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BRIEF COMMUNICATION

Comparison of the effects of salt-stress and alkali-stress on photosynthesis and energy storage of an alkali-resistant halophyte *Chloris virgata*

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Abstract

Seedlings of *Chloris virgata* were treated with varying (0–160 mM) salt-stress (SS; 1 : 1 molar ratio of NaCl to Na_2SO_4) or alkali-stress (AS; 1 : 1 molar ratio of $NaHCO_3$ to Na_2CO_3). To compare these effects, relative growth rates (RGR), stored energy, photosynthetic pigment contents, net photosynthetic rates, stomatal conductance, and transpiration rates were determined. Both stresses did not change significantly the photosynthetic parameters of *C. virgata* under moderate stress (below 120 mM). Photosynthetic ability decreased significantly only at high stress (160 mM). Thus *C. virgata*, a natural alkali-resistant halophyte, adapts better to both kinds of stress. The inhibition effects of AS on RGR and energy storage of *C. virgata* were significantly greater than that of SS of the same intensity. The energy consumption of *C. virgata* was considerably greater while resisting AS than while resisting SS.

Additional key words: carotenoids; chlorophyll; leaf area; net photosynthetic rate; relative growth rate; stomatal conductance; transpiration rate; water content.

The salinization and alkalization of soil is a widespread environmental problem. Although the world's land surface occupies about 13.2×10^9 ha, no more than 7.0×10^9 ha are potentially arable and only 1.5×10^9 ha are currently cultivated. Of the cultivated lands, about 0.34×10^9 ha (23 %) are saline and another 0.56×10^9 ha (37 %) are sodic (Läuchli and Lüttge 2002). Saline and sodic soils exist in over 100 countries, and cover about 10 % of total arable lands. In saline and sodic soils, Na^+, Ca^{2+}, Mg^{2+}, and K^+ are the main cations of dissoluble mineral salts, and Cl^-, SO_4^{2-}, HCO_3^-, CO_3^{2-}, and NO_3^- are the corresponding main anions (Läuchli and Lüttge 2002). These ions all come from neutral salts or alkaline salts. We can further classify natural salt stress, in terms of the salt characteristics, into neutral salt stress, alkaline salt stress, and mixed salt stress. The alkaline salt stress and the neutral salt stress are two distinct kinds of stresses for plants and should be called alkali-stress (AS) and salt-stress (SS), respectively (Shi and Yin 1993). Alkaline salts ($NaHCO_3$ and Na_2CO_3) induce much stronger destructive effects on plants than neutral salts (NaCl and Na_2SO_4) (Shi and Yin 1993). When salinized soil contains HCO_3^- and/or CO_3^{2-}, which raise the soil pH, plants suffer damaging effects of both SS and AS. However, relatively little attention has been given to AS. There are some reports about high pH of calcareous soils (Brand *et al*. 2002, Nuttall *et al*. 2003), alkaline soil (Hartung *et al*. 2002), alkaline salt stress (Shi and Yin 1992, 1993, El-Samad and Shaddad 1996, Campbell and Nishio 2000), and mixed salt stress (Shi and Sheng 2005,

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Abbreviations: AS – alkali stress; Car – carotenoid; Chl – chlorophyll; DM – dry mass; E – transpiration rate; ESR – energy storage rate; FM – fresh mass; g_s – stomatal conductance; P_N – net photosynthetic rate; P_{NC} – colony net photosynthetic rate; RGR – relative growth rate; SS – salt stress; WC – water content.

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Shi and Wang 2005). These reports not only demonstrate the actual existence of AS, but also show that the AS is more severe than the SS (Shi and Yin 1993).

Soil salinization and alkalization frequently co-occur. For example, in northeast China, alkalinized grassland has reached more than 70 % and is expanding (Kawanabe and Zhu 1991). No plants can survive there with the exception of a few alkali resistant halophytes. Alkali resistant halophytes are natural species with high resistance to both SS and AS. Therefore, they are the ideal choice for researching the differences between these stresses.

