

Effects of NaCl stress on the growth and photosynthetic characteristics of *Ulmus pumila* L. seedlings in sand culture

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Abstract

The effects of NaCl stress on the growth and photosynthetic characters of *Ulmus pumila* L. seedlings were investigated under sand culture condition. With increasing NaCl concentration, main stem height, branch number, leaf number, and leaf area declined, while Na⁺ content and the Na⁺/K⁺ ratio in both expanded and expanding leaves increased. Na⁺ content was significantly higher in expanded leaves than in those just expanding. Chlorophyll (Chl) *a* and Chl *b* contents declined as NaCl concentration increased. The net photosynthetic rate, intercellular CO₂ concentration, stomatal conductance, and transpiration rate also declined, but stomatal limitation value increased as NaCl concentration increased. Both the maximal quantum yield of PSII photochemistry and the effective quantum yield of PSII photochemistry declined as NaCl concentration rose. These results suggest that the accumulation of Na⁺ in already expanded leaves might reduce damage to the expanding leaves and help *U. pumila* endure high salinity. The reduced photosynthesis in response to salt stress was mainly caused by stomatal limitation.

Additional key words: chlorophyll fluorescence; elm; gas exchange; growth; salt stress; sodium ion.

Introduction

Soil salinization is an increasing problem throughout the world (Munns 2002). Salt stress interferes with plant growth and development; it causes great losses in agricultural production (Herrero and Pérez-Coveta 2005, Rozema and Flowers 2008), and it also restricts afforestation. More than 950 million ha of land are salt-affected in the world. In China, 10.5% of the saline land occurs mainly in the northeast, northwest interior, and coastal areas north of the Yangtze River (Song *et al.* 2009). The problem worsens due to poorly managed irrigation, which causes secondary salinization of fertile farmland and leads to further loss of the nonsaline soil suitable for cultivation (Munns and Tester 2008).

Although biotechnology has generated crops resistant to plant pests and diseases, it has not delivered yet salt-tolerant cultivars for use in saline agriculture (Rozema and Flowers 2008). Therefore, the development of saline agri-

culture currently depends both on identifying plants with high salt tolerance and on understanding and exploiting their salt tolerance (Bhatnagar-Mathur *et al.* 2008).

Salinity can reduce plant growth as a consequence of osmotic stress, ion toxicity, and nutritional stress (Munns and Tester 2008). High salt concentrations damage the semipermeability of the plasma membrane as intracellular ion, K⁺, moves out of cells and extracellular ion, Na⁺, moves into cells; this disrupts the interstitial ionic homeostasis and results in reduced growth and development, and even death (Tavakkoli *et al.* 2011).

Salt stress also damages chloroplast structure, reduces Chl content, and decreases photosynthesis (Ma *et al.* 2012). NaCl inhibits photosynthesis as a consequence of osmotic stress, which leads to a decrease in water potential and stomatal conductance (g_s), sugar accumulation, which causes feedback inhibition, and ion toxicity (*e.g.*, an excess

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Abbreviations: C_a – ambient CO₂ concentration; Chl – chlorophyll; C_i – intercellular CO₂ concentration; DM – dry mass; E – transpiration rate; F₀ – minimal fluorescence yield of the dark-adapted state; F_m – maximal fluorescence yield of the dark-adapted state; F_m' – maximal fluorescence yield of the light-adapted state; F_s – steady-state fluorescence yield; F_v – variable fluorescence; F_v/F_m – maximal quantum yield of PSII photochemistry; FM – fresh mass; g_s – stomatal conductance; LA – leaf area; L_s – stomatal limitation value; P_N – net photosynthetic rate; Q_A – primary quinone acceptor of PSII; Q_B – secondary quinone acceptor of PSII; S0, S100, S200, S300 – treatment with 0, 100, 200, and 300 mM NaCl, respectively; Φ_{PSII} – effective quantum yield of PSII photochemistry.

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of Na⁺ and Cl⁻) accompanied by a reduction of K⁺ and Ca²⁺ (Silva *et al.* 2010). The reduction in photosynthesis caused by salt stress depends on the kind and concentration of the salt, how the stress occurs, and the sensitivity of a plant (Qiu *et al.* 2003). Research on the effects of NaCl stress on photosynthesis has focused mostly on crops (Gill *et al.* 2013, Gong *et al.* 2013) and herbaceous plants (Wani *et al.* 2013); it has been less often focused on woody plants (Fu *et al.* 2013). The salt tolerance of Chinese elm, *U. pumila* (Ulmaceae), has not been previously investigated in sand culture.

