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Effects of salt stress on growth, photosynthesis and solute accumulation in three poplar cultivars

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Abstract

This study compared the effects of salt (NaCl) stress on growth, photosynthesis and solute accumulation in seedlings of the three poplar (*Populus bonatii*) cultivars *Populus* × BaiLin-2 (BL-2), *Populus* × BaiLin-3 (BL-3), and *Populus* × Xjiajiali (XJJL). The results showed that BL-2 and BL-3 could not survive at a salinity level of 200 mM but XJJL grew well. The effect of moderate salt stress on leaf extension of the three cultivars was only slight. At a high level of salinity, however, NaCl clearly inhibited leaf extension of BL-2 and BL-3, whereas it did not affect that of XJJL, and the net photosynthetic rate (P_N) in XJJL was much higher than those of BL-2 and BL-3. The lower P_N of BL-2 and BL-3 might be associated with the high concentration of Na^+ and/or Cl^- accumulated in the leaves, which could be toxic in photosynthesis system. In summary, the greater salt-tolerance of XJJL compared with that of BL-2 and BL-3 might be explained by the higher P_N and photosynthetic area, the lower Na^+/K^- ratio and Cl^- in the leaf, and the greater accumulation of soluble sugars and SO_4^{2-}.

Key words: growth; photosynthesis; poplar; salt stress; solute accumulation.

Introduction

The salinization of soil is a widespread environmental problem and an important factor in limiting agricultural productivity (Läuchli and Lüttge 2002). In northeast China, alkalinized grassland covers more than 70 % of the land area, and is still expanding (Kawanabe and Zhu 1991, Zheng and Li 1999). Overgrazing and destruction of the ground vegetation are the main reasons for the expansion of the area of salinized land. Thus, it is very important to increase the vegetation productivity and improve plant biodiversity within those areas in order to control the salinization/alkalization and to repair the damaged ecosystem. Salinization is a severe problem in China that limits the establishment and production of forests, which can have a significant role in stabilizing such damaged systems (Ma *et al.* 1997). Therefore, it is necessary to assess the salt tolerance of any trees to be used for large-scale afforestation and the recovery of damaged ecosystems. *Populus* × BaiLin-2 (BL-2), *Populus* × BaiLin-3 (BL-3), and *Populus* × Xjiajiali (XJJL), three poplar (*Populus bonatii*) cultivars distributed in the saline lands of northeast China, are salt- and drought-resistant. The timber can be used in house construction, for the production of charcoal and agricultural facilities. In this study, we compared the effects of salt stress on the growth, photosynthesis and solute accumulation of these three poplar cultivars, to provide a reference for the cultivation of salt-tolerant trees.

Materials and methods

Plants: Three poplar (*Populus bonatii*) cultivars, *Populus* × BaiLin-2 (BL-2), *Populus* × BaiLin-3 (BL-3) and *Populus* × Xjiajiali' (XJJL), were chosen for this research. The cultivars were all bred by the Baicheng Institute of Agricultural Sciences, China. BL-2 was bred from the female parent *Populus* × *nigra* and the male

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Abbreviations: ALA – average leaf area; BL-2 − *Populus* × BaiLin-2; BL-3 − *Populus* × BaiLin-3; C_i − intercellular CO_2 concentration; DM − dry mass; E − transpiration rate; FM − fresh mass; g_s − stomatal conductance; LA – leaf area; L_N – number of leaves; P_N − net photosynthetic rate; SS − soluble sugar; TLA – total leaf area; WUE – water use efficiency; XJJL− *Populus* × Xjiajiali.

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parent *Populus* × *pyramidalis*. BL-3 was bred from the female parent *Populus* × *simonii* and the male parent *Populus* × *nigra*. XJJL was obtained by graft of *Populus* × *canada* onto *Populus* × *siberia*. For each cultivar, a total of 108 seedlings, 6/pot, were grown outdoors in plastic pots (30 cm diameter) containing a 2:1 (w/w) mixture of sand and soil). Water lost by evaporation was replaced daily with distilled water.

