain yield, grain number, spikelet number, straw dry weight and above-ground dry weight at plant maturity, were determined. Inorganic ion content in young leaves at day 55 after sowing was also analyzed. The results showed that the above-ground dry weight and leaf area in the subtillers (T1 and T2) at day 55 after sowing were greatly reduced by salinity. Compared with the effect of salinity on subtiller growth, the mainstem was much less affected during the vegetative growth stages, whereas there was a similar effect of salinity on the grain yield between the mainstem and subtillers. The reduction in the grain yield of Sakha 8 by moderate salinity mainly resulted from a decrease in the number of tillers, whereas in addition to a reduction in the number of tillers in the salt-sensitive genotype Thasos, the grain yield in mainstem and subtillers was further reduced during the grain filling. Both wheat genotypes are more sensitive to salt stress during the vegetative growth stages than in the reproductive stages. The salt-tolerant genotype Sakha 8 is characterized by the exclusion of Na^+ in the leaves. Thus, under moderate saline conditions the greater reduction in subtillers may result from an ion imbalance in the salt-tolerant genotype Sakha 8 and from Na^+ toxicity in the salt-sensitive genotype Thasos.

Key words: chloride, mainstem, salinity, subtillers, wheat.

INTRODUCTION

Salinity has drawn extensive attention throughout the world because over 6% of the earth's land area (800 million hectares) is affected by either salinity or the associated condition of sodicity (Food and Agriculture Organization 2006). Hence, increases in crop salt tolerance are needed to sustain food production in many regions of the world. Wheat represents a major food crop in most countries where saline soils exist or might develop (Ashraf and McNeilly 1988), and is reported by Maas and Hoffman (1977) to be moderately tolerant to salinity.

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The yield capacity of wheat is highly dependent on the number of spike-bearing tillers and the grain yield per spike. Salinity as an environmental factor depresses wheat growth because of a reduction in tiller number and biomass (El-Hendawy *et al*. 2005a; Hu *et al*. 1997; Maas and Grieve 1990; Nicolas *et al*. 1993). It has been reported that among the tillers, the mainstem in salt-stressed wheat does not suffer from a reduction in yield with increasing salinity as much as the subtillers suffer (Hu *et al*. 1997; Maas *et al*. 1994, 1996), which may be caused by competition among the tillers for nutrients. The inhibitory effects of salinity on plant growth are related to Na^+ and Cl^- accumulation together with the uptake of essential nutrients, such as K^+ and Ca^{2+} (El-Hendawy *et al*. 2005b; Hu and Schmidhalter 1997; Wang and Han 2007). However, most studies on wheat have focused on the effects of high salinity. In agricultural fields, moderate levels of salinity are becoming a common problem, especially in the irrigation areas. It is still unclear whether the conclusions from

studies on the effects of high salinity on wheat hold true for wheat under moderate saline conditions. Therefore, it is necessary to investigate the growth of individual tillers and the distribution of mineral elements among the different tillers under moderate saline conditions.

Recently, the two wheat cultivars Sakha 8 and Thasos have been identified according to multiple agronomic parameters at the different growth stages as being salt-tolerant and relatively salt-sensitive genotypes, respectively (El-Hendawy *et al.* 2005a). This finding provides a unique opportunity to understand the influences of salinity on tillering in contrasting wheat genotypes. Therefore, the objectives of the present study were to investigate the relationship between plant growth and ion distribution among tillers under moderate salinity in these two contrasting wheat genotypes to provide a comprehensive understanding of the reduction in tillering under saline conditions.

MATERIALS AND METHODS

Plant growth

Thirty seeds of each Sakha 8 and Thasos cultivar were sown in 11-L plastic pots containing 10 kg of dry loamy soil with or without salt stress. One after sowing, the seedlings were thinned to 15 plants per pot. Soil collected from the soil surface (0–15 cm) was air-dried, sieved through a 5-mm screen and mixed with 30% sand to achieve good leakage. The initially air-dried soil with 7.5% gravimetric water content was filled layer-wise in four layers in pots. To reach a final soil water content of 25% on a dry soil basis, tap water or NaCl solution was added to the control or salinity treatments, respectively. According to the preliminary experiments, the salt-stressed pots were salinized by adding 400 mL of 120 mmol L^{-1} NaCl solutions to each soil layer to achieve an electrical conductivity (EC) of approximately 7.0 dS m^{-1}. The soil pH was 6.9. The EC and pH value were measured before sowing and at day 55 after sowing. There was only a slight change in the EC between the two measurements, whereas the pH values decreased from 6.9 to 6.0. To maintain 25% of soil water content, the pots were weighed daily during the experiment and the loss of water was replaced by adding tap water. To ensure that no nutrient deficiency existed during plant growth, 0.57 g NH_4NO_3 was applied to each pot at days 20, 40 and 60 after sowing, and 0.2 g KH_2PO_4 and 0.2 g K_2SO_4 were similarly applied at day 20 after sowing. At the two-leaf stage, the seedlings were thinned to twenty per pot.

The experiment consisted of a split-plot layout with three replicates. The main plot consisted of salt levels, with the two genotypes being allocated to the subplots. Plants were grown in a greenhouse at day/night temperatures of approximately 18/13°C, with a 14-h light period of photon flux density 550 μmol photon m^{-2} s^{-1}.

Before heading (i.e. at day 55 after sowing), six randomly selected plants were harvested per pot and the two youngest fully developed leaves were separated from the mainstem and the two subtillers (i.e. the primary tillers from leaves 1 and 2, T1 and T2, on the mainstem). Leaf areas for the mainstem, subtillers (T1 and T2) and remaining tillers were determined using a leaf-area meter. Plant material was dried at 65°C for 48 h for the determination of dry weight.

