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Positive correlation between potassium uptake and salt tolerance in wheat

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Abstract

The aim of our study was to answer whether any positive correlation exists between K^+ uptake and salt tolerance in wheat. We carried out a sand-culture experiment with salt-tolerant, DK961 (ST), and salt-sensitive, JN17 (SS), wheat cultivars, where photosynthesis, the K^+/Na^+ ratio, growth, and the biomass yield were examined. The seeds were exposed for four weeks to six NaCl concentrations (50, 100, 150, 200, 250, and 300 mM), which were embodied in the Hoagland solution. Salinity-induced decrease of K^+ or increase in the Na^+ content was much smaller in ST than that in SS. The reductions in the light-saturated photosynthetic rate (P_{Nmax}) and chlorophyll content caused by salinity were smaller in the ST compared to SS. Stomatal conductance decreased in both cultivars under saline conditions; nevertheless, it was lower in SS than in ST. The antioxidative capacity was higher in ST than that in SS under saline conditions. Significant positive correlations were observed in both cultivars between K^+ contents and P_{Nmax}/biomass yields. We suggest that higher-affinity K^+ uptake might play a key role in higher salt tolerance and it might be a reliable indicator for breeding new species of salt-tolerant wheat.

Additional key words: gas exchange; malondialdehyde; peroxidase; reactive oxygen species; *Triticum aestivum* L.

Introduction

Salinity is a common stress limiting crop growth and productivity worldwide (Munns 2002, Bartels and Sunkar 2005). One of the primary plant responses to salinity is net influx of Na^+ and outflux of K^+, resulting in a decrease of the K^+/Na^+ ratio in plant tissues (Maathuis *et al*. 1996, Qi and Spalding 2004). Generally, K^+ is utilized by plant cells as one of the major cations and its main function is to maintain electroneutrality and osmotic equilibrium (Cakmak 2005). In some biochemical processes, K^+ is used for regulatory purposes, while elsewhere it is involved in protein activities that depend on K^+-protein interactions, which cannot be mimicked by Na^+ or by any other cations. Therefore, K^+ is a crucial element for living cells (Tomemori *et al*. 2002, Cuin *et al*. 2003, Chérel 2004). The K^+ dependence does not confine plant growth in the normal soil, where K^+ is abundant, but it becomes a limiting factor in saline soil, where the K^+/Na^+ ratios are considerably lowered (Rodríguez-Navarro and Rubio 2006, Zheng *et al*. 2008). Therefore, the higher-affinity K^+ uptake by plants may be a key factor for better growth under saline conditions.

Sodium is considered to be nonessential for C_3 glycophytes, and thus the substitution of K^+ by Na^+ may lead to ionic imbalance and to physiological disorder under saline conditions (Carden *et al*. 2003, Tester and Davenport 2003). Plant growth may be limited by K^+ starvation induced by salinity stress which influences the capacity of unidirectional K^+ influx and net K^+ uptake. The internal K^+ concentration is exerted by both K^+ influx and cell K^+ conservation (Chérel 2004). In addition, K^+ starvation often activates overlapping cell signaling pathways and cellular responses, such as the reductions of Chl production and photosynthetic capacity (Lacan and Durand 1996, Rus *et al*. 2004). Wheat cultivars with different salt tolerance might have different affinity of K^+ uptake and capacity of K^+ conservation in plant tissues under saline conditions (Zheng *et al*. 2008). Therefore, high-affinity K^+ uptake and cell K^+ conservation of wheat may positively correlate with its salt tolerance.

An adequate internal K^+ concentration is crucial for the

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Abbreviations: Chl – chlorophyll; DM – dry mass; FM – fresh mass; g_s – stomatal conductance; MDA – malondialdehyde; P_{Nmax} – light-saturated photosynthetic rate; POD – peroxidase; ROS – reactive oxygen species; SS – salt-sensitive; ST – salt-tolerant.
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adjustment of cell osmoregulation, turgor maintenance, function of stomata, activation of enzymes, protein synthesis, oxidant metabolism, and photosynthesis (Amtmann *et al*. 1999, Blokhina *et al*. 2003, Sofo *et al*. 2005). However, overproduction of reactive oxygen species (ROS) caused by salinity usually leads to lipid peroxidation and induces K^+ leakage from cells by activating K^+ efflux channels (Blokhina *et al*. 2003, Cuin and Shabala 2007). Malondialdehyde (MDA) content is a direct indicator of cellular membrane lipid peroxidation caused by stresses, including salinity stress (Blokhina *et al*. 2003). The ability of scavenging ROS is determined by the antioxidant enzymes activities (Sofo *et al*. 2005). Nevertheless, the relationship between internal K^+ supply and plant antioxidative capacity is still not clear.