Photosynthesis, the primary step to energy production in the biosphere, is inhibited by SS (Ma *et al.* 1997), often through affecting photosynthetic enzymes (Sultana *et al.* 1999), chlorophyll (Chl) and carotenoids (Car) (Qiu *et al.* 2003), and chloroplast structure (Fidalgo *et al.* 2004). Photosynthetic characteristics and accumulation of energy and materials under SS have often been studied. Environmental acidic pH significantly affects photosynthesis and photosynthetic electron transport (Gerloff-Elias *et al.* 2005), but to our knowledge, the effects of AS on photosynthetic productivity and energy storage have not been reported.

C. virgata is a natural annual alkali tolerant halophyte species, a grass with high protein content, which makes it a high quality forage plant (Zheng and Li 1999). It grows naturally on heavily alkalized soil over pH 10, and even colonizes bare alkaline patches as a pioneer species to form a single preponderant species halophyte community. This species also maintains the relative stability and productivity of the community (Zheng and Li 1999). Because of *C. virgata*'s two-tier resistances not only to SS but also to AS, it was chosen to study the differences in physiological responses to these two stresses.

C. virgata seeds were collected from the alkalization grassland located in the west of Jilin Province of China (44°40'–44°45' N, 123°44'–123°47' E). The mean annual precipitation of this area is 470 mm. The mean annual evaporation capacity is 1 668 mm. The mean air temperature in summer is 22–24 °C. The full seeds were sown in 17-cm diameter plastic pots (5 plants per pot) containing washed sand. Every day after emergence the seedlings were once sufficiently watered with Hoagland nutrient solution. All pots were placed in the artificial greenhouse (25.0±1.5 °C during the day and 19.0±1.5 °C during the night). Plants grew at uniform irradiance in a greenhouse under photoperiod of 15/9 h (light/dark).

Two neutral salts were mixed in a 1 : 1 molar ratio (NaCl : Na_2SO_4), and applied to the SS group. Two alkaline salts were mixed in a 1 : 1 molar ratio ($NaHCO_3$: Na_2CO_3), and applied to the AS group. Within each group, four total salt concentrations were applied: 40, 80, 120, and 160 mM. Therefore, in the 160 mM solution for SS, a mixture of 80 mM NaCl and 80 mM Na_2SO_4 would result in total ion concentrations of 240 mM Na^++80 mM Cl^-+80 mM SO_4^{2-}. The pH ranges in the SS and AS groups were 6.28–6.65 and 9.93–9.97, respectively.

When the seedlings of *C. virgata* were 4 weeks old, 30 pots with seedlings growing uniformly were selected and randomly divided into 10 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 8 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 17:00–18:00 h with the application of nutrient solutions containing the appropriate salts. All pots were watered thoroughly with 500 cm^3 treatment solution applied in three portions. Control plants were maintained by watering with nutrient solution. To avoid stress shock, stress intensities were increased gradually by 40 mM every day until the desired concentration was reached. After the highest concentration group reached the desired concentration, treatment continued for another 10 d. The entire treatment duration was 14 d.

Net photosynthetic rate (P_N), stomatal conductance (g_s), and transpiration rate (E) of leaves were determined between 08:30 and 10:30 in fully expanded third blades, using a portable open flow gas exchange system *LI-6400* (*LI-COR*, USA). The photosynthetically active radiation (PAR) was 800 µmol m^{-2} s^{-1}. Measurements were repeated five times for each blade, for five blades per pot, and the averages were recorded. After the above measurements, all plants were harvested carefully and were washed, first with tap water and then with distilled water. Water remaining on the surface of the plants was blotted with filter paper. All plants were separated into roots and shoots and their fresh masses (FM) were determined. The leaf area was determined with an area meter (model *1671-VHA*). Colony net photosynthetic rate (P_{NC}), *i.e.* the total P_N of all plants in a pot, was calculated using the formula $P_{NC} = P_N \times$ leaf area.