At plant maturity, five plants per pot were harvested at random and then separated into the mainstem, T1, T2 and remaining tillers from which the leaves, stem and spikes were removed as appropriate. After drying at 65°C for 48 h, straw dry weight, spike dry weight, grain number per spike, grain yield per spike and spikelet number per spike were measured in each of the mainstem, T1, T2 and remaining tillers. The above-ground dry weight at plant maturity was equal to the spike dry weight plus the straw dry weight.

Analysis of ion contents

The two youngest fully developed leaf samples from the mainstem, T1 and T2 harvested at day 55 after sowing were ground after oven-drying into a fine powder by passing them through a 0.5-mm diameter sieve. To determine Na^+, K^+, Mg^{2+} and Ca^{2+} concentrations, 150-mg plant samples were ashed at 560°C in a muffle furnace for 6 h and then digested with 2 mL of 20% HCl for 5 min at 60°C using a heating block, and finally diluted to a volume of 25 mL with distilled deionized water. The concentrations of Na^+, K^+, Mg^{2+} and Ca^{2+} were determined using an Inductively Coupled Plasma Emission Spectrometer (ICP model Liberty 200; Varian Australia, Mulgrave, Victoria, Australia).

For determination of NO_3^- and Cl^- concentrations, 50 mg of the ground sample was shaken with 25 mL distilled water for 1 hour and then filtered. Chloride and NO_3^- were determined using an ion chromatography analyzer (Model LC20–1; Dionex, Sunnyvale, CA, USA).

Statistical analysis

All variables were analyzed using the General Linear Model (GLM) procedure implemented in SAS (SAS Institute 2004). All growth parameters were analyzed using individual ANOVAs with individual models for the mainstem, T1, T2 and the total plant. Individual models for the mainstem, T1 and T2 were also used for the individual ANOVAs for each inorganic ion. All tests used a nominal alpha level of 0.05.

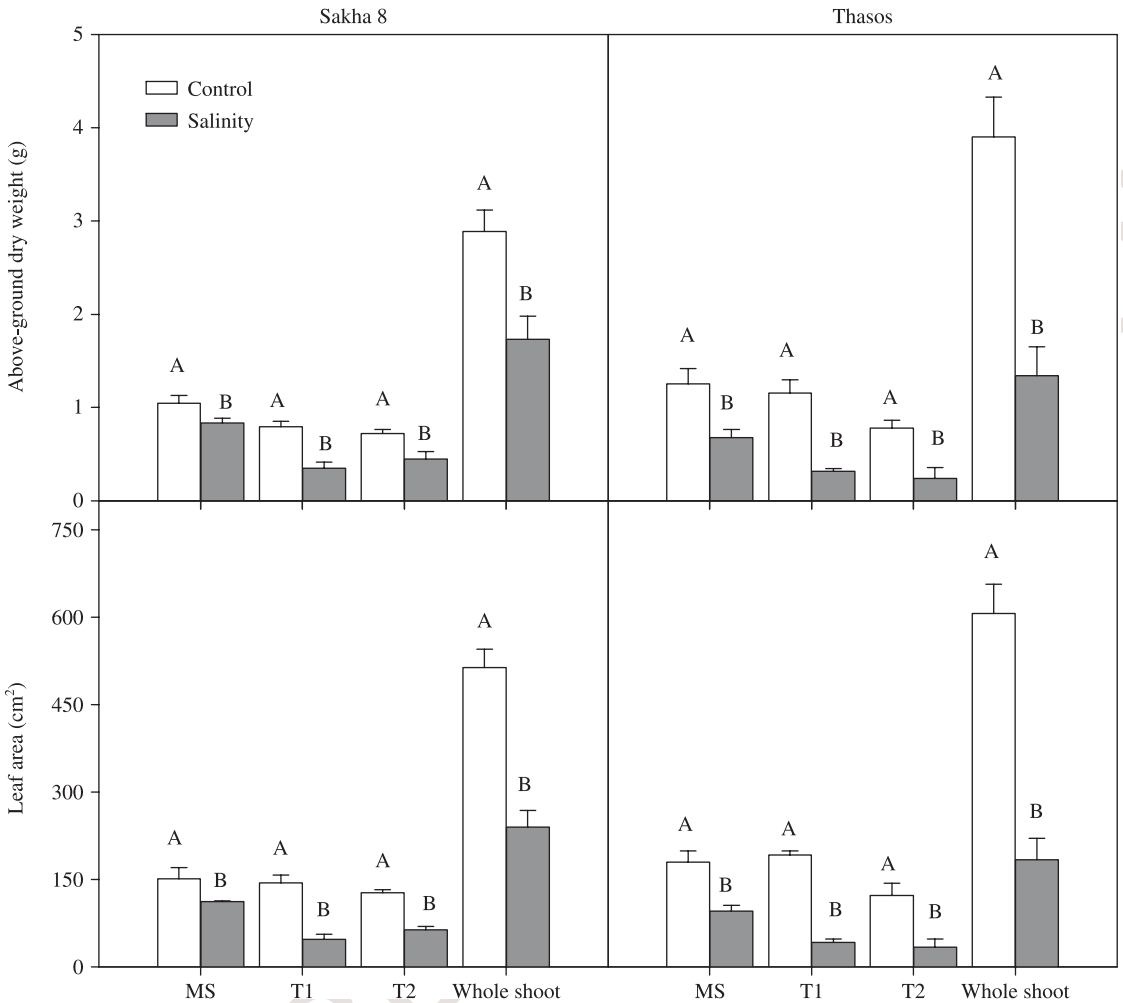

Figure 1 Effect of salinity on above-ground dry weight (g per tiller or per plant) and leaf area (cm^2 per tiller or per plant) of the mainstem (MS), T1, T2 and the whole shoot for Sakha 8 and Thasos at day 55 after sowing. Bars with the same letter are not statistically different ($P \leq 0.05$) between the control and salinity treatments.

