

NaCl salinity-induced changes in water status, ion contents and photosynthetic properties of *Shepherdia argentea* (Pursh) Nutt. seedlings

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ABSTRACT

Two-year old seedlings of Silver buffaloberry (*Shepherdia argentea* (Pursh) Nutt.) were exposed to NaCl salinity (0, 200, 400 and 600 mmol/l) for 30 days. Leaf water potential (Ψ_w), chlorophyll contents (Chl a, b, and a + b) and K⁺ content decreased with an increase in salinity. Relative water content (RWC) declined significantly with 400 and 600 mmol/l NaCl. However, salinity induced an excessive accumulation of Na⁺ in the leaves of plants. Light responses of photosynthesis showed that net photosynthetic rate (P_N) values were continuously raised with the increase of photosynthetic photon flux density (PPFD) at all salinity levels and plants treated with 600 mmol/l salinity suffered from photoinhibition with the lowest P_N values. The reduction of P_N and stomatal conductance (g_s) associated with a sharp increase of intercellular CO₂ concentration (C_i) in the leaves at 600 mmol/l salt-treated plants showed that non-stomatal limitations might have prevailed over stomatal limitations under severe saline conditions, due to severe cellular dehydration, inhibited synthesis of chlorophyll and ionic imbalance and toxicity. It is concluded that *S. argentea* possesses high salt tolerance capacity and can be widely cultivated in salt-affected areas.

Keywords: leaf water potential; ion accumulation; chlorophyll contents; net photosynthetic rate; non-stomatal limitations; salinity

High salinity is the most widespread abiotic stress and constitutes the most stringent factor in limiting plant distribution and productivity (Iqbal and Ashraf 2005, Yildirim et al. 2009). The main negative effects of high salinity that influence plant growth and development are photosynthesis inhibition (Sharma et al. 2005), water deficit (Suárez and Medina 2008), ion toxicity associated with excessive Cl⁻ and Na⁺ (Afzal et al. 2008, Patel and Pandey 2008), interference with nutrition leading to nutrient imbalance (Misra et al. 1997). Bastías et al. (2004) have reported that high concentrations of salt disrupt homeostasis in

water relations and change the ion distribution at both cellular and whole plant levels. Later, altered water homeostasis leads to molecular damage, growth arrest and even death. The reduction in growth under saline conditions is a consequence of several physiological responses and photosynthesis is thought to be the most important process (Stępień and Kłbus 2006). Salinity-induced limitation of photosynthesis under salinity is not only attributed to stomatal closure leading to a reduction of intercellular CO₂ concentration (C_i), but also to non-stomatal factors. There are increasing evidences that salt affects photosynthetic

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enzymes, chlorophylls and carotenoids (Misra et al. 1997, Youssef and Awad 2008). It has also been observed by Biswal et al. (2002) that NaCl salinity affects photosystem 2 (PS 2) photochemical efficiency, charge separation of primary charge pairs in PSII and pigment-protein complexes of thylakoid membranes. However, plants seem to lack unique mechanism of resistance to salt stress and, despite an increasing number of studies, the data concerning effects of salt stress on photosynthesis are still fragmentary.

Utilization of salt-tolerant plants is expected to be an effective method to improve saline soil. Hence, better understanding of the mechanisms that enable plants to adapt to salt stress is necessary for exploiting saline soil (Patel and Pandey 2008). Silver buffaloberry (*Shepherdia argentea* (Pursh) Nutt.) is considered to be able to bear cold, drought, leanness and salinity (Geng and Wang 2007, Qin et al. 2009a). It was introduced from America to China in 2002 and has been successfully planted in large scale in China's Loess Plateau and coastal area. Drought stress studies conducted by Geng and Wang (2007) showed that the soil-water compensation point for hydration of *S. argentea* was 4.4% and the optimum soil moisture to maintain the maximum net photosynthetic rate (P_N) was 18.5% with the highest water use efficiency (WUE) compared to *Zygophyllum xanthoxylum* and *Atraphaxis mandshurica*. Qin et al. (2009a) has analyzed the comparison of physiology responses to salt stress in *S. argentea* and *Hippophae rhamnoides*, as a native tree species widely distributed in the northwest of China. It has been reported that *S. argentea* possesses higher salt tolerance than *H. rhamnoides* and can bear the stress of 600 mmol/l NaCl for above 30 days. Nevertheless, studies on the tolerance of *S. argentea* to salt stress are still incomplete and preliminary. In the present study, to understand the adaptive features of *S. argentea* that allow it to grow and survive in saline regions, we analyzed changes of leaf water potential, relative water content, ion and chlorophyll contents and photosynthesis in *S. argentea* in four salinity treatments.