We investigated the effects of salinity on the leaf K^+/Na^+ ratio, Chl content, gas exchange, MDA content, and peroxidase (POD) activity, and the correlations between leaf K^+ contents and P_{Nmax}/plant biomass yields, respectively, in two wheat cultivars with contrasting salt tolerance. The results might offer an indicator for breeding and selecting new wheat varieties with high salt tolerance.

Materials and methods

Plant culture: The sand-culture experiment was carried out in a temperature-controlled, double-glass greenhouse. Two contrasting winter wheat (*Triticum aestivum* L.) cultivars, salt-tolerant (ST), DK961, and salt-sensitive (SS), JN17, were used. Thirty seeds of individual species were sown in each of 48 plastic boxes (31 × 19 × 12 cm), which were filled with 3 kg of sand, washed and sterilized prior use. Controls were irrigated with full strength Hoagland nutrient solution (0 mM NaCl, C0). Treated seeds were irrigated with modified Hoagland solutions containing six concentrations of NaCl (50, 100, 150, 200, 250, and 300 mM; NC50, NC100, NC150, NC200, NC250, and NC300, respectively). Six replications were used for each treatment. Water lost by evapotranspiration was replenished daily during the experiment. Young plants were thinned to 20 individuals per box after 10 d from sowing. The PPFD in chambers was 1,600 μmol m^{-2} s^{-1} at canopy level during the 14-h photoperiod. The temperature fluctuated from 17°C (night) to 36°C (day), and the relative humidity (RH) was 75–86% during the experiment. In this study, no plant of SS survived after the NC300 treatment.

Stomata scanning and gas exchange: Sections of lamina (about 9 mm^2) taken from the middle of the most recent, fully-expanded leaves of the ST and SS plants were excised at the end of the experiment. Eight lamina sections were selected from both cultivars under salinity treatments. Excised lamina sections were fixed in a solution of buffered glutaraldehyde (2.5%) for 24 h. Thereafter, the laminae were dehydrated in a series of ethanol-water solutions (30, 50, 60, 70, 80, 90, and 100% ethanol) and incubated in an ethanol-isoamyl acetate mixture for 1 h. The laminae were dried and then coated with gold. The mounted specimens were examined and photographed with a scanning electron microscope operated at 12 kV (*Hitachi S-570*, *Hitachi*, Japan).

Gas exchange was measured on the most recent, fully-expanded leaves using a portable gas-exchange fluorescence system (*GFS-3000*, *Heinz Walz*, Germany) 30 d after the treatment. RH was maintained at 70% and leaf temperature was set at 25°C in the leaf chamber. The flow rate was set at 600 μmol s^{-1}, and CO_2 concentration in the leaf chamber was maintained at 400 μmol mol^{-1}. The leaf was illuminated with 1,200 μmol m^{-2} s^{-1} PPFD (light-saturated) from an internal light source in the leaf chamber. As the conditions for gas-exchange measurements became stable, light-saturated net photosynthetic rate (P_{Nmax}) and stomatal conductance (g_s) were simultaneously recorded.

Leaf K^+ and Na^+ content: Dry leaf samples of the most recent, fully-expanded leaves of ST and SS were finely ground before passing through a 2-mm sieve. About 0.5 g of the sample was soaked for 12 h in digesting tubes with 10 mL of concentrated nitric acid and 3 mL of perchlorate acid, then digested at 300°C for another 6 h. The extraction solution volume was completed to 50 mL with deionized water. The contents of K^+ and Na^+ were measured using an atomic absorption spectrophotometer (*SP9-400*, *PYE*, England).

Chlorophyll (Chl) content was measured following the method described by Hiscox and Israelstam (1979). Frozen leaf samples (0.2 g) were crushed into a fine homogenate and extracted in 95% ethanol. The absorbance of the extract was recorded at 663 and 645 nm with a UV/visible light spectrophotometer (*UV-365*, *Shimadzu*, Japan), and Chl content was calculated using the following formula: Chl content [mg g^{-1}(FM)] = 8.02 × A_{663} + 20.20 × A_{645}, where A_{663} and A_{645} is absorbance at 663 and 645 nm, respectively.