Stress treatment: The seedlings were subjected to salt stress when they were 2 weeks old. The 18 pots of uniformly growing seedlings were divided randomly into 6 sets of 3 pots for each cultivar. Each pot was considered a single replicate and each set contained 3 replicates. One set was used as an untreated control and the remaining 5 sets were treated with NaCl at various concentrations (40, 80, 120, 160 and 200 mM). Stress treatments were applied at 17:00–18:00 h with nutrient solutions containing the appropriate concentration of NaCl every 7 days. Water lost by evaporation was replaced with distilled water at other times. The duration of the treatment was 21 days.

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 at 08:30–10:30 h on fully expanded leaves, using a portable open-flow, gas-exchange system (*LI-6400; LI-COR Biosciences*, Lincoln, USA). The PAR was 1200 μmol m^{-2} s^{-1} (*i.e.* saturation). The ambient CO_2 concentration was set at 360 μmol mol^{-1}. The water use efficiency (WUE) was calculated as the ratio P_N/E. The leaf area (LA) was determined with an area meter (*1671-VHA*; Burwell, Cambridge). The average leaf area (ALA) was calculated using the formula:

$$\text{ALA} = \text{TLA} / N_L \text{ cm}^2 \text{ leaf}^{-1}$$

where TLA is total leaf area and N_L is leaf number. All plants were harvested in the morning after the final treatment. The plants were washed first with tap water and then with distilled water. The fresh mass (FM) was determined for each plant. The plant samples were air-dried at 80 °C for 15 min, then dried *in vacuo* at 40 °C to constant weight to measure the dry mass (DM).

Samples (100 mg) of the dried plant leaves were treated with 20 ml of deionized water at 100 °C for 2 h, and the extract was used to determine the content of free inorganic ions. NO_3^-, Cl^- and SO_4^{2-} were determined by ion chromatography (*DX-300* ion chromatographic system; *AS4A-SC* ion-exchange column; *CD M-II* electrical conductivity detector; mobile phase $Na_2CO_3/NaHCO_3$ = 1.7 mM/1.8 mM; *DIONEX*, Sunnyvale, USA). Na^+ and K^+ contents were determined by atomic absorption spectroscopy (*TAS-990, Purkinje General*, Beijing, China). Proline and total soluble sugars were measured using ninhydrin and anthrone, respectively.

Statistical analysis: The analysis of variance and regression calculations were done with the statistical program *SPSS 13.0* (*SPSS*, Chicago, USA), with the level of statistical significance set at $p<0.05$. All treatments were done in triplicate, and the results are reported as mean and standard error (SE).

Results

Growth: The results of this study showed that BL-2 and BL-3 could not survive at a salinity level of 200 mM; however, XJJL grew well. Changes of LA, DM, FM and branch length showed similar trends. With increasing salinity, the four indices all decreased significantly ($p<0.01$), and the reductions in BL-2 and BL-3 were much greater than those for XJJL (Fig. 1). L_N of BL-2 and BL-3 decreased with increasing stress intensity, whereas the low degree of salt stress enhanced L_N in XJJL (Fig. 1*E*). The increasing salt stress did not result in a decrease of ALA in XJJL (Fig.1*D*). In BL-2 and BL-3, the lower salt stress did not reduce ALA (Fig. 1*D*); however, when the degree of salinity was 80 mM or greater, ALA decreased sharply with increasing salinity. Linear regression analysis between salinity (x) and each growth index (y) was used to compare the inhibitory effects of salt stress on growth in the three cultivars (Table 1). The strain rate, the decreased value caused by one unit of salinity (d_y/d_x), represents the degree of salt stress on growth. A larger value of d_y/d_x indicates a stronger stress action. All the growth indices were negatively correlated with salinity. Linear regression analysis showed that the salt stress induced inhibitory effect on the growth of BL-2 and BL-3 was greater than that of XJJL (Table 1).

Photosynthesis: The responses of P_N, E and g_s to salt stress were similar; the low degree of salt stress enhanced all of these indices. However, when salinity was greater than 80 mM NaCl, these indices in BL-2 and BL-3 were significantly lower than those in the controls. In XJJL, however, indices were significantly lower than those in the controls only when salinity was greater than 120 mM NaCl (Fig. 1*I-J*). At a low degree of salinity, the P_N values for XJJL and BL-3 were similar, and higher than that for BL-2. However, the P_N of XJJL was much higher than those of the other two cultivars at high degrees of salinity (80–200 mM NaCl). With increasing salinity, C_i in BL-2 and BL-3 was increased (Fig. 1*J*, $p<0.01$), but it remained relatively unchanged in XJJL ($F = 0.567$; $p=0.724$). WUE of XJJL also was higher than those of the other two cultivars. With increasing salinity, the WUE of BL-2 and BL-3 decreased sharply, whereas it was little changed for XJJL (Fig. 1*K*).