MATERIAL AND METHODS

Experimental design. *S. argentea* seedlings were obtained from the experimental base (latitude 36°39'N, longitude 101°46'E and altitude 2309 m) of Research Institute of Forestry, Qinghai Academy of Agriculture and Forestry, China. In April 2007,

the seedlings of *S. argentea* were planted in plastic pots (one per pot), filled with 11 kg native chernozem soil and irrigated every three days, in order to maintain soil water at field capacity. In July 2008, the experiment was carried out for 30 days under native condition in the open air. Twenty two-year old seedlings, uniform in size, were subjected to salt stress by adding NaCl solutions of four concentrations: 0 (control), 200, 400 and 600 mmol/l, with the calculated amount of NaCl dissolved in water. The final salt concentration was progressively adjusted with increasing NaCl solutions (50 mmol/l per day). At the same time, the plants were irrigated with fresh water every three days to maintain soil water at field capacity and avoid drought stress. Five replicates of each treatment were used to measure leaf water status, ion accumulation and chlorophyll contents of *S. argentea* at the end of the experiment before harvest, while three replicates were used to measure leaf photosynthetic parameters at 25 days after the salt treatments.

Leaf water status. Predawn leaf water potential (Ψ_w) was measured on medial leaves of each plant, using HR-33T Dew Point Mikrovolt-meter (Wescor Inc., Logan, UT, USA). Relative water content (RWC) was determined on medial leaves of each plant and calculated from the equation: $RWC (\%) = 100 \times (FW - DW) / (TW - DW)$, where FW, DW, and TW denote leaf fresh, dry or turgid weight, respectively (Yildirim et al. 2009).

Ion contents. The contents of Na^+ and K^+ in leaves were determined from dry matter and were quantified by an inductively coupled plasma optical emission spectrometry (ICP-OES, Leeman Labs Inc., NH, USA) after nitric-perchloric acid (1%) digestion (Bastías et al. 2004).

Chlorophyll contents. Chlorophyll (Chl) was extracted from dry leaves after harvest at the end of experiment with 80% acetone and absorbance values were determined on a spectrophotometer (SP-756, Beijing, China) at 663 and 645 nm, respectively. Chl a, Chl b and total Chl (Chl a + b) contents were calculated as described by Arnon (1949).

Photosynthetic parameters. Measurements of net photosynthetic rate (P_N), stomatal conductance (g_s), transpiration rate (E) and intercellular CO_2 concentration (C_i) were carried out on the third fully expanded leaf (from top) of each plant (3 plants for each treatment), using a Li-6400 portable photosynthesis system (Li-Cor Inc., Lincoln, NE, USA). The photosynthetic photon flux density (PPFD) sequence for generating light response curves was set as 0, 50, 100, 150, 200, 400, 600, 800, 1000, 1200, 1500, 1800, 2000, 2200 and

