Responses of salt-tolerant and intolerant wheat genotypes to sodium chloride: photosynthesis, antioxidants activities, and yield

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Abstract

Physiological responses of two wheat (*Triticum aestivum* L.) genotypes (salt-tolerant DK961 and salt-sensitive JN17) to increased salt concentrations (50, 100, 150 mM NaCl: $NaCl^{50}$, $NaCl^{100}$, $NaCl^{150}$) were studied. Photosynthetic capacity, irradiance response curves, contents of soluble sugars, proteins, and chlorophyll (Chl), K^+/Na^+ ratio, and activities of antioxidant enzymes (superoxide dismutase, peroxidase, and catalase) in flag leaves were measured on 7 d after anthesis. In control ($NaCl^0$) plants, non-significant ($p>0.05$) differences were found in gas exchange and saturation irradiance (SI) between salt-tolerant (ST) and salt-sensitive (SS) wheat genotypes. However, we found higher soluble sugar and protein contents, K^+/Na^+ ratio, and antioxidant enzyme activities, but lower Chl content and yield in ST wheat. Salinity stresses remarkably increased soluble sugar and protein contents and the antioxidant activities, but decreased K^+/Na^+ ratio, Chl contents, SI, photosynthetic capacities, and yield, the extent being considerably larger in JN17 than DK961. Although the soluble sugar and protein contents and the antioxidant activities of JN17 elevated more evidently under salt stresses, those variables never reached the high levels of DK961. The antioxidant enzyme activities of SS wheat increased in $NaCl^{50}$ and $NaCl^{100}$, but decreased rapidly when the NaCl concentration reached 150 mM. Thus the ST wheat could maintain higher grain yield than the SS one by remaining higher osmoregulation and antioxidative abilities, which led to higher photosynthetic capacity. Hence the ST wheat could harmonize the relationship between CO_2 assimilation (source) and the grain yield (sink) under the experimental conditions.

Additional key words: catalase; genotype differences; peroxidase; reproductive stage; salinity stress; salt tolerance; stomatal conductance; superoxide dismutase; *Triticum aestivum*; yield.

Introduction

Salinity negatively affects the growth and productivity of most plants (Able *et al.* 2003). It reduces the growth of wheat, at least partially, by leading to specific ion toxicity and enhances the generation of reactive oxygen species (ROS), resulting in a decrease of photosynthetic capacity (Able *et al.* 2003, Zheng *et al.* 2008). The K^+/Na^+ ratio plays a key role in adjusting cell osmoregulation, stomatal function, activation of enzymes, protein synthesis, oxidant metabolism, and photosynthesis (Cherel 2004). Normally, the K^+/Na^+ ratio tends to decrease under salinity stress as a result of either excessive Na^+ accumulation in plant tissue or enhanced K^+ leakage from the cell by activating K^+ efflux channels (Cuin and Shabala 2007).

Although the adverse symptoms caused by salinity could be partially corrected by implementing schemes to remedy salt-stressed (SS) soils, such as plastic foil covers (Makela *et al.* 1996), KNO_3 supply (Zheng *et al.* 2008), or foliar application of glycine betaine (Ma *et al.* 2006), understanding the salt tolerant (ST) metabolism and demonstrating ST wheat cultivars is the most promising

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Abbreviations: CAT − catalase (EC 1.11.1.6); Chl − chlorophyll; cv. − cultivar; FM – fresh mass; g_s, − stomatal conductance; LAI − leaf area index; PAR − photosynthetically active radiation; P_N − net photosynthetic rate; POD − peroxidase (EC 1.11.1.7); RH – relative humidity; ROS − reactive oxygen species; RWC − relative water content; SI − saturation irradiance; SOD − superoxide dismutase (EC 1.15.1.1).
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strategy (Chen *et al.* 2005). Numerous studies were carried out under either hydroculture or sand culture, focusing on physiological variations at seedling stage (Sairam *et al.* 2002, Stepien and Klobus 2005). Few reports are on responses of contrasting wheat genotypes grown in saline field soil at reproductive stage. However, reproductive stage is the key phase for fruitful productions of high plants, including wheat (Poustini and Siosemardeh 2004), thus a careful study on the responses of wheat to salt stress at this stage is urgently needed.