MDA content and POD activity: Frozen samples (0.5 g) of leaves mixed with 5 mL of phosphate buffer (pH 7.8) were crushed into fine powder using a mortar and pestle in liquid nitrogen. The homogenate was centrifuged at 1,200 × *g* for 20 min at 4°C; the supernatant was used for MDA content and POD activity measurements. MDA content and POD activity were determined following the method described by Zheng *et al.* (2008).

For MDA content measurements, 1 mL of the extract and 2 mL of 0.6% thiobarbituric acid (TBA) were mixed, boiled for 15 min, cooled, and centrifuged for 10 min (1,200 × *g*). Absorbance of supernatant was recorded at 600, 532, and 450 nm, and MDA content was calculated using the following formula: MDA [μmol g^{-1}(FM)] =

$[6.45 \times (A_{532} - A_{600}) - 0.56A_{450}] \times V/M$, where A_{532}, A_{600}, and A_{450} is the absorbance at 600, 532, and 450 nm, respectively; V is the volume of extraction, and M is the fresh mass of the sample.

POD (EC 1.11.1.7) was determined through measuring the oxidation of guaiacol. The assay mixture contained 50 mL of 0.1 M sodium phosphate (pH 6.0), 28 µL of guaiacol (99%), and 19 µL of 30% H_2O_2. The absorbance was continuously recorded five times at 470 nm at 30-s intervals. POD activity was calculated according to the variation of absorbance and expressed in µmol g^{-1}(FM) min^{-1}. All spectrophotometric analyses were performed at 0–4°C with a UV/visible light spectrophotometer (*UV-365*, *Shimadzu*, Japan).

Results and discussion

Salinity-induced changes in K^+ and Na^+ contents: K^+ leakage and Na^+ accumulation are major causes of salinity injury in plants growing under saline condition (Munns 2002, Demidchik *et al*. 2003). The K^+/Na^+ ratio is used as an important indicator in breeding new species of plants with higher salt tolerance (Chen *et al*. 2005). In this study, insignificant differences were noted in K^+ and Na^+ contents between ST and SS under C0 (Fig. 1). Salinity induced considerable decline in the K^+ content but enhanced the Na^+ content in both cultivars, with the extents being larger in SS than that in ST. Salinity-induced changes were not significant in the K^+ and Na^+ contents in ST, but were significant in SS under mild/moderate (<200 mM NaCl) salt stress. The results might indicate that (*1*) cellular membrane integrity remained better preserved in the ST wheat than that in the SS under salt stress; (*2*) the higher affinity K^+ uptake and retention might exist in the ST than that in the SS under saline condition.

Previous studies reported that plant genomes contain more genes encoding K^+ transporters and channels in the salt-tolerant plants than those in salt-sensitive ones; these transporters show the specific capacity of K^+ uptake from saline soil (Yao *et al*. 2010). Rapid reduction of the K^+/Na^+ ratio in SS wheat may considerably cause K^+ starvation and Na^+ poisoning (Lacan and Durand 1995, Carden *et al*. 2003), leading to severe limitations of plant growth. One of the important reasons for K^+ starvation limiting plant growth may be the decrease of K^+-dependent enzyme activities (Armengaud *et al*. 2009). In addition, low antioxidant enzyme activities may seriously decline the capacity to eliminate ROS, and may result in severe secondary oxidative stress (Sairam and Srivastava 2001, Simova-Stoilova *et al*. 2009). Therefore, the combination of K^+ starvation and Na^+ poisoning might be the crucial factor limiting plant metabolism and growth under saline conditions. Overall, the high-affinity K^+ uptake might be positively correlated with plant salt tolerance of wheat under salinity stress.

Plant growth and biomass yield: Twenty individual wheat plants were randomly harvested 28 d after the treatments. Plant height and root length were measured, and then samples were oven-dried at 75°C to constant mass to record the biomass yield.

Statistical analysis: This experiment consisted of a randomized block of seven NaCl treatments with two contrasting winter wheat cultivars. There were six replicates for each treatment. Data for each independent variable were analyzed separately using *General Linear Models of SPSS* package (*Ver. 11*, *SPSS*, Chicago, USA). Regression line was made using *Sigmaplot 10.0*. Differences between treatments were considered significant at 0.05 and 0.01, respectively.