Plants have developed several salt-tolerance mechanisms. For example, some plants are able to regulate the kind, quantity, and proportion of intracellular and extracellular inorganic ions in order to maintain ionic stability.

Materials and methods

Growth conditions and NaCl treatments: *U. pumila* seedlings (1-year-old, collected from Huimin County of Shandong Province, China) of the similar size (18 ± 2 cm, from the sand surface to the tip of the main stem) were transplanted into plastic pots (24 cm high × 26 cm in a diameter) containing 5 kg of rinsed river sand on September 1, 2011. The plants were grown in a controlled greenhouse in Jinan City, Shandong, at 30 ± 3°C/20 ± 3°C day/night temperature, light intensity of 600 μmol(photon) m⁻² s⁻¹ during 15-h photoperiod, and 70 ± 10% relative humidity. Hoagland nutrient solution [2.5 mM Ca(NO₃)₂, 2.5 mM KNO₃, 1 mM MgSO₄, 0.5 mM KH₂PO₄, 45 μM Fe-EDTA, 23 μM H₃BO₃, 4.55 μM MnCl₂, 0.16 μM CuSO₄, 0.38 μM ZnSO₄, 0.28 μM Na₂MoO₄, pH adjusted to 5.7 ± 0.1 with NaOH and HCl] was supplied every day.

Uniform seedlings were treated with 0, 100, 200, and 300 mM NaCl (S0, S100, S200, and S300, respectively). The treatment with Hoagland nutrient solution supplemented with NaCl started on May 13, 2012. To avoid osmotic shock, the NaCl concentration was rising by 50 mM per day. To avoid salt accumulation in the sand due to evaporation, 2 l of nutrient solution containing NaCl was supplied twice every day; it equaled the amount that was flushed from the drained pots. The experiment was terminated 21 d after the final salinity concentrations had been reached. Each treatment was represented by 5 pots.

Plant growth: At the beginning and at the end of the experiment, the length of the main stem of each seedling (from the sand surface to the tip of the main stem), the number of all branches, and number of leaves per plant were determined. The leaf area (LA) per plant was estimated by *Epson Perfection V750 PRO* photo scanner (*Epson America Inc.*, Long Beach, CA, USA).

Inorganic ions: At the end of the experiment, expanded and expanding leaves were harvested separately from the same leaf position of each plant. The leaves were washed, they were placed at 105°C for 15 min to deactivate the

Other plants accumulate small organic molecules (*e.g.*, betaine, proline, organic acids, and soluble sugars) for osmotic adjustment (Ghoulam *et al.* 2002, Moghaieb *et al.* 2004). We could screen for new salt-tolerant plants and understand how to improve their growth in saline soil, if we know more about the salt-tolerance mechanisms.

NaCl is the main compound that causes salt stress in plants (Tarchoune *et al.* 2012). Seedlings are usually more sensitive to salt stress than plants in more advanced stages (Wu *et al.* 2012). The overall goal of our research was to identify salt-tolerant tree species that can be used for the afforestation of saline-alkaline soils. The specific objective of this study was to determine the effects of NaCl stress on the growth and photosynthetic characteristics of *U. pumila* seedlings grown in sand culture.

enzymes, and then dried at 80°C to a constant dry mass (DM). A 50-mg dry sample was processed in a muffle stove at 550°C for 2 d, and the ash was dissolved in 1 ml of concentrated nitric acid. The volume of the solution was adjusted to 25 ml with deionized water, then it was filtered, and the Na⁺ and K⁺ concentrations were determined with a flame photometer (*Flame Photometer 410*, *Sherwood Scientific Ltd*, Cambridge, UK) (Song *et al.* 2009).