Aliquots of the fresh plant materials (500 mg) were randomly sampled to determine Chl and Car contents in acetone extracts spectrophotometrically as described by Zhu (1993). Other fresh samples were oven-dried at 105 °C for 15 min, then vacuum-dried at 40 °C to constant mass, and the dry mass (DM) recorded. Water content (WC) was calculated as the difference between dry and fresh masses. Relative growth rates (RGR) were determined as described in Kingsbury *et al.* (1984). Caloric values of shoot and root were determined using a bomb calorimeter (*PARR1281*, USA). The energy storage rate (ESR) was defined as follows: ESR = (total caloric value after treatment – total caloric value before treatment)/duration of treatment [d]. Statistical analyses were performed using the program *SPSS 14.0.*

The RGR of *C. virgata* decreased slightly with increasing salt concentrations under SS (p<0.01), but decreased greatly under AS (p<0.001) (Fig. 1*A*). With increasing SS, the WC of *C. virgata* shoots decreased, and the extent of reduction under AS (p<0.001) was greater than that under SS (p<0.001) (Fig. 1*B*).

The contents of Chl *a* ($p<0.05$), Chl *b* ($p<0.05$), and Car ($p<0.05$) under SS were greater than in control (Table 1). Each parameter initially increased gradually, with increasing stress. However, the contents declined again at 160 mM salt concentration. The Chl *a/b* ratio under SS was lower than that of the control, and decreased with rising stress at first, followed by an increase at >160 mM. Thus the moderate SS enhanced the content of photosynthetic pigments in the leaf of *C. virgata*, increasing the relative amount of Chl *b*. The effect was weakened when the intensity of SS exceeded a certain limit. A similar change was observed under AS. However, the extents of change in Chl contents and Chl *a/b* under moderate AS were obviously less than those observed under moderate SS, and the turning point came at a stress between 80 and 120 mM. The content of Car was scarcely changed by alkali-stress ($p>0.9$) except at 120 mM. This response was significantly different from the SS response.