RESULTS

Effects of salinity on growth parameters of the whole shoot, mainstem and subtillers (T1 and T2)

The tiller number per plant at first harvest was five in the control and four in the salinity treatment for Sakha 8, and seven in the control and four in the salinity treatment for Thasos.

Above-ground dry weights and leaf areas of the whole shoot and individual tillers (mainstem, T1 and T2) at day 55 after sowing decreased significantly with increasing salinity for both genotypes (Fig. 1). However, compared with Sakha 8, the reductions in above-ground dry weight and leaf area in the mainstem, T1, T2 and the whole shoot were greater for Thasos. Importantly, the above-ground dry weights and leaf areas of the subtillers (T1 and T2) at day 55 after sowing were reduced to a greater degree in both genotypes under salt stress than in the mainstem. For example, the above-ground dry weights of the mainstem, T1 and T2 were reduced by 20%, 56% and 38%, respectively, for Sakha 8 and by 46%, 72% and 69%, respectively, for Thasos.

Compared with the control treatment, grain yield, grain number and above-ground dry weight per plant at plant maturity in Sakha 8 were reduced by salinity by 22%, 23% and 29%, respectively. For Thasos, the corresponding values were 32%, 32% and 34% (Figs 2,3). By contrast, larger reductions for both straw dry weight and spikelet number per plant for Sakha 8 (41% and 38%, respectively, compared with the control treatment) than for Thasos (38% and 28%) were apparent (Fig. 3). Furthermore, whereas the reductions in grain yield and straw dry weight per plant in Thasos were significant,

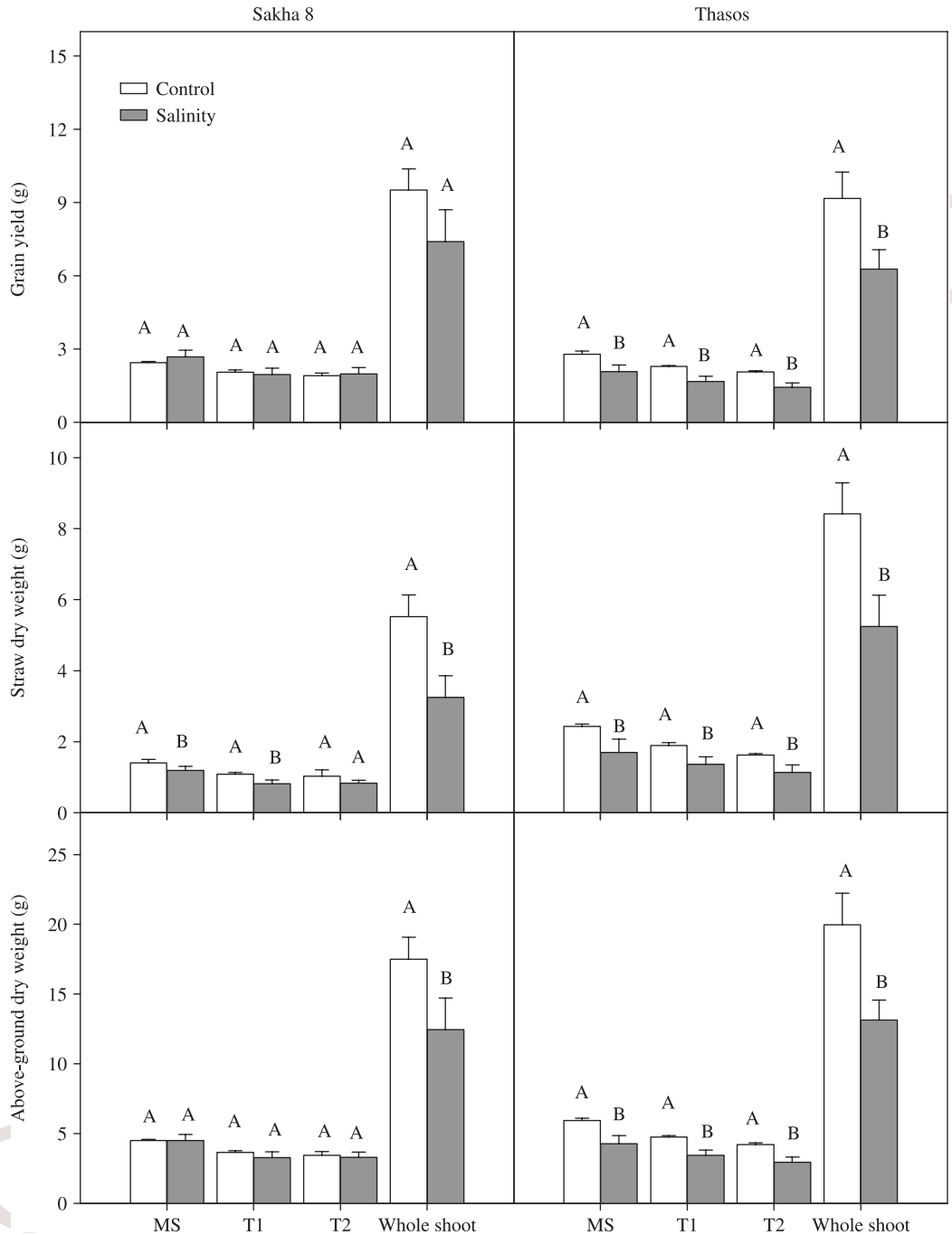

Figure 2 Effect of salinity on grain yield, straw dry weight and above-ground dry weight (per tiller or per plant) of the mainstem (MS), T1, T2 and the whole shoot for Sakha 8 and Thasos at plant maturity. Bars with the same letter are not statistically different ($P \leq 0.05$) between the control and salinity treatments.

