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Growth and leaf gas exchange in *Populus euphratica* across soil water and salinity gradients

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Abstract

Soil water and salinity conditions of the riparian zones along the Tarim River, northwest China, have been undergoing alterations due to water use by human or climate change, which is expected to influence the riparian forest dominated by an old poplar, *Populus euphratica*. To evaluate the effects of such habitat alterations, we examined photosynthetic and growth performances of *P. euphratica* seedlings across experimental soil water and salinity gradients. Results indicated that seedlings were limited in their physiological performance, as evidenced by decreases in their height and biomass, and the maximal quantum yield of photosystem II (PSII) photochemistry (F_v/F_m), the effective quantum-use efficiency of PSII (F_v'/F_m'), and photochemical quenching (q_P) under mild (18% soil water content, SWC; 18.3 g kg^{-1} soil salt content, SSC) and moderate (13% SWC, 22.5 g kg^{-1} SSC) water or salinity stress. However, seedlings had higher root/shoot ratio (R/S), increased nonphotochemical quenching (NPQ), and water-use efficiency (WUE) relative to control under such conditions. Under severe (8% SWC, 27.9 g kg^{-1} SSC) water or salinity stress, *P. euphratica* seedlings had only a fifth of biomass of those under control conditions. It was also associated with damaged PSII and decreases in WUE, the maximal net photosynthetic rate (P_{Nmax}), light-saturation point (LSP), and apparent quantum yield (α). Our results suggested that the soil conditions, where *P.euphratica* seedlings could grow normally, were higher than ~13% for SWC, and lower than ~22.5 g kg^{-1} for SSC, the values, within the seedlings could acclimate to water or salinity stress by adjusting their R/S ratio, improving WUE to limit water loss, and rising NPQ to dissipate excessive excitation energy. Once SWC was lower than 8% or SCC higher than ~28 g kg^{-1}, the seedlings suffered from the severe stress.

Additional key words: chlorophyll fluorescence; photosynthesis; seedling; water and salt stress.

Introduction

Desert riparian forest in the Tarim River Basin, northwestern China, is an important ecosystem that provides valuable services, among which fixation of the mobile dunes in the basin is the most important. Unfortunately, this valuable ecosystem has undergone a great decline in the past decades, primarily as a result of flow regime

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Abbreviations: C_i – intercellular CO_2 concentration; Chl – chlorophyll; E – transpiration rate; F_m – maximal fluorescence in dark-adapted state; F_m' – maximal fluorescence in light-adapted state; F_s – steady-state fluorescence yield; F_v/F_m – maximal quantum yield of PSII photochemistry; F_v'/F_m' – effective quantum use efficiency of PSII; F_0 – minimal fluorescence in dark-adapted state; F_0' – minimal fluorescence in light-adapted state; g_s – stomatal conductance; LCP – light-compensation point; LSP– light-saturation point; L_s – stomatal limitation; NPQ – nonphotochemical quenching; P_N – net photosynthetic rate; P_{Nmax} – leaf maximal net photosynthetic rate; PPFD – photosynthetic photon flux density; PSII – photosystem II; q_p – photochemical quenching; R_D – respiration rate; R/S – root/shoot ratio; SWC – soil water content; SSC – soil salt content; WUE – water-use efficiency; α – apparent quantum yield ; θ – the convexity of the light-response curve.
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alterations (such as a reduction of flooding and groundwater decline in riparian zones) due to human activities and/or climate change (Chen *et al*. 2003). As soil physical and chemical properties are closely related to flow regimes (Castelli *et al*. 2000), these alterations greatly influence the soil water and salinity conditions in the riparian zones, on which riparian plant establishments depend. Therefore, the evaluation of riparian plant response to soil water and salinity gradients is important for understanding the ecosystem decline and further for any restoration effort.

Plant responses to drought and salinity have much in common (Munns 2002). Severe water and salinity stress decreases a plant growth rate, leaf area, biomass accumulation (Rodríguez *et al*. 2005), and it generates osmotic stress (Munns 2002). Together with these aspects, photosynthesis is among the primary processes to be affected. Drought and salt stress leads to a decrease in photosynthetic efficiency (Sayed 2003), chlorophyll (Chl) content in leaves (Fedina *et al*. 2003), CO_2 gain caused by stomatal limitation (Flexas *et al*. 2007), and synthesis of ribulose-1,5-bisphosphate (Bertolli *et al*. 2012) that may further increase a plant susceptibility to photodamage (Krause 1988) and result in irreversible impairment of photosynthetic apparatus (Delfine *et al*. 1999). Plant adaptations to drought and salinity stress involve morphological and physiological mechanisms, such as alterations in cell wall elasticity, leaf area, or biomass compartmentation between shoot and roots (Kozlowski 1991). Plants control water loss *via* stomata closure during drought (Chaves 1991, Sharkey 1990), at the cost of a possible imbalance between photochemical activities in PSII and electron requirement for photosynthesis (Krause 1988), which results in a decrease of carbon assimilation (Chaves 1991).

