PHOTOSYNTHETICA 46 (1): 107-114, 2008

Comparison of effects of salt and alkali stresses on the growth and photosynthesis of wheat

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Abstract

The seedlings of wheat were treated by salt-stress (SS, molar ratio of NaCl : Na_2SO_4 = 1 : 1) and alkali-stress (AS, molar ratio of $NaHCO_3$: Na_2CO_3 = 1 : 1). Relative growth rate (RGR), leaf area, and water content decreased with increasing salinity, and the extents of the reduction under AS were greater than those under SS. The contents of photosynthetic pigments did not decrease under SS, but increased at low salinity. On the contrary, the contents of photosynthetic pigments decreased sharply under AS with increasing salinity. Under SS, the changes of net photosynthetic rate (P_N), stomatal conductance (g_s), and transpiration rate (E) were similar and all varied in a single-peak curve with increasing salinity, and they were lower than those of control only at salinity over 150 mM. Under AS, P_N, g_s, and E decreased sharply with rising salinity. The decrease of g_s might cause the obvious decreases of E and intercellular CO_2 concentration, and the increase of water use efficiency under both stresses. The Na^+ content and Na^+/K^+ ratio in shoot increased and the K^+ content in shoot decreased under both stresses, and the changing extents under AS were greater than those under SS. Thus SS and AS are two distinctive stresses with different characters; the destructive effects of AS on the growth and photosynthesis of wheat are more severe than those under SS. High pH is the key feature of the AS that is different from SS. The buffer capacity is essentially the measure of high pH action on plant. The deposition of mineral elements and the intracellular unbalance of Na^+ and K^+ caused by the high pH at AS might be the reason of the decrease of P_N and g_s and of the destruction of photosynthetic pigments.

Additional key words: carotenoids; chlorophyll; NaCl; Na_2CO_3; $NaHCO_3$; Na_2SO_4; stomatal conductance; transpiration rate; *Triticum*; water use efficiency.

Introduction

In saline and sodic soils, Na^+, Ca^{2+}, Mg^{2+}, K^+, Cl^-, SO_4^{2-}, HCO_3^-, CO_3^{2-}, and NO_3^- are main ions (Läuchli and Lüttge 2002). All these ions come from neutral salts or alkaline salts. We can further classify the natural salt-stress, in terms of the salt characteristics, into neutral salt-stress, alkaline salt-stress, and mixed salt-stress. When a salinized soil contains HCO_3^- and/or CO_3^{2-}, which consequentially elevate the soil pH, plants undergo the damaging effects of both salt stress (SS) and alkali stress (AS). Relatively little attention has been given to AS. Even so, there have been some reports about high-pH calcareous soils (Brand *et al.* 2002, Nuttall *et al.* 2003), alkaline soils (Hartung *et al.* 2002), alkaline salt-stress (Shi and Yin 1992, 1993, El-Samad and Shaddad 1996, Campbell and Nishio 2000, Shi *et al.* 2002), and mixed salt-stress (Shi and Sheng 2005, Shi and Wang 2005). These reports not only clearly demonstrate the actual existence of AS, but also show that the effects of AS are more severe than those of SS (Shi and Yin 1993).

Soil salinization and alkalization frequently co-occur, and this has caused severe problems in some areas, such as northeast China (Kawanabe and Zhu 1991). There are numerous reports on photosynthetic characteristics under SS (Qiu *et al.* 2003, Koyro 2006, Wei *et al.* 2006).

Received 28 June 2007, *accepted* 20 September 2007.
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Abbreviations: AS – alkali stress; C_i – internal CO_2 concentration; Car – carotenoids; Chl – chlorophyll; E – transpiration rate; g_s – stomatal conductance; P_N – net photosynthetic rate; RGR – relative growth rate; SS – salt stress; WC – water content; WUE – water use efficiency.
Acknowledgements: This work was supported by grants from the National Natural Science Foundation of China (No. 30671491 and No. 30571318) and the Program for Changjiang Scholars and Innovative Research Team in University from the Ministry of Education of China (IRT0519), and the National Key Basic Research Program of China (No. 2007CB106800).