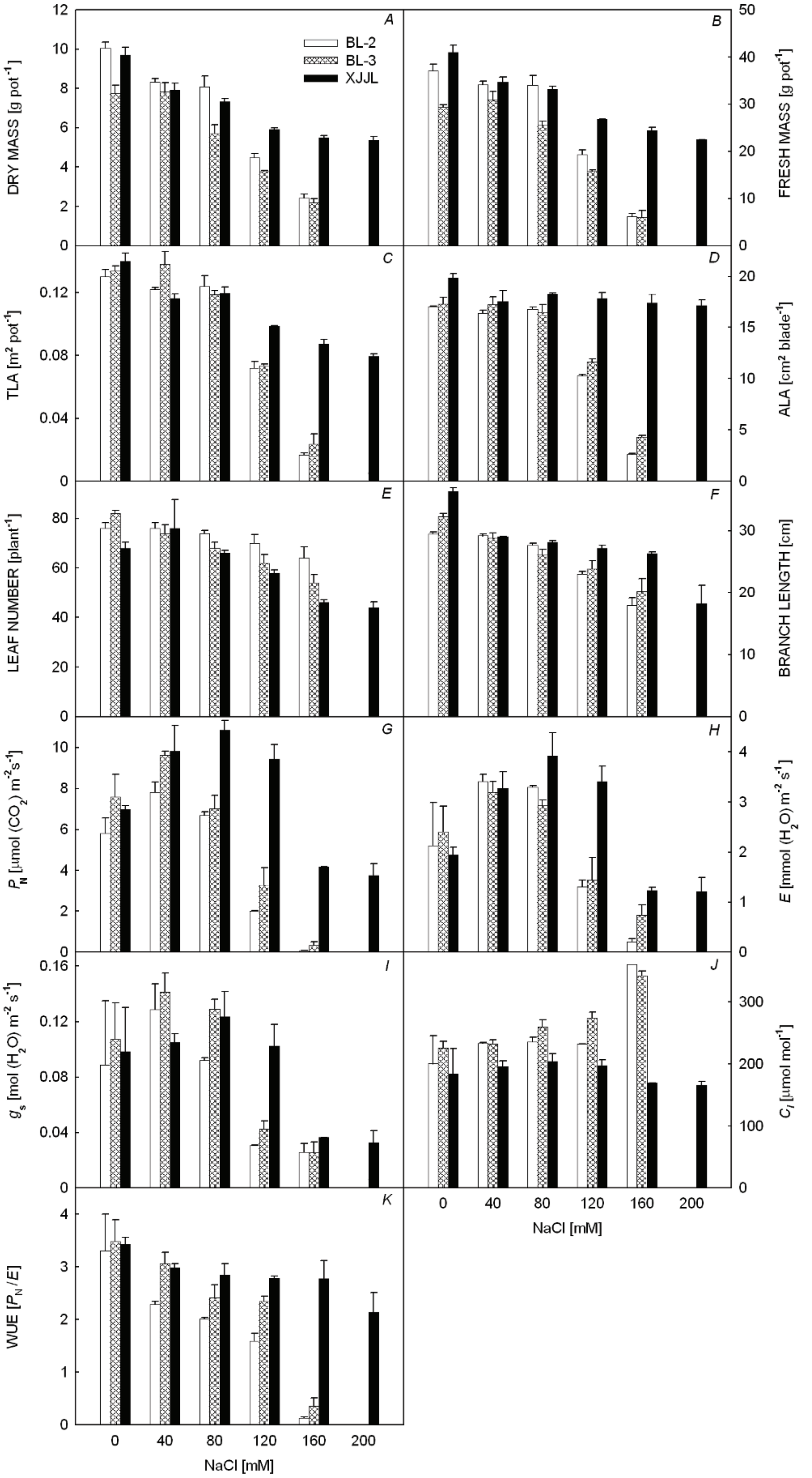

Fig. 1. Effect of the degree of salinity on: *A*: dry mass (DM); *B*: fresh mass (FM); *C*: total leaf area (TLA); *D*: average leaf area (ALA); *E*: leaf number (L_N); *F*: branch length; *G*: net photosynthetic rate (P_N); *H*: transpiration rate (E); *I*: stomatal conductance (g_s); *J*: intercellular CO_2 concentration (C_i); and *K*: water use efficiency (WUE) in the seedlings of three poplar cultivars *Populus* × BaiLin-2 (BL-2), *Populus* × BaiLin-3' (BL-3), and *Populus* × Xjiajiali' (XJJL). Two weeks old seedlings were subjected to NaCl stress for 21 d. The values are reported as mean ± SE of three replicates.

Table 1. Result of linear regression analysis between growth index (y) and salinity (x). $^{*}p<0.05$; $^{**}p<0.01$. BL-2 – *Populus* × BaiLin-2; BL-3 – *Populus* × BaiLin-3; XJJL – *Populus* × Xjiajiali, DM – dry mass; FM – fresh mass; TLA – total leaf area; d_y/d_x.slope of regression equation.

y	Regression equation	r^2	d_y/d_x
DM	$y_{BL\text{-}2} = -0.0477\,x + 10.48$	0.9350^{**}	-0.0477
	$y_{BL\text{-}3} = -0.0378\,x + 8.471$	0.9416^{**}	-0.0378
	$y_{XJJL} = -0.0217\,x + 9.119$	0.9195^{**}	-0.0217
FM	$y_{BL\text{-}2} = -0.1915\,x + 41.44$	0.8512^{*}	-0.1915
	$y_{BL\text{-}3} = -0.1544\,x + 33.87$	0.8686^{*}	-0.1544
	$y_{XJJL} = -0.0922\,x + 39.64$	0.9615^{**}	-0.0922
TLA	$y_{BL\text{-}2} = -0.0007\,x + 0.1485$	0.8130^{*}	-0.0007
	$y_{BL\text{-}3} = -0.0007\,x + 0.1544$	0.8597^{*}	-0.0007
	$y_{XJJL} = -0.0003\,x + 0.1360$	0.9440^{**}	-0.0003