In order to understand why ST wheat could relieve the saline adverse effects and obtain higher grain yield than the SS one, two wheat genotypes with different salt tolerance were treated by various NaCl (50, 100, and 150 mM: $NaCl^{50}$, $NaCl^{100}$, $NaCl^{150}$) concentrations. Photosynthetic capacities, K^+/Na^+ ratios, contents of chlorophyll (Chl), soluble sugars, and proteins, and antioxidant activities of both cultivars were measured at 7 d after anthesis. The objectives were to compare the differential responses of two genotypes to NaCl at reproductive stage, and try to offer evidence on whether the same variation tendency existed as that at seedling stage.

Materials and methods

Plant growth and treatments: On 12 October 2006, seeds of two winter wheat (*Triticum aestivum* L.) cultivars, DK961 (ST) and JN17 (SS), were sown in 24 blocks (length×breadth×depth = 0.5×0.5×0.5 m) in a greenhouse of Shandong Academy of Agricultural Science. Blocks were filled with field soil, which was classified as a light loam. Organic C, available N, P, and K in the soil were 0.86 %, 121.86, 175.71, and 80.51 mg kg^{-1}, respectively. Control ($NaCl^0$) plants were irrigated with tap water (no NaCl). Experimental seeds were exposed to saline water. Water lost by evapotranspiration was replenished each day. The average day/night temperature was kept at 16−32/10−16 ºC, respectively, with a mean photoperiod of 14 h, and the relative humidity (RH) of 65−86 %. The maximal photosynthetically active radiation (PAR) was approximately 1 800 μmol m^{-2} s^{-1} at canopy height during a mean photoperiod of 14 h.

Gas exchange and irradiance response: Simultaneous measurements of gas exchange and irradiance response were taken on flag leaf at 7 d after anthesis, with a *LCA-4* portable IRGA photosynthesis system (*Analytical Development Co.*, Herts, England). RH was maintained at 70 % and leaf temperature was 25 ºC in the leaf chamber. The flow rate was set at 600 μmol s^{-1} and CO_2 concentration in the leaf chamber was the same as the ambient atmosphere (375~385 μmol mol^{-1}). The leaf was irradiated with PAR of 1 500 μmol m^{-2} s^{-1} of internal light source. The irradiance response curve was recorded automatically in the same leaf inserted into the leaf chamber by means of operation program. During irradiance response measurements, CO_2 concentration was maintained at 700 μmol mol^{-1}. CO_2 assimilation in response to (PAR) of 1 800, 1 600, 1 400, 1 200, 1 000, 800, 600, 400, 200, and 0 μmol m^{-2} s^{-1} at the leaf surface was measured. Each PAR step lasted 3 min and data were recorded 5 times. The data obtained for each leaf were analyzed with the program photosynthetic assistant (*V*ersion *1.1, Dundee Scientific,* Dundee, UK) to obtain saturation irradiance (SI) of two wheat cultivars under different salt stress.

Contents of Chl and soluble sugars: Chl contents were measured by a modified method of non-maceration (Hiscox and Isrealstam 1979). Samples (0.02 g) were crushed into a fine powder with $CaCO_3$ and 95 % ethanol. The absorbance of the supernatant was recorded at 645 (A_{645}) and 663 (A_{663}) nm, respectively, using an UV/visible spectrophotometer (*UV-365*, *Shimadzu*, Kyoto, Japan). The spectral slit-width was 1 nm. Soluble sugar contents were measured following the method of Yemm and Willis (1954): 0.05 g ground dry samples were kept in 6−7 cm^3 of de-ionized water and boiled for 30 min to extract soluble sugars, then centrifuged under 1 200×*g* for 10 min using a centrifuge (*Sigma 3k15,* Heidelberg, Germany)., The extracts were decanted and the residue was re-extracted two more times; then the extracts were completed to 50 cm^3. The absorbance of the mixture (0.1 cm^3 extracts and 3 cm^3 anthrone reagent: 0.15 g anthrone+84 cm^3 oil of vitriol+16 cm^3 H_2O) was recorded at 620 nm. The content of soluble sugars was calculated from a standard colorimetric curve of glucose at 620 nm.

Content of soluble proteins and activities of antioxidant enzymes: Frozen flag leaf samples (0.5 g) were crushed into a fine powder using a mortar and pestle under liquid nitrogen. The homogenate was centrifuged at 1 200×*g* for 20 min at 4 ºC. In the supernatants, soluble protein content was measured according to Sairam *et al.* (2002). The absorbance of the mixture containing 20 mm^3 supernatant and 3 cm^3 Coomassie brilliant blue G-250 was recorded at 595 nm 2 min after mixing. The soluble protein content was calculated from a standard curve of bovine albumin at 595 nm by colorimetry.