Chl concentration: Fresh leaves from the same position (the 3rd to 5th expanded leaf on the third branch from the bottom of the main stem) were crushed in 5 ml of 80% acetone and dimethyl sulfoxide (DMSO). The samples were sealed, shaken, and placed in a water bath at 65°C until the leaf tissue turned white. The Chl content in the supernatant after centrifugation (1,000 g for 10 min) was estimated by reading the absorbance at 645 and 663 nm with a UV spectrophotometer (*UV-120-02*, *Spectrophotometr*, Shimadzu, Kyoto, Japan). Chl *a* and Chl *b* concentrations were calculated using the equations of Porra *et al.* (1989):

$$\text{Chl } a = 12.7 A_{663} - 2.69 A_{645}$$

$$\text{Chl } b = 22.9 A_{645} - 4.68 A_{663}$$

Photosynthetic parameters: Net photosynthetic rate (P_N), intercellular CO₂ concentration (C_i), stomatal conductance (g_s), and transpiration rate (E) were measured with a *Portable Photosynthesis System LI-6400* (*LI-COR Inc.*, Lincoln, NE, USA). All parameters were measured between 10:00 and 11:00 h (local time) under a photosynthetically active radiation of 2,100 μmol(photon) m⁻² s⁻¹ (saturated light intensity), leaf temperature of 30 ± 2°C, relative humidity of 60 ± 5%, and 390 μmol(CO₂) mol⁻¹ (C_a). The 3rd to the 5th expanded leaf on the third branch from the bottom upward were measured and readings were repeated five times per leaf. The stomatal limitation value (L_s) was calculated as $1 - C_i/C_a$ (Chen *et al.* 2006, Ma *et al.* 2012).

Chl fluorescence: A portable fluorometer (*FMS-2*, *Hansatech*, King's Lynn, UK) was used to determine the maximal quantum yield of PSII photochemistry, which was expressed as $F_v/F_m = (F_m - F_0)/F_m$, and to determine the effective quantum yield of PSII photochemistry (Φ_{PSII}), which was calculated as $(F_m' - F_s)/F_m'$. The plant was dark adapted for at least 30 min before the measurement of F_0 , and then a pulse saturation light of $17,000 \mu\text{mol m}^{-2} \text{s}^{-1}$ was turned on for 2.5 s to measure F_m . The plant was kept under day light ($600 \mu\text{mol m}^{-2} \text{s}^{-1}$) for at least 30 min, then F_s was

measured, last F_m' was determined (Qiu *et al.* 2003, Dongsansuk *et al.* 2013).

Statistical analysis: All values were the means \pm SD of 5 replicate seedlings. The data were analyzed using *SPSS 16.0* (*SPSS Inc.*, Chicago, IL, USA). Treatment significance was determined with one-way analyses of variance (*ANOVA*), and means denoted by different lowercase letters were significantly different at $P < 0.05$ based on *Duncan's* multiple range test.

Results

Shoot and root growth: NaCl stress inhibited significantly the growth of *U. pumila* seedlings and the inhibition increased with rising concentrations of NaCl (Table 1, Fig. 1). Compared with the control (S0), the main stem height, branch number, leaf number, and LA decreased due to salinity by 82.2, 82.6, 79.5, and 85.4%, respectively. All leaves remained green and many new roots were detected when the plants were exposed to the low NaCl concentration (lower than S200) for 21 d. Chlorosis occurred in the leaves of S200 plants, although few new roots generated. Moreover, S300 lead to severe chlorosis, abscission of the older leaves, and no new roots (Fig. 1).

Na⁺ content and Na⁺/K⁺ ratio: Na⁺ is the main toxic ion and the Na⁺/K⁺ ratio is often used to represent the degree of salt injury in plants. The presence of NaCl in the

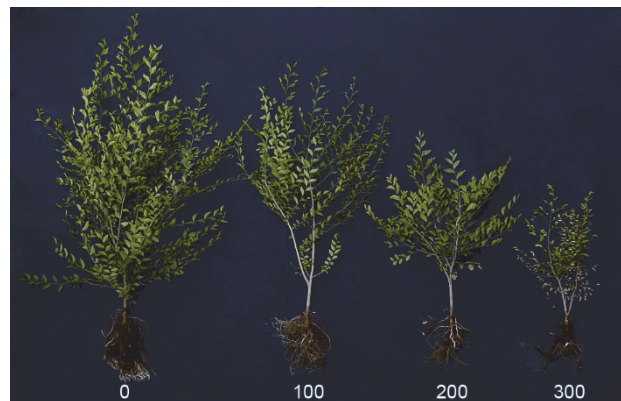


Fig. 1. A photograph of representative *Ulmus pumila* seedlings after treatment with 0, 100, 200, and 300 mM NaCl for 21 d.

Table 1. Effects of NaCl treatments on the growth of *Ulmus pumila* seedlings. Values indicate the changes in main stem height, branch number, leaf number, and leaf area from the day when the treatments were fully implemented until 21 d of the experiment. Means \pm SD, $n = 5$. Values in a column followed by different lowercase letters are significantly different at $P < 0.05$ according to *Duncan's* multiple range test. LA – leaf area.

