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# Water transport and water use efficiency differ among *Populus euphratica* Oliv. saplings exposed to saline water irrigation

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**Abstract:** *Populus euphratica* Oliv. is a unique woody tree that can be utilized for vegetation restoration in arid and semi-arid areas. The effects of saline water irrigation (0.00, 2.93, 8.78 and 17.55 g/L NaCl solutions) on water transport and water use efficiency (WUE) of *P. euphratica* saplings were researched for improving the survival of *P. euphratica* saplings and vegetation restoration in arid and semi-arid areas of Xinjiang, China in 2011. Results showed that hydraulic conductivity and vulnerability to cavitation of *P. euphratica* saplings were more sensitive in root xylem than in twig xylem when irrigation water salinity increased. Irrigation with saline water concentration less than 8.78 g/L did not affect the growth of *P. euphratica* saplings, under which they maintained normal water transport in twig xylem through adjustment of anatomical structure of vessels and kept higher WUE and photosynthesis in leaves through adjustment of stomata. However, irrigation with saline water concentration up to 17.55 g/L severely inhibited the photochemical process and WUE of *P. euphratica* saplings, resulting in severe water-deficit in leaves and a sharp reduction in water transport in xylem. Thus, it is feasible to irrigate *P. euphratica* forest by using saline groundwater for improving the survival of *P. euphratica* saplings and vegetation restoration in arid and semi-arid areas of Xinjiang, China.

**Keywords:** photosynthesis; photochemical process; water use efficiency; hydraulic conductivity; cavitation resistance

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## 1 Introduction

Soil salinization is a global concern, particularly in arid and semi-arid areas (Evelin et al., 2009; Parihar et al., 2015; Baath et al., 2017). The total area of salt-affected soils in the world, including saline and sodic soils currently comprising approximately  $8.31 \times 10^8$  hm<sup>2</sup>, is continually increasing (Martinez-Beltran and Manzur, 2005; Nikolskii-Gavrilov et al., 2015; Mehdi-Tounsi et al., 2017). Salt stress is one of the most critical factors hindering the growth and development of plants, especially due to excess Na<sup>+</sup> (FAO, 2008; Baath et al., 2017; Hu et al., 2017). This is because high salt concentrations, especially of Na<sup>+</sup> and Cl<sup>-</sup>, decrease the osmotic potential of soil solution, thereby lowering the availability of water to plants and resulting in dehydration stress of plants

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(Brinker et al., 2010). Moreover, excess  $\text{Na}^+$  concentration negatively affects plant nutrition and ion homeostasis (Shabala and Cuin, 2008). High  $\text{Cl}^-$  concentration interferes with  $\text{NO}_3^-$  and  $\text{HPO}_4^{3-}$  absorption in plants, causing nutrient imbalances and negatively-affected carbohydrate transportation (Apostol et al., 2004; López-Perez et al., 2007). Since most plant species have very limited capacities to cope with excess  $\text{Na}^+$ , productivity of saline soil is greatly diminished and plant growth may even become impossible (Brinker et al., 2010). The adaptive mechanisms of salt-tolerant species have attracted considerable research interests in recent years (Munns, 2005; Yamaguchi and Blumwald, 2005; Munns and Tester, 2008; Chen and Polle, 2010; Wang et al., 2016; Baath et al., 2017; Mehdi-Tounsi et al., 2017).

Up to now, adaptive mechanisms including osmotic and metabolic adjustment and  $\text{Na}^+$  absorption and allocation of salt-tolerant plants to salt stress have been reported (Kang and Zhang, 2004; Schachtman and Goodger, 2008; Rahnama et al., 2010). Water uptake, transport and use in roots, xylem and leaves constitute the complete water path and play important roles in the survival of terrestrial vascular plants. However, researches regarding water transport and water use efficiency (WUE) in salt-tolerant plants is still limited, and the related studies have been restricted to the effects of mild salt stress over short time periods (from a few minutes to 24 h or a few days) (Guo et al., 2006; Horie et al., 2011; Muries et al., 2011; Sutka et al., 2011; Calvo-Polanco et al., 2014). Knowledge of the effects of severe salt stress over long time periods on water uptake, water transport, and WUE in salt-tolerant plants is not enough.