Peroxidase (POD) was determined through measuring the oxidation of guaiacol. The assay mixture contained 50 cm^3 of 0.1 M sodium phosphate (pH 6.0), 28 mm^3 guaiacol, and 19 mm^3 of 30 % H_2O_2. The absorbance was recorded five times at 470 nm at 30 s intervals. Variation of absorbance stands for enzyme activity. Superoxide dismutase (SOD) activity was determined following the method of Giannopolitis and Ries (1977). The super

natant was desalted by *Sephadex G-25* gel filtration to remove interfering materials and used as the crude enzyme extract. One unit of SOD activity [U] was defined as the amount of crude enzyme extract required for inhibiting the reduction rate of nitro-blue tetrazolium (NBT) by 50 %. Catalase (CAT) activity was determined following the method described by Aebi (1984).

K^+ and Na^+ contents: About 0.5 g finely ground dry samples were soaked for 12 h in digesting tubes with 10 cm^3 concentrated nitride acid and 3 cm^3 perchloric acid, then digested at 300 ºC for 6 h. The extractions were completed to 50 cm^3 with de-ionized water. The amount of K^+ and Na^+ contents were determined byd using an atomic absorption spectrophotometer (*SP9-400*, *Pye*, *Unicam Ltd.*, Cambridge, England).

Growth parameters and yield components: Leaf area index (LAI) was computed as the ratio between photosynthetic area of total leaves and the corresponding land area. For relative water content (RWC) measurement, leaf samples were taken immediately after determining gas exchange, and weighed to obtain their fresh mass (FM), then soaked in distilled water in the dark at 22 ºC for 6 h. After the hydration period, the turgid leaf samples were blotted, dried, and weighed to obtain the turgid mass. The leaf samples were then dried at 80 ººC for 24 h, and then the dry mass (DM) was determined. Leaf RWC was calculated according to Muranaka *et al.* (2002). Spikes per m^2 and seeds per spike were counted at mature stage. The 1000-seed mass and yield were obtained after harvest.

Statistical analysis: The experiment consisted of a randomized block of four NaCl concentrations with two wheat cultivars. There were six replications for each treatment. Statistical analysis of data was processed using analysis of variance (ANOVA) in the General Linear Model procedure of *SPSS* (version *11.5*, *SPSS*, Chicago, IL, USA). The effects of SS on physiological parameters and yield were verified using one-way ANOVA. Significant effects were determined at $p \leq 0.05$

Results

Gas exchange and SI: Non-significant differences ($p<0.05$) were observed in net photosynthetic rate (P_N) between ST cv. DK961 and SS cv. JN17 in $NaCl^0$ plants (Fig. 1). Salinity remarkably reduced the P_N of both cultivars, with the largest reductions occurring under $NaCl^{150}$ treatment. Such adverse effects were more serious in JN17 than in DK961. Considerable reductions (21, 57, and 67 %, respectively) occurred in increased NaCl treatments. However, non-significant reductions were found in P_N of DK961 in $NaCl^{50}$ and $NaCl^{100}$ treatments, while evident reduction (40 %) was observed under $NaCl^{150}$. The responding trends of stomatal conductance (g_s) to NaCl stresses were consistent with P_N. The reductions of g_s were always smaller in DK961 than in JN17 salt stresses. P_N and g_s in ST cv. DK961 were always higher than in the SS cv. JN17 at all salt concentrations.

Distinct PAR-P_N curves (Fig. 2) were established after analyzing the data set measured in different treatments. For ST cv. DK961, two PAR-P_N curves monitored under $NaCl^{50}$ and $NaCl^{100}$ were close to $NaCl^0$, with the SI of ~1 300 μmol m^{-2} s^{-1}. However, the slope of PAR-P_N curve was much lower under $NaCl^{150}$, with SI of ~900 μmol m^{-2} s^{-1}. The extent was larger in JN17 than DK961. Two PAR-P_N curves of JN17 measured under $NaCl^0$ and $NaCl^{50}$ were close, with SI of ~1 300 μmol m^{-2} s^{-1}. The SI of JN17 was only ~900 μmol m^{-2} s^{-1} in $NaCl^{100}$ treatment and 800 μmol m^{-2} s^{-1} in $NaCl^{150}$ treatment.