NaCl [mM]	Main stem height [cm]	Branch number per plant	Leaf number per plant	LA per plant [cm ²]
0	34.0 \pm 3.2 ^a	127.0 \pm 18.0 ^a	1,196.0 \pm 183.0 ^a	3,235.8 \pm 689.4 ^a
100	24.8 \pm 1.5 ^b	66.0 \pm 9.0 ^b	630.0 \pm 70.0 ^b	1,529.5 \pm 316.9 ^b
200	6.4 \pm 1.5 ^c	23.0 \pm 7.0 ^c	246.0 \pm 89.0 ^c	474.3 \pm 105.1 ^c
300	2.8 \pm 0.8 ^d	6.0 \pm 4.0 ^d	40.0 \pm 10.0 ^d	62.2 \pm 11.6 ^d

Hoagland nutrient solution induced an important increase in Na⁺ content in leaves. The Na⁺ content increased substantially in the expanding leaves but even more in the expanded leaves (Fig. 2A). In the leaves, the K⁺ concentration gradually decreased in response to NaCl (data not shown). The Na⁺/K⁺ ratio in leaves also increased with increasing NaCl quantity, and the ratio was substantially greater in the expanded leaves than in the expanding leaves (Fig. 2B). After S300, the Na⁺ content in the expanded leaves was nearly twice as high as in the expanding leaves (Fig. 2A) and the ratio was 3 times higher in the expanded leaves than in the expanding leaves (Fig. 2B).

Photosynthetic pigments: Compared with the control

(S0), both Chl *a* and Chl *b* content declined as the quantity of NaCl added increased (Fig. 3), *e.g.*, Chl *a* and Chl *b* content in the S300 plants decreased by 40%, and 67%, respectively.

Photosynthetic gas-exchange parameters: P_N , C_i , g_{s_s} , and E declined, while L_s increased with the increasing of NaCl concentration (Fig. 4). Compared with S0, S100 led to a slight decline of g_{s_s} ; the marked reduction of g_{s_s} occurred when the NaCl concentration was higher than 100 mM (Fig. 4C). When NaCl concentration reached 300 mM, the inhibition of photosynthetic gas-exchange parameters was very severe, *e.g.*, P_N , C_i , g_{s_s} , and E decreased by 82.6, 57.8, 83.3, and 63.3%, respectively.

