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Salt acclimation induced salt tolerance in wild-type and chlorophyl *b*-deficient mutant wheat

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Abstract: Salt acclimation can promote the tolerance of wheat plants to the subsequent salt stress, which may be related to the responses of the photosynthetic apparatus. The chlorophyl (*Chl*) *b*-deficient mutant wheat *ANK 32B* and its wild type (WT) were firstly saltly acclimated with 30 mmol NaCl for 12 days, then subsequently subjected to 6-day salt stress (500 mmol NaCl). The *ANK 32B* mutant plants had lower *Chl b* concentration, which was manifested in the lower total *Chl* concentration, higher ratio of *Chl a/b* and in reduced photosynthetic activity (P_n). The effect of salt acclimation was manifested mainly after salt stress. Compared to non-acclimated plants, the salt acclimation increased the leaf water potential, osmotic potential (Ψ_o) and K concentration, while decreased the amount of Na^+ and H_2O_2 in WT and *ANK 32B* under salt stress, except for Ψ_o in *ANK 32B*. In addition, the salt acclimation enhanced the APX (ascorbate peroxidase) activity by 10.55% and 33.69% in WT and *ANK 32B* under salt stress, respectively. Compared to the genotypes, under salt stress, the Ψ_o, F_v/F_m, P_n and g_s of mutant plants were 5.60, 17.62, 46.73 and 26.41% lower than that of WT, respectively. These results indicated that although the salt acclimation could alleviate the negative consequences of salt stress, it is mainly manifested in the WT, and the *ANK 32B* plants had lower salt tolerance than WT plants, suggesting that lower *Chl b* concentration has a negative effect on the salt acclimation induced salt tolerance in wheat.

Keywords: salinity; *chlorina* mutant; water relation; photosynthesis; chlorophyll *a* fluorescence

High salinity is critical environmental stress in native and agricultural land, which limits the availability of soil water, modulating the plant water relations (Dinneny 2014). The ability of sodium ions to enter the transpiration stream and accumulate in leaves results in indirect damage to the photosynthetic apparatus and ion homeostasis (Müller et al. 2014, Bargaz et al. 2016). Wheat (*Triticum aestivum* L.) is sensitive to soil salinity; it has been reported that soil salinity-induced grain yield loss is up to 60% in wheat (El-Hendawy et al. 2017).

Soil salinity inhibits crop growth *via* modulating multiple physiological processes (Munns and Tester

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2008, Zhao et al. 2020). Initially, soil salinity triggers osmotic stress leading to the reduction of plant water uptake and cell dehydration (Janda et al. 2016, Li et al. 2020). Soil salinity also causes a significant reduction of stomatal conductance, which partly depresses the photosynthetic capacity in wheat (Rahnama et al. 2010). When sodium ions enter the transpiration stream and accumulate in leaves, the major injury of salinity involves ionic imbalance, toxic sodium effect, and salinity induced oxidative stress (Munns and Tester 2008). This further causes a disruption of selectivity of the plasma membrane, lipid reprogramming and depression of metabolic activities (Janda et al. 2016).

Recent work has demonstrated that single, short experiences of salt can improve the tolerance of plants to the subsequent severe salt stress (Janda et al. 2016, Wang et al. 2017, Zuo et al. 2019). In maize, NaCl acclimated (25 mmol, 7 days) plants retain more K^+ while accumulating less Na^+ in roots and have better vacuolar Na^+ sequestration ability in leaves under salt stress (Pandolfi et al. 2016). Our previous study in wheat showed that the salt acclimation-induced salt tolerance could be enhanced by abscisic acid priming, which is due to higher antioxidant capacity and photosynthetic electron transport efficiency (Wang et al. 2017). The NaCl acclimation (50 mmol, 7 days) obviously enhanced leaf water potential (Ψ_l), relative water content, chlorophyll (*Chl*) *a* concentration, photosynthetic rate (P_n) and stomatal conductance (g_s) in rice plants, compared with the non-acclimation treatment under salt stress (Djanaguiraman et al. 2006). This suggests that the changes in the photosynthetic process reflect the effect of salt stress on plants (Sun et al. 2016).