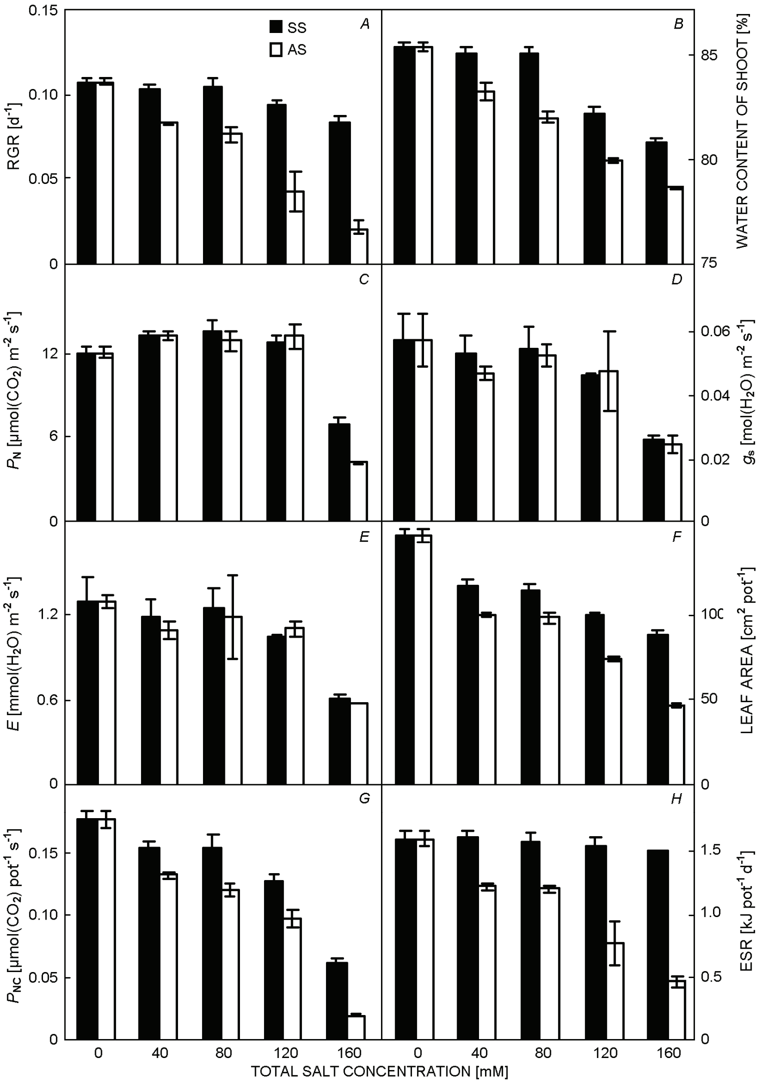

Fig. 1. Effects of salt- (SS) and alkali- (AS) stresses on (*A*) relative growth rate, RGR, (*B*) water content (WC) of shoots, (*C*) net photosynthetic rate (P_N), (*D*) stomatal conductance (g_s), (*E*) transpiration rate (*E*), (*F*) leaf area, (*G*) colony net photosynthetic rate (P_{NC}), and (*H*) energy storage rate (ESR) of *C. virgata.* Four-week-old *C. virgata* seedlings were treated with salt-stress (NaCl : Na_2SO_4 = 1 : 1; pH 6.28–6.65) and alkali-stress ($NaHCO_3$: Na_2CO_3 = 1 : 1; pH 9.93–9.97) for 14 d. Means (±S.E.) of three replications.

The P_N of *C. virgata* increased slightly under moderate SS or AS (below 160 mM), and there was no difference between the two responses (Fig. 1*C*). The P_N declined dramatically at 160 mM, and the extent of reduction, relative to the control, under AS (64 %) was much greater than under SS (42 %). The changes of g_s (Fig. 1*D*, $p>0.45$) and *E* (Fig. 1*E*, $p>0.40$) were small at less than 120 mM with increasing salt concentrations. Only when the stress was greater than 80 mM, g_s ($p<0.05$) and *E* ($p<0.05$) decreased sharply. The effects of SS and AS on g_s and *E* were similar. Leaf areas under SS or AS decreased with increasing stress. However, the decrease under AS ($p<0.001$) was greater than that under SS ($p<0.001$) (Fig. 1*F*).

Photosynthetic ability of plant colony depends on P_{NC}, *i.e.* the P_N of all plants in a colony (a pot in this paper). The P_{NC} index represents the photosynthesis productivity of plants. In agreement with the decrease of leaf area induced by SS and AS, P_{NC} decreased dramatically with rising stress, more under AS ($p<0.001$) than under

SS ($p<0.001$) (Fig. 1*G*). The total caloric value of the incremental biomass per unit of time represents the energy storage rate (ESR). ESR of *C. virgata* under SS decreased only slightly, but that under AS decreased steeply ($p<0.001$) (Fig. 1*H*).

P_{NC} is dependent variable (Y) and stress intensity (viz. total salt concentration) is an independent variable (X), to perform a linear regression analysis of the SS or AS data. The linear regression equations of SS (1) and AS (2) were calculated as follows:

$$\text{SS: Y } (P_{NC}) = -0.0006384\,\text{X} + 0.1854,\ r^2 = 0.8306,\ p<0.05 \qquad (1)$$

$$\text{AS: Y } (P_{NC}) = -0.0008656\,\text{X} + 0.1781,\ r^2 = 0.9094,\ p<0.05 \qquad (2)$$

Using the linear regression equations, we deduced that P_{NC} would decrease by 0.006384 μmol(CO_2) pot^{-1} s^{-1} for every increase of 10 mM stress intensity for SS, and 0.008656 μmol(CO_2) pot^{-1} s^{-1} for AS. Under these experimental conditions, the extent of decrease in P_{NC} caused by AS was about 1.3 times larger than that caused by SS, at a given stress intensity.

The ESR was defined as a dependent variable (Y), and stress intensity as an independent variable (X), to perform a linear regression analysis on the SS or AS data. Both linear regression equations of SS (3) and AS (4) were calculated as follows:

$$\text{SS: Y (ESR)} = -0.0006\,\text{X} + 1.613,\ r^2 = 0.8954,\ p<0.05 \qquad (3)$$

$$\text{AS: Y (ESR)} = -0.0068\,\text{X} + 1.591,\ r^2 = 0.9536,\ p<0.01 \qquad (4)$$

According to the linear regression equations, we deduced that ESR would decrease by 0.006 kJ pot^{-1} d^{-1} for every increase of 10 mM stress for SS, and 0.068 kJ pot^{-1} d^{-1} for AS. Under these experimental conditions, the extent of reduction in the ESR caused by AS was about 11.3 times that caused by SS at a given stress intensity.