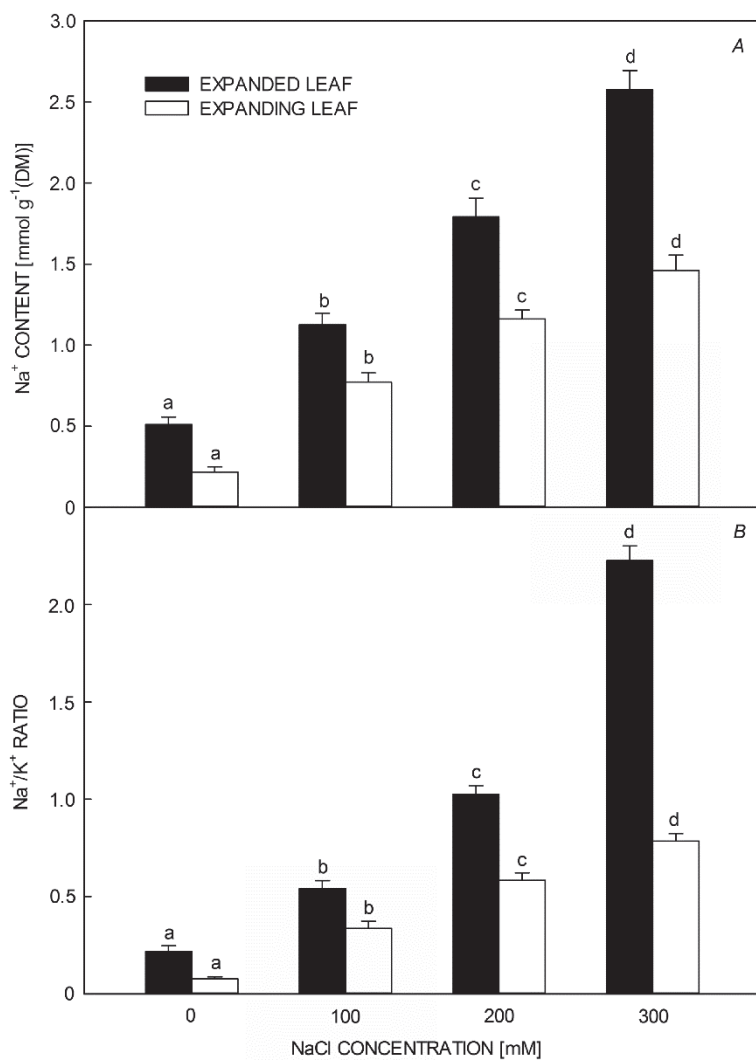


Fig. 2. Leaf Na⁺ content (A) and Na⁺/K⁺ ratio (B) of *Ulmus pumila* seedlings treated with 0, 100, 200, and 300 mM NaCl for 21 d. Values are means ± SD (*n* = 5). For each kind of leaf (expanded and expanding), means with different lowercase letters are significantly different at *P* < 0.05 according to Duncan's multiple range test.

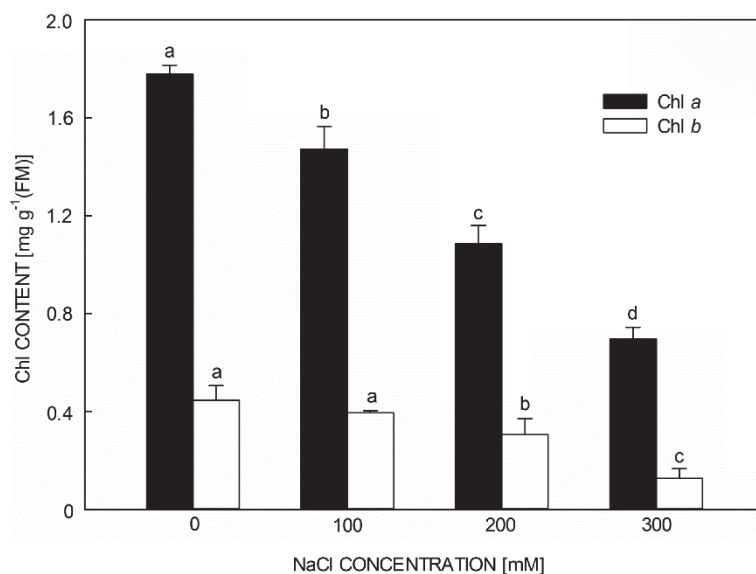


Fig. 3. Chlorophyll (Chl) *a* and Chl *b* concentration in expanded leaves of *Ulmus pumila* seedlings treated with 0, 100, 200, and 300 mM NaCl for 21 d. Values are means ± SD (*n* = 5). For each variable, means with different lowercase letters are significantly different at *P* < 0.05 according to Duncan's multiple range test.

F_v/F_m and Φ_{PSII}: F_v/F_m and Φ_{PSII} declined as NaCl concentration increased (Fig. 5). In the case of F_v/F_m, no signifi-

cant difference was observed between S100 and S200, but it decreased significantly at S300 (Fig. 5A).

Discussion

Plant sensitivity to salt stress is manifested by changes in growth and morphology (*e.g.*, slow growth, leaf abscission, and death) and changes in physiology (*e.g.*, decline in the photosynthetic capacity and an increase in plasma membrane permeability) (Munns 2005). Therefore, biomass provides a dependable criterion for evaluating salt stress and tolerance (Huang *et al.* 2012). On the other hand, plants may adapt to environmental stress (*i.e.*, they may increase their chances of survival) by reducing the growth

rate and adjusting biomass allocation (Grotkopp *et al.* 2002). In the current study, NaCl addition reduced the growth of *U. pumila* seedlings, and the severity of the reduction correlated with the concentration of NaCl added. However, no visible damage was detected, when the plants were treated with 100 mM NaCl for 21 d, while the higher concentrations, *e.g.*, 200 mM or 300 mM NaCl, led to leaf chlorosis, death, and even abscission. This indicated that *U. pumila* could endure higher salinity environment.