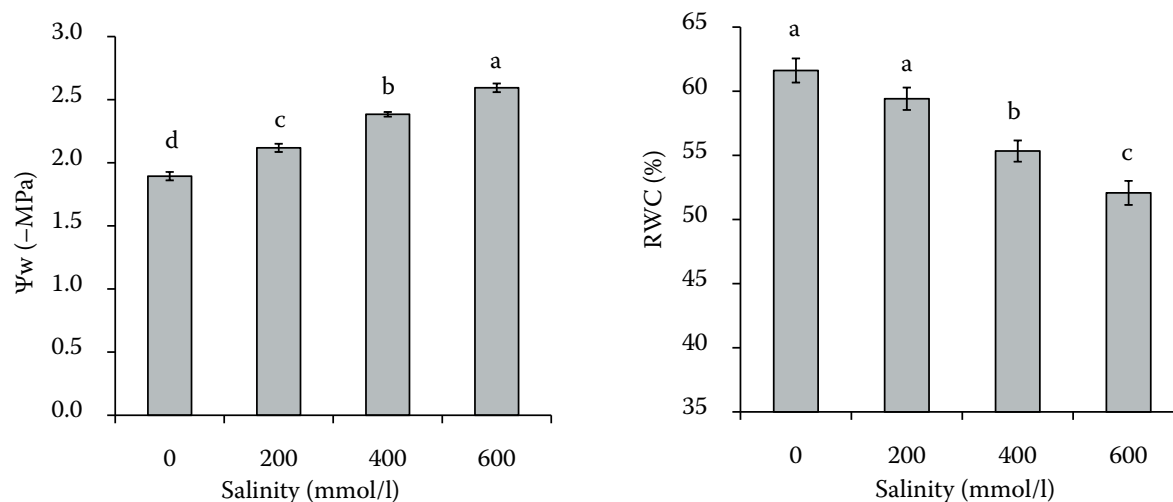


Figure 1. Effects of salt stress on leaf water potential (Ψ_w) and relative water content (RWC) in leaves of *S. argentea* seedlings. Values are means of five replicates \pm SE. Bars with different letters are significantly different at $P < 0.05$ level, as determined by DMRT

2500 $\mu\text{mol/mol}$ with the LI-6400-02B LED light source (Qin et al. 2009b). The maximum P_N ($P_{N_{\max}}$), light saturation point (LSP), light compensate point (LCP) and apparent quantum yield (AQY) were calculated from the regression equation of light response curves. All measurements were made between 9:00–11:00 a.m. in the native environment, with the following specifications and adjustments: ambient CO_2 concentration 385.7 ± 4.4 $\mu\text{mol/mol}$, air temperature $22.7 \pm 1.9^\circ\text{C}$ and relative humidity $39.4 \pm 4.3\%$.

Statistical analysis. One way analysis of variance (ANOVA) at a significance level $P < 0.05$ was

performed using the SPSS software (version 15.0). Duncan's Multiple Range Test (DMRT) was used when significant differences were found among salt treatments. Relationships between PPFD and P_N were examined with linear regression models.

RESULTS

Salinity effects on leaf water status. There was a marked and progressive decline in leaf water potential (Ψ_w) in leaves of seedlings with increasing salinity (Figure 1). The decrements of