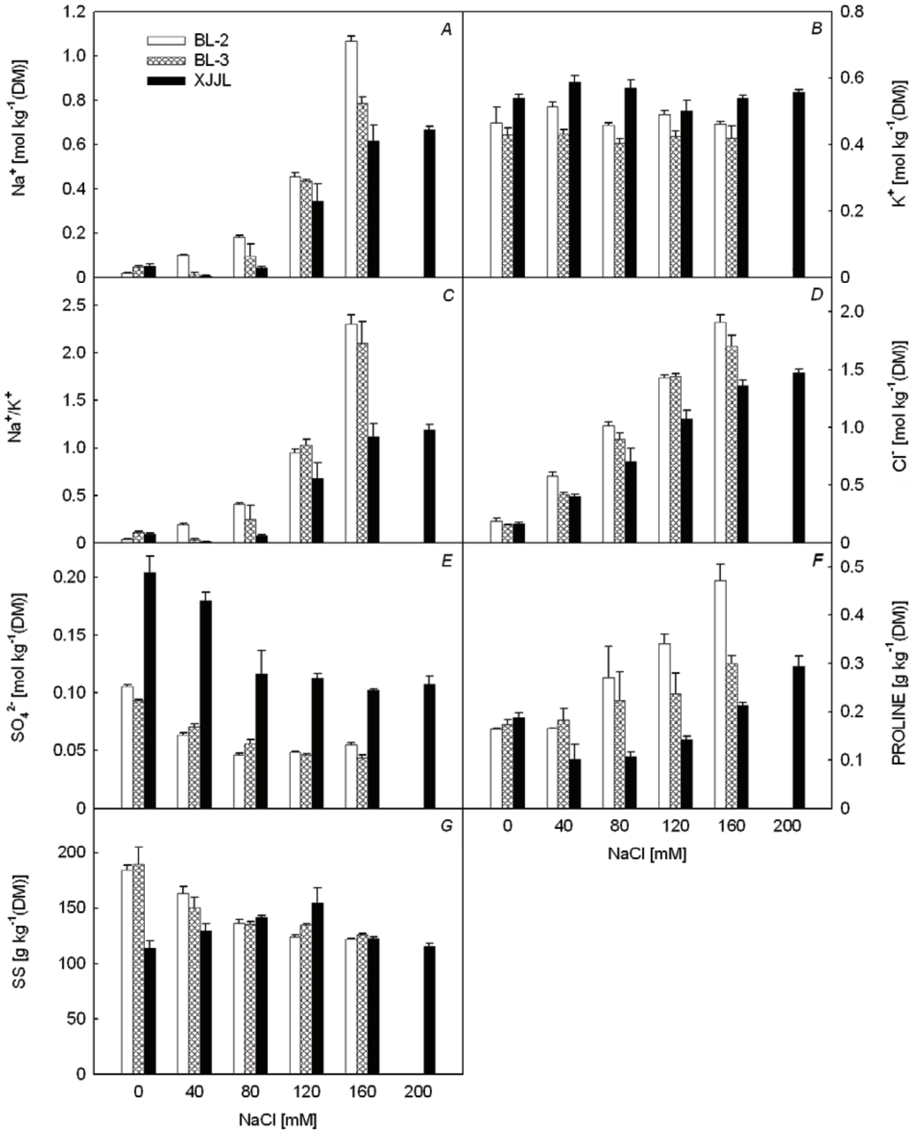

Fig. 2. Effects of the degree of salinity on: *A*: Na^+; *B*: K^+; *C*: Na^+/K^+; *D*: Cl^-; *E*: SO_4^{2-}; *F*: proline; and *G*: soluble sugars (SS) in the leaves of the seedlings of three poplar cultivars *Populus* × BaiLin-2 (BL-2), *Populus* × BaiLin-3 (BL-3), and *Populus* × Xjiajiali (XJJL). Two weeks old seedlings were subjected to NaCl stress for 21 d. The values are reported as mean ±SE of three replicates.

Solute accumulation: Soluble carbohydrates are major secondary metabolites in poplar, and reach very high levels (11–18 % of DM). The soluble sugar contents in BL-2 and BL-3 both decreased with increasing degree of salinity (Fig. 2*G*, $p<0.01$). In contrast, the contents were increased in XJJL with increasing degree of salinity, and decreased slightly at the highest salt stress (Fig. 2*G*; $p<0.01$). Free proline contents increased with increasing degree of salinity. The lowest degree of salinity did not cause an increase of Na^+ content or Na/K ratio; however, when the degree of salinity was ≥80 mM, they increased sharply with increasing salinity (Fig. 2; $p<0.01$). The salt stress did not result in a decreased K^+ content (Fig. 2; $p<0.1$). At the same degree of salinity, the Na content and Na/K ratio of BL-2 and BL-3 were much higher that those in XJJL. With increasing salinity, the Cl^- content increased, while the SO_4^{2-} content decreased, and the amount of change was much greater in BL-2 and BL-3 than that in XJJL (Fig. 2; $p<0.01$). NO_3^- was not detected in the leaves.

Discussion

Growth: High salinity can inhibit the growth and development of plants and even result in their death (Shi and Wang 2005, Shi and Sheng 2005, Moghaieb *et al.* 2004, Khan *et al.* 2000, Short and Colmer 1999). Many reports have showed clearly that salt stress inhibits the growth of poplar (Wang *et al.* 2008, Chang *et al.* 2006, Evers *et al.* 1997). The results of our experiment showed that growth of BL-2 and BL-3 was inhibited significantly, and these cultivars cannot survive in 200 mM NaCl. However, at the same degree of salinity, XJJL grew well. In addition, salt stress induced a greater reduction of DM, FM, TLA and branch length in BL-2 and BL-3 compared with XJJL (Fig.1 and Table 1), demonstrating that the tolerance of salt stress is greater in XJJL than that in BL-2 and BL-3, and that the difference might be due to different salt-tolerance mechanisms. Unitary linear regression analysis showed that salt stress had a greater inhibitory effect on BL-2 and BL-3 (Table 1). The huge difference in salt-tolerance among cultivars indicates a high degree of ecophysiologic plasticity, and provides important benchmark values for breeding salt-tolerant tree cultivars.