only the reduction in straw dry weight was significant in Sakha 8. Under saline conditions, significant decreases in grain number, spikelet number per plant and the thousand-grain weight (TGW) were recorded in Thasos, but only spikelet number per plant was reduced in Sakha 8 (Figs 2,3).

Similar to the responses of the whole shoot to salinity, the mainstem, T1 and T2 of Sakha 8 also showed better salt tolerance than those of Thasos with respect to grain yield, grain number and above-ground dry weight at plant maturity. However, straw dry weights, spikelet numbers and the TGW of the mainstem, T1 and T2

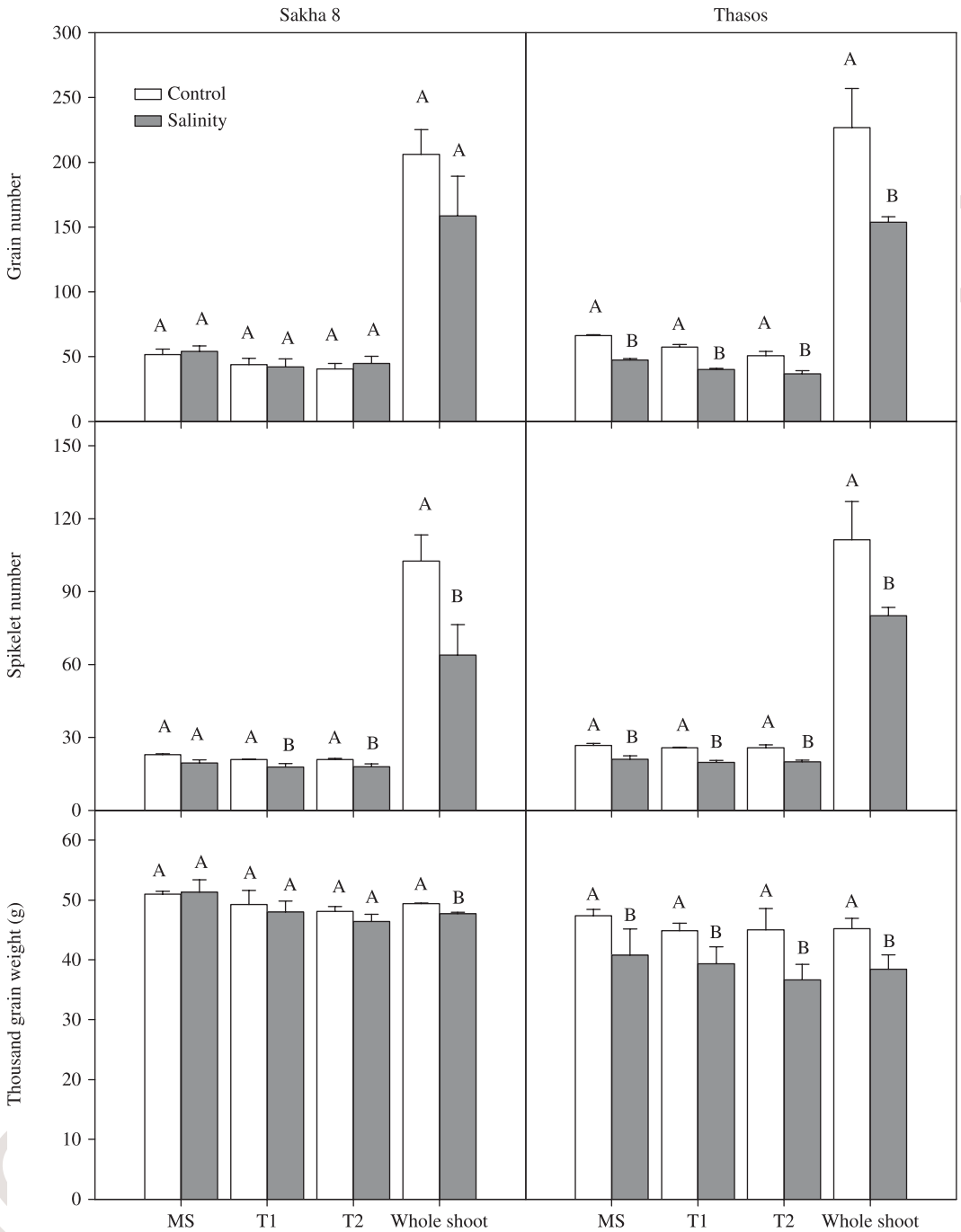

Figure 3 Effect of salinity on grain number, spikelet number and thousand-grain weight (per tiller or per plant) of the mainstem (MS), T1, T2 and the whole shoot for Sakha 8 and Thasos at plant maturity. Bars with the same letter are not statistically different ($P \leq 0.05$) between the control and salinity treatments.

underwent smaller reductions in Sakha 8 than in Thasos compared with the whole shoot (Figs 2,3). The slightly increased grain yields and grain numbers of the mainstem and T2 for Sakha 8 under salinity suggest that the remaining tillers were mainly responsible for the reduction in these parameters per plant (Figs 2,3). For Thasos, salinity caused significant reductions in grain yield, grain number, spikelet number, straw dry weight and above-ground dry weight at maturity in the mainstem, T1 and T2.