Contents of Chl, soluble sugars, and proteins: Chl content of DK961 was lower (by 5 %) than that of JN17 under $NaCl^0$ (Fig. 3). Salt stresses caused decreases in Chl contents of both cultivars. However, the reductions in DK961 were lower than those in JN17, especially under $NaCl^{50}$ and $NaCl^{100}$. As a result, the Chl contents of DK961 were 8 and 22 % higher than those of JN17, respectively, in $NaCl^{50}$ and $NaCl^{100}$ treatments. Although the Chl content of DK961 declined significantly (by 43 %) in $NaCl^{150}$ treatment, it was still higher (7 %) than that of JN17 at the same NaCl treatment.

As important osmoregulatory compounds, soluble sugars and proteins accumulated significantly in both cultivars under NaCl stresses (Table 1). Soluble sugar content of DK961 was considerably higher (by 19 %) than that of JN17 in $NaCl^0$ plants. Non-significant variations were noted in DK961 in $NaCl^{50}$ and $NaCl^{100}$ treatments compared with $NaCl^0$, however, considerable increment was observed in $NaCl^{150}$ treatment. Although the increments in JN17 were more considerable than those in DK961 at all NaCl concentrations, they never reached the high levels of DK961. The variation tendency of the soluble protein contents under NaCl stresses was much similar to the trends of soluble sugar contents.

Antioxidant enzyme activities: The increments of antioxidant enzymes activities induced by long-term salt stress were compared between ST and SS wheat. As shown in Fig. 4, even in $NaCl^0$ plants the activities of SOD, POD, and CAT were significantly higher (by 21, 7, and 47 %) in DK961 than in JN17. Salinity stresses remarkably elevated the activities of those antioxidant enzymes in both cultivars. Although the enzyme activities of JN17 increased considerably before the salt concentration approached 150 mM, they were always lower than those of DK961. The enzymes activities of JN17 were

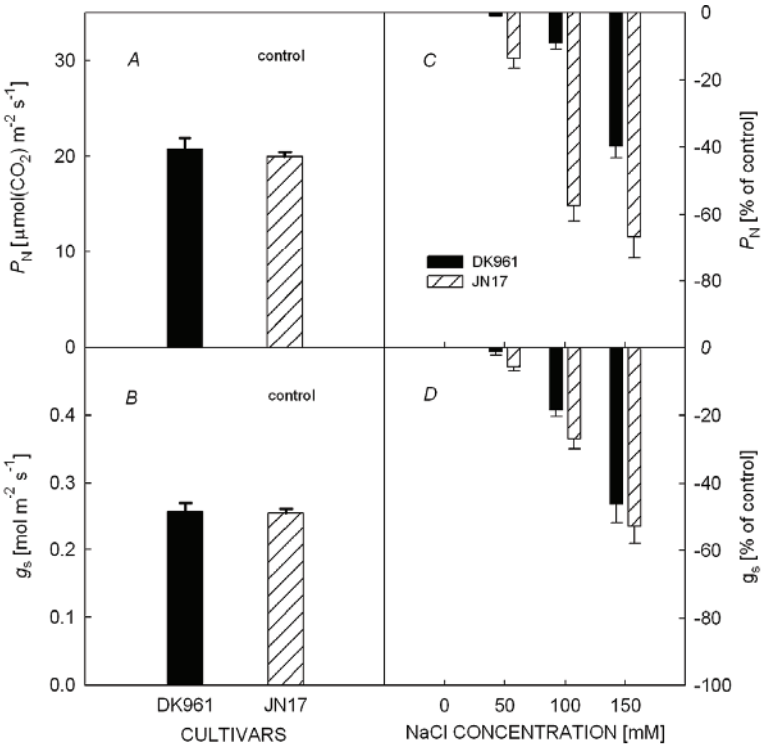

Fig. 1. Net photosynthetic rate (P_N) and stomatal conductance (g_s) in salt-tolerant (DK961) and salt-sensitive wheat (JN17) at 7 d after anthesis. (*A, B*) Plants grown under control conditions ($NaCl^0$), (*C, D*) changes of contents [%] under $NaCl^{50}$, $NaCl^{100}$, and $NaCl^{150}$ in relation to $NaCl^0$. *Vertical bars* indicate SE (n = 6).