Chl fluorescence analysis is helpful for understanding changes in photosynthetic apparatus induced by abiotic stresses (Van Heerden *et al*. 2007). Previous works indicate that the changes in the Chl fluorescence parameters are strongly related to environmental factors, such as high CO_2 concentration, temperature, irradiance, salinity, and water deficit (Flexas *et al*. 2007, Zribi *et al*. 2009, Silva *et al*. 2010, Kalaji *et al*. 2011, Song *et al*. 2011, Xue *et al*. 2012). For example, F_v/F_m has been frequently used to evaluate the damage in PSII reaction centers of plants under severe stress (Sayed 2003). Values of F_v/F_m and F_v'/F_m' are effective to indicate the point, at which plants suffer from a stress (Percival *et al*. 2003, Faraloni *et al*. 2011). To attain maximal photosynthetic efficiency and minimal photodamage, plants protect themselves by a dissipation of excess energy in chloroplasts through increasing NPQ in Chl fluorescence emission (Roháček and Barták 1999). It can be evidenced by a great increase in NPQ in *e.g*., *Cerasus humilis* seedlings exposed to water stress, followed by a decrease in subsequent recovery (Song *et al*. 2011, Bertolli *et al*. 2012). In this mechanism, the excitation pressure, resulted from the surplus energy in PSII, is alleviated by diverting light energy into heat (Calatayud *et al*. 1999), which effectively prevents the ATP synthesis from damage and which restrains the reduction in photosynthetic electron transport and phosphorylation (Bertolli *et al*. 2012). Chl fluorescence methods enable to understand different aspects of photosynthesis, such as energy-utilizing strategies and the extent of plant tolerance to environmental stress (Maxwell and Johnson 2000).

P. euphratica responses to stress have attracted much attention (Ma *et al*. 1997, Chen *et al*. 2003, 2006) possibly due to the ecosystem degradation over the past decades. However, the adaptive strategies and tolerance of *P. euphrarica* seedlings to drought and salinity stresses are not well understood. Plant seedlings are more prone subject to environmental stress. This is especially true for *P. euphrarica* seedlings, because (*1*) they establish on riparian zones, where soil water and salinity change greatly over time due to high variations in flow in arid regions, and (*2*) they do not develop a deep root system to get a stable water resource from groundwater.

In this study, we measured the growth and leaf gas exchange of 2-year-old *P. euphratica* seedlings across soil water and salinity gradients under controlled conditions. Our objectives were: (*1*) to assess the morphological and physiological responses of the seedlings to soil water and salinity gradients, (*2*) to determine the critical water and salinity levels that allow the seedlings to grow and survive.

Materials and methods

Plant materials and experimental conditions: The experiments were carried out at the Aksu Water Balance Station, Chinese Academy of Sciences (40°27′N, 80°45′E), which is located *ca*. 30 km north of the Tarim River. The station has an annual average rainfall of *ca*. 45.7 mm and an evaporation potential of 2,500 mm. Average annual sunshine in 2008 and solar radiation were 2,940 h and 6,000 MJ m^{-2}, respectively.

Two-year-old *P. euphratica* seedlings, obtained from a common garden nearby the station, were planted in pots of 24 cm in height and 32 cm in diameter. Each pot was filled with 11 kg of sandy loam with SSC of ~15 g kg^{-1}. Three seedlings were grown in each pot. During two months (in May and June) prior to the onset of treatments, plants were well watered to promote establishments. Then on July 10, experimental treatments were initiated and lasted 60 days. Experiments were conducted outdoor and a rain shelter was used during treatment period to exclude the effects of rain.

Water stress: The seedlings were subjected to 4 SWC treatments: 22% (control, CK_w), 18% (W2), 13% (W3),

and 8% (W4). There were 6 pots in each treatment. SWCs were maintained by weighing and daily water addition. Each pot was weighed daily using an electronic balance (*ACS-15A*, *Shanghai Yousheng Weighing Apparatus Co. Ltd.*, Shanghai, China), then the amount of water needed for desired SWC was calculated and corresponding amount of water was added at 20:00 h local time. Due to evapotranspiration, actual SWCs in pots ranged 21.6–24.0%, 16.8–19.2%, 12.0–14.4%, and 7.2–9.6% for CK_w, W2, W3, and W4 treatments, respectively.