An explanation for the different injurious extents of the two stresses might be their different mechanisms of action. The injurious effects of salinity are a result of low water potentials and ion toxicities (Soussi *et al.* 1998, Khan *et al.* 2000, Ghoulam *et al.* 2002, De-Lacerda *et al.* 2003). The AS exerts the same stress factors as SS but with the added influence of high pH stress. The high pH environment surrounding the roots can directly cause decreases in the activity and free concentrations of essential mineral nutrient ions, and cause some, such as Ca^{2+}, Mg^{2+}, HPO_4^{2-}, and $H_2PO_4^-$, 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 trans-membrane electrochemical-potential gradients in root cells, and the loss of normal physiological root functions such as ion absorption. Seriously alkalized environments may also result in destruction of the structure of root cells and, thus, a loss of function. Therefore, for adapting to AS, plants not only need a special mechanism, different from their reaction to SS, but also have to expend more materials and energy than for adapting to SS.

We found that under SS the contents of Chl *a* and *b* and Car increased initially with rising stress intensity, then decreased once the salinity reached 160 mM. Under AS, with the exception of Car which barely changed, the Chl contents also initially increased, then decreased with increasing stress intensity, similarly to the SS response (Table 1). Accumulation of photosynthetic pigments under moderate stress may be an adaptive manner to SS or AS. However, the turning point of change was lower at 80 mM salinity. Thus there might be dual effects, stimulation and inhibition, of SS and AS on the photosynthetic pigments, particularly Chl. At feeble stresses, the stimulation effect might overshadow the inhibition effect but this effect would gradually strengthen with rising stress intensity and finally exceed the stimulation effect. In such a case, because AS is stronger than SS at the same salinity, the salinity at which the inhibition effect exceeded the stimulation effect for AS would be lower than that for SS. This phenomenon not only implies that SS and AS are two distinct kinds of stress, it also reveals that the resistance of *C. virgata* to SS is stronger than that to AS.

We observed that photosynthetic pigment contents under AS were lower than under SS (Table 1), possibly the result of AS causing Mg to precipitate and inhibit Chl synthesis (Shi and Zhao 1997). Alternatively, AS may have increased the activity of the Chl-degrading enzyme chlorophyllase (Reddy and Vora 1986). The non-proportional changes of Chl *a* and Chl *b* under SS and AS were probably not simply due to the change of leaf WC, and may be closely related to the metabolic regulation of Chl. In addition, the effects of the two stresses on Car content were significantly different.

The g_s and E of many plants decreases with increasing SS intensity (Sultana *et al.* 1999, Zheng *et al.* 2002, Koyro *et al.* 2006, Wei *et al.* 2006), but the g_s and E of *C. virgata* decreased only when the stress was greater than 80 mM. The differences of g_s and E between the two stresses were not significant. This demonstrates that the high pH caused by AS did not affect the gas exchange of *C. virgata*. The decrease of g_s and E under both stresses (Fig. 1*D,E*) may be an adaptive response to the decreased WC (Fig. 1*B*) or may be not correlated to WC but rather induced by the physical or chemical signal materials of roots stimulated by salt or alkali (Munns and Termaat 1986, Zheng *et al.* 2002).

P_N of a plant usually decreases with rising stress intensity (Ma *et al.* 1997, Sultana *et al.* 1999, Koyro *et al.* 2006). However, we found that P_N of *C. virgata* did not decrease but increased slightly under moderate SS or AS (below 160 mM; Fig. 1*C*). Only when the intensity of stress was at 160 mM, did the P_N decrease. Within the normal physiological adaptability of *C. virgata* (stress

Table 1. Effects of salt- (SS) and alkali- (AS) stresses on contents of photosynthetic pigments (Chl – chlorophyll, Car – carotenoids) [g kg^{-1}(FM)] in the seedlings of *C. virgata.* Four-week-old *C. virgata* seedlings were treated with salt-stress (NaCl : Na_2SO_4 = 1 : 1; pH 6.28–6.65) and alkali-stress ($NaHCO_3$: Na_2CO_3 = 1 : 1; pH 9.93–9.97) for 14 d. Means (±SE) of three replications.