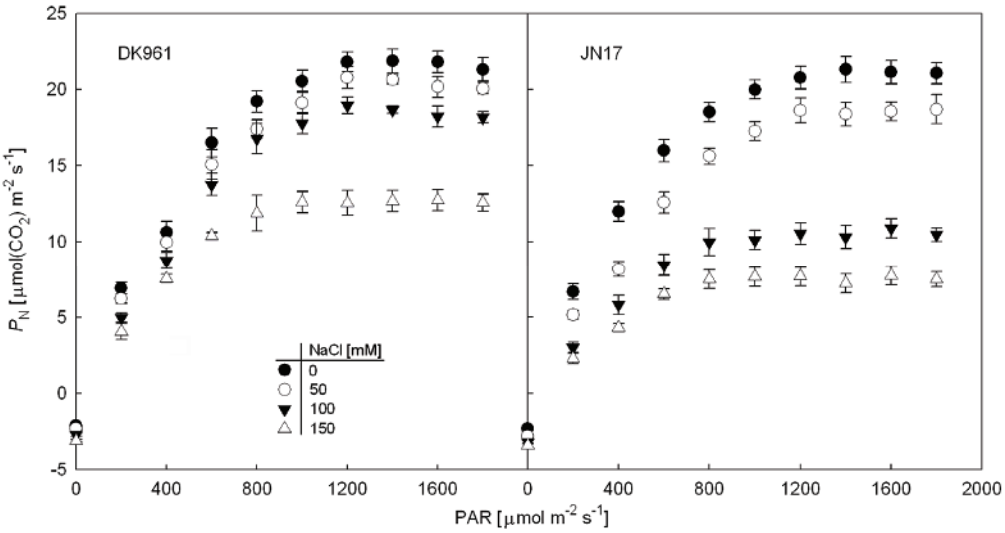

Fig. 2. Functional relationship between net photosynthetic rate (P_N) and photosynthetically active radiation (PAR) in flag leaves of salt-tolerant DK961 and salt-sensitive JN17 wheat at 7 d after anthesis under a series of $NaCl^{50}$, $NaCl^{100}$, and $NaCl^{150}$. $NaCl^0$ was control. *Error bars* show S.E., n=3.

lower in $NaCl^{150}$ than in $NaCl^{100}$. Salt-induced increments in POD were the highest among the antioxidant enzymes.

Contents of K^+ and Na^+: Even in $NaCl^0$ plants, the K^+ content was remarkably higher and the Na^+ content was considerably lower, leading to the K^+/Na^+ ratio higher in DK961 than in JN17 (Table 1). Salinity stresses decreased K+ contents, but increased Na+ contents, with reduced K^+/Na^+ ratios in both cultivars. However, the variable extent was smaller in DK961 than JN17, especially in $NaCl^{50}$ and $NaCl^{100}$ treatments. When the salt concentration approached 150 mM, the K^+ content and the K^+/Na^+ ratio decreased significantly in both cultivars, but they were still higher in DK961 than in JN17.

Growth and yield components: Plant height and LAI were higher, but spike length and flag leaf RWC were lower in DK961 than JN17 under $NaCl^0$ (Table 2).