Generally, photosynthesis is inhibited by SS (Ma *et al.* 1997, Sultana *et al.* 1999, Qiu *et al.* 2003, Koyro 2006). Salt also affects photosynthetic components (Ma *et al.* 1997, Qiu *et al.* 2003) and chloroplast structure (Fidalgo *et al.* 2004). But to our knowledge, the effects of AS on photosynthesis have not been reported. Under AS, plants are simultaneously exposed to action of salt and high pH. Environmental pH significantly affects photosynthesis and photosynthetic electron transport (Gerloff-Elias *et al.* 2005). The high pH caused by AS may destroy photosynthetic activity of plants and be the key feature of the AS that is different from SS.

In this study, we treated wheat seedlings with varying 0–150 mM SS (molar ratio of NaCl : Na_2SO_4 = 1 : 1) and 0–75 mM AS (molar ratio of $NaHCO_3$: Na_2CO_3 = 1 : 1) to compare the effects of the both stresses on growth and photosynthesis.

Materials and methods

Plants: Seeds of Xiaobingmai 33, a salt-resistant wheat cultivar, were sown in plastic pots of 17-cm diameter. Each pot contained 13 seedlings. Seedlings were sufficiently watered with Hoagland nutrient solution once every day. All pots were placed in the greenhouse (25.0±1.5 °C during the day and 19.0±1.5 °C during the night). Plants grew at uniform irradiance under photoperiod of 15/9 h light/dark and photosynthetic photon flux density (PAR) of 250 μmol m^{-2} s^{-1}.

Simulated salt and alkaline conditions: Within the SS group, five concentration treatments were applied: 30, 60, 90, 120, and 150 mM (labelled as S_1–S_5). Within the AS group, five concentration treatments were applied: 15, 30, 45, 60, and 75 mM (labelled as A_1–A_5) (Table 1). These treatments referred to the total salt concentrations of NaCl+Na_2SO_4 or $NaHCO_3$+Na_2CO_3. Therefore, in the salt-stress solution of 150 mM, a mixture of 75 mM NaCl and 75 mM Na_2SO_4 would result in total ion concentrations of 225 mM Na^++75 mM Cl^-+75 mM SO_4^{2-}. The buffer capacity was defined according to Shi and Sheng (2005) and Shi and Wang (2005) by titration with HCl as the mM amount of H^+ needed to drop the pH of 1 000 cm^3 of treatment solution to the same pH as the control. The buffer capacity represents the degree of AS. The correlation coefficient between Na^+ concentration and salinity was 1 in this design of stress conditions. Therefore, Na^+ concentration could be represented by salinity.

Stress treatments: When the seedlings were 2 weeks old, 36 pots with seedlings growing uniformly were selected and randomly divided into 12 sets, 3 pots per set. One set was used as a control, a second set was used for growth index determination at the beginning of treatment, and the remaining 10 sets were used as various stress treatments. Each pot was considered a single replicate; therefore there were three replicates per set. Stress treatments were performed once every day around 17 and 18 h with the application of nutrient solutions containing the appropriate salts. All pots were watered thoroughly with 500 cm^3 of treatment solution applied in three portions. Control plants were watered with nutrient solution. The entire treatment duration was 15 d.

Table 1. Stress factors of various treatments. Salt-stresses: S_1-S_5, alkali-stresses: A_1-A_5.

	Salinity [mM]	pH	Buffer capacity [H^+ mmol]
Control	0	6.60	0.00
S_1	30	6.61	0.00
S_2	60	6.62	0.00
S_3	90	6.63	0.00
S_4	120	6.64	0.00
S_5	150	6.65	0.00
A_1	15	9.75	17.5
A_2	30	9.92	34.7
A_3	45	9.93	52.5
A_4	60	9.97	68.1
A_5	75	9.96	90.5

Measurement of physiological indices: Net photosynthetic rate (P_N), stomatal conductance (g_s), transpiration rate (E), and intercellular CO_2 concentration (C_i) of leaves were determined between 08:30 and 10:30 from fully expanded third blades, using a portable open flow gas exchange system *LI-6400* (*Li-Cor*, USA). The photosynthetically active radiation (PAR) was 1 200 μmol m^{-2} s^{-1} (saturation irradiance). Measurements were repeated five times for each blade, for five blades per pot, and the averages were recorded. The water use efficiency (WUE) was calculated as the ratio of P_N/E (Nieva *et al.* 1999). The leaf area was determined with an area meter (model *1671-VHA*). Water content (WC) was calculated from dry mass (DM) and fresh mass (FM). Carotenoids (Car) and chlorophyll (Chl) *a* and *b* were extracted with acetone, and spectrophotometeric determination at 440, 645, and 663 nm of each sample was done 3 times. The calculation used the methods of Zhu (1993). A flame photometer was used for the determination of K^+ and Na^+ contents. Relative growth rate (RGR) was determined as described in Kingsbury *et al.* (1984).