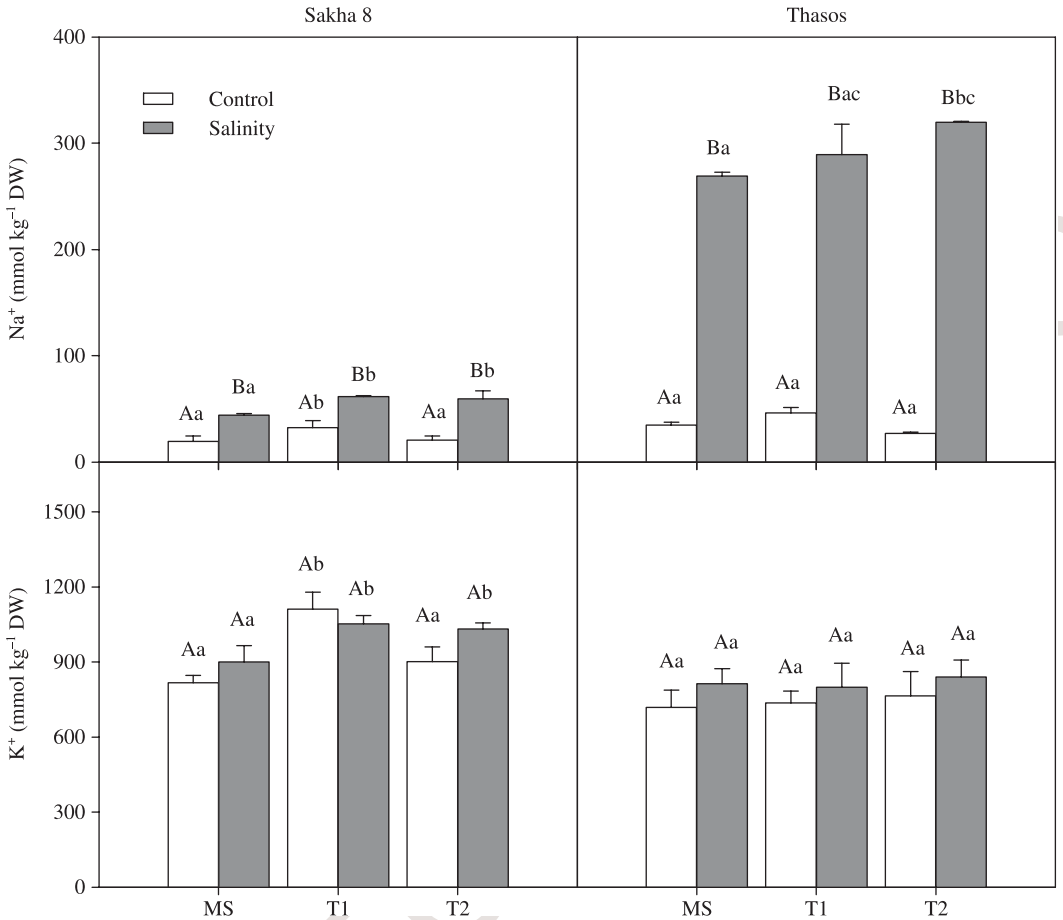

Figure 4 Effect of salinity on the Na^+ and K^+ concentrations of the two youngest fully developed leaves of the mainstem (MS), T1 and T2 for Sakha 8 and Thasos. The same uppercase letters on the different color bars or lowercase letters on the same color bars are not statistically different ($P \leq 0.05$). DW, dry weight.

Distribution of inorganic ions in the mainstem, T1 and T2 at day 55 after sowing

In both genotypes, salinity significantly increased the Na^+ concentration in the mainstem, T1 and T2 (Fig. 4). Compared with the control treatment, the Na^+ concentration in Sakha 8 was increased approximately twofold in the mainstem and T1, and approximately threefold in T2. The accumulation of Na^+ in Thasos under saline conditions was even higher, approximately eightfold in the mainstem, sixfold in T1, and 12-fold in T2. Thasos was also observed to accumulate significantly higher Na^+ levels in the mainstem, T1 and T2 than Sakha 8.

The effect of salinity on the K^+ concentration in the leaf tissues differed depending on the combination of the tillers and of the genotypes. For example, K^+ concentrations in the mainstem and T2 of both Thasos and Sakha 8 and in T1 of Thasos increased slightly under saline conditions, whereas the concentration in T1 of Sakha 8 decreased slightly (Fig. 4). Compared with the mainstem, the K^+ concentration significantly increased in T1 and T2 of Sakha 8 under salinity, whereas there was no significant difference between the mainstem and subtillers in Thasos (Fig. 4). Regardless of the treatment, all tillers of Sakha 8 accumulated higher K^+ concentrations in the young leaves than those of Thasos. However, no differences between the two treatments were significant for any individual tiller of either Sakha 8 or Thasos. Large differences in the Na^+:K^+ ratios between the two genotypes under saline conditions were observed, ranging from 0.05 to 0.06 for the tillers of Sakha 8 and from 0.33 to 0.38 for the tillers of Thasos. An increase in the Na^+:K^+ ratio for T1 or T2 compared with the mainstem was observed in both genotypes.