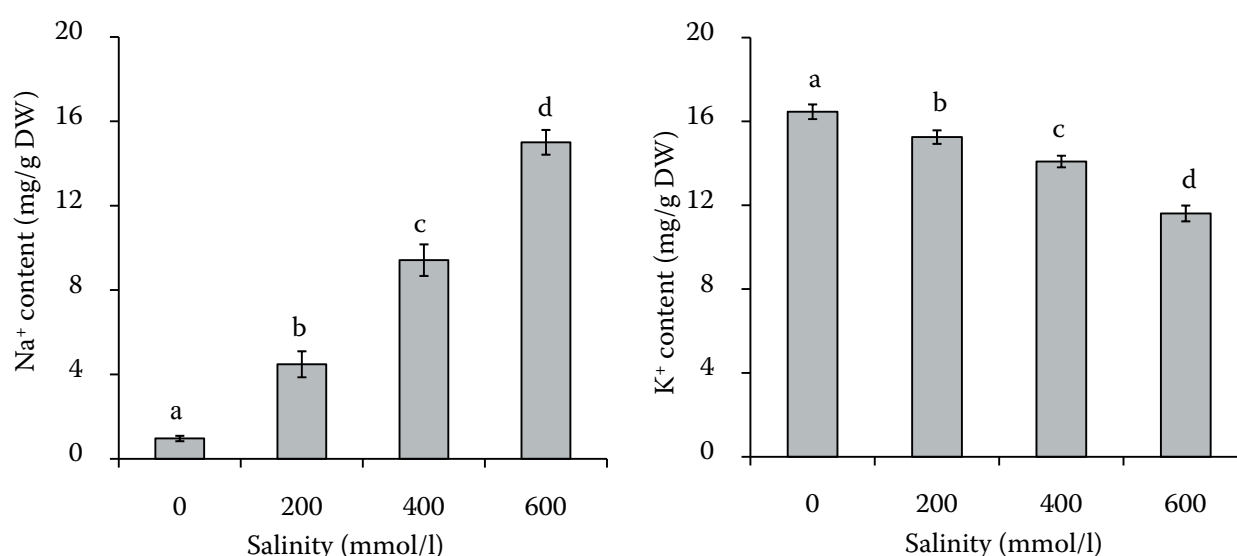


Figure 2. Effects of salt stress on Na^+ and K^+ contents in leaves of *S. argentea* seedlings. Values are means of five replicates \pm SE. Bars with different letters are significantly different at $P < 0.05$ level, as determined by DMRT

Table 1. Salinity effects on chlorophyll a (Chl a), chlorophyll b (Chl b) and total chlorophyll (Chl a + b) contents in leaves of *S. argentea* seedlings

Salinity (mmol/l)	Chl a	Chl b (mg/g DW)	Chl a + b	Chl a/b
0	2.25 ± 0.06 ^a	0.43 ± 0.01 ^a	2.68 ± 0.06 ^a	5.17 ± 0.07 ^a
200	2.04 ± 0.05 ^b	0.41 ± 0.01 ^{ab}	2.46 ± 0.05 ^b	4.93 ± 0.12 ^a
400	1.72 ± 0.07 ^c	0.38 ± 0.03 ^{bc}	2.10 ± 0.10 ^c	4.62 ± 0.28 ^a
600	1.37 ± 0.04 ^d	0.35 ± 0.01 ^c	1.72 ± 0.04 ^d	3.93 ± 0.25 ^b

Values are means of five replicates ± SE. Different letters in the same column are significantly different at $P < 0.05$ level, as determined by DMRT

Ψ_w were 11.8%, 24.9% and 37.0% at 200, 400 and 600 mmol/l, respectively, when compared with the control. Salinity also significantly reduced RWC in leaves of plants treated with 400 and 600 mmol/l (Figure 1). The decrement of RWC in 400 mmol/l salt-treated plants was 10.2%, and that in 600 mmol/l salt-treated plants was 15.5%.

Salinity effects on ion contents. Saline conditions significantly altered the tissue concentration of Na^+ and K^+ (Figure 2). Na^+ content in the leaves of plants sharply increased with increasing salinity and was 4.6, 9.8 and 15.6 times higher than the control at 200, 400 and 600 mmol/l salt treatments, respectively. In contrast, K^+ content was significantly decreased with the increase of salinity (Figure 2) and had a lower changing range than Na^+ (only decreased by 7.3%, 14.4% and 29.5% of the control).

Salinity effects on chlorophyll contents. A continuous and significant decrease in Chl a, Chl b and Chl a + b contents in leaves of *S. argentea* seedlings due to salt stress was detected (Table 1). The rate of decrease in these parameters was greater at the higher salinity. Compared with the controls, Chl a content declined by 9.0%, 23.4% and 39.2%, Chl b content declined by 4.5%, 12.9% and 19.2%, and Chl a + b content was reduced by 8.3%, 21.7% and 35.9%, at 200, 400 and 600 mmol/l NaCl concentrations, respectively. Chl b was less sensitive or better protected against salt stress than Chl a under the same salinity level, which resulted in the drop in the Chl a/b ratio, especially for 600 mmol/l salt-treated plants (75.9% of the controls; Table 1).