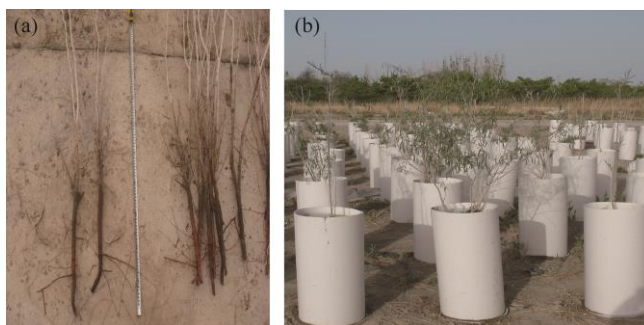
*Populus euphratica* Oliv. is distributed from northwestern Africa, western South Asia to Central Asia (Browicz, 1977). In fact, *P. euphratica* growing on river banks or areas with deep water tables in China accounts for 54% of the whole areas in the world (Hukin et al., 2005; Zhuang et al., 2010). In Xinjiang, *P. euphratica* accounts for 89% of the areas in China (Chen et al., 2006). The groundwater salinity is 3.00–10.00 g/L, or even reaches up to 10.00–30.00 g/L in some areas in Xinjiang (Wang et al., 2010). *P. euphratica* is a salt-tolerant species that can grow in saline environments (Sixto et al., 2005; Fu et al., 2010; Rajput et al., 2016). Thus, *P. euphratica* is an optimal woody tree utilized for vegetation restoration due to the limited water resources and high salinity of groundwater in arid and semi-arid areas (Abassi et al., 2014). In this study, we studied the effects of saline water irrigation (0.00, 2.93, 8.78 and 17.55 g/L NaCl solutions) on the water transport and WUE of *P. euphratica* saplings for three months and tried to answer the following scientific questions: (1) how saline water changes the water transport in xylem and WUE in leaves when *P. euphratica* saplings are irrigated by saline water? And (2) what is the saline water threshold that *P. euphratica* maintains its normal growth?

## 2 Materials and methods

### 2.1 Materials and experimental design

*P. euphratica* saplings used in the study were collected from a nursery in the lower reaches of the Tarim River, Xinjiang, China. Bare-rooted *P. euphratica* saplings (2–3-year old) with similar heights and diameters were transferred to polyvinyl chloride (PVC) pipes from the nursery to the Xinjiang Agricultural University Test Station in Urumqi in April 2011 (Fig. 1). Each pipe was placed with one sapling. The PVC pipes (32 cm in diameter and 75 cm in depth with an artificially sealed bottom) were filled with approximately 60 kg soil. The soils were sandy loam with a total salt content of 0.69 ( $\pm 0.15$ ) g/kg. Soil pH was 7.8 ( $\pm 0.1$ ). Soil bulk density was 1.34 ( $\pm 0.36$ ) g/cm<sup>3</sup> and field capacity was 0.33 ( $\pm 0.07$ ) cm<sup>3</sup>/cm<sup>3</sup>. Soil organic matter content was 6.05 ( $\pm 0.52$ ) g/kg. Available nitrogen, phosphorus and potassium contents were 18.98 ( $\pm 2.01$ ), 2.50 ( $\pm 0.31$ ) and 640.00 ( $\pm 83.00$ ) mg/kg, respectively. The saplings were maintained under the above soil for one month until the saplings sprouted. During this period, soil moisture in the 0–30 cm soil layer was maintained in the range of 15%–20% by using drinking water. Soil moisture was measured with the FDR-100 Soil Water Content Sensor (FDR-100, Shijiazhuang, China). After one month, the healthy saplings with similar heights and diameters were treated with four saline water irrigation treatments, i.e., 0.00 (Control), 2.93 ( $S_1$ ), 8.78 ( $S_2$ ) and 17.55 g/L ( $S_3$ ) NaCl

solutions for three months. Each treatment was comprised of five saplings. All of saplings under saline treatments were irrigated with different NaCl concentrations every 7 d, and the amount of irrigation water for each sapling was 2 L every time to maintain the soil moisture in the pipe close to saturated soil water content. In order to evenly irrigate the soil in the pipes without disturbing soil, we inserted a porous tube (2.5 cm in diameter) into the soil permanently in each pipe when we transplanted the plant. The porous was 8.0 cm away from the saplings, and there were pores with a 0.3-cm diameter spaced at 5.0 cm intervals on the porous. Irrigation occurred via the porous tube. A waterproof tarp was utilized to prevent rain influencing. The tarp was temporarily installed above the canopy if it rained. The irrigation experiment was ended in August 2011. During the experiment, the average daily temperature was 24°C, the average daily relative humidity was approximately 45%, and the average daily potential evaporation was 300–400 mm.