Salinity stress: NaCl solution was used to impose salinity stress on *P. euphratica* seedlings. There were 4 treatments with different NaCl concentrations: 0 mM (control, CK_s), 50 mM (S2), 100 mM (S3), and 200 mM (S4). There were also 6 pots in each treatment. Each pot was supplemented with 100 ml of the corresponding NaCl solution every 5 d. SWC in all pots was maintained at 70–80% of the field capacity throughout the treatment period.

Soil salt content: SSC was measured at the end of the experiment. Soil in each pot was sampled at 5–20 cm depth. Extracts of soil samples (dried soil:deionised water = 50 g:0.25 L) were used for soil salinity measurement. Soil pH was determined by potentiometry method (*pHS-2C*, *Shanghai LIDA Instrument Factory*, China).

Plant growth: Heights and the stem diameters of all plants were measured at the beginning and at the end of the treatments. Destructive harvesting was carried out at the end of the experiment. For each seedling, leaves, stem, and roots were separated. Roots were rinsed in deionized water and carefully blotted with tissue paper. Then the biomasses of different parts were oven-dried at 75ºC until the constant mass.

Gas-exchange measurements: Net photosynthetic rate (P_N), stomatal conductance (g_s), intercellular CO_2 concentration (C_i), and transpiration rate (E) were determined using a portable photosynthesis system (*LI-6400*, *LI-COR Inc*., Lincoln, NE, USA) with a 2 × 3 cm^2 chamber at ambient air CO_2 concentration (380 μmol mol^{-1}). The relative air humidity and leaf temperature in the chamber were maintained at about 35% and 27ºC, respectively. Photosynthetic photon flux density (PPFD) ranged from 1,200 to 1,400 μmol m^{-2} s^{-1}. Measurements were made between 10:30 and 13:30 h, local time, on clear days in September. For each treatment, fully expanded leaves from 6 randomly selected seedlings were measured.

Light-response curves were determined using the chamber with a light source (*6400-02B, LI-COR Inc*., Lincoln, NE, USA). During response-curve measurements, CO_2 concentration, relative air humidity, and leaf temperature in the chamber were maintained at 380 μmol mol^{-1}, 35%, and 27ºC, respectively. PPFD was set at 18 levels, decreasing from 3,500 to 0 μmol m^{-2} s^{-1} at varying intervals. Response-curve measurements were taken on 3 seedlings for each treatment.

Chl fluorescence was measured by the *LI-6400* system with the fluorescence chamber (*LI-6400-40*, *LI-COR Inc*., Lincoln, NE, USA). Measurements, including dark- and light-adapted fluorescence, were made between 11:00 and 13:30 h, local time, on clear days in September, repeated 6 times for each treatment. The minimal (F_0) and maximal (F_m) fluorescences in dark-adapted state were determined with a modulated irradiation (<1 μmol m^{-2} s^{-1}) shortly after keeping the leaves in the dark (2 h). A saturating pulse of 7,000 μmol m^{-2} s^{-1} by 0.8 s was applied for measurements of F_m. The variable fluorescence (F_v) was calculated as $F_v = F_m - F_0$. The leaves were continuously illuminated with actinic light at the intensity of 1,500 μmol m^{-2} s^{-1}, the steady-state (F_s), and maximal (F_m') fluorescence were measured by applying a second saturating pulse. Minimal fluorescence in light-adapted state (F_0') was measured after far-red illumination of the previously exposed leaves. These variables were used to calculate $F_v/F_m = (F_m - F_0)/F_m$, $F_v'/F_m' = (F_m' - F_0')/F_m'$, $q_p = (F_m' - F_s)/(F_m' - F_0')$, and $NPQ = (F_m - F_m')/F_m'$ (Roháček 2002).

Data analysis: WUE was calculated as P_N/E (Galmés *et al*. 2007) and stomatal limitation (L_s) was calculated as $1 - C_i/C_a$, where C_a was the ambient CO_2 concentration (Berry and Downton 1982).

Light-response curve was fitted to a nonrectangular hyperbola model (Farquhar and von Caemmerer 1982) using *SPSS 13.0* (*SPSS*, Chicago, USA). This model was expressed as:

$$P_N = \frac{\alpha PPFD + P_{Nmax} - \sqrt{(\alpha PPFD + P_{Nmax})^2 - 4\theta\alpha PPFD P_{Nmax}}}{2\theta} - R_D$$

where θ is the convexity of the light response curve, α is the initial slope of the linear regression between P_N and PPFD below 200 μmol m^{-2} s^{-1}, and R_D is the dark respiration rate. The light-compensation point (LCP) and light-saturation point (LSP) were calculated as the PPFD at P_N equal(ed) to zero and P_{Nmax} for each curve, respectively.