Salinity effects on photosynthetic properties. Net photosynthetic rate (P_N) values were continuously raised with the increase of photosynthetic photon flux density (PPFD) at all salinity levels; however, there was a significant difference in the in-

crease amplitude of P_N values under different NaCl concentrations (Figure 3). P_N values of plants grown under non-saline conditions were the highest and did not decline when PPFD exceeded 2500 $\mu\text{mol/mol}$, whereas those of 200 and 400 mmol/l salt-treated plants were relatively low and maintained constant above 2000 $\mu\text{mol/mol}$ PPFD. However, plants treated with 600 mmol/l salinity seriously suffered from photoinhibition and had the lowest P_N values compared to others. The changes of stomatal conductance (g_s) and transpiration rate (E) in the leaves of *S. argentea* seedlings subjected to varying salinity had the same tendency as P_N under different PPFD (Figure 3). Non-obvious difference in intercellular CO_2 concentration (C_i) values in the plants were observed when salinity was below 400 mmol/l, whereas C_i values in 600 mmol/l salt-treated plants was significantly higher when PPFD exceeded 1000 $\mu\text{mol/mol}$ (Figure 3).

To analyze the effects of NaCl salinity on the maximum P_N ($P_{N_{\max}}$), light saturation point (LSP) and apparent quantum yield (AQY), regression of light response curves and the initial slope of the curves between P_N and PPFD were made (Figure 4, Table 2). Compared with the control, $P_{N_{\max}}$ was decreased by 29.2%, 43.7% and 87.1%, and AQY decreased by 9.8%, 26.8% and 82.9% at 200, 400 and 600 mmol/l NaCl concentrations, respectively (Table 2). Salinity also reduced LSP values to a certain extent but there was no obvious difference among saline conditions (Table 2).

DISCUSSION

Water status is the main factor affecting the plants' growth and development. Decreasing external water potential produces a net accumulation of solutes in cells, which lowers the cell osmotic potential neces-