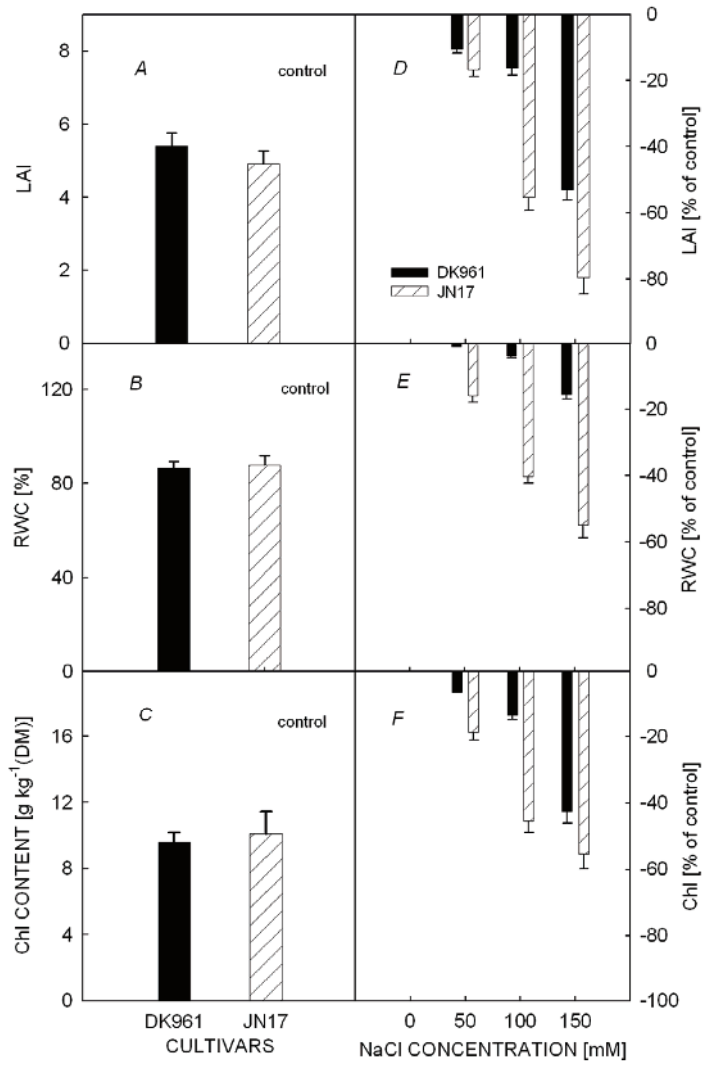

Fig. 3. Leaf area index (LAI), relative water content (RWC), and chlorophyll (Chl) content in flag leaves of salt-tolerant DK961 and salt-sensitive JN17 wheat at 7 d after anthesis. (*A*−*C*) Plants grown under control conditions ($NaCl^0$), (*D*−*F*) changes of contents [%] of $NaCl^0$ under $NaCl^{50}$, $NaCl^{100}$, and $NaCl^{150}$. *Vertical bars* indicate SE (n = 6).

Table 1. Contents of soluble sugars and proteins [g kg^{-1}(FM)], K^+, and Na^+ [g kg^{-1}] and K^+/Na^+ ratio in flag leaves of salt-tolerant DK961 and salt-sensitive JN17 under control conditions ($NaCl^0$) or increased NaCl ($NaCl^{50}$, $NaCl^{100}$, and $NaCl^{150}$) treatments at 7 d after anthesis. Means±SE (n = 6). *Different letters* within a column indicate significant differences (p<0.05, t-test).

Cv.	NaCl	Soluble sugars	Soluble proteins	K^+	Na^+	K^+/Na^+
DK961	$NaCl^0$	187.41±10.50a	71.44±3.02a	23.89±1.50a	4.94±0.69a	4.83±0.52a
	$NaCl^{50}$	201.24±12.23a	76.05±3.11a	19.09±1.67a	9.56±1.91ab	2.00±0.34a
	$NaCl^{100}$	228.91±14.63a	84.29±4.02b	17.57±1.85a	16.59±1.96b	1.06±0.16a
	$NaCl^{150}$	281.31±15.16b	96.15±4.17c	12.51±1.56b	33.66±2.02c	0.37±0.07b
JN17	$NaCl^0$	157.41±10.66a	59.55±3.16a	22.19±0.64a	5.24±0.63a	4.23±0.53a
	$NaCl^{50}$	189.24±11.87b	67.71±3.67b	11.02±1.04b	30.28±2.35b	0.36±0.06a
	$NaCl^{100}$	218.91±13.68c	77.12±3.88c	7.29±0.69c	59.73±3.34c	0.12±0.04b
	$NaCl^{150}$	261.30±16,79d	86.11±4.12d	4.51±0.39d	120.75±4.67d	0.04±0.01c

Salinity stresses caused decreases in the above mentioned parameters of both cultivars. However, the extents of reduction were still larger in JN17 than in DK961. Especially the flag leaf RWC was less than 50 % in $NaCl^{150}$ treatment. Seeds per spike, 1 000-seed mass, and the yield of DK961 were lower than those of JN17 under $NaCl^0$. However, salt-induced decreases in yield components of ST cv. DK961 were much lower than those of JN17, especially at $NaCl^{50}$ and $NaCl^{100}$. DK961 maintained high yields under $NaCl^{50}$ and $NaCl^{100}$ (only 6 and 9 % lower than in $NaCl^0$, respectively), while the yields of JN17 decreased significantly (being 23 and 54 % lower than in $NaCl^0$, respectively). Nevertheless, the yields of both cultivars were reduced considerably

(DK961 and JN17: 42 and 80 %) by $NaCl^{150}$ treatment than in $NaCl^0$. Although the yield of DK961 was lower (by 2 %) than that of JN17 in $NaCl^0$, it was higher than that of JN17 under each salt treatment.