An one-way *ANOVA* with an the least significant differences (LSD) test at $P<0.05$ and 0.01 was employed to determine the effects of soil water and salinity treatments on the growth and leaf gas-exchange parameters. All statistical tests were performed using *SPSS 13.0* (*SPSS*, Chicago, USA).

Results

Soil pH and salinity: At the end of the experiment, soil pH and salinity were similar across SWC gradients (Table 1), suggesting that soil water treatment had little effect on soil salinity. During salinity treatment, while SSC increased significantly with increasing NaCl concentration, soil pH did not change (Table 1). The soil salinity in S2, S3, and S4 was 18.3 g kg^{-1}, 22.5g kg^{-1}, and 27.9 g kg^{-1}, respectively, after being 10 times irrigated with 100 ml of different NaCl solutions.

Table 1. Soil pH and salinity. Soil samples were taken at 5–20 cm depth in pots. Data are means ± SE (n = 6). The different *capital* and *lowercase letters* indicate significant differences at P<0.01 and 0.05 according to LSD test, respectively, within their own treatments.

Treatment	W1	W2	W3	W4	S1	S2	S3	S4
pH	7.4^{a}	7.6^{a}	7.5^{a}	7.4^{a}	7.6^{a}	7.5^{a}	7.4^{a}	7.4^{a}
Soil salinity [g(NaCl) kg^{-1}(soil)]	14.3^{a}	14.4^{a}	14.6^{a}	14.7^{a}	14.8^{A}	18.3^{B}	22.5^{C}	27.9^{D}

Table 2. Height, stem diameter, and root, stem, and leaf dry mass [g $plant^{-1}$] for *Populus euphratica* seedlings under water- and salt-stress conditions. CK_W, W2, W3, and W4 stand for soil water content of 22%, 18%, 13%, and 8%, respectively and CK_S, S2, S3, and S4 stand for NaCl concentrations of 0, 50, 100 and 200 mM, respectively. Data are means ± SE (n = 18). The different *lowercase letters* indicate significant differences at P<0.05 according to LSD test, respectively, within their own treatments.

Treatments	Height [cm]		Stem diameter [mm]		Biomass [g]				Root/shoot
	0 d	60 d	0 d	60 d	Root	Stem	Leaf	Total	
CK_W	19.80^{a}	52.40^{a}	1.99^{a}	4.76^{a}	8.66^{a}	3.72^{a}	4.71^{a}	17.09^{a}	1.03^{b}
W2	18.10^{a}	42.90^{b}	2.02^{a}	3.77^{b}	4.06^{b}	1.46^{b}	1.58^{b}	7.10^{b}	1.34^{a}
W3	19.17^{a}	38.50^{b}	1.95^{a}	3.64^{b}	2.86^{c}	1.11^{b}	1.23^{bc}	5.20^{c}	1.22^{a}
W4	19.71^{a}	26.90^{c}	2.00^{a}	3.30^{c}	1.01^{d}	0.62^{c}	0.50^{c}	2.13^{d}	0.91^{b}
CK_S	18.10^{a}	42.90^{a}	2.16^{a}	3.77^{a}	3.93^{a}	1.41^{a}	1.53a	6.87^{a}	1.30^{a}
S2	19.80^{a}	36.10^{b}	2.21^{a}	3.42^{a}	2.62^{b}	1.08^{b}	0.92^{b}	4.62^{b}	1.32^{a}
S3	18.90^{a}	27.40^{c}	2.20^{a}	3.17^{a}	1.85^{c}	0.63^{c}	0.73^{c}	3.21^{c}	1.36^{b}
S4	19.10^{a}	24.10^{d}	2.18^{a}	2.83^{b}	0.72^{d}	0.32^{d}	0.21^{d}	1.25^{d}	1.36^{b}

Seedling growth and biomass: Seedling height, base stem diameter, and biomass declined significantly with decreasing SWC and increasing SSC (Table 2). This pattern was particularly clear in biomass, with values for CK_w and CK_s about 8 and 5 times greater than in W4 and S4 treatments, respectively. The root/shoot ratio (R/S) presented different patterns within soil water and salinity experiments (Table 2). In soil water experiment, the greatest R/S occurred in W2 and W3 seedlings, followed by CK_w and it was the lowest in W4. In contrast, R/S increased with SSC in soil salinity experiment.