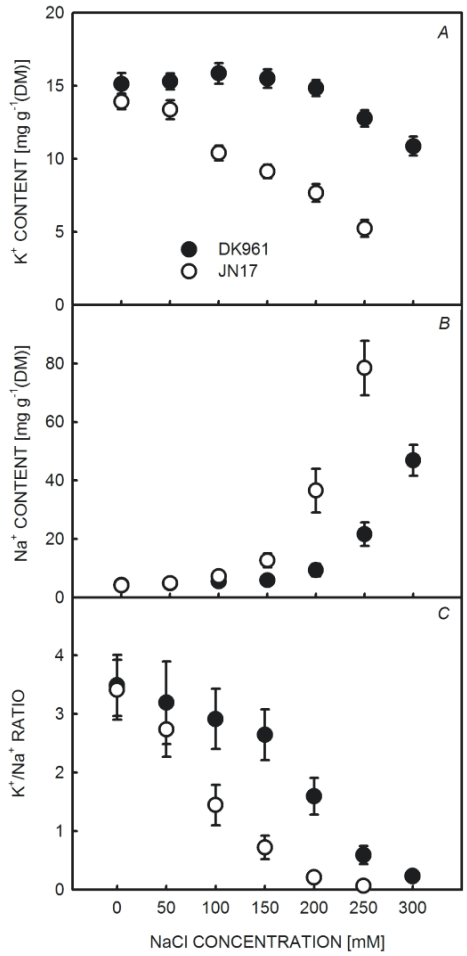

Fig. 1. Leaf K^+ content (*A*), Na^+ content (*B*), and the K^+/Na^+ ratio (*C*) in salt-tolerant wheat cultivar DK961 and salt-sensitive wheat cultivar JN17 under different NaCl treatments. Values are means ± SE ($n = 6$).

Salinity-induced changes in stomata and P_N: Salinity significantly reduced the size of stomata (Fig. 2*A*) in both

cultivars, with the extent being larger in SS than that in ST. For instance, the reductions caused by salinity in the stomatal length were 19% in SS, but only 3% in ST at the NC100 treatment. No significant changes were noted in g_s (Fig. 2*B*) in ST, while a considerable reduction was measured in SS under moderate salt (NC100) stress. However, the significant decrease occurred in both cultivars under the severe saline conditions (NC200). Nevertheless, the ST cultivar always maintained higher g_s than SS in each treatment. The greater g_s is a key factor for better photosynthesis and plant growth under saline conditions (Walker *et al*. 1996, Zheng *et al*. 2010, Redman *et al*. 2011). Stomata opening may be significantly affected by the guard cell water potential (Hattori *et al*. 2007), hence, salinity-induced changes of ion concentrations in guard cells should be further investigated.

Similarly, the P_{Nmax} decreased by salinity in both cultivars, with the extents being larger in SS than that in ST (Fig. 3). No significant reduction was measured in P_{Nmax} of ST below NC200 treatment, while drastic decrease was noted at the NC250 and NC300 concentrations. Nevertheless, the P_{Nmax} of SS decreased significantly when the salt concentration reached NC100. The positive correlation between P_{Nmax} and g_s exists (Shabala *et al*. 2003), therefore, the decrease of P_{Nmax} might be caused by the salinity-induced decline of g_s. Stomata shrinkage may reduce the intercellular CO_2 concentration (C_i), leading to a shortage of CO_2 available for photosynthesis and resulting in a decrease of photosynthesis (Zheng *et al*. 2010). In addition, the decline of P_{Nmax} might be caused also by nonstomatal limitations.

Salinity-induced changes in Chl content: Chl plays a key role and determines a plant photosynthetic capacity under salt stress (Zheng *et al*. 2010). Salinity reduced Chl contents in both cultivars, with the extents being greater in