To explore the roles of the photosynthesis system in salt acclimation induced salt tolerance and the physiological mechanisms in wheat, the *Chl b*-deficient mutant wheat *ANK 32B* and its wild type (WT) were firstly saltly acclimated with 30 mmol NaCl for 12 days, then the plants were subsequently subjected to 6-day salt stress under 500 mmol NaCl. It has reported that *ANK 32B* plants have lower *Chl b* concentration and photo-oxidizable photosystem (PS) I than WT (Brestic et al. 2015, 2016, Zivcak et al. 2019). The objective was to test whether lower *Chl b* concentration could affect the salt acclimation induced salt tolerance in wheat.

MATERIAL AND METHODS

Genetic materials and experimental design. The chlorophyll *b* deficient mutant *chlorina ANK 32B* and the WT were used in this study. The *ANK 32B* mutant is the near-isogenic hexaploid line containing a *chlorina* mutation of the cn-A1 locus introduced from a *chlorina* mutant line of AN-215 (Brestic et al. 2015). The WT and *ANK 32B* seeds were sown in plastic pots (15 cm high and 25 cm in diameter). The clay soil was sieved by passing through a 1 cm mesh, and each pot was filled with 4.8 kg soil. Four wheat seedlings remained in each pot after thinning at the 3-leaf stage. At the 6-leaf stage, wheat plants were exposed to four treatments: C – non-stress control; AC – salt acclimation treatment with 30 mmol NaCl solution irrigated for 12 days; ST – salt stress control with 500 mmol NaCl solution irrigated for 6 days; AC + ST – combination treatment of salt acclimation plus salt stress. The plants were grown in a greenhouse. The active photosynthetic radiation was set as > 500 μmol/m^2/s, and the photoperiod was 12 h. The relative humidity was 70 ± 5%. The experiment was a randomised block design. Each treatment consisted of three replicates, and each replicate consisted of 4 pots. Thus, 48 plants were included in each treatment.

Physiological trait determination. The net photosynthetic rate (P_n) and stomatal conductance (g_s) were measured on the latest fully expanded leaves with a portable photosynthesis system (LI-6400, Li-Cor, Lincoln, USA) at a CO_2 concentration of 400 μmol/mol and photosynthetically active radiation of 1 200 μmol/m^2/s after salt treatment. The maximum quantum yield of PS II (F_v/F_m) and performance index on the absorption basis (PI_{ABS}) were determined on the same leaves as for the gas exchange with the plant efficiency analyser (Pocket-PEA, Hansatech, Norfolk, UK) after a 30 min of dark adaptation. Three leaves from different plants were selected for the measurements of gas exchange and *Chl a* fluorescence parameters. Fresh leaf samples (0.1 g) were used to determine the total chlorophyll, *Chl a* and *Chl b* concentrations according to Arnon (1949). The Ψ_l and osmotic potential (Ψ_o) of the latest fully expanded leaves were measure with a pressure chamber (soil moisture equipment, Santa Barbara, USA) and a psychrometer (C-52 sample chambers, Wescor, Logan, USA) connected with a microvolt meter (HR-33T, Wescor, Logan, USA), respectively. One hundred milligrams of leaf sample was used for the analysis of Na^+ and K^+ concentrations, which were analysed after high-pressure nitric acid digestion (UltraClave III, MLS, Leutkirch, Germany) with inductively coupled plasma optical emission spectrometry (ICP-OES 720, Varian, Palo Alto, USA). Three leaves were homogenised for measurements of H_2O_2 concentration and antioxidant enzyme activities. The H_2O_2 concentration was measured by monitoring the absorbance of the titanium peroxide complex at 410 nm following the methods of Li et al. (2013). The SOD (superoxide dismutase) activity was determined by monitoring the inhibition of photochemical reduction of nitroblue tetrazolium, the activity of APX (ascorbate peroxidase) was measured following ascorbate oxidation by monitoring the decrease at 290 nm, and the CAT (catalase) activity was determined following Li et al. (2014).

Statistical analysis. All data were firstly tested for homogeneity of variance with boxplot and subjected to the one-way ANOVA using SigmaSTAT (V3.5, Systat Software Inc., Chicago, USA).