Leaf gas exchange: The seedlings showed the significant decrease in P_N, g_s, and L_s with increasing both the soil water and the salinity stress (Table 3). The similar pattern was also observed in E. Contrary to it, C_i presented an opposite pattern, with the value increasing with lower SWC and greater SSC (Table 3). For WUE, the greatest value occurred in W2, followed by W3, and both were significantly higher than that of CK_w and W4 in the soil water experiment (Table 3). In the soil salinity experiment, WUE was the greatest in S2, followed by S3 and S4, and all were significantly higher than that of CK_s.

Similar patterns as P_N were also observed across soil water and salinity gradients in P_{Nmax}, α, θ, and LSP calculated from light-response curves, as shown in Table 4. Values of these variables under W4 and S4 treatments decreased at least 30%, compared with controls. As the pattern of C_i, LCP increased significantly with lower SWCs or higher SSCs (Table 4).

Chl fluorescence: Similarly to the above-mentioned pattern, F_v/F_m, F_v'/F_m', and q_P decreased significantly with lower SWCs or higher SSCs (Fig.1 *A*,*B*). NPQ presented different patterns within soil water and salinity experiments, *i.e.*, NPQ significantly increased with SSC in the soil salinity experiment (Fig. 1*B*), whereas in the soil water experiment, the lowest value occurred in W2, significantly lower than CK_w, W3, and W4 (Fig. 1*A*).

Discussion

Effects of soil water and salinity on the growth of *P. euphratica* seedlings: Plants evolved many morpho-physiological characteristics that allow them to survive in adverse conditions (Villagra and Cavagnaro 2006). Phenotypic plasticity is the most intuitive performance for plants to adapt to stress conditions, despite there are many internal and ecological factors, which can limit their expression under a given environmental factor (Valladares 2007). The effect of drought and salinity stress on a plant growth is manifested mainly in the diminution of cell dilation, and it causes the diminution of the biomass. Therefore, the proportion of a biomass reduction under stress in relation to the control can be used to estimate a stress tolerance in a species (Munns 2002). Gindaba *et al*. (2005) found that *Eucalyptus* produced more biomass than the deciduous species under a severe water deficit indicating that *Eucalyptus* was more tolerant to water stress. Our experiments indicated that the growth of the seedlings was significantly limited by the soil water and salinity, as evidenced by seedlings with the lower height under lower SWCs or greater SSCs. The growth of seedlings under severe (8% SWC, 27.9 g kg^{-1} SSC) stress was seriously inhibited as indicated by the higher reduction (~80%) in the height and biomass compared with control. However, the limitation effects of both treatments were more evident on the leaf and the stem than on the root biomass accumulation, resulting in varying increases in R/S of seedlings across SWC and SSC gradients (Table 2). Under stress condition, plant roots usually continue to grow, whereas the shoot growth stops (Wilkinson and Davies 2002), which is favorable for exploiting limited soil resources and improving hydraulic conductance (Pan *et al*. 2011). Thus, the proportionally decreased aboveground biomass, particularly the leaf biomass of the seedlings across SWC and SSC gradients, could be a morphological mechanism that allowed plants to acclimate to stress environments by increasing soil resource acquisition and minimizing water loss (Savé *et al*. 1994).

Table 3. Leaf net photosynthetic rate (P_N), stomatal conductance (g_s), intercellular CO_2 concentration (C_i), transpiration rate (E), water-use efficiency (WUE), and stomatal limitation (L_s) for *Populus euphratica* seedlings under water and salinity treatments. The PPFD was in a range of 1,200−1,400 μmol m^{-2} s^{-1}. CK_W, W2, W3, and W4 stand for soil water contents of 22%, 18%, 13%, and 8%, respectively, CK_S, S2, S3, and S4 stand for NaCl concentrations of 0, 50, 100, and 200 mM, respectively. Data are means ± SE (n = 6). The different *capital* and *lowercase letters* indicate significant differences at P<0.01 and 0.05 according to LSD test, respectively, within their own treatments.