Discussion

Significant positive correlations existed between P_N and g_s (Ma *et al.* 2006). We found that P_N and g_s of both cultivars decreased with the increase of salt concentration, however, the extent was larger in SS than ST wheat (Fig. 1). Hence high salt concentrations might decrease the available water resources in soil (Liu *et al.* 2005), and plants sensed the water availability around the roots and responded by sending chemical signals to the shoot to elicit adaptive responses, finally leading to stomata closure (Warren and Dreyer 2006). However, the ST wheat cv. performed higher ability in absorbing water from saline soil (Fig. 3). Thus it could maintain higher g_s and P_N under salinity.

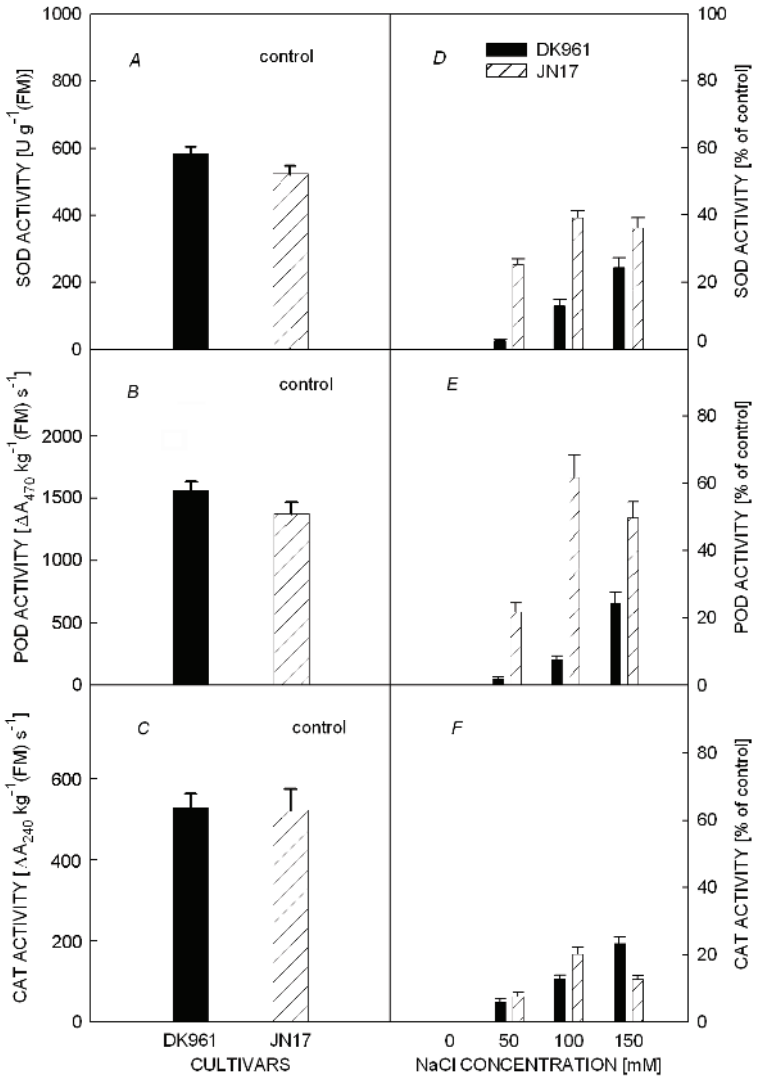

Fig. 4. Superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT) activities in flag leaves of salt-tolerant (DK961) and salt-sensitive (JN17) wheat at 7 d after anthesis. (*A*−*C*) Plants grown under control conditions ($NaCl^0$), (*D*−*F*) changes of antioxidant enzyme activities [%] of $NaCl^0$ under $NaCl^{50}$, $NaCl^{100}$, and $NaCl^{150}$. *Vertical bars* indicate SE ($n = 6$).