RESULTS AND DISCUSSION

It has been reported that *ANK 32B* mutant plants have a significantly higher *Chl a* to *b* ratio while lower total chlorophyll concentration than WT plants, due to lower *Chl b* concentration in leaves (Brestic et al. 2015). In the present study, salt stress significantly reduced the concentrations of *Chl a*, *Chl b* and total chlorophylls, compared with the non-stress control in both *ANK 32B* and WT (Figure 1). It seems that the decrease was more pronounced for *Chl a* than for *Chl b*, which also resulted in a decrease of *Chl a/b* too. The *Chl a/b* of salt acclimated plants was 16.72% higher than the control plants in *ANK 32B*. The total chlorophyll concentration of salt acclimated plants was 14.74% and 10.68% higher than that of non-acclimated plants in *ANK 32B* and WT; however, these are observed only in the higher *Chl a* of WT plants, neither the *Chl a* in mutant plants, nor the *Chl b* in both genotypes showed significant differences (Figure 1, ST *vs.* ST + AC). Higher chlorophyll content was found in salt acclimated barley compared to non-acclimated plants when the SPAD indexed chlorophyll content was determined (Zuo et al. 2019). Though the ratio of *Chl a* to *b* was significantly higher in *ANK 32B* than that in WT without salt stress, neither salt acclimation nor salt stress affected the *Chl a/b* ratio in both *ANK 32B* and WT. Under salt stress, the salt acclimation increased the *Chl a* concentration by 23.65% in WT; however, it had no significant effect in *ANK 32B*.

Under the control condition, a similar level of Ψ_1 and Ψ_o was found in *ANK 32B* and WT plants (Figure 2), indicating that lower *Chl b* concentration did not influence the plant water relations. However, the salt acclimation slightly reduced the Ψ_o in WT plants, which might be due to the salt acclimation-induced changes in the concentration of total soluble sugar

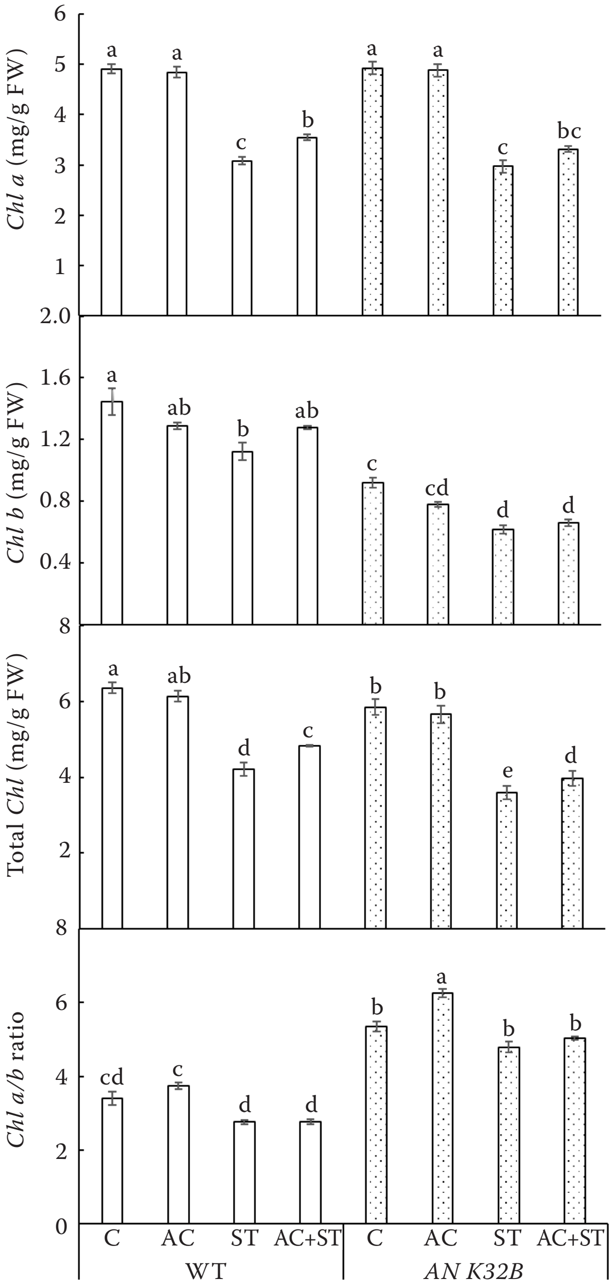

Figure 1. Concentrations of photosynthetic pigment (*Chl a*, *Chl b* and total *Chl*) and *Chl a* to *Chl b* ratio in wheat (wild type (WT) and *ANK 32B*) as affected by salt acclimation and salt stress. C – non-stress control; AC – salt acclimation; ST – salt stress; AC + ST – salt acclimation + salt stress. Different small letters indicate significant difference at the $P < 0.05$ level; FW – fresh weight