Treatment	P_N [μmol(CO_2) m^{-2} s^{-1}]	g_s [mol(H_2O) m^{-2} s^{-1}]	C_i [μmol mol^{-1}]	E [mmol(H_2O) m^{-2} s^{-1}]	WUE [μmol $mmol^{-1}$]	L_s
CK_W	23.08 ± 1.06^{A}	0.609 ± 0.034^{A}	284 ± 2.35^{a}	11.98 ± 0.61^{A}	1.93 ± 0.35^{A}	0.253 ± 0.015^{A}
W2	21.03 ± 0.56^{A}	0.462 ± 0.014^{B}	285 ± 1.98^{a}	4.366 ± 0.34^{C}	4.82 ± 0.26^{B}	0.250 ± 0.011^{A}
W3	18.10 ± 0.97^{B}	0.350 ± 0.023^{C}	291 ± 2.67^{b}	6.820 ± 0.44^{B}	2.65 ± 0.14^{C}	0.234 ± 0.012^{B}
W4	7.82 ± 0.75^{C}	0.190 ± 0.039^{D}	293 ± 1.55^{b}	3.729 ± 0.26^{C}	2.10 ± 0.13^{A}	0.229 ± 0.014^{B}
CK_S	21.08 ± 0.63^{A}	0.467 ± 0.017^{A}	277 ± 2.88^{a}	6.866 ± 0.48^{A}	3.07 ± 0.057^{a}	0.271 ± 0.018^{A}
S2	16.52 ± 0.74^{B}	0.349 ± 0.008^{B}	282 ± 1.98^{a}	4.31 ± 0.32^{B}	3.83 ± 0.081^{b}	0.258 ± 0.011^{A}
S3	9.47 ± 0.12^{C}	0.162 ± 0.012^{C}	292 ± 5.01^{b}	2.687 ± 0.12^{C}	3.52 ± 0.096^{c}	0.232 ± 0.013^{B}
S4	4.34 ± 0.53^{D}	0.080 ± 0.010^{D}	304 ± 6.12^{c}	1.257 ± 0.24^{D}	3.45 ± 0.033^{c}	0.200 ± 0.015^{C}

Table 4. Leaf maximum net photosynthetic rate (P_{Nmax}), apparent quantum yield (α), light-compensation point (LCP), and light-saturation point (LSP) for *Populus euphratica* seedlings under water- and salt-stress conditions. CK_w, W2, W3, and W4 stand for soil water content of 22%, 18%, 13%, and 8%, respectively, and CK_s, S2, S3, and S4 stand for NaCl concentrations of 0, 50, 100, and 200 mM, respectively. Data are means ± SE (n = 6). Means denoted by the different *capital* and *lowercase letters* are significantly different at P<0.01 and 0.05 according to LSD test, respectively, within their own treatments.

Treatment	P_{Nmax} [μmol(CO_2) m^{-2} s^{-1}]	α [μmol m^{-2} s^{-1}]	LCP [μmol m^{-2} s^{-1}]	LSP [μmol m^{-2} s^{-1}]	θ
CK_w	35.9 ± 2.78^{A}	0.060 ± 0.004^{A}	32 ± 3^{a}	916 ± 73^{A}	0.721 ± 0.005^{A}
W2	31.2 ± 3.62^{B}	0.054 ± 0.006^{B}	45 ± 6^{b}	723 ± 65^{B}	0.689 ± 0.005^{B}
W3	22.4 ± 1.85^{C}	0.049 ± 0.002^{C}	53 ± 4^{c}	610 ± 36^{C}	0.452 ± 0.004^{C}
W4	15.2 ± 2.33^{D}	0.042 ± 0.003^{D}	62 ± 3^{d}	491 ± 52^{D}	0.317 ± 0.004^{D}
CK_s	33.5 ± 3.32^{A}	0.054 ± 0.005^{A}	44 ± 5^{a}	810 ± 87^{A}	0.638 ± 0.003^{A}
S2	17.7 ± 4.41^{B}	0.042 ± 0.006^{B}	46 ± 7^{b}	540 ± 89^{B}	0.402 ± 0.003^{B}
S3	14.7 ± 3.12^{B}	0.037 ± 0.003^{C}	48 ± 6^{c}	431 ± 68^{C}	0.326 ± 0.005^{C}
S4	5.8 ± 1.96^{C}	0.033 ± 0.004^{C}	52 ± 5^{c}	219 ± 32^{D}	0.195 ± 0.002^{D}