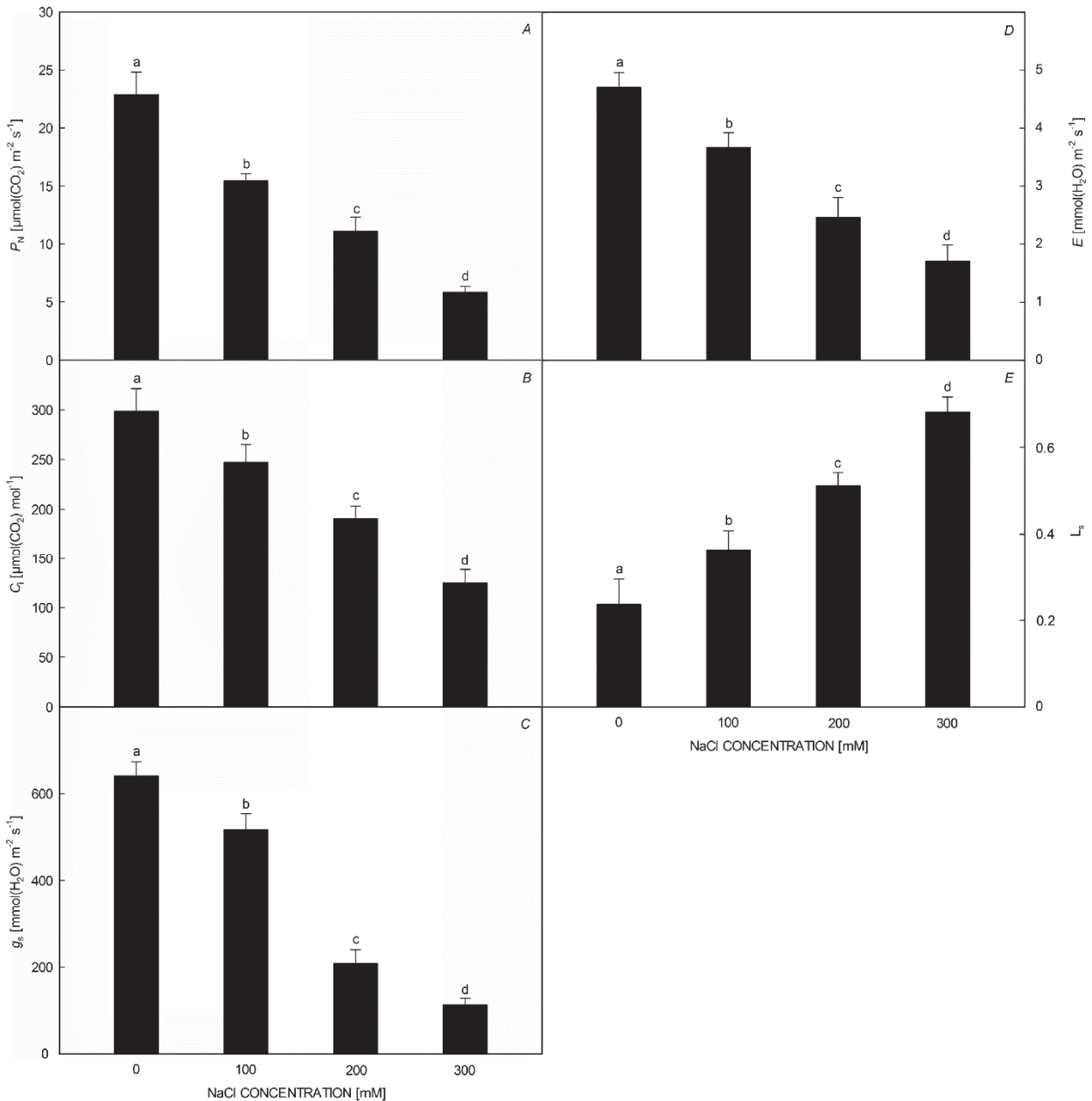


Fig. 4. Effects of NaCl treatments (0, 100, 200, and 300 mM for 21 d) on A: net photosynthetic rate (P_N), B: intercellular CO_2 concentration (C_i), C: stomatal conductance (g_s), D: transpiration rate (E), and E: stomatal limitation value (L_s) of *Ulmus pumila* seedlings. Values are means \pm SD ($n = 5$). Means followed by different lowercase letters are significantly different at $P < 0.05$ according to Duncan's multiple range test.