	[mM]	Chl *a*	Chl *b*	Chl (*a*+*b*)	Chl *a/b*	Car
Control	0	1.38±0.16	0.37±0.05	1.69±0.17	3.71±0.07	0.41±0.01
SS	40	1.78±0.21	0.51±0.07	2.29±0.28	3.52±0.12	0.45±0.06
	80	1.95±0.09	0.58±0.04	2.52±0.12	3.37±0.06	0.55±0.08
	120	2.29±0.07	0.73±0.01	3.03±0.07	3.13±0.11	0.68±0.03
	160	1.94±0.23	0.60±0.09	2.54±0.32	3.27±0.10	0.46±0.07
AS	40	1.37±0.16	0.38±0.05	1.75±0.21	3.59±0.08	0.42±0.08
	80	1.73±0.08	0.48±0.03	2.21±0.10	3.57±0.05	0.42±0.09
	120	1.39±0.19	0.38±0.05	1.77±0.24	3.70±0.04	0.37±0.06
	160	1.22±0.14	0.32±0.03	1.53±0.17	3.84±0.06	0.42±0.09

lower than 160 mM), its RGR decrease was a result of decreasing photosynthetic area, and was basically independent of its P_N. Marcelis and Van-Hooijdonk (1999) also reported that the reduction of plant growth at higher salinities was mainly due to the reduction of photosynthetic area. For a halophyte growing in natural salt-alkali conditions over a long term, photosynthesis tends to stabilize, which suggests that the effects of salt-alkali stress on plant growth are mainly through the reduction of photosynthetic area rather than through a change in P_N. Reduced plant P_N under higher SS is probably a result of the reduction of intracellular CO_2 partial pressure caused by stomatal closure or of 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 *et al.* 2006), ion toxicities in the cytosol (James *et al.* 2006), *etc*. The above-mentioned results showed that the inhibition effect of higher AS on P_N of *C. virgata* was greater than that of SS, the reason for which might be complex and deserving further research.

At salt concentration <160 mM, the effects of both stresses on the P_N of *C. virgata* were similar (Fig. 1*C*). The P_N values under both stresses were all slightly higher than that of control. This phenomenon provides strong evidence that *C. virgata*, as an alkali-resistant halophyte, has a great tolerance to SS and AS. Although the mechanisms of both stresses are different (Shi and Yin 1993), their effects on P_N are similar within the range of physiological adaptability of *C. virgata*. This suggests that a high pH surrounding roots, caused by AS, may be resisted by root cells, and prevented from invading the intracellular environment. Consequentially, the basal physiological functions of *C. virgata*, such as intracellular photosynthesis, were not interfered with by the high pH. We propose that pH adjustment outside of the roots may be a key physiological mechanism by which *C. virgata* resists AS.

Both SS and AS caused a decrease in P_{NC} of *C. virgata* (Fig. 1*G*), the major cause of which was the decrease in photosynthesis productivity (below 160 mM stress). However, under higher stress (160 mM or over), the decrease in P_{NC} of *C. virgata* may be also a result of the destruction of photosynthetic system. The energy storage rate of *C. virgata* was inhibited by SS and AS in a fashion similar to the P_{NC} (Fig. 1*H*). The photosynthetic productivity of plants under stress provides the energy and materials not only for their normal growth and development, but also for their adapting to stress (Flexas *et al.* 2006).

P_{NC} is an index reflecting the photosynthesis productivity of plants. The decrease in photosynthetic productivity of *C. virgata* was greater under AS than under SS, but the difference between both was only 30 %. However, the decrease of energy storage induced by AS was 11.3 times larger than that induced by SS. Thus, energy consumption of *C. virgata* while resisting AS was much greater than it was while resisting SS. Plants under AS need more energy and materials to resist high pH stress than plants under SS. The high energy consumption of plants adapting to AS is the main reason that inhibition effects of AS on plant growth exceed the effects of SS. In terms of photosynthesis productivity and the energy cost of resisting stress, our experimental results support the hypothesis that SS and AS are actually two distinct kinds of stress (Shi and Sheng 2005, Shi and Wang 2005, Yan *et al.* 2005).