The influence of salinity on Ca^{2+} concentrations in the young leaves also varied according to tiller and genotype. Under salt stress, Ca^{2+} concentrations in Sakha 8 declined slightly in all tillers, whereas they increased slightly in Thasos. In Sakha 8, the degree of

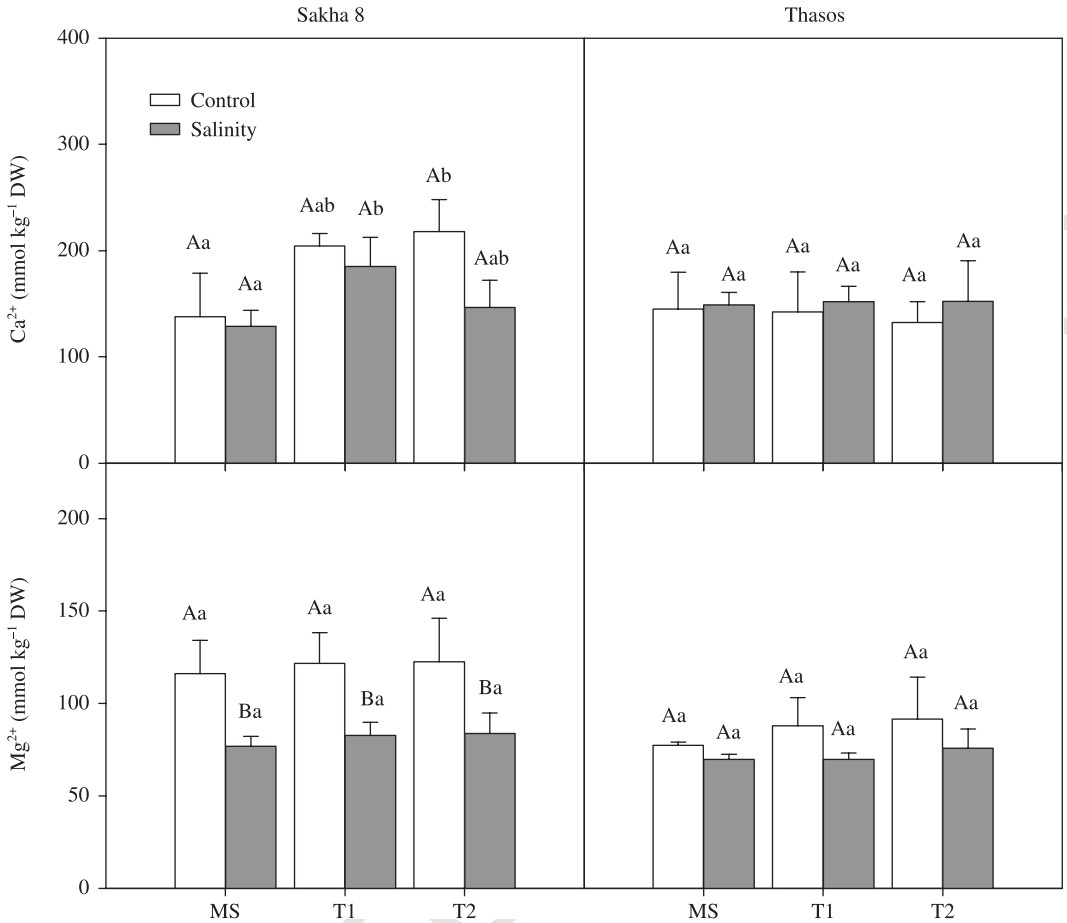

Figure 5 Effect of salinity on the Ca^{2+} and Mg^{2+} concentrations of the two youngest fully developed leaves of the mainstem (MS), T1 and T2 for Sakha 8 and Thasos. The same uppercase letters on the different color bars or lowercase letters on the same color bars are not statistically different ($P \leq 0.05$). DW, dry weight.

the reduction in Ca^{2+} concentration induced by salinity increased from the mainstem to T1 and T2, although these differences were not significant. By contrast, Mg^{2+} concentrations in the mainstem, T1 and T2 decreased with salinity in both genotypes (Fig. 5). In general, Mg^{2+} concentrations in tillers of Sakha 8 were higher than the corresponding tillers of Thasos, although the reduction in Mg^{2+} concentrations under salinity was greater in Sakha 8. Finally, there was no significant difference in Mg^{2+} concentration among tillers under saline conditions regardless of the genotypes.

Similar to Na^+, Cl^- concentrations in the young leaf tissue of all tillers of both genotypes increased significantly under salinity. However, all tillers in Sakha 8 accumulated less Cl^- than those in Thasos (Fig. 6). Chloride concentrations in T1 and T2 in both Sakha 8 and Thasos were higher than those in the mainstem, although this difference was only significant between the mainstem and T1 in Sakha 8. Salinity greatly decreased the NO_3^- concentrations in all tillers for both genotypes (Fig. 6), and a greater reduction in Sakha 8 was observed. Similar to the findings for K^+ and Mg^{2+}, NO_3^- concentrations in T1 and T2 were higher than those in the mainstem regardless of the genotype and treatment. However, the mainstem tiller showed a smaller reduction in NO_3^- concentration than did the subtillers in both genotypes. This trend is identical to Ca^{2+} in Sakha 8 and Mg^{2+} in Thasos.