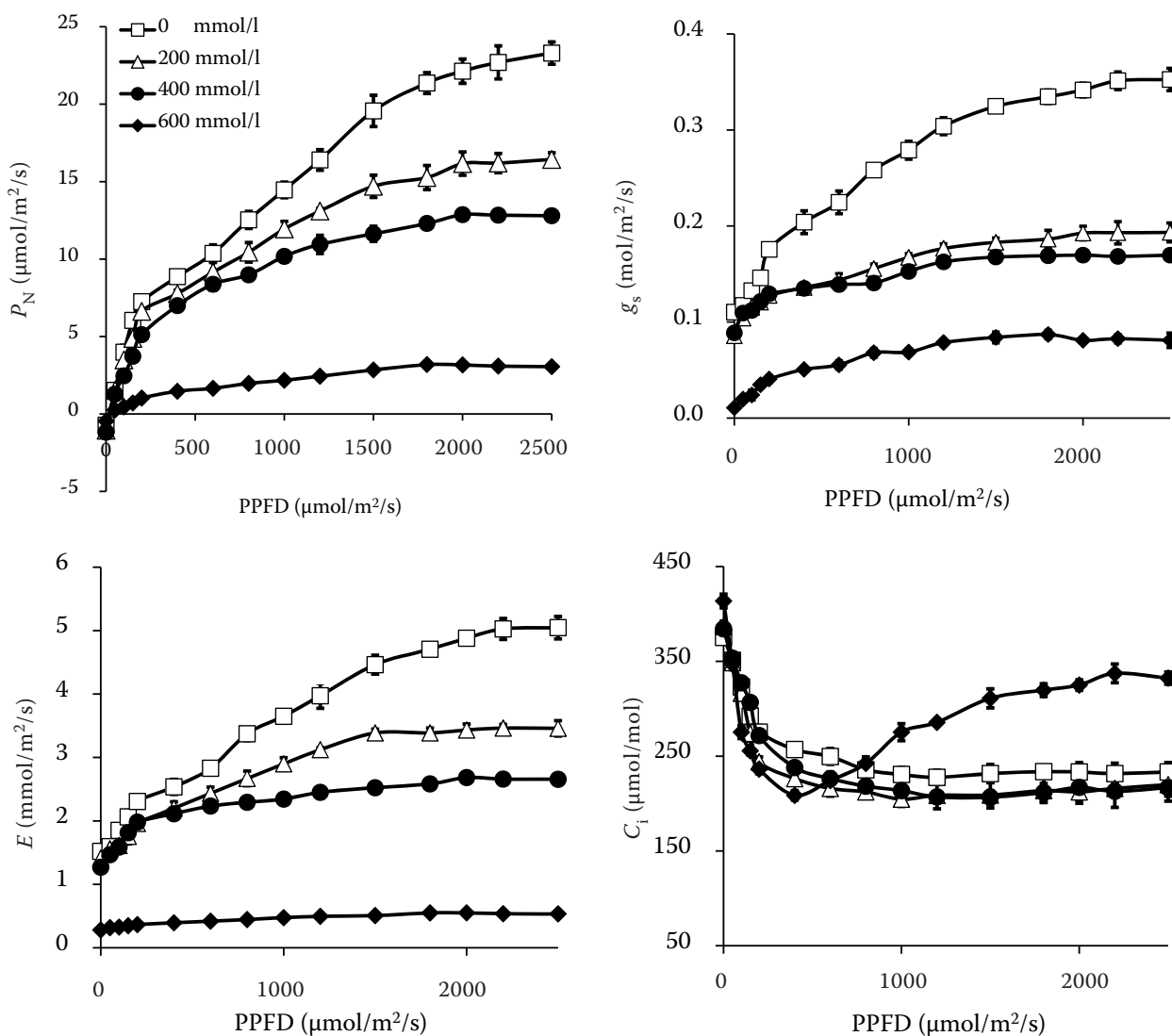


Figure 3. Light responses of net photosynthetic rate (P_N), stomatal conductance (g_s), transpiration rate (E) and intercellular CO_2 concentration (C_i) in the leaves of *S. argentea* seedlings grown under different NaCl concentrations. Values are means of three replicates \pm SE and SE is not shown when smaller than symbol

sary for maintaining the turgor pressure (Navarro et al. 2003). Through the analysis of water relations in the leaves of *S. argentea*, we observed that plants adjusted their Ψ_w to more negative levels as salinity increased (Figure 1), which is a common reaction to salinity similar to those reported for other species (Navarro et al. 2003, Suárez and Medina 2008). Significant reduction of RWC in leaves of plants treated with 400 and 600 mmol/l (Figure 1) indicated that salinity also resulted in dehydration at cellular level and dehydration symptoms were greater in higher NaCl concentration treatment because of the increasing cellular water loss.

Ion uptake is the cheapest form of osmotic adjustment under soil saline conditions, but it could also lead to problems of decline in leaf function and ionic imbalance and toxicity (Bastías et al.

2004, Yildirim et al. 2009). In particular, salinity alters uptake and absorption rates of all mineral nutrients resulting in deficiency symptoms. Bonilla et al. (2004) found that most toxic effects of NaCl can be attributed to Na^+ toxicity. Excessive accumulation of Na^+ can cause a range of osmotic and metabolic problems for plants (Hoai et al. 2003). In the present study, Na^+ content in the leaves of plants was 4.6, 9.8 and 15.6 times of the controls at 200, 400 and 600 mmol/l, respectively (Figure 2), which indicated that *S. argentea* seedlings had no efficient capacity to restrict sodium movement to the photosynthetic parts of the plant. Potassium is a major plant macro-nutrient that plays important roles related to stomatal behavior, osmoregulation, enzyme activity, cell expansion, neutralization of non-diffusible negatively charged