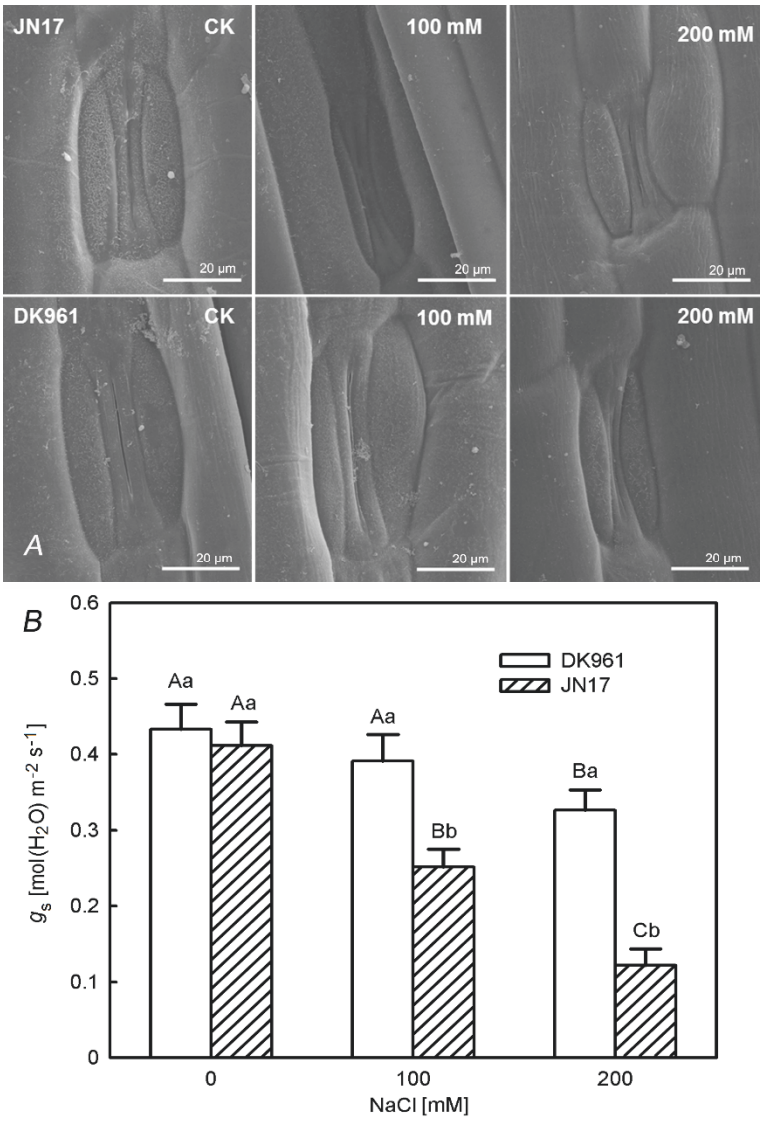

Fig. 2. Photographs from a scanning electron microscope of leaf stomata (*A*) and stomatal conductance (g_s) (*B*) of salt-tolerant wheat cultivar DK961 and salt-sensitive wheat cultivar JN17 28 d after NaCl treatments. Values are means ± SE (n = 6). Different *uppercase letters* indicate significant differences between salinity treatments, while different *lowercase letters* indicate significant differences between cultivars.

SS than in ST (Fig. 4). During mild/moderate salinity treatments (<200 mM NaCl), the ST plants maintained the Chl content similar to C0, while it decreased significantly in SS. Nevertheless, the Chl content decreased considerably in both cultivars under severe salt stress (>200 mM NaCl). Insignificant differences were noted in the Chl content between SS and ST at C0, but it became considerably smaller in SS than in ST under saline conditions. Some studies report that salinity-induced excessive K^+ leakage may not only delay the Chl biosynthesis, but also accelerate the degradation of original Chl (Walker *et al*. 1996, Redman *et al*. 2011). The ST wheat retained the higher K^+ content than that in the SS plants under mild/moderate (<200 mM NaCl) salt stress. Adequate internal K^+ supply might result in higher Chl synthesis

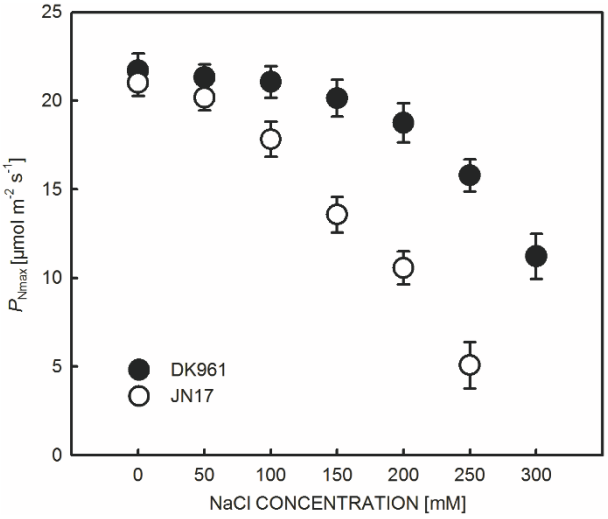

Fig. 3. Light-saturated photosynthetic rate (P_{Nmax}) of salt-tolerant wheat cultivar DK961 and salt-sensitive wheat cultivar JN17 under different NaCl concentrations. Values are means ± SE (n = 6).