**Fig. 1** Pictures of plant material and experimental condition. (a), 2–3-year old *P. euphratica* saplings before transplant; (b), growth of *P. euphratica* saplings in polyvinyl chloride (PVC) pipes.

## 2.2 Gas exchange and chlorophyll fluorescence

The second or third fully expanded leaf of each tree was selected to measure the net photosynthetic rate ( $P_n$ ), stomatal conductance ( $g_s$ ), transpiration rate ( $T_r$ ), intercellular  $\text{CO}_2$  concentration ( $C_i$ ) and air  $\text{CO}_2$  concentration ( $C_a$ ) on clear days. These measurement data were automatically recorded by a portable gas exchange system (Li 6400, LiCOR, Lincoln, NE, USA) at different photosynthetically active radiation (PAR) levels. Considering the PAR values during plants' growing period (April to September) varied from 1871 to 2044  $\text{MJ}/\text{m}^2$  in the Tarim River, Xinjiang, China (Li and Xie, 2000), we set the following PAR level, i.e., 0, 20, 50, 100, 400, 600, 800, 1000, 1200, 1500 and 2000  $\mu\text{mol}/(\text{m}^2\cdot\text{s})$ , with an ambient  $\text{CO}_2$  concentration of 375  $\mu\text{mol}/\text{mol}$  and an air temperature of 28°C. WUE was calculated from the  $P_n/T_r$  ratio. The dark-adapted maximum fluorescence ( $F_m$ ), minimum fluorescence ( $F_0$ ), light-adapted steady-state chlorophyll fluorescence ( $F_v$ ) and maximum fluorescence ( $F_m'$ ) in the leaves of *P. euphratica* were measured by a portable modulated fluoro-meter (Mini-Pam-2000, Walz, Germany). The maximum quantum efficiency of photosystem II (PS II) was calculated as  $F_v/F_m = (F_m - F_0)/F_m$ , and the potential activity of PS II was calculated by the  $F_v/F_0$  ratio. We calculated the actual photochemical energy conversion quantum yield of PS II (Yield) according to the method of Genty et al. (1989). The electron transport rate (ETR) was calculated as  $\text{ETR} = \text{Yield} \times \text{PAR} \times 0.5 \times 0.84$ . We calculated the quantum yields of regulated (Y(NPQ)) and non-regulated (Y(NO)) non-photochemical energy loss in PS II according to Kramer et al. (2004). We estimated the light-adapted minimum fluorescence ( $F_0'$ ) using the following equation:  $F_0' = F_0 / (F_v/F_m + F_0/F_m')$  (Oxborough and Baker, 1997). The Y(NPQ)/Y(NO) ratio, a measure of the capacity of photo-protective reactions (Klughammer and Schreiber, 2008) was also calculated.

## 2.3 Leaf water potential ( $\Psi$ ) and relative water content

We measured leaf  $\Psi$  of *P. euphratica* saplings at the predawn (06:00, Local Standard Time (LST)) and midday (13:00) using a HR-33T Dew Point Microvolt meter (WESCOR, USA). One healthy leaf in the upper part of each tree crown was immediately collected in polyethylene bags at predawn and midday. We cut three small discs with a diameter of 5 mm for avoiding the vein from each leaf, and then placed these discs in C-52 sample chambers connected to the HR-33T

Dew Point Microvoltmeter. After the discs samples were equilibrated with chamber air in the C-52 sample chamber for 2 h, the dew-point value ( $\mu\text{V}$ ) was measured.  $\Psi$  (MPa) was measured as follows:  $\Psi = \mu\text{V}/7.5$ . After the measurements of  $\Psi$ , 2–3 leaves from each tree were collected to determine the fresh weight (FW) of leaves, and then these leaves were placed in deionized water for 24 h to absorb water to saturation. The saturated leaves were removed from the deionized water, cleaned water on the surface of leaves, and then determined their saturation fresh weight (SFW). The clean and saturated leaves were placed in a drying oven at  $105^\circ\text{C}$  for 30 min, and then dried at  $75^\circ\text{C}$  for at least 24 h until the weight of leaves was stabilized, then we determined the dry weight (DW). The relative water content (RWC) of leaves was calculated as follows:  $\text{RWC} = (\text{FW} - \text{DW}) / (\text{SFW} - \text{DW}) \times 100\%$ .