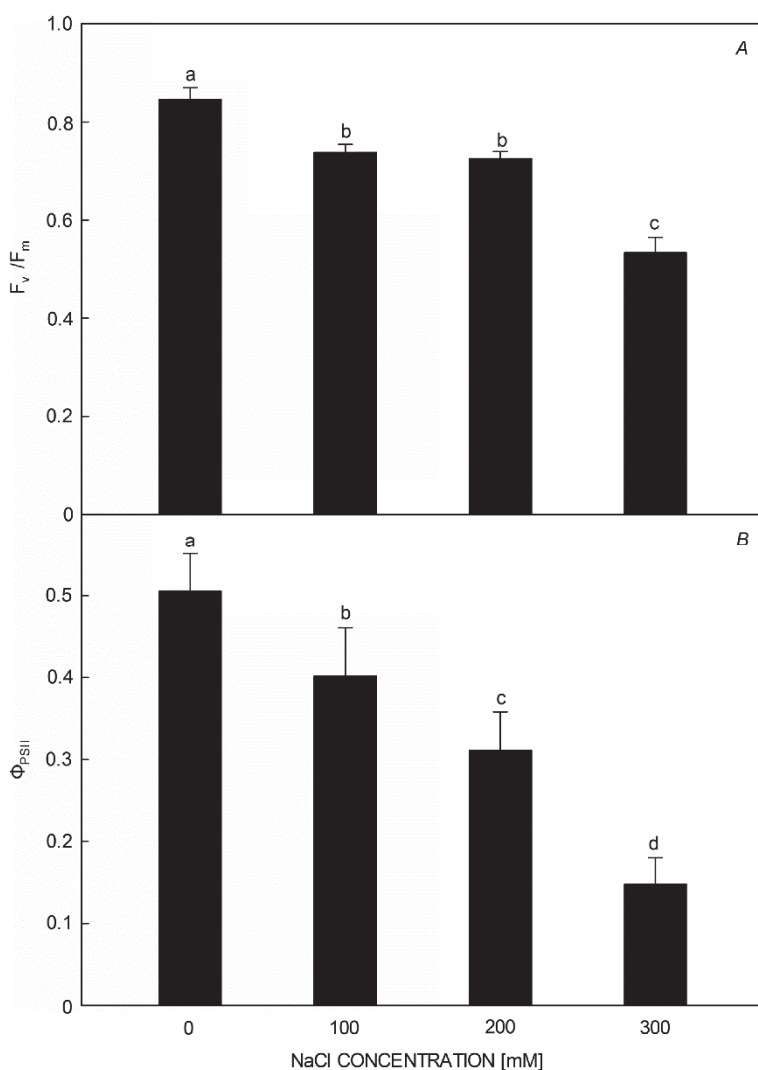


Fig. 5. Effects of NaCl treatments (0, 100, 200, and 300 mM for 21 d) on *A*: the maximal quantum yield of PSII photochemistry (F_v/F_m) and *B*: the effective quantum yield of PSII photochemistry (Φ_{PSII}) of *Ulmus pumila* seedlings. Values are means \pm SD ($n = 5$). Means followed by different lowercase letters are significantly different at $P < 0.05$ according to Duncan's multiple range test.

To explain the reduced growth, we suggest that NaCl stress not only altered the ion balance but also the photosynthetic capacity, which caused growth reduction. In this study, NaCl stress affected negatively P_N and LA of *U. pumila* seedlings; it was the main reasons for the decline in seedlings biomass.

Salt tolerance depends to a great extent on the metabolism of ions, especially on Na^+ , K^+ , and Cl^- . Salt-tolerant plants can reduce injury from salt stress by decreasing their cellular Na^+ content and increasing their cellular K^+ content, and thus they maintain the low Na^+/K^+ ratio (Munns and Tester 2008). The high concentration of Na^+ infiltrated into cells damages plasma membranes and leads to the imbalance of ions including a loss of Ca^{2+} and K^+ , metabolic disorder, and reduced plant growth (Clapham 1995, Carter *et al.* 2006). Therefore, maintaining K^+ concentration in the cytoplasm is important for salt tolerance. A large difference in ion content between different parts of the same plant was found under salinity (Greenway and Munns 1980). In the current study, the Na^+ content was substantially greater in the expanded leaves than in the