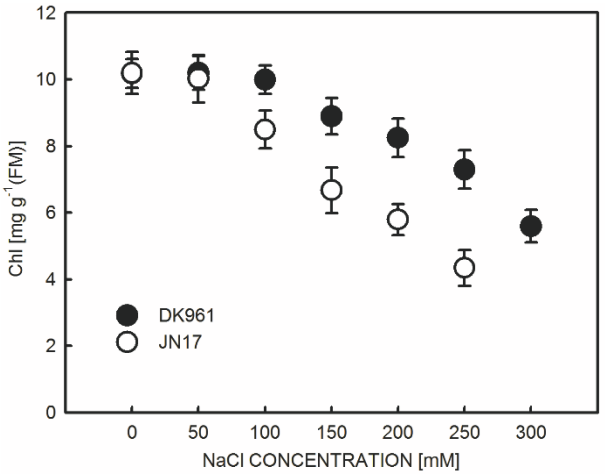

Fig. 4. Chlorophyll (Chl) content of salt-tolerant wheat cultivar DK961 and salt-sensitive wheat cultivar JN17 under different NaCl treatments. Values are means ± SE (n = 6).

in ST than in SS. However, the Chl contents decreased significantly under severe (>200 mM NaCl) salt stress; it might be due to the considerable reduction of the K^+ content in both cultivars.

Salinity-induced changes in MDA content and POD activity: We observed only the insignificant increase in the POD activity (Fig. 5*A*) and the MDA content (Fig. 5*B*) under mild/moderate salinity (<200 mM NaCl) stress in both cultivars; but significant changes occurred under severe salt stress conditions, with the extents being larger in ST than that in SS. The POD activity decreased rapidly at high salinity (>200 mM NaCl), while the MDA contents increased continuously with the increases of the NaCl concentration. Salinity may induce secondary oxidative stress and produce ROS, leading to plant cellular membrane lipid peroxidation and ion leakage (Blokhina *et al*. 2003). Antioxidant enzymes may effectively scavenge the ROS and reduce the oxidative injuries (Simova-Stoilova *et al*. 2009). However, the decrease of the POD activity under high salinity might indicate that the plant antioxidative system was severely damaged by excessive salt stress. The

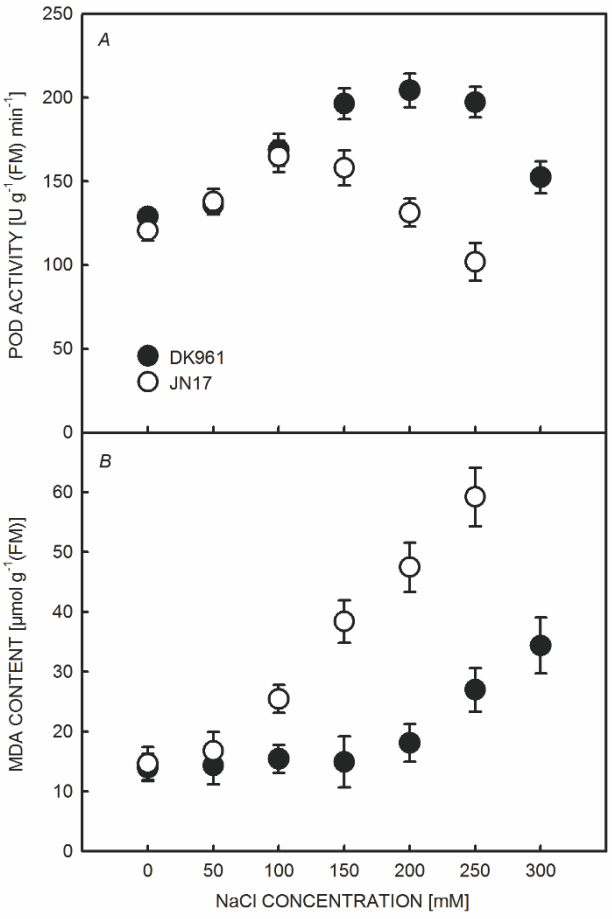

Fig. 5. Peroxidase (POD) activity (*A*) and malondialdehyde (MDA) content (*B*) of salt-tolerant wheat cultivar DK961 and salt-sensitive wheat cultivar JN17 under different NaCl concentrations. Values are means ± SE (n = 6).

increment of the MDA content is an indicator of membrane lipid peroxidation (Davenport *et al*. 2005). Salinity-induced enhancement of the MDA content was always smaller in the SS wheat than in the ST. It might indicate that the cell membrane was damaged more seriously by salinity in the SS than in the ST. The trend of plant POD activity is quite consistent with that of the K^+ content in both wheat cultivars, therefore, it may be conceivable that plant ROS scavenging ability is positively correlated with the plant K^+ affinity.