References

Bethke, P.C., Drew, M.C.: Stomatal and non-stomatal components to inhibition of photosynthesis in leaves of *Capsicum annuum* during progressive exposure to NaCl salinity. – Plant Physiol. **99**: 219-226, 1992.

Brand, J.D., Tang, C., Rathjen, A.J.: Screening rough-seeded lupins (*Lupinus pilosus* Murr. and *Lupinus atlanticus* Glads.) for tolerance to calcareous soils. – Plant Soil **245**: 261-275, 2002.

Campbell, S.A., Nishio, J.N.: Iron deficiency studies of sugar beet using an improved sodium bicarbonate-buffered hydroponics growth system. – J. Plant Nutr. **23**: 741-757, 2000.

De Lacerda, C.F., Cambraia, J., Oliva, M.A., Ruiz, H.A., Prisco, J.T.: Solute accumulation and distribution during shoot and leaf development in two sorghum genotypes under salt stress. – Environ. exp. bot. **49**: 107-120, 2003.

El-Samad, H.M.A, Shaddad, M.A.K.: Comparative effect of sodium carbonate, sodium sulphate, and sodium chloride on the growth and related metabolic activities of pea plants. – J. Plant Nutr. **19**: 717-728, 1996.

Fidalgo, F., Santos, A., Santos, I., Salema, R.: Effects of long-term salt stress on antioxidant defence systems, leaf water relations and chloroplast ultrastructure of potato plants. – Assoc. appl. Biol. **145**: 185-192, 2004.

Flexas, J., Bota, J, Galmés, J., Medrano, H., Ribas-Carbó, M.: Keeping a positive carbon balance under adverse conditions: responses of photosynthesis and respiration to water stress. – Physiol. Plant. **127**: 343-352, 2006.

Gerloff-Elias, A., Spukerman, E., Proschold, T.: Effect of external pH on the growth, photosynthesis and photosynthetic electron transport of *Chlamydomonas acidophila* Negoro, isolated from an extremely acidic lake (pH 2.6). – Plant Cell Environ. **28**: 1218-1229, 2005.

Ghoulam, C., Foursy, A., Fares, K.: Effects of salt stress on growth, inorganic ions and proline accumulation in relation to osmotic adjustment in five sugar beet cultivars. – Environ. exp. Bot. **47**: 39-50, 2002.

Hartung, W., Leport, L., Ratcliffe, R.G., Sauter, A., Duda, R., Turner, N.C.: Abscisic acid concentration, root pH and anatomy do not explain growth differences of chickpea (*Cicer arietinum* L.) and lupin (*Lupinus angustifolius* L.) on acid and alkaline soils. – Plant Soil **240**: 191-199. 2002.

James, R.A., Munns, R., Caemmerer, S. von, Trejo, C., Miller, C., Condou, T. (A.G.).: Photosynthetic capacity is related to the cellular and subcellular partitioning of Na^+, K^+ and Cl^- in salt-affected barley and durum wheat. – Plant Cell Environ. **29**: 2185-2197, 2006.

Kawanabe, S., Zhu, T.C.: Degeneration and conservation of *Aneurolepidium chinense* grassland in Northern China. – J. jap. Grassland Sci. **37**: 91-99, 1991.

Khan, M.A., Ungar, I.A., Showalter, A.M.: Effects of salinity on growth, water relations and ion accumulation of the subtropical perennial halophyte, *Atriplex griffithii* var. *stocksii*. – Ann. Bot. **85**: 225-232, 2000.

Kingsbury, R.W., Epstein, E., Peary, R.W.: Physiological responses to salinity in selected lines of wheat. – Plant Physiol. **74**: 417-423, 1984.

Koyro, H.-W.: Effect of salinity on growth, photosynthesis, water relations and solute composition of the potential cash crop halophyte *Plantago coronopus* (L.). – Environ. exp. Bot. **56**: 136-146, 2006.

Läuchli, A., Lüttge, U.: Salinity in the soil environment. – In: Tanji, K.K. (ed.): Salinity: Environment-Plants-Molecules. Pp. 21-23. Kluwer Academic Publ., Boston 2002.