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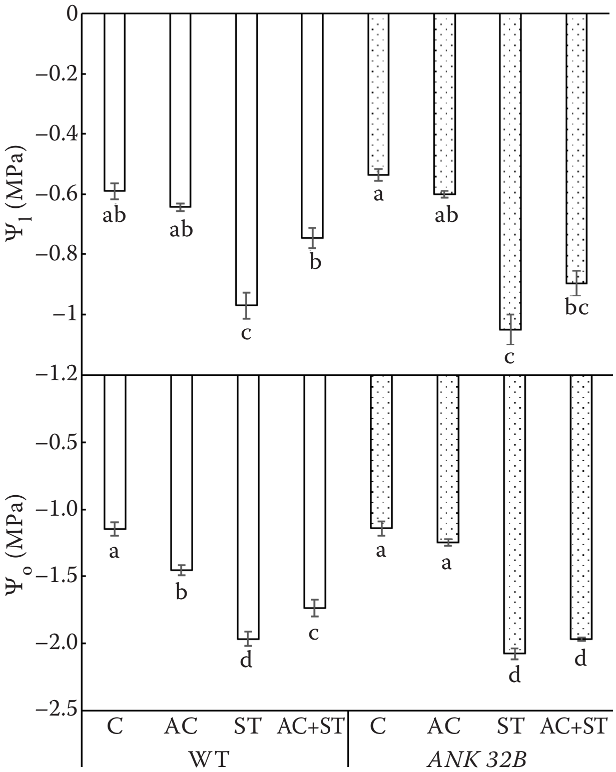

Figure 2. Leaf water potential (Ψ_l) and osmotic potential (Ψ_o) in wheat (WT and *ANK 32B*) as affected by salt acclimation and salt stress. C – non-stress control; AC – salt acclimation; ST – salt stress; AC + ST – salt acclimation + salt stress. Different small letters indicate significant difference at the $P < 0.05$ level

(Zuo et al. 2019). As indicated by Munns (2005), soil salinity-induced decrease of soil water potential modifies the plant water relations. Under salt stress, the Ψ_l and Ψ_o decreased significantly in both salt acclimation (AC + ST) and non-acclimated (ST) plants, but the decrease was less pronounced in acclimated plants as compared to non-acclimated plants in WT. In *ANK 32B* mutant plants, neither Ψ_l nor Ψ_o was affected by salt acclimation. In addition, the Ψ_o in salt acclimated WT plants was14.22% higher than that of salt acclimated *ANK 32B* plants. This indicated that the soil salinity induced osmotic stress resulted in different dehydration levels in plant tissues in *ANK 32B* and WT plants (Parida and Das 2005). It was suggested that the salt acclimation benefited the balance of plant water relations in WT plants, while it was not the same case in *ANK 32B* plants.

The salinity-induced ionic effect is one of the major damages to the plants (Mandhania et al. 2006), and the excessive accumulation of Na^+ negatively affects the metabolic activities in plants (Zhao et al. 2020). In the present study, salt acclimation slightly increased the amount of Na and reduced the amount of K in both WT and *ANK 32B* plants. These changes were similar in both genotypes. Salt stress increased the Na^+ concentration while decreased the K^+ concentration in leaves; however, salt acclimation alleviated the adverse effect of salt stress on ionic balance in wheat (Figure 3, AC + ST *vs*. ST). As significant differences were not found between the *ANK 32B* and WT genotypes, the similar trends indicated that *Chl b* deficiency had no significant effect on ionic balance in wheat under salt stress.