Salinity-induced changes in plant growth and biomass: K^+ is one of the most needed elements for plant growth (Gassmann *et al*. 1996) and a key activator for some synthetic enzymes (Hirsch *et al*. 1998). In this study, the insignificant decrease was noted in several plant growth parameters (plant height, root length, and biomass yield) in ST, while they changed significantly in SS under mild/moderate salinity (< NC100) stress (Fig. 6). Those parameters decreased significantly in both cultivars under severe salinity (> NC100). Salinity-induced injuries were larger in SS than that in ST; salinity might cause more K^+ outflow in the SS than in the ST. K^+ represents a crucial osmotic adjustment substance and acts also as the important activating agent for some K^+-dependent enzymes (Fu and Luan 1998). Severe K^+ starvation may lead to physiological disorder and limitation of plant growth (Bañuelos *et al*. 2002). Therefore, higher affinity K^+ uptake and adequate internal K^+ supply might be the key factors for better growth of plants growing in saline conditions.

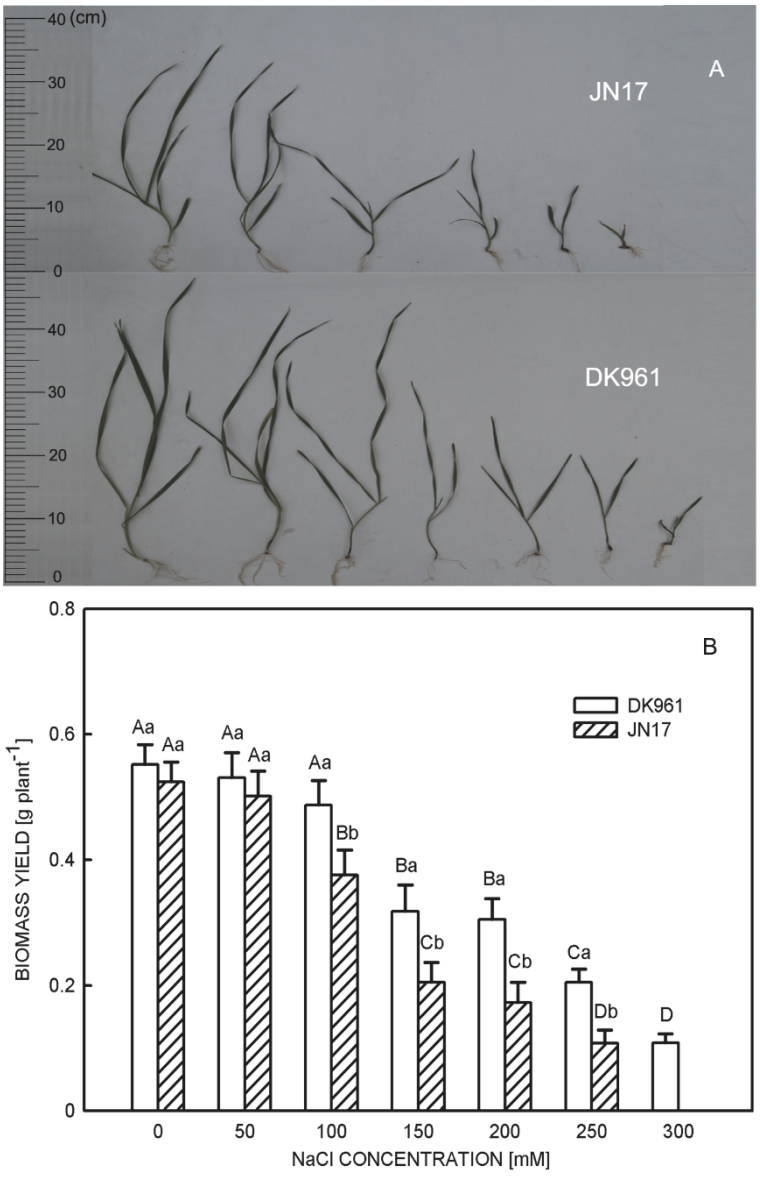

Fig. 6. Photographs of plant growth (*A*) and biomass yields (*B*) of salt-tolerant wheat cultivar DK961 (ST) and salt-sensitive wheat cultivar JN17 (SS) 28 d after NaCl treatments. Values are means ± SE (n = 6). Different *uppercase letters* indicate significant differences between salinity treatments, while different *lowercase letters* indicate significant differences between cultivars.