Statistical analyses of variance and correlation were performed using the statistical program *SPSS 13.0*. All of the treatments were repeated three times, and the means and calculated standard errors (S.E.) are reported. The significance was tested at the 5 % level.

Results

Wheat growth: With increasing salt concentrations, the RGR and WC of wheat shoots decreased, and their reducing extents under AS (p<0.01) were greater than those under SS (p<0.01) (Fig. 1*A,B*).

Pigment contents (Fig. 1*C–F*): Under SS, the contents of Chls and Car were all higher than those of control at 30 mM salinity, but then turned to decrease slightly with increasing salinity. Under AS, except the content of Chl *b*, that was greater than that of control at the salinity of 15 mM (A_1), the contents of photosynthetic pigments decreased sharply with increasing stress (p<0.01). The effect of SS on Chl *a/b* was insignificant (p=0.035). Under AS, the Chl *a/b* was lower than that of control at A_1 and A_2, whereas at salinity of 60 and 75 mM the Chl *a/b* was significantly higher than that of control (p<0.01).

Photosynthesis and leaf area: Under SS, P_N of wheat was enhanced and higher than that of control at S_1, but then turned to decrease slightly with increasing salinity (Fig. 1*G*). However, P_N became lower than that of control (p<0.01) when stress reached 150 mM. Under AS, the P_N decreased sharply with increasing stress, especially at salinity higher than 45 mM. Under SS, the changes of g_s and E were similar and varied all in a single-peak curve with increasing salinity (Fig. 3*H,I*). The values of g_s and E were the highest at 60 mM salinity and at 150 mM salinity much lower than those of control. However, g_s (p<0.01) and E (p<0.01) decreased sharply under AS with increasing stress intensity. The WUE (p<0.01) increased sharply with increasing salinity under AS (Fig. 1*J*). But under SS, WUE increased with rising salinity only at salinities greater than 60 mM. With increasing stress, C_i declined (Fig. 1*K*), and the extent of reduction under AS (p<0.01) was greater than that under SS (p<0.01). Leaf area decreased under both stresses with increasing salinity and under AS it was always lower than that under SS at the same salinity (Fig. 1*L*).

Contents of Na^+, K^+, and Na^+/K^+ ratio: With increasing stress, the contents of Na^+ (p<0.01) and Na^+/K^+ ratio increased (p<0.01), while K^+ content decreased (p<0.01), and the changes under AS were greater than those under SS (Fig. 2).

Correlation and multiple linear regressions: The correlations between salinity and all the photosynthetic indices were insignificant, but the correlations between buffer capacity and all the photosynthetic indices were very significant (Table 2). The correlations between buffer capacity and the photosynthetic indices were greater than that between pH and the photosynthetic indices (Table 2). Consequently, it would be more reasonable to use the buffer capacity as the strength value of AS than to use pH (Tables 1 and 2). Table 2 shows that there was a significant negative correlation between each photosynthetic index and Na^+ content or Na^+/K^+ ratio, and a significant positive correlation between each photosynthetic index and K^+ content in shoot of wheat. But there was a significant positive correlation between WUE and Na^+ content or Na^+/K^+ ratio, and a significant positive correlation between WUE and the K^+ content in shoot of wheat.

A multiple linear regression analysis was performed for each photosynthetic index (Table 3). The r^2 values were larger than 0.84 (p<0.01), indicating a high linear correlation between each physiological index and the three stress factors. The analysis indicated that the buffer capacity was a dominant factor that affected photosynthesis.

Discussion

Effects of SS and AS on growth: RGR reflects the life-sustaining activities of the plant, and it is an optimum index for measuring degrees of stress and the responses of plants to various stresses. We observed the decreases in RGR and the WC of wheat under both SS and AS with rising stress intensity (Fig. 1*A,B*). However, the extents of the decreases in RGR and WC under AS were obviously greater than those observed under SS. The injurious effect caused by AS was greater than that by SS at the same salinity, which was consistent with previous reports (Shi and Yin 1992, 1993, Shi and Sheng 2005, Shi and Wang 2005). An explanation for the different injurious extents of the two stresses might be their different mechanisms of action. The injurious effects of salinity may be a result of low water potentials and ion toxicities (Munns 2002, Moghaieb *et al.* 2004, Parida and Das 2005). AS consists of the same stress factors as SS, but the influence of high pH is added. The high pH environment surrounding the roots can direct some ions, *e.g.* Ca^{2+}, Mg^{2+}, to precipitate (Shi and Zhao 1997), which may destroy the nutrient supply and ion balance around the roots. Moreover, a high pH may lead to the lack of protons, the destruction or inhibition of transmembrane electrochemical-potential gradients in root cells, and the loss of normal physiological root functions such as ion absorption. Under AS, plant survival depends not only on the ability to cope with physiological drought and ion toxicity, but also on the resistance to high pH.