Ma, H.-C., Fung, L., Wang, S.-S., Altman, A., Hüttermann, A.: Photosynthetic response of *Populus euphratica* to salt stress. – Forest Ecol. Manage. **93**: 55-61, 1997.

Marcelis, L.F.M., van Hooijdonk, J.: Effect of salinity on growth, water use and nutrient use in radish (*Raphanus sativus* L.). – Plant Soil **215**: 57-64, 1999.

Munns, R., Termaat, A.: Whole-plant response to salinity. – Aust. J. Plant Physiol. **13**: 143-160, 1986.

Nuttall, G., Armstrong, R.D., Connor, D.J.: Evaluating physicochemical constraints of Calcarosols on wheat yield in the Victorian southern Mallee. – Aust. J. agr. Res. **54**: 487-497, 2003.

Qiu, N., Lu, Q., Lu, C.: Photosynthesis, photosystem II efficiency and the xanthophyll cycle in the salt-adapted halophyte *Atriplex centralasiatica*. – New Phytol. **159**: 479-486, 2003.

Reddy, M.P., Vora, A.B.: Changes in pigment composition, Hill reaction activity and saccharides metabolism in bajra (*Pennisetum typhoides* S & H) leaves under NaCl salinity. – Photosynthetica **20**: 50-55, 1986.

Shi, D., Sheng, Y.: Effect of various salt-alkaline mixed stress conditions on sunflower seedlings and analysis of their stress factors. – Environ. exp. Bot. **54**: 8-21, 2005.

Shi, D., Wang, D.: Effects of various salt-alkali mixed stresses on *Aneurolepidium chinense* (Trin.) Kitag. – Plant Soil **271**: 15-26, 2005.

Shi, D.C., Yin, L.J.: Difference between salt (NaCl) and alkaline (Na_2CO_3) stresses on *Puccinellia tenuiflora* (Griseb.) Scribn *et* Merr. plants. – Acta bot. sin. **35**: 144-149, 1993.

Shi, D.C., Yin, L.J.: Strain responses in Na_2CO_3-stressed *Leymus chinensis* seedlings and their mathematical analysis. – Acta bot. sin. **34**: 386-393, 1992.

Shi, D.C., Zhao, K.F.: Effects of NaCl and Na_2CO_3 on growth of *Puccinellia tenuiflora* and on present state of mineral elements in nutrient solution. – Acta pratacu. sin. **6**(2): 51-61, 1997.

Soussi, M., Ocaña, A., Lluch, C.: Effects of salt stress on growth, photosynthesis and nitrogen fixation in chick-pea (*Cicer arietinum* L.). – J. exp. Bot. **49**: 1329-1337, 1998.

Sultana, N., Ikeda, T., Itoh, R.: Effect of NaCl salinity on photosynthesis and dry matter accumulation in developing rice grains. – Environ. exp. Bot. **42**: 211-220, 1999.

Wei, Y., Xu, X.., Tao, H., Wang, P.: Growth performance and physiological response in the halophyte *Lycium barbarum* grown at salt-affected soil. – Ann. appl. Biol. **149**: 63-269, 2006.

Yan, H., Zhao, W., Sheng, Y.M., Shi, D.C., Zhou, D.W.: Effects of alkali-stress on *Aneurolepidium chinense* and *Helianthus annuus*. – Chin. J. appl. Ecol. **16**: 1497-1501, 2005.

Zheng, G.Q., Xu, X., Xu, Y.Z., Liu, Z.L.: The effect of salt stress on the stomatal and non-stomatal limitation of photosynthesis of *Lycium barbarum*. – Acta bot. boreal-occident sin. **22**: 1355-1359, 2002.

Zheng, H.Y., Li, J.D.: Form and dynamic trait of halophyte community. – In: Zheng, H.Y., Li, J.D. (ed.): Saline Plants in Songnen Plain and Restoration of Alkaline-Saline Grass. Pp. 137-138. Science Press, Beijing 1999.

Zhu, G.L.: Carotenoid and chlorophyll determination. – In: Zhu, G.L. (ed.): Laboratory Manual of Plant Physiology. Pp. 51-54. Beijing University Press, Beijing 1993.