Photosynthesis: Photosynthetic productivity is dependent upon P_N and TLA. It was proved in this study that increasing soil salinity caused a dramatic decrease of L_N and TLA (Fig. 1), and that TLA of XJJL under high salt stress was much larger than that of the other two cultivars (Fig. 1). ALA is equal to the ratio TLA/L_N, changes of which can reflect the effect of salt stress on the leaf extension. The ALA of BL-2 and BL-3 was not affected by moderate salt stress, whereas high salt stress inhibited leaf extension significantly and resulted in considerable decreases of ALA and TLA (Fig. 1). Compared with them, the leaf extension in XJJL was not inhibited under high salt stress, which maintained a relatively large photosynthetic leaf area.

P_N usually decreases with rising stress intensity (Sultana *et al.* 1999, Koyro *et al.* 2006, Wei *et al.* 2006). However, we found that moderate salt stress could clearly enhance P_N of poplar seedlings, which may be an adaptive response to salt stress (Yang *et al.* 2008). At the lowest degree of salinity in this study, the inhibition of growth by salt stress was a result of decreasing LA and L_N, and was essentially independent of P_N. The photosynthetic system of a plant growing long-term in naturally saline conditions tends to stabilize, suggesting that the effect of salt stress on plant growth is mainly through the reduction of photosynthetic area rather than through a change in P_N. The reduction of plant P_N under a high level of salt- stress is generally considered to be the result of a reduction of intracellular CO_2 partial pressure caused by stomatal closure, or of non-stomatal factors (Bethke and Drew 1992). The non-stomatal factors depend mainly on the cumulative effects of factors such as leaf water content and osmotic potential, biochemical constituents (Sultana e*t al.* 1999), contents of photosynthetic pigments (Ma *et al.* 1997, Koyro *et al.* 2006), ion toxicity in the cytosol (James *et al.* 2006). Although P_N in XJJL was decreased under high salt stress, its C_i changed only slightly (Fig. 1), which implied that the salt stress might not affect its ability to assimilate CO_2, and the reduction of P_N under high salt-stress was a result of the reduction of g_s. However, in BL-2 and BL-3, when g_s decreased, C_i increased dramatically. All these data indicated that a high salt stress might destroy the chloroplast structure in BL-2 and BL-3, and lead to the decrease or loss of their ability to assimilate CO_2 and the reduction of P_N. Such damage of the photosynthetic system might be attributed to ion toxicity in the cytoplasm. The decrease of g_s and *E* under salt stress might be correlated to an intercellular Na^+-K^+ imbalance (Fig. 1), and could be an adaptive response to osmotic stress.

Solute accumulation: The injurious effects of salinity are commonly thought to be a result of low water potential and ion toxicity (Parida and Das 2005). Na^+ is the main poisonous ion in salinized soil, and plants growing in saline conditions generally compartmentalize Na^+ into vacuoles, which avoids Na^+ toxicity in the cytosol. Low Na^+ and high K^+ in the cytoplasm are essential for the maintenance of a number of enzymatic processes (James *et al.* 2006, Zhu 2003, Munns 2002), and the Na^+/K^+ ratio is an important index indicating the salt-tolerance ability of a plant (Parida and Das 2005). Na^+ enters plant cells principally through K^+ pathways (Blumwald 2000). The similarity of the hydrated ionic radius of Na^+ and K^+ makes it difficult to discriminate between them and this is the basis of Na^+ toxicity (Blumwald 2000). Plants under salt-alkaline stress usually absorb Na^+ and simultaneously inhibit K^+ absorption (Shi and Wang 2005, Shi and Sheng 2005, Moghaieb *et al.* 2004, Khan *et al.* 2000, Short and Colmer 1999, Munns 2002). However, our results showed that the increase of Na^+ content in the leaf was not accompanied by a decrease of K^+ content. This phenomenon implied that there was no competitive inhibition between the absorptions of Na^+ and K^+ for poplar, and poplar might have a unique pathway of Na^+ absorption that does not depend on the K^+ pathway. Further, it might be the result of controlling the transportation of Na^+ and K^+ in the leaf cell. The majority of woody plant species are salt-sensitive. The long-distance transportation of water and ions is likely to be the main factor limiting compartmentalization of toxic ions and salt resistance. Therefore, we suggest that when researching and breeding salt-resistant woody plants, we should pay attention to controlling the transport of Na^+ and K^+ in leaves. By comparing the accumulation traits of ions among the three poplar cultivars, it is obvious that under the same degree of salinity, Na^+, Cl^- and Na^+/K^+ were much lower in XJJL than those of BL-2 and BL-3, showed the greater capacity of XJJL in controlling Na^+. At the higher degree of salinity, the reduction of P_N in BL-2 and BL-3 might be attributal to intercellular ion imbalance and could be the result of a large afflux of toxic ions such as Na^+ and Cl^- into leaves (Fig. 1). High concentrations of Na^+ and Cl^- in leaves might disturb sub-cellular partition of them, which would cause high-level accumulation in the cytoplasm and destruction of the structure and function of chloroplasts (James *et al.* 2006). This might be the reason why the three cultivars showed different levels of salt resistance.