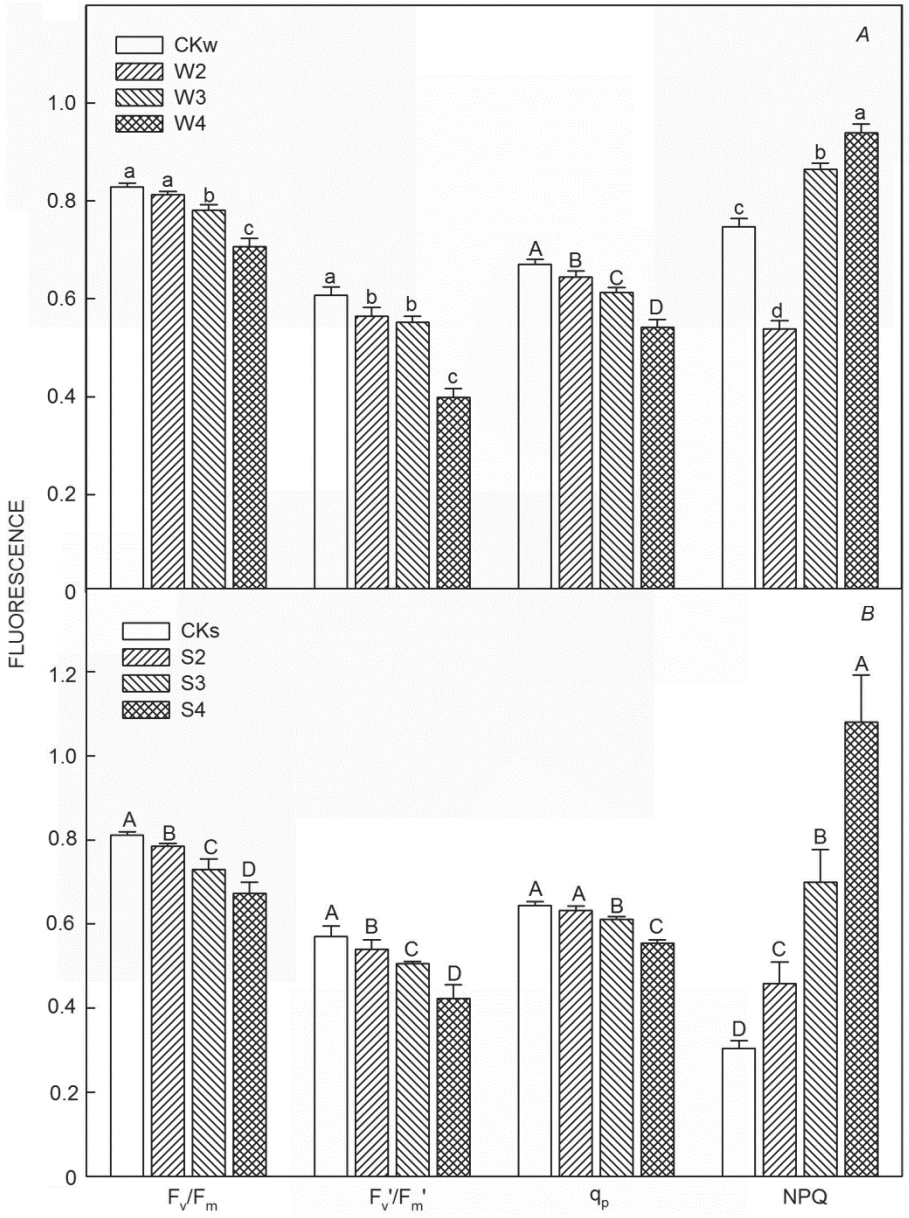

Fig.1. The chlorophyll fluorescence of *Populus euphratica* seedlings exposed to water and salinity treatments. Maximal quantum yield of PSII photochemistry (F_v/F_m), effective quantum-use efficiency of PSII (F_v'/F_m'), photochemistry quenching coefficient (q_P), and nonphotochemical quenching (NPQ) of the seedlings under water stress (*A*) (CK_w,W2, W3, and W4 stand for soil water contents of 22%, 18%, 13%, and 8%, respectively) and salt stress (*B*) (CK_s, S2, S3, and S4 stand for NaCl concentration of 0, 50, 100, and 200 mM, respectively). Bars are means ± SE (n = 6). The different *capital* and *lowercase letters* indicate a significant difference at the p<0.01 and 0.05 according to LSD test, respectively, within their own treatments.

Effects of water and salinity on photosynthesis: Reductions in P_N, g_s, and L_s for *P. euphratica* seedlings across SWC and SSC gradients were not associated with a parallel reduction in C_i (Table 3). In general, P_N reduction as response to an initial osmotic shock, caused by moderate drought or salinity stress, resulted from a stomata closure (Sharkey 1990). Thus, P_N decline has been reported as an early response (24 h) to salinity stress in the seedlings (Wang *et al*. 2007). Whereas under severe, long-term stress, the reduction is largely due to nonstomatal limitations (Ma *et al*. 1997), as a result of the inhibition of photosynthetic electron transport as well as the impairment of metabolic and photophosphorylation capacity (Sharkey and Seemann 1989). The limitation of photosynthesis by stomata occurs only when P_N reduction is associated with decreased g_s and C_i, as well as increased L_s (Farquhar and Sharkey 1982). Therefore, P_N reduction of the seedlings was largely due to nonstomatal factors in our study.