Our results showed that the injurious effects of AS on wheat are more severe than those of SS. The analyses of correlation and multiple linear regression indicated that the buffer capacity was the dominant factor of AS and should be taken as an optimal index to represent the intensity of AS. High pH is the key feature of AS, which

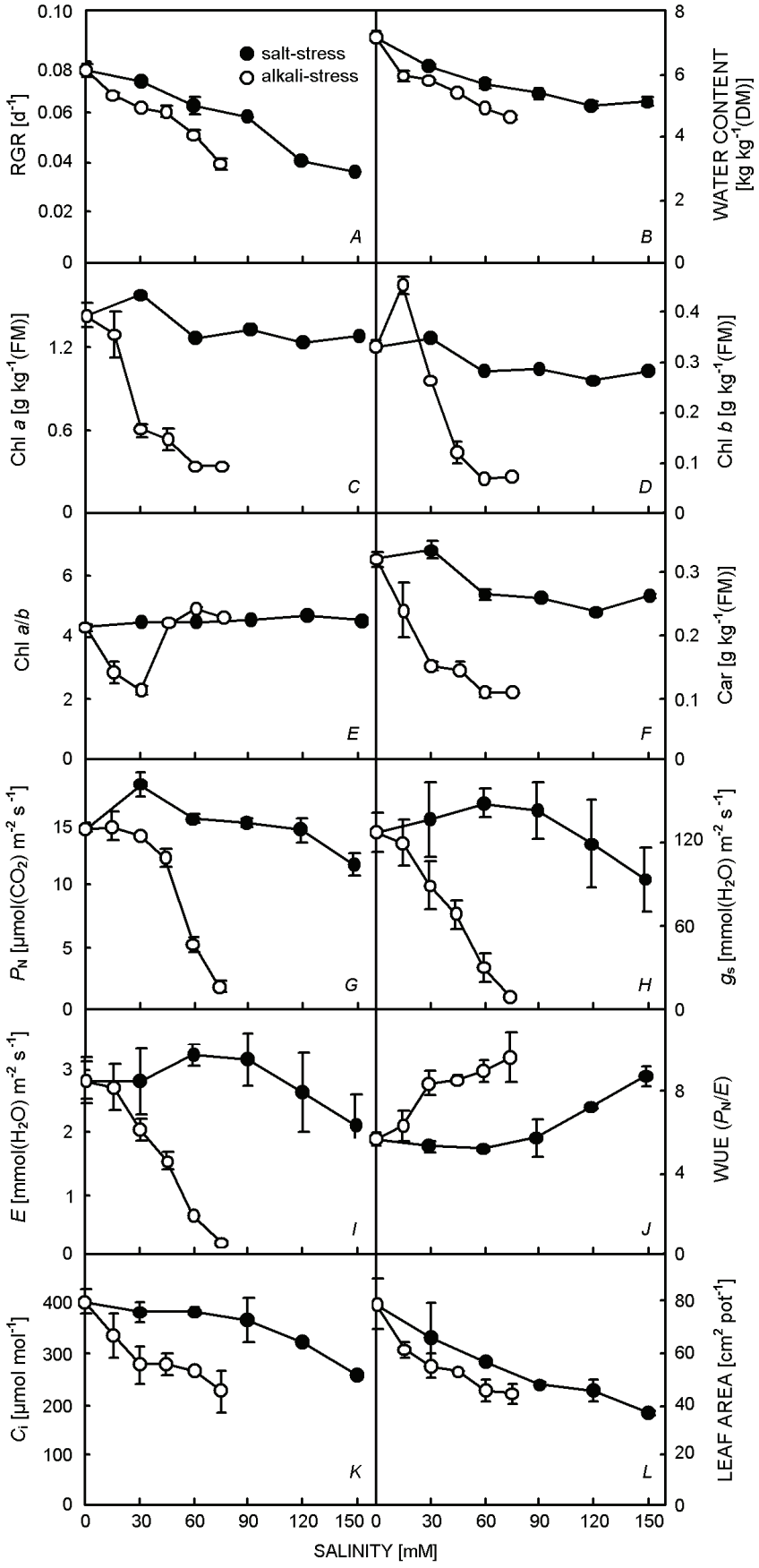

Fig. 1. Effects of salt (●) and alkali (○) stresses on (*A*) relative growth rate (RGR), (*B*) water content, chlorophyll (Chl) *a* (*C*) and *b* (*D*) contents, (*E*) Chl *a/b* ratio, (*F*) content of carotenoids (Car), (*G*) net photosynthetic rate (P_N), (*H*) stomatal conductance (g_s), (*I*) transpiration rate (*E*), (*J*) water use efficiency (WUE), (*K*) intercellular CO_2 concentration (C_i), and (*L*) leaf area of wheat. Means±S.E. of three replicates.

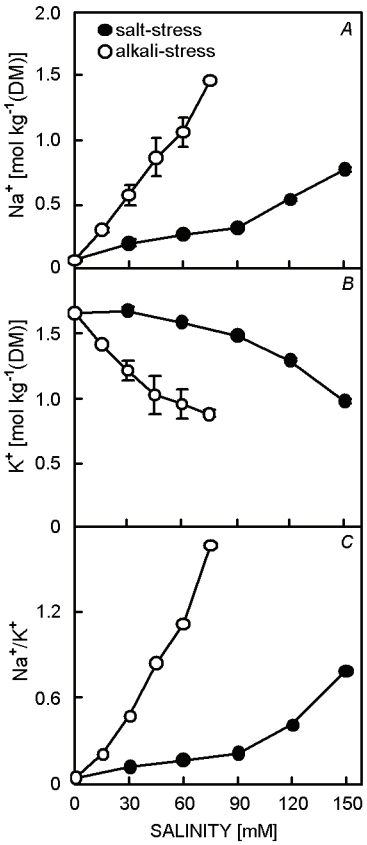

Fig. 2. Effects of salt (●) and alkali (○) stresses on (*A*) contents of Na^+ and K^+, and Na^+/K^+ ratio of wheat seedlings. Means±S.E. of three replicates.

is different from SS. Buffer capacity is a measure of action of high pH on plants. Under high pH and low buffer capacity, such as A_1 (pH 9.75, buffer capacity 17.5 mmol H^+), despite of the high pH, wheat was adjusted the high pH easily and grew well because of the low buffer capacity. Only at high buffer capacity, alkali injury caused by high pH was found. Consequently, we propose that the buffer capacity should be taken as an important parameter for reflecting the alkalinity of salt-alkalized soil.