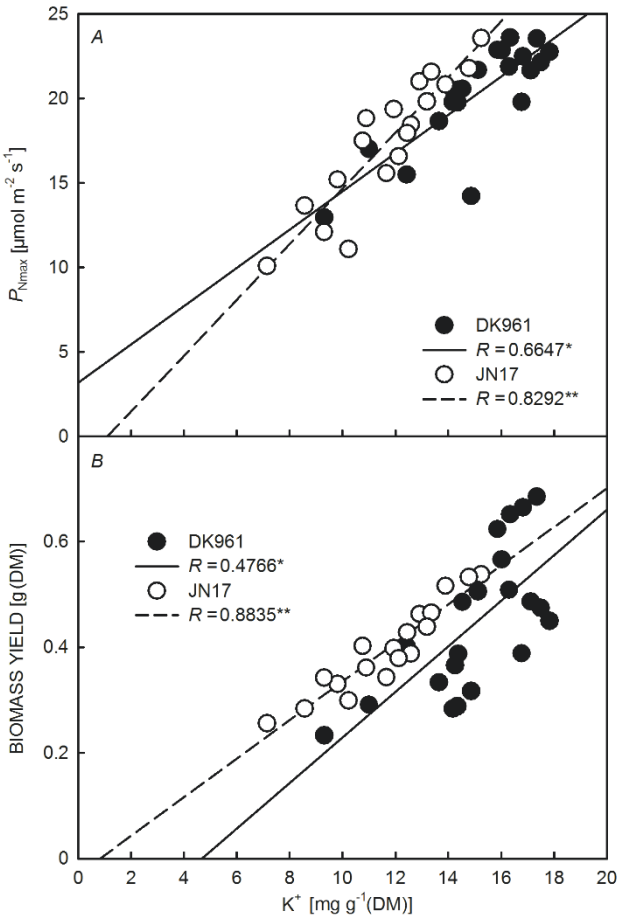

Fig. 7. Correlations between leaf K^+ contents and light-saturated photosynthetic rates (P_{Nmax}) (*A*) and biomass yields (*B*) in salt-tolerant wheat cultivar DK961 and salt-sensitive wheat cultivar JN17. Regression line was made using *Sigmaplot 10.0* in *SPSS* package. * – significant at $p = 0.05$, ** – significant at $p = 0.01$.

Correlations between K^+ affinity and P_{Nmax}/biomass yield: Significant positive correlations were found in both ST (Fig. 7*A*) and SS (Fig. 7*B*) between the K^+ contents and the P_{Nmax}/biomass yields. Salinity-induced reductions in the K^+ contents and the P_{Nmax}/biomass yields were larger in SS than that in ST, indicating saline injuries were more serious in the former than in the latter one. As a result, the correlation coefficient was significant at 0.01 level in SS contrary to 0.05 level in ST.

Previous studies reported that differential shrinkage of protoplast volume may play a role in the genotypic difference in K^+ retention (Liebersbach *et al*. 2004). However, there is a controversy regarding the underlying molecular mechanisms implicated in K^+ transport into the root symplasm of wheat from saline soil. This ability might depend on the plant K^+ transporter and K^+-affinity uptake (Maathuis *et al*. 1996, Amtmann *et al*. 1999). Current evidence indicates that some members of the *TRK-HKT*, *Kup-HAK*, and the *AKT-KAT* families of the K^+ transporters can be involved in the process (Gassmann *et al*. 1996, Bañuelos *et al*. 2002, Liebersbach *et al*. 2004, Gierth *et al*. 2005). Therefore, plant salt tolerance might be positively correlated with plant abilities for K^+ transport and retention. A further elucidation of these steps as well as the control of Na^+ partitioning within plant tissue seems to be crucial in the search for genes actually involved in different K^+/Na^+ selectivity and, consequently, in the growth response of plants to salt stress.

Conclusion: Significant positive correlations exist between plant salt tolerance and K^+ affinity in wheat. Higher K^+ affinity may be a key factor for better growth of winter wheat in saline condition. Therefore, it is possible to use the K^+/Na^+ ratio as the indicator in selecting new winter wheat species with higher salt tolerance.

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