Salt stress triggers the production of reactive oxygen species (ROS), leading to oxidative stress (Alscher et al. 1997). Here, the H_2O_2 concentration was significantly increased in WT and *ANK 32B* under salt stress compared with that under normal conditions; however, the salt acclimation induced reduction of H_2O_2 concentration in leaf was larger in WT than *ANK 32B* under salt stress (Figure 4). This indicated that salt acclimation alleviated the injury of salt-induced oxidative stress in WT, but it cut no ice in *ANK 32B*. For the ROS scavenging, SOD catalyses the

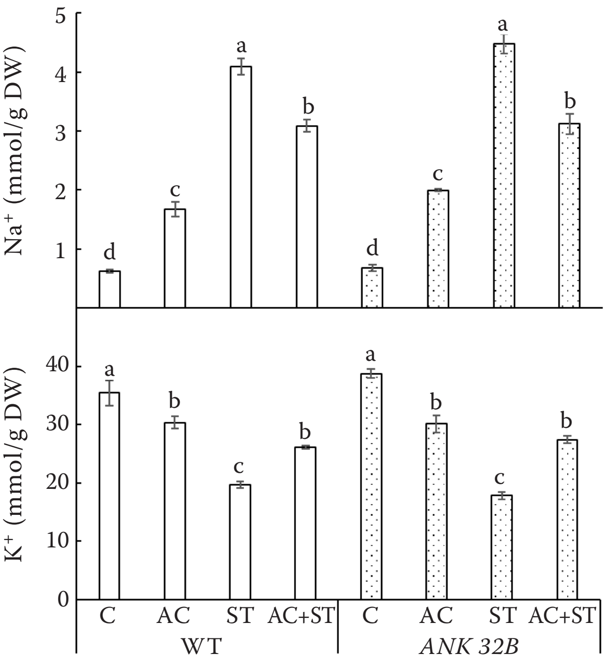

Figure 3. Concentrations of Na^+ and K^+ in wheat (wild type (WT) and *ANK 32B*) as affected by salt acclimation and salt stress. C – non-stress control; AC – salt acclimation; ST – salt stress; AC + ST – salt acclimation + salt stress. Different small letters indicate significant difference at the $P < 0.05$ level; DW – dry weight