Low Na^+ and high K^+ in the cytoplasm are essential for the maintenance of many enzymatic processes (James *et al.* 2006). Plants grown under saline-alkaline stress usually absorb Na^+ and simultaneously inhibit K^+ absorption, which results in the increase of Na^+ content and the decrease of K^+ content (Short and Colmer 1999, Khan *et al.* 2000, Moghaieb *et al.* 2004, Shi and Sheng 2005, Shi and Wang 2005). Plants generally compartmentalize Na^+ into vacuoles to avoid Na^+ toxicity in the cytosol (Munns 2002, Parida and Das 2005) and synthesize the compatible organic solutes in the cytoplasm to prevent dehydration (Murakeözy *et al.* 2002a,b). Results shown in Fig. 2 indicated that with increasing stress intensity the Na^+ content and Na^+/K^+ ratio in shoot increased, while K^+ content decreased, and the degrees of change under AS were greater than those under SS. This indicated that high pH caused by AS interfered the selective absorption of K^+-Na^+ in roots and resulted in imbalance of intracellular K^+-Na^+.

Effects of SS and AS on photosynthetic pigments and photosynthesis: Chl and Car are the main photosynthetic pigments of higher plants. The accumulation of Chl and Car was not inhibited but stimulated by low SS (30 mM). With increasing stress, the contents of Chl and Car decreased slightly under SS over 30 mM only, but decreased sharply under AS. This might be ascribed to the fact that AS caused Mg precipitation and led to inhibition of Chl synthesis (Shi and Zhao 1997). Alternatively, AS might enhance the activity of the Chl-degrading enzyme chlorophyllase (Reddy and Vora 1986). The effects on the Chl *a/b* in wheat between SS and AS were significantly different, and this might be closely related to the metabolic regulation of Chl, which should be researched in depth.