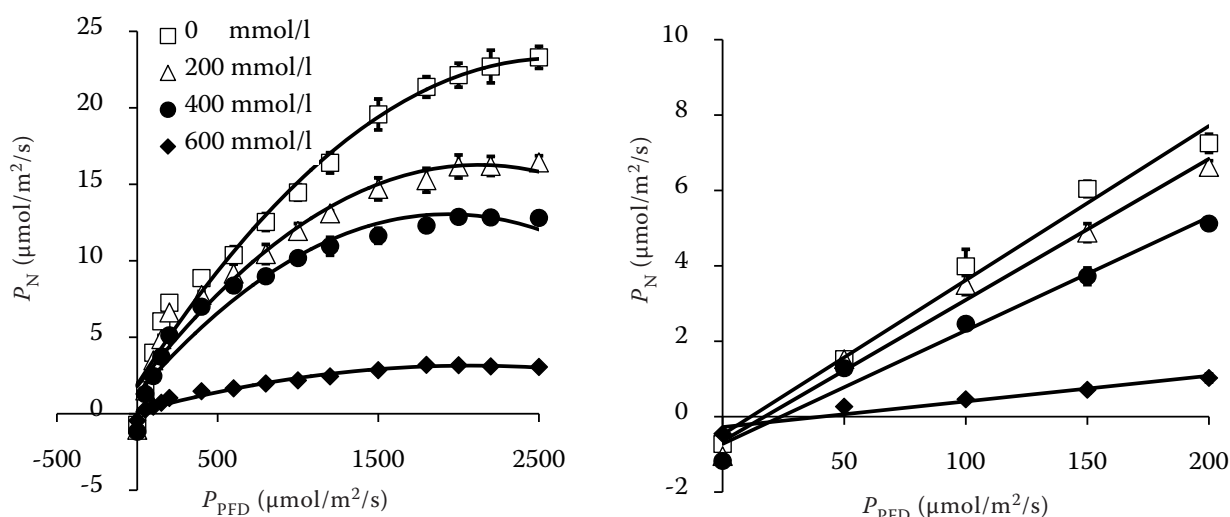


Figure 4. Relationship between photosynthetic photon flux density (P_{PFD}) and net photosynthetic rate (P_{N}) in the leaves of *S. argentea* seedlings grown under different NaCl concentrations. The expressions of $y = ax^2 + bx + c$ for light response curves is shown in Table 4

ions and membrane polarization. Moreover, it is known that toxic effects of Na^+ are largely due to its ability to compete with K^+ for binding site essential for cellular function (Yildirim et al. 2009). We found that the salt treatments decreased K^+ content with increasing NaCl level (Figure 2). However, our results might disagree with the view of Blumwald et al. (2000) that many K^+ transport systems have significant affinity for Na^+ and thus reduction in K^+ uptake is mainly caused by Na^+ , since the decrement of K^+ content was much lower when Na^+ content sharply increased with varying salinity (Figure 2).

Concentrations of chlorophyll components of the photosynthetic apparatus are normally used to quantify leaf senescence in salt-stressed plants. Most studies show that salinity adversely affects Chl content (Meloni et al. 2003). The observed

decrease in Chl contents in the leaves of *S. argentea* seedlings grown under saline conditions (Table 1) may be attributed to both an inhibited synthesis of that pigment and damaged PS antenna system (Youssef and Awad 2008). The higher Chl a/b ratio in 600 mmol/l salt-treated plants compared to that in other treatments obtained in this study (Table 1) indicates that the ratio of PS 2/PS 1 content was changed in stressed leaves under severe salinity level (Stępień and Kłbus 2006).