expanding leaves of *U. pumila* exposed to NaCl stress. It was consistent with a previous report concerning the concentration of Na^+ in barley (*Hordeum vulgare* L.) growing under saline conditions. The Na^+ content was lower in actively growing tissues than in mature tissues (Tavakkoli *et al.* 2011). Compartmentalization of Na^+ in organelles or tissues is an important mechanism of salt tolerance in plants (Chinnusamy *et al.* 2005). In this paper, when the NaCl concentration was lower than 200 mM, all leaves of *U. pumila* remained green and new roots were formed during the treatments and the Na^+/K^+ ratio maintained low in both expanded and expanding leaves. However, higher NaCl suppressed growth, and it led even to leaf chlorosis, death, and abscission. For example, when *U. pumila* seedlings were treated with 300 mM NaCl for 21 d, chlorosis, death and abscission in expanded leaves occurred, and the Na^+/K^+ ratio in expanded leaves was 2.75 times higher than that in expanding leaves. These results suggest that preferential accumulation of Na^+ in the expanded leaves under salt stress presumably reduces the damage to expanding leaves, which perhaps helps

U. pumila survive in high salinity environments.

Both the Chl *a* and Chl *b* contents of *U. pumila* were reduced by salt stress in the current study. Their contents indicate still the ability to use light (Ma *et al.* 2012). The progressive decrease in Chl content with rising NaCl concentration was consistent with previous results obtained with *Ocimum basilicum* (Tarchoune *et al.* 2012). Chl *b* is more sensitive than Chl *a* to NaCl stress, because chlorophyllase degrades preferentially Chl *b*.

Na⁺ plays an important role in maintaining photosynthesis in some plants, such as dicotyledonous euhalophytes, *Suaeda salsa* and *Atriplex nummularia* (Lu *et al.* 2003, Tester and Davenport 2003). However, the excessive accumulation of Na⁺ causes shortage of other ions, reduces transport of mineral elements and water, and reduces photosynthesis (Lee *et al.* 2007). At the same time, the excess of Na⁺ can accelerate carbohydrate accumulation and starch hydrolysis in mesophyll cells of some plants, which slows photosynthetic output and causes the feedback inhibition of photosynthesis (Gorai *et al.* 2011), and it further inhibits CO₂ fixation by damaging the photosystems (Silva *et al.* 2011). The *g_s* was reduced under NaCl stress. It limits CO₂ uptake and water evaporation and thus it limits photosynthesis and transpiration (Raschke 1975). *P_N*, which indicates carbon assimilation capacity per unit of LA, is an effective indicator of salt tolerance in plants under salt stress (Ma *et al.* 2012). In the current paper, both *P_N* and *E* of *U. pumila* declined as NaCl concentrations increased. In previous studies concerning salinity effects, a decreased carbon assimilation capacity was caused by both stomatal and nonstomatal factors in *Phaseolus vulgaris* (Seemann and Sharkey 1986) and *Porphyra perforata* (Satoh *et al.* 1983). *L_s* is an index to

reflect the influence degree on photosynthesis caused by stomata. When plants suffer from stress, decline in photosynthesis is indicated by decrease in *C_i* and increase in *L_s*. According to the optimization theory of stomatal regulation suggested by Farquhar and Sharkey (1982), the reduction in *P_N* under stress is probably caused by stomatal limitation, if stress does not decrease the photosynthetic capacity of mesophyll cells, but decreases *g_s*, *C_i*, and increases *L_s*. On the contrary, if the photosynthetic capacity of mesophyll cells significantly decreases, it will reduce CO₂ utilization capacity, then *C_i* increases, so the decrease in *P_N* under stress results mainly from non-stomatal factors. When *U. pumila* seedlings were subjected to NaCl in the current study, *g_s* and *C_i* declined, while *L_s* increased, indicating that the primary reason for the decrease in photosynthesis was the stomatal limitation. A similar inference was done by Wu *et al.* (2012) for the nonhalophyte *Solanum melongena*.

When plants suffer from environmental stress, *F_v/F_m* decreases (Zribi *et al.* 2009). The addition of NaCl caused the decline of *F_v/F_m* values; it showed that *U. pumila* suffered from salt stress. Φ_{PSII} declined with increasing NaCl concentration. The decrease of Φ_{PSII} may be related to the inhibition of electron transfer from *Q_A⁻* to *Q_B* (Baker 2008, Abdeshahian *et al.* 2010).

In conclusion, the partial accumulation of Na⁺ in the expanded leaves rather than in the expanding leaves might help *U. pumila* tolerate and survive high salinity. The inhibition of *U. pumila* photosynthesis by salt stress apparently resulted from stomatal effects. Finally, additional research is needed to quantify and understand the mechanism of Na⁺ accumulation in different parts of *U. pumila*.

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