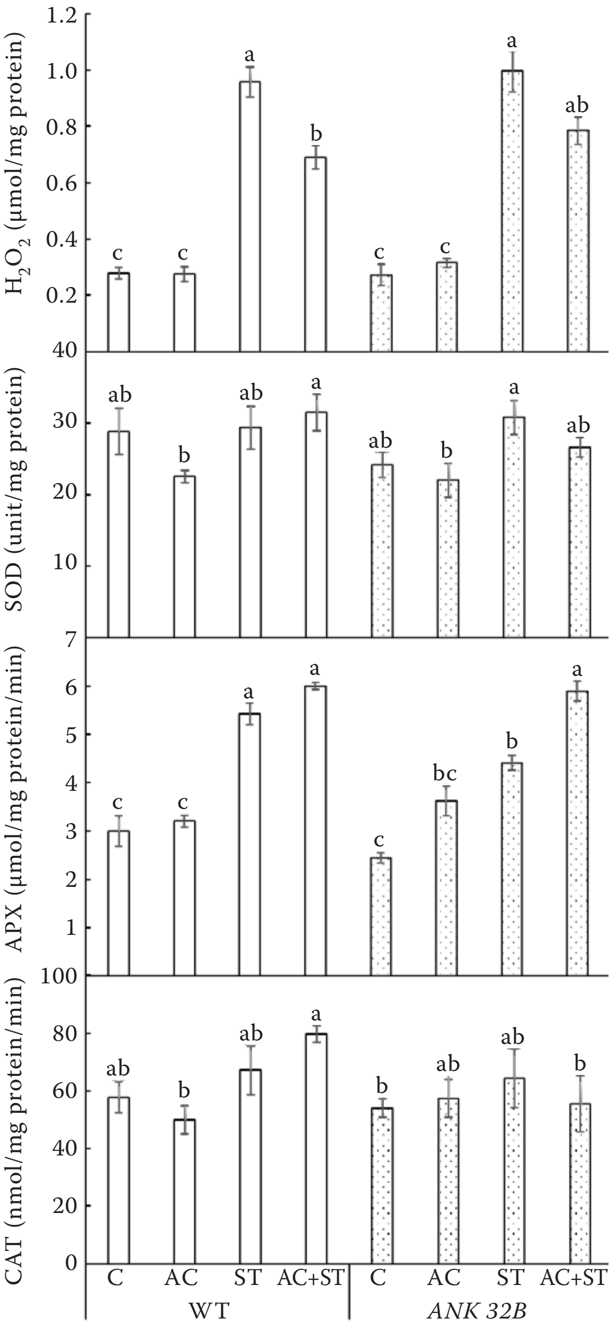

Figure 4. Concentrations of H_2O_2, activities of superoxide dismutase (SOD), ascorbate peroxidase (APX) and catalase (CAT) in wheat (wild type (WT) and *ANK 32B*) as affected by salt acclimation and salt stress. C – non-stress control; AC – salt acclimation; ST – salt stress; AC + ST – salt acclimation + salt stress. Different small letters indicate significant difference at the $P < 0.05$ level

disproportionation of single oxygen ($^1O_2$) generated mainly from chloroplasts, and produces H_2O_2, then CAT decomposes H_2O_2 to H_2O and O_2, together with APX (Keunen et al. 2013). In the present study, the salt stress enhanced the APX activity in both WT and *ANK 32B* but did not affect the activities of SOD and CAT in any genotypes. The significant difference between salt acclimated and non-acclimated plants was found only in the APX activity of *ANK 32B* leaves. Various responses of antioxidant enzyme activity to salt acclimation and salt stress were observed in wheat and rapeseed (Wang et al. 2017, Santangeli et al. 2019). For instance, salt acclimated wheat plants have significantly higher CAT activity than non-acclimated plants under salt stress, while no significant difference was found in SOD activity (Wang et al. 2017). In rapeseed, salt acclimation enhanced the APX activity while reduced the SOD activity under salt stress (Santangeli et al. 2019). The variations in antioxidant enzyme activity might be due to the responses of different enzyme activities to the salt acclimation with various NaCl levels. Based on the results, it is unlikely that antioxidant enzymes play a major role either in salt acclimation or in the procession against salt stress in either genotype.

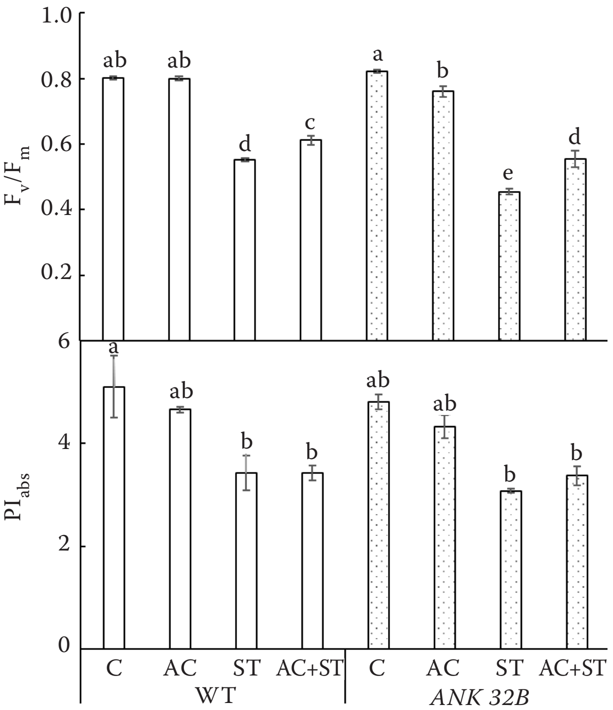

Figure 5. The maximum quantum efficiency of photosystem II (F_v/F_m) and performance index on absorption basis (PI_{abs}) in wheat (wild type (WT) and *ANK 32B*) as affected by salt acclimation and salt stress. C – non-stress control; AC – salt acclimation; ST – salt stress; AC + ST – salt acclimation + salt stress. Different small letters mean significant difference at the $P < 0.05$ level