Under both stresses, the environment water potential and WC of wheat (Fig. 1*B*) decreased with increasing stress intensity. The g_s was closely correlated with the change of environment water potential. But the responses of g_s in wheat to increasing SS and AS were different. The g_s of wheat was lower than that of control only at 150 mM AS, but decreased sharply under AS of increasing salinity. This phenomenon showed that the change of g_s of wheat might be not the results of response to the decrease of environment water potential and intracellular WC, which was also proved by the results of correlation analysis. The correlation coefficient between g_s and salinity was merely –0.11 (Table 2). Regulation of stomata movement is generally related to the change of the K^+ concentration in guard cells. Our experimental results indicated that the g_s of wheat was closely related to Na^+ content, K^+ content, and Na^+/K^+ ratio in whole plant; the correlation coefficients between g_s and these characteristics were –0.947 (p<0.01), 0.889 (p<0.01), and –0.955 (p<0.01), respectively. The AS caused serious imbalance of intracellular Na^+-K^+ in wheat (Fig. 2). The content of Na^+ was significantly higher under AS than under SS, especially under high AS. For example, the Na^+ content at 75 mM AS was 23 times as great as in control, while the g_s was very low (0.0096), and therefore stomata were almost closed. Therefore, the decrease of g_s of wheat might be closely correlated with the K^+ transport inhibited by Na^+ in guard cells, or might be induced by physical or chemical signals from roots stimulated by AS. The decrease of g_s might cause the obvious decreases of E (Fig. 1*I*) and C_i (Fig. 1*K*) under AS. However, the increase of WUE under both stresses might be a result of plant response to the decrease of WC (Fig. 1*B*).

P_N of a plant usually decreases with rising stress intensity (Sultana *et al.* 1999, Koyro 2006, Wei *et al.* 2006). However, we found that P_N of wheat was not lower than that of control until the intensity of SS reached 150 mM, but decreased sharply under AS with increasing salinity (Fig. 1*G*). This implied that SS and AS were actually not only two distinct stresses, but also that the resistance of wheat to SS was stronger than that to AS. Under moderate SS, the decrease of wheat RGR was

a result of decreasing photosynthetic area (Fig. 1*L*), and was basically independent of its P_N. For a plant growing in natural salt conditions over a long term, its photosynthesis tends to stabilize, which suggests that the effects of SS on plant growth are rather mediated by the reduction of photosynthetic area than by a change in P_N. The reduction of plant P_N under high SS is generally considered to be a result of the reduction of C_i caused by stomatal closure or by non-stomatal factors (Bethke and Drew 1992). The non-stomatal factors mainly depend on the cumulative effects of leaf water and osmotic potential, biochemical constituents (Sultana et *al*. 1999), contents of photosynthetic pigments (Ma *et al*. 1997, Koyro 2006), ion toxicities in the cytosol (James *et al*. 2006), *etc*. We found that the visible reduction of the P_N of wheat under AS was related not only to both destroying photosynthetic pigments and decreasing g_s (Figs. 2 and 3), but also to imbalance of intracellular Na^+-K^+. Fig. 3 showed that P_N of wheat decreased slightly with increasing Na^+/K^+ ratio when the ratio in shoot was lower than 1, and decreased sharply when the Na^+/K^+ ratio in shoot was higher than 1. Furthermore, when under both stresses the Na^+/K^+ ratios in shoot were of similar value, their P_N values were also similar. The above analysis showed that the photosynthetic ability of wheat under AS was related to regulating Na^+-K^+ metabolism, which was confirmed by the results of correlation analysis. The P_N of wheat was negatively correlated significantly with Na^+ content (r = –0.920) and Na^+/K^+ ratio (r = –0.945) in shoot and positively correlated significantly with the K^+ content (r = 0.818) in shoot (Table 2). James *et al*. (2006) also reported that photosynthetic capacity was related to the cellular and sub-cellular partitioning of Na^+, K^+, and Cl^-.