The value of SI reflects the efficiency of photon energy utilization (Munns 2002). SI of the SS cv. decreased more significantly than that of ST cv. under salt stresses (Fig. 2). Some reports suggest that photon energy efficiency mostly determines the ability of photosystem 2, which plays the key role in response of leaf photosynthesis to salt stress (Xu *et al.* 1995, Anderson and Barber 1996). The ST wheat had higher ability in catching photon energy which might be explained by lower salt-induced degradation of CP_{43} or by higher salt-enhanced synthesis of D_1 protein those in ST wheat (Sairam *et al.* 2002).

NaCl impaired plant growth by specific ion toxicity (Chen *et al.* 2005). The reason for more significant decrease of K^+/Na^+ ratio of SS wheat than of ST one

Table 2. Plant height and spike length [cm], and yield components, *i.e.* spikes per m^2 [×100], seeds per spike, 1 000 seed mass, and yield [kg m^{-2}] in salt-tolerant DK961 and salt-sensitive JN17 wheat under control conditions ($NaCl^0$) or increased NaCl ($NaCl^{50}$, $NaCl^{100}$, $NaCl^{150}$) treatments. Means±SE (n = 6). *Different letters* within a column indicate significant differences (p<0.05, t-test).

Cv.	NaCl	Plant height	Spike length	Spikes m^{-2}	Seeds per spike	1000-seed	Yield
DK961	$NaCl^0$	96.44±4.22a	8.56±0.24a	5.89±0.19a	32.76±0.04a	41.15±0.82a	0.68±0.03a
	$NaCl^{50}$	99.92±3.57a	8.51±0.18a	5.77±0.07a	31.97±0.46ab	40.55±0.34a	0.64±0.02a
	$NaCl^{100}$	92.80±6.20a	7.36±0.17b	5.67±0.13a	30.90±0.52b	40.90±0.56a	0.61±0.04a
	$NaCl^{150}$	69.24±7.12b	6.18±0.18c	5.21±0.18b	24.27±0.64c	36.23±0.75b	0.39±0.03b
JN17	$NaCl^0$	81.06±5.23a	9.34±0.18a	5.68±0.16a	33.65±0.57a	42.30±0.53a	0.69±0.04a
	$NaCl^{50}$	71.20±3.20b	7.58±0.17b	4.81±0.02b	31.27±0.64b	41.42±0.64a	0.53±0.02b
	$NaCl^{100}$	54.14±6.12c	5.20±0.14c	4.23±0.06c	26.77±0.64c	32.60±0.64b	0.31±0.02c
	$NaCl^{150}$	37.80±7.50d	4.12±0.13d	3.64±0.14d	14.43±0.67d	30.30±0.92c	0.14±0.02d

under salt stresses might be involved in two aspects: (*1*) The membrane integrity was damaged more seriously (Zheng *et al.* 2008). Poor membrane integrity induced more K^+ leakage and Na^+ accumulation in plant cells, and as a result unbalanced ions in plant tissues limited plant growth. (*2*) The K^+ selectivity of cell membrane of ST wheat was better than that of SS one, which was testified by always higher K^+ content in ST wheat than in SS one, even in $NaCl^0$ plants (Table 1). Higher soluble sugar and protein accumulation in ST wheat than in SS one also indicated that ST wheat had higher ability of osmotic adjustment under salinity (Muranaka *et al.* 2002).

The alleviation of oxidative stress could contribute to salt-induced increases in activities of antioxidant enzymes (Mittova *et al.* 2004). Higher activities of antioxidant enzymes in ST than SS wheat indicated that ST wheat had higher ability to eliminate free active radicals than the SS one (Lawlor 1995, Stepien and Klobus 2005). The enzyme activities of SS wheat in $NaCl^{150}$ were lower than those in $NaCl^{100}$. The reason for this difference might be the salt-induced limitation of plant growth in excessive NaCl treatment, with the plants being too weak to grow at 7 d after anthesis.

We suggest that the ST wheat was better equipped than the SS one in maintaining gas exchange, SI, Chl content, K^+/Na^+ ratio, and in mechanisms resistant to secondary oxidative stress that results from increased formation of ROS under salinity stress. ST wheat could effectively relieve the inhibition of salt stresses and obtain high grain yield. However, the damage caused by salt stresses in reproductive stage might be more serious than that in the seedling stage.

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