DISCUSSION

The yield potential of wheat under saline conditions is highly dependent on the number of tillers per plant and the grain yield per spike (El-Hendawy *et al.* 2005a; Maas and Grieve 1990; Salam *et al.* 1999). As there was no difference in grain yield in the mainstem, subtillers 1 and 2 of Sakha 8 between the control and the salinized treatments, the results in this study suggest that the reduction in the grain yield of Sakha 8 by salinity mainly results from the decreased number of tillers

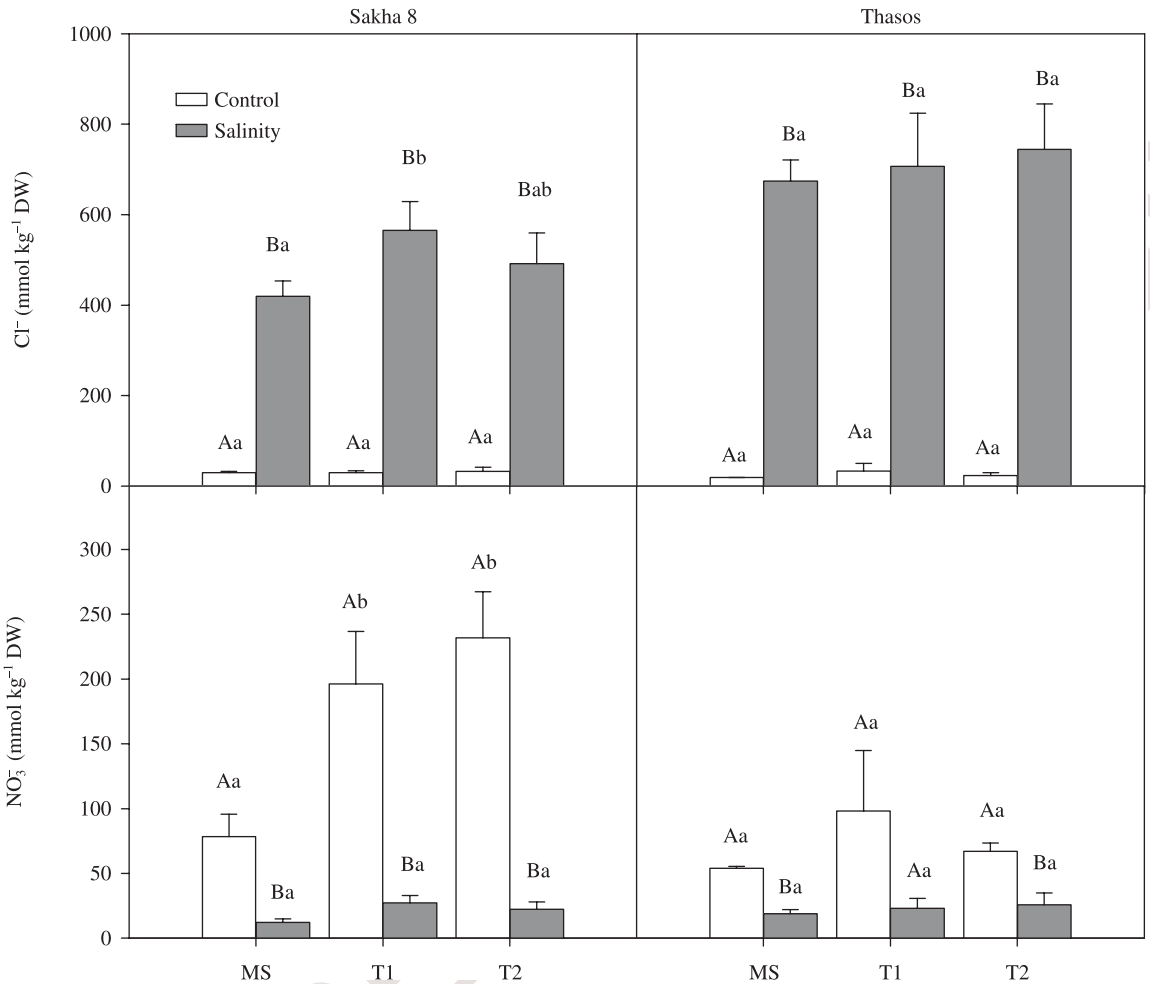

Figure 6 Effect of salinity on the Cl^- and NO_3^- concentrations of the two youngest fully developed leaves of the mainstem (MS), T1 and T2 for Sakha 8 and Thasos. The same uppercase letters on the different color bars or lowercase letters on the same color bars are not statistically different ($P \leq 0.05$). DW, dry weight.

(Fig. 2). In contrast, the results indicate that in addition to the reduction in the number of tillers in the salt-sensitive genotype Thasos, the grain yield in the mainstem and subtillers is further reduced during grain filling (Fig. 2). Previous studies have shown that wheat is more sensitive to salt stress during the vegetative growth stages than in the reproductive stages (e.g. Francois *et al*. 1994; Hu *et al*. 1997). This is also the case for both genotypes tested in the present study. Compared to the difference in the above-ground dry weight of both genotypes between the control and the saline treatments at day 55 after sowing, less reduction as a result of salinity at the final harvest was observed (Figs 1,2). The vegetative growth stages of wheat plants are characterized by tiller initiation and leaf appearance and growth. The spikelet is initiated early in the vegetative growth stages (Grieve *et al*. 1993). Our study showed that salinity reduced the number of spikelets in both genotypes, especially Thasos (Fig. 3). As the TGW may indicate a further effect of salinity on grain filling during the reproductive stages, the difference in TGW between the two treatments only in Thasos may suggest that there is a further reduction in grain filling in the salt-sensitive wheat. Although under saline conditions the reduction in wheat grain yield that is related to the initiation of tiller number and spikelets and grain filling may be caused by many factors, such as the inhibition of photosynthesis, ionic toxicity and nutrient imbalance, the direct effects are probably Na and Cl ionic toxicity and/or nutrient imbalance (El-Hendawy *et al*. 2005a; Maas and Poss 1989; Nicolas *et al*. 1993).