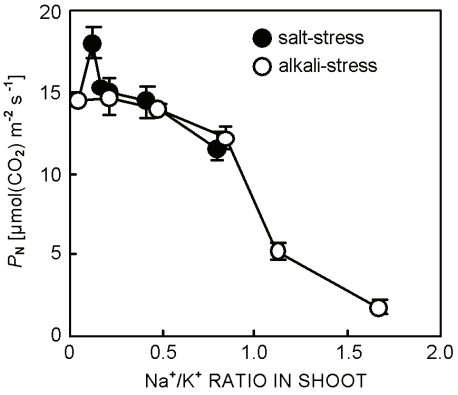

Fig. 3. Effects of Na^+/K^+ ratio in shoot on net photosynthetic rate (P_N) of wheat seedlings under salt (●) and alkali (○) stresses. Means±S.E. of three replicates.

Table 2. Correlation coefficients between photosynthetic indices and stress factors, and correlation coefficients between photosynthetic indices (Car – carotenoids, Chl – chlorophyll, E – transpiration rate, g_s – stomatal conductance, WUE – water use efficiency) and the contents of Na^+, K^+, and Na^+/K^+ ratio in shoot. *,**correlations significant at 0.05 and 0.01 levels of probability. $r_{0.05}$ = 0.602, $r_{0.01}$ = 0.735, n = 11.

	Salinity [mM]	pH	Buffer capacity [H^+ mmol]	Na^+ content	K^+ content	Na^+/K^+
P_N	–0.218	–0.579	–0.875**	–0.920**	0.818**	–0.945**
Chl *a*	0.009	–0.828**	–0.940**	–0.858**	0.816**	–0.838**
Chl *b*	–0.248	–0.462	–0.810**	–0.856**	0.760**	–0.849**
Car	–0.075	–0.846**	–0.906**	–0.855**	0.838**	–0.821**
E	–0.103	–0.720*	–0.944**	–0.945**	0.871**	–0.956**
g_s	–0.110	–0.739**	–0.943**	–0.947**	0.889**	–0.955**
WUE	0.350	0.656*	0.782**	0.920**	–0.975**	0.901**

Table 3. Analysis of multiple linear regressions between each photosynthetic index (see Table 2) and three stress factors: n = 11; X_1 = salinity; X_2 = pH; X_3 = buffer capacity; β_1,–β_3: standardized regression coefficients corresponding to X_1–X_3. The larger β value indicates stronger effect of the stress factor on photosynthetic index.

Regression equation	r^2	ANOVA test	β_1	β_2	β_3
$P_N = 9.69 – 0.024\ x_1 + 1.037\ x_2 – 0.177\ x_3$	0.895	p<0.01	–0.227	0.372	–1.217
Chl a =1.999 – 0.002 x_1 – 0.078 x_2 – 0.01 x_3	0.910	p<0.0001	–0.164	–0.290	–0.711
Chl b = 0.073 – 0.001 x_1 + 0.041 x_2 – 0.005 x_3	0.844	p<0.01	–0.201	0.579	–1.325
Car = 0.500 – 0.001 x_1 – 0.027 x_2 – 0.001 x_3	0.925	p<0.0001	–0.313	–0.583	–0.443
E = 2.723 – 0.004 x_1 + 0.059 x_2 – 0.032 x_3	0.935	p<0.0001	–0.183	0.101	–1.049
g_s = 0.144 – 0.00022 x_1 + 0.00015 x_2 – 0.0014 x_3	0.935	p<0.0001	–0.214	0.006	–0.971
WUE = 1.650 + 0.020 x_1 + 0.472 x_2 + 0.021 x_3	0.855	p<0.01	0.559	0.491	0.425

AS interfered the selective absorption for K^+-Na^+ in roots and resulted in high intracellular content of Na^+ (Fig. 2*A*). The destroying action of AS on photosynthetic pigments and photosynthetic capacity might be ascribed

to the disturbed sub-cellular partition of Na^+, which would cause the high Na^+ in cytoplasm and the destruction of structure and function of chloroplasts. This was significantly different from *Chloris virgata*, a natural alkali-resistant halophyte. Under moderate stress, the effects of both stresses on photosynthesis and Na^+-K^+ selective absorption of *C. virgata* were similar (Yang *et al*., unpublished). This indicates that high pH surrounding roots caused by AS may be resisted by the root cells of *C. virgata*, and prevented from invading the intracellular environment. Therefore, we propose that the pH adjustment of the roots may be a key physiological mechanism for *C. virgata* resisting AS. The function of pH regulation may occur outside root, or in apoplast of root, or both outside root and in apoplast of root. Therefore, cells participating in pH regulation of root may be epidermal cells, cortical cells, or xylem parenchyma cells.

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