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The F_v/F_m and PI_{ABS} are two important indicators widely used to present the photosynthetic electron transport efficiency under stress conditions (Kalaji et al. 2017, Zivcak et al. 2017, Faseela et al. 2020). In this study, salt stress decreased the F_v/F_m and PI_{ABS} in both *ANK 32B* and WT plants, but salt acclimated plants had significantly higher F_v/F_m than non-acclimated plants in both *ANK 32B* and WT under salt stress (Figure 5). Under non-stress conditions, there was no significant difference between C and AC plants in F_v/F_m and PI_{ABS} except for the F_v/F_m in *ANK 32B*. In addition, the F_v/F_m was significantly higher in WT than that in *ANK 32B* under salt stress, indicating that the lower *Chl b* concentration depressed the maximum quantum efficiency of PS II under stress conditions. The PI_{ABS} was reduced by salt stress in *ANK 32B* and WT. However, the PI_{ABS} was similar in salt acclimated and non-acclimated plants in both *ANK 32B* and WT under salt stress.

Salt stress usually causes stomatal closure and limits the net photosynthetic rate (Dinneny 2014). Under non-stress conditions, no significant difference was found in P_n and g_s between the control and salt acclimated plants in both *ANK 32B* and WT. Salt stress reduced the P_n, which should be partly due to the decrease in g_s (Figure 6). The salt acclimated plants had higher P_n and g_s than the non-acclimated plants under salt stress, except for the g_s in *ANK 32B*. In addition, the P_n and g_s in WT were 87.75% and 35.88% higher than that in *ANK 32B* under salt stress, respectively. This indicated that lower *Chl b* concentration had a negative effect on photosynthetic carbon assimilation, hence reduced the plant growth in wheat under salt stress.

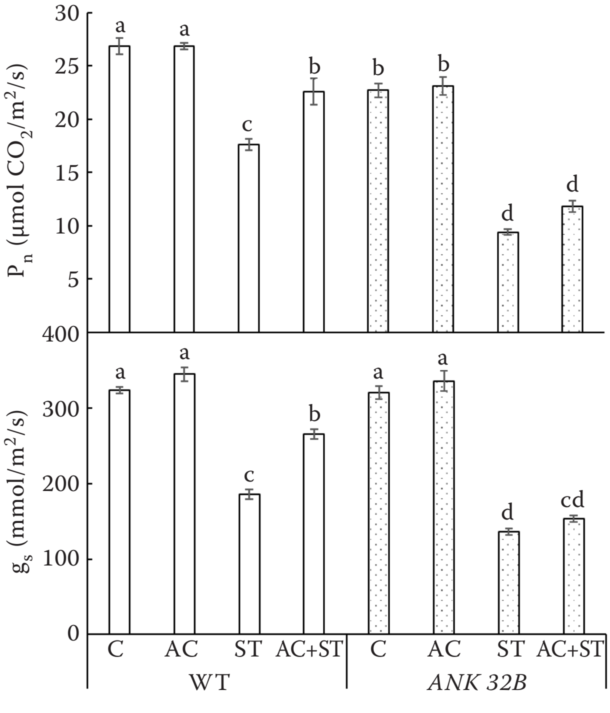

Figure 6. Net photosynthetic rate (P_n) and stomatal conductance (g_s) in wheat (wild type (WT) and *ANK 32B*) as affected by salt acclimation and salt stress. C – non-stress control; AC – salt acclimation; ST – salt stress; AC + ST – salt acclimation + salt stress. Different small letters mean significant difference at the $P < 0.05$ level

In conclusion, salt stress caused a decrease of Ψ_l, Ψ_o and K concentration and an increase in concentrations of Na and H_2O_2 in WT and *ANK 32B*, but the salt acclimation was able to alleviate the adverse effects of salt stress, especially in WT plants. The protection was not linked to the antioxidant systems, as only the APX was activated under salt stress (the SOD and CAT activities did not change), and the activity of the antioxidant enzymes did not differ between the salt acclimated and non-acclimated in WT and *ANK 32B* plants except APX in mutant plants, where APX was higher in acclimated plants than in non-acclimated plants under salt stress conditions. The elevated activity of APX could not reduce the adverse effect of salt since the acclimated mutants have significantly lower Ψ_o, F_v/F_m, P_n and g_s than WT under salt stress. Thus, salt acclimated *ANK 32B* plants had lower salt tolerance than WT plants. This suggested that lower *Chl b* concentration has a negative effect on the salt acclimation induced salt tolerance in wheat.

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