## 2.4 Xylem hydraulic conductivity and xylem vulnerability to cavitation

Xylem hydraulic conductivity ( $K$ ) was measured by a xylem embolism meter (Bronkhorst, Montigny-les-cormeilles, France). The vessel length of *Populus* varied from 4.88 to 7.61 cm (Zhang, 2013) and the maximum vessel length of *P. euphratica* was approximately 8.70 ( $\pm 2.60$ ) cm (Ayup et al., 2015). The fresh twigs or lateral roots with diameters of 2–5 mm from each tree were cut into 3–5 segments with 8–12 cm in length. Twig and root segments were placed in deionized water and immediately connected to the xylem embolism meter. Initial xylem hydraulic conductivity ( $K_{p0}$ ) of sample was measured at a low hydraulic pressure (1–2 kPa for roots and 2–3 kPa for twigs) using 1 mM  $\text{CaCl}_2/\text{MgCl}_2/\text{KCl}$  mixed solution ( $\text{pH}=6$ ) filtered through a 0.22- $\mu\text{m}$  filter membrane. Then, the sample was flushed at a high pressure (175 kPa) with the same mixed solution for 10 min, and a new  $K$  value was re-measured at a low pressure. The procedure was repeated until  $K$  reached the maximum xylem hydraulic conductivity ( $K_{\text{max}}$ ).

The curves of xylem vulnerability to cavitation were measured by air-injection method (Salleo et al., 2004; Trifilò et al., 2007) through a pressure collar (Pressure Chamber Instrument, Model 1505D-EXP-XC-100, PMS Instrument Company, USA). The pressure collar sequentially applied pressures ( $P$ ) of 0.5, 1.0, 1.5, 2.0, 2.5, 3.0, 3.5, 4.0 and 4.5 MPa to the sample. Each pressure level was maintained for 3 min, and  $K_p$  (xylem hydraulic conductivity under an applied pressure) was measured at a hydraulic pressure range of 1–3 kPa using the same mixed solution. The specific hydraulic conductivity ( $K_{\text{sp}}$ ) was calculated as follows:  $K_{\text{sp}} = K_p \times \text{sample length} / \text{sample area}$ , and the percentage loss of hydraulic conductivity (PLC) was calculated as  $\text{PLC} = 100\% \times (1 - K_{\text{spi}} / K_{\text{smax}})$ , where  $K_{\text{spi}}$  was the  $K_{\text{sp}}$  value under specific air pressure level ( $\text{kg}/(\text{m} \cdot \text{s} \cdot \text{MPa})$ );  $K_{\text{smax}}$  was the maximum specific hydraulic conductivity ( $\text{kg}/(\text{m} \cdot \text{s} \cdot \text{MPa})$ ).

## 2.5 Xylem vessel anatomy

Three fresh twigs with 1–2-cm in length were collected from each tree in the morning, then immediately placed into 2-cm-high glass bottles and fixed in FAA solution (75% ethanol:formalin:acetic acid=90:5:5). A sliding microtome (Leica CM1900, Wetzlar, Germany) was used to sample cross-sections of the twigs. The cross-sections were then stained with 0.1% (w:v) safranin (staining red lignified cell walls) and 1% (w:v) fast green (staining blue-green cellulosic walls). We photographed the stained cross-sections by a microscope (Olympus, BX51, Japan) then measured and calculated average vessel diameter, average vessel density, thickness of vessel wall, thickness of interval between vessels and mechanical strength of vessel wall ( $h = t^2/b^2 \times 100\%$ , where  $h$  is the mechanical strength of vessel wall (%);  $t$  is the inner diameter of vessel ( $\mu\text{m}$ ); and  $b$  is the thickness of interval between vessels ( $\mu\text{m}$ )) by a WinCELL image analysis system (WinCELL Regent Instruments Inc., Sainte-Foy, QC, Canada). Average vessel diameter was calculated as follows:  $\text{average vessel diameter} = (\sum D^4/N)^{1/4}$ , where  $D$  is the inner diameter of vessel ( $\mu\text{m}$ ); and  $N$  is the total vessel numbers.

## 2.6 Soil salt content

At the end of the experiment, three soil samples from each PVC pipe were taken using a soil auger in the 0–30 and 30–60 cm soil layers, and then mixed the samples. The mixed sample was

air-dried, ground and passed through a 