Except for the different characteristics of accumulation of inorganic ion, the three cultivars showed differences in the accumulation of organic solutes. Proline, which had a similar role in the adaptation to salt stress, is accumulated mainly in the cytoplasm for coping with the osmotic stress resulted from vacuole and apoplast. Despite the high content of soluble sugars in the leaves (maximum of 18.4 % of FM), soluble sugars might have different roles in the response of different cultivars to salt stress. With increasing salinity, the contents of soluble sugars in BL-2 and BL-3 decreased (Fig. 2), while that in XJJL increased, and eventually decreased slightly at higher degrees of salinity. Thus, we propose that the accumulation of soluble sugars might be important to cytoplasmic osmotic regulation of XJJL. The decrease of soluble sugars in BL-2 and BL-3 is probably caused by the interruption or conversion of their metabolism.

In summary, XJJL showed greater salt tolerance than the other cultivars in this study. Higher P_N and larger photosynthetic area, lower Na/K ratio and Cl^- in the leaf, greater accumulation of soluble sugars and SO_4^{2-} might explain the greater salt-tolerance of XJJL compared with that of BL-2 and BL-3. The salt-stress physiology of trees should be the major research objective of a future work.

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S.Z. Ryang, S.Y. Woo, S.Y. Kwon, S.H. Kim, S.H. Lee, K.N. Kim, and D.K. Lee: Changes of net photosynthesis, antioxidant enzyme activities, and antioxidant contents of *Liriodendron tulipifera* under elevated ozone – Photosynthetica 47: 19-25, 2009.

Please correct:

On p. 21, replace Table 1 as follows:

Table 1. Protocol of exposure to ozone. O_3 concentrations [$\mu g\ kg^{-1}$] and AOT40 [$\mu g\ kg^{-1}\ h^{-1}$] are shown. Plants were not exposed to ozone on some days (17, 26, and 31 July).

Date	17	18	19	20	22	23	24	25	27	28	29	30
O_3	100	100	100	100	150	150	200	200	250	250	300	300
AOT40	480	960	1 440	1 920	**2 800**	**3 680**	**4 960**	**6 240**	**7 920**	**9 600**	**11 680**	**13 760**

On p. 23, replace the legends of Fig. 3 and Fig. 4 as follows:

Fig. 3. Antioxidant enzyme activities (APX − ascorbate peroxidase, DHAR − dehydroascorbate reductase, GR − glutathione reductase, MDHAR − monodehydroascorbate reductase, SOD − superoxide dismutase) [%NBT inhibition rate for SOD, nmol kg^{-1}(protein) s^{-1} for others] expressed as ratio of ozone affected to control plants during gradual O_3 exposure from 100 to 300 $\mu g\ kg^{-1}$ (cf. Table 1). *Dotted lines* indicate constant value of control. Statistical differences between control and O_3 treatment are shown above bars: $^{***}p$<0.001, $^{**}p$<**0.01**, $^{*}p$<**0.05**, n.s. non significant ($n = 3$).

Fig. 4. Peroxidase (POD) and catalase (CAT) activities [nmol kg^{-1}(protein) s^{-1}] expressed as ratio of ozone affected to control plants during gradual O_3 exposure from 100 to 300 $\mu g\ kg^{-1}$ (cf. Table 1). *Dotted lines* indicate constant value of control. Statistical differences between control and O_3 treatment are shown above bars: $^{***}p$<0.001, $^{**}p$<**0.01**, $^{*}p$<**0.05**, n.s. non significant ($n = 3$).

The publisher and authors apologize for these errors and for inconveniences they may have caused.