Photosynthesis is often reduced by salt stress, irrespective of the type of salts used (Misra et al. 1997). In the present study, when compared to the control, P_{N} values of 200 and 400 mmol/l salt-treated plants were relatively low, whereas plants treated with 600 mmol/l salinity seriously suffered from photoinhibition and had the lowest P_{N} values (Figure 3). In addition, $P_{\text{N max}}$ and AQY declined

Table 2. Effects of salt stress on the maximum P_{N} ($P_{\text{N max}}$), light saturation point (LSP) and apparent quantum yield (AQY) in the leaves of *S. argentea* seedlings as determined by regression equation: $y = P_{\text{N}}$, $x = P_{\text{PFD}}$

Salinity (mmol/l)	Regression equation	R^2	$P_{\text{N max}}$	LSP	AQY
			(μmol/m ² /s)		
0	$y = -3 \times 10^{-6} x^2 + 0.0164x + 1.9052^{**}$	0.98	24.32	2733	0.041
200	$y = -3 \times 10^{-6} x^2 + 0.0136x + 1.7962^{**}$	0.961	17.21	2267	0.037
400	$y = -3 \times 10^{-6} x^2 + 0.0122x + 1.2849^{**}$	0.955	13.69	2033	0.03
600	$y = -7 \times 10^{-7} x^2 + 0.0029x + 0.1285^{**}$	0.968	3.13	2071	0.007

**indicate extremely significant difference in the regression equation at $P < 0.01$ level

progressively with the increase of salinity (Table 2, Figure 4), especially in 600 mmol/l salinity level (only 12.9% and 17.1% of the control, respectively). Meanwhile, LSP values were also reduced to a certain extent under saline conditions (Table 2). Our results are in agreement with the findings of Krauss and Allen (2003), suggesting that salinity negatively affects the efficiency of solar energy utilization in *S. argentea* seedlings. The close relationship between P_N and Na^+ concentration in leaf tissue was reported by Iqbal and Ashraf (2005), indicating that P_N was affected by Na^+ in the leaf mesophyll. Salinity-induced excessive accumulation of Na^+ in the leaves of plants which was also obtained in the present study (Figure 2); it is in agreement with the opinion that high accumulation of Na^+ in the cytoplasm or chloroplast can affect the integrity and function of photosynthetic membranes, when the vacuole can no longer sequester toxic ions (Bastías et al. 2004). Moreover, the reduced photosynthesis at high salinity could be also attributed, in part, to the reduced content of K^+ (Figure 2) which is indispensable in maintaining the steady-state photosynthetic rate and contributes to better regulation of stomata opening (Stępień and Kłbus 2006).

Stomatal closure is well known to be an effective mechanism for economical water utilization under salinity and limitation of the harmful salt ions uptake (Hasegawa et al. 2000). However, the decrease in g_s also caused a simultaneous decrease in both P_N and E (Figure 3). According to our study, the changes of g_s and E in the leaves of *S. argentea* seedlings subjected to varying salinity had the same tendency as P_N under different PPFD. On the contrary, C_i values in 600 mmol/l salt-treated plants were significantly higher than those in other treatments when PPFD exceeded 1000 $\mu\text{mol/mol}$ (Figure 3). The high salinity-induced increase of C_i values was also observed by Yang et al. (2006) and supported the hypothesis that the inhibition of photosynthesis caused by salt accumulation in the mesophyll produces an increase in C_i , which reduces the stomatal aperture (Mansfield et al. 1990). It was reported that both stomatal and non-stomatal limitations account for a reduction of photosynthesis (Farquhar and Sharkey 1982). According to our results, the great reduction of P_N and g_s associated with a sharp increase of C_i in the leaves of *S. argentea* seedlings subjected to 600 mmol/l concentration showed that non-stomatal limitations (chloroplast capacity to fix CO_2) at the biochemical level might have prevailed over stomatal or mesophyll limitations under se-

vere saline conditions, which was mainly due to serious cellular dehydration, inhibited synthesis of chlorophyll and ionic imbalance and toxicity. Thus, we can conclude that *S. argentea* introduced from abroad possesses high salt tolerance capacity which can help to adapt to moderate salinity levels (200 and 400 mmol/l NaCl), and can be widely cultivated in salt-affected areas.

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