Photosynthesis is the most important process for

forming organic matter in plants, and the effects of water and salinity on photosynthesis determine the growth and survival of the plants. Though there was a decline in P_N for mild (18% SWC, 18.3 g kg^{-1} SSC) and moderate (13% SWC, 22.5 g kg^{-1} SSC) stress-treated seedlings, the notable reduction in E and high WUE indicated that the seedlings were possible to alleviate water- or salinity stress by controlling their water loss and improving WUE. These results suggested that the seedlings under mild and moderate drought and salinity stress could maintain water relations as efficiently as possible through self-regulation strategies (Gindaba *et al*. 2005, Silva *et al*. 2010). However, such self-regulation mechanism cannot offset the stress effects on photosynthesis once the seedlings were exposed to severe soil water or salinity stress, as evidenced by declined P_N accompanied with low WUE for seedlings grown at W4 (8% SWC) or S4 (27.9 g kg^{-1} SSC). This might mean that such water and salinity conditions might not be feasible for seedlings.

Plants with higher LSP and lower LCP can use a wider irradiation range and they have higher photosynthetic capacity. Our light-response results indicated that LSP, P_{Nmax}, α, and θ of the seedlings decreased, whereas LCP dramatically increased with the increasing drought or soil salinity stress, which was consistent with reports concerning of *Cyclobalanopsis* under water stress (Wei *et al*. 2009) and of *P. euphratica* exposed to salinity stress (Wang *et al*. 2007). Our results confirmed that the quantum yield of CO_2 assimilation declined and the light adaptability of the seedlings became weaker with the increasing soil water or salinity stress.

Nonstomatal limitation of photosynthesis in drought- and salt-stressed plants may be a result of impairment of photochemical activities (Souza *et al*. 2004), that may be attributed to the reduced RuBP regeneration, the reduced amount of functional Rubisco and/or other metabolic responses (Pankovic *et al*. 1999). Our Chl fluorescence results showed that the photochemical activities of the seedlings were significantly limited under soil water and salinity treatments.

F_v/F_m is a good indicator for the effect of environmental stresses on photosynthesis, especially for the activity of PSII. Zribi *et al*. (2009) found the constant F_v/F_m associated with a progressive decrease in F_v'/F_m' in tomato undergone 4-week salt-stress treatment, indicating the photosynthetic electron transport still intact (Signarbieux and Feller 2011). Song *et al*. (2011) reported that the reduction of F_v/F_m may suggest a disorder in PSII. Therefore, our findings of the significant decline in F_v/F_m, combined with the decrease in the photosynthetic rate, might indicate some degree of damage in the photosynthetic apparatus and the occurrence of the photoinhibition. According to Souza *et al*. (2004), the significant reduction in the F_v/F_m, F_v'/F_m', and q_p indicated the occurrence of an overexcitation of the photochemical systems. The large decrease in F_v'/F_m' and q_p, which was found in the seedlings grown in the severe stress treatments, *i.e.*, W4 and S4, further confirmed the damage of PSII in seedlings.

NPQ represents the proportion of excitation energy dissipated at the expense of photochemical utilization (Brestic *et al.* 1995). Once photosynthetic capacity is too low to use all incident radiation absorbed, plants dissipate the excess excitation energy in the thylakoids as heat to avoid the photoinhibition (Song *et al*. 2011) or allocate extra energy to photorespiration, which acts as an alternative electron sink that reduces the possible effects of oxidative stress (Lawlor and Cornic 2002). In our experiments, the pattern of NPQ, increasing with the soil drought or salinity stress, coincided with the pattern of decreasing P_N under the same conditions, indicated that *P. euphratica* seedlings dissipated more and more excitation energy as the soil drought or salinity stress increased to protect the photosynthetic apparatus from further photodamage.

Conclusions: Growth and photosynthesis of *P. euphratica* seedlings were highly dependent upon the soil water and salinity conditions. They were limited under mild and moderate stress conditions, but they were able to grow normally through a serie of strategies, such as changing the biomass allocation, improving WUE, increasing heat dissipation to prevent photosynthetic reaction centers from damage. Under severe water and salinity stress, the seedlings showed markedly the reduced biomass and photosynthesis, associated with the decreased WUE and impaired PSII function, which indicated that above-mentioned mechanisms could not offset the stress effects. Our results suggested that the top soil drying and salinization of riparian habitats along the Tarim River resulted from recent flow regime changes, might be unfavorable for the regeneration of *P. euphratica* forests.

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