Data of ion distribution among tillers (Figs 4,6) show that Na^+ and Cl^- concentrations in leaves at day 55 after sowing increased significantly with increasing salinity regardless of genotypes and orders of tillers. Compared to Sakha 8, the Na^+ concentration in the leaves of Thasos was approximately sixfold higher, whereas the Cl^- concentration was only 20% higher (Figs 4,6),

indicating that the salt-tolerant wheat is able to exclude most of the Na^+, which is considered to be an important trait of salt tolerance. This finding is in agreement with our previous studies (El-Hendawy *et al.* 2005a, 2005b). It has been reported that Na^+ is more toxic to the plant tissues of wheat than Cl (Munns *et al.* 1986), which may explain why there was a greater reduction in the number of tillers and further inhibition of seed development in Thasos. The possible mechanisms of Na^+ exclusion in Sakha 8 under saline conditions may be that the salt-tolerant wheat genotype may result from restricting the xylem loading and delivering from the roots to the shoots (Gorham *et al.* 1990; McCully *et al.* 1987; Santa-María and Epstein 2001; Shone *et al.* 1969), re-circulating Na^+ from the shoots to the roots by the phloem (Lohaus *et al.* 2000; Munns *et al.* 1988), having a low transpiration rate (Ball 1988; El-Hendawy *et al.* 2005b; Sharma *et al.* 2005), and re-allocating ion content between different leaves (Munns 1993; Rashid *et al.* 1999; Salam *et al.* 1999). In contrast, Saneoka *et al.* (1999) reported that salt-tolerant wheat SARC from Pakistan was characterized by the inclusion of Na^+ and Cl^-. Furthermore, under saline conditions there were higher ratios of Na^+:K^+ and Na^+:Ca^{2+}, especially for Thasos. Tester and Davenport (2003) pointed out that high Na^+:K^+ ratios could disrupt protein synthesis in the cell, given that Na^+ competes with K^+ for binding sites essential for cellular function, but cannot substitute for K^+ to activate functional enzymes (Bhandal and Malik 1988; Munns and Greenway 1980). Under saline conditions, Cl^- competes with anions, such as NO_3^-, and depresses NO_3^- uptake, which may cause ion imbalance (Hu and Schmidhalter 1997; Hu *et al.* 2005). Trewavas (1985) proposed that NO_3^- might be a plant growth regulator, which affects metabolism and development. He argued that this system could operate via an effect on the Ca^{2+} concentration of the cytoplasm: energy is directed towards NO_3^- reduction when NO_3^- enters a cell, so that a change in NO_3^- uptake would change the energy available for Ca^{2+} expulsion. Thus, the great decrease in the NO_3^- concentration under saline conditions, especially for Sakha 8 (Fig. 6), may indicate a disturbance in metabolism, resulting in a reduction in the number of tillers.

Although studies have shown that grain yield on the mainstem in salt-stressed wheat was much less reduced compared with that in the subtillers (Hu *et al.* 1997; Maas *et al.* 1996), our results showed that the effect of salinity on the grain yield in the mainstem was slightly different from that in the subtillers. However, there was a higher reduction in leaf area and dry weight of subtillers 1 and 2 of both genotypes compared with the mainstem during the vegetative growth stages (Fig. 1). In wheat plants, the early growth of subtillers imported photoassimilates and nutrients from the mainstem entirely (Kemp and Whingwiri 1980; Lauer and Simmons 1985). Studies have shown competition for carbohydrates between the mainstem and the subtillers (Kirby and Jones 1977). For the mineral nutrients, the results showed that there was a different effect of salinity on the distribution of K^+, Ca^{2+}, Mg^{2+} and NO_3^- in the individual tillers between the two genotypes (Figs 4,5,6). The effect of salinity on K^+, Ca^{2+}, Mg^{2+} and NO_3^- concentrations in the leaves was similar in the individual tillers of the salt-sensitive genotype Thasos. For Sakha 8, however, there was a greater effect of salinity on Ca^{2+} and NO_3^- in subtillers, suggesting that insufficient nutrient uptake may lead to a reduction in tillers or tiller abortion in the salt-tolerant wheat. As the difference in Na^+ or Cl^- concentrations in leaves among tillers is much less than the difference between the control and salinity treatments (Figs 4,6), if a toxic effect of Na^+ and Cl^- could occur in wheat under moderate salt stress, it would happen only to whole plants. As the mainstem and/or main subtillers are a major source for subtillers, we would expect that the affected mainstem under saline conditions would cause further (even greater) reduction in the subtillers, especially in the salt-sensitive genotype Thasos.

In conclusion, the results from the present study showed that both wheat genotypes are more sensitive to salt stress during the vegetative growth stages than in the reproductive stages. The reduction in the grain yield of Sakha 8 under moderate salinity was mainly because of the decreased number of tillers, whereas in addition to the reduction in the number of tillers in the salt-sensitive genotype Thasos, grain yield in the mainstem and subtillers was further reduced during grain filling. The salt-tolerant genotype Sakha 8 is characterized by the exclusion of Na in the leaves. Under moderate saline conditions, the greater reduction in subtillers may result from ion imbalance in the salt-tolerant genotype Sakha 8 and from Na toxicity in the salt-sensitive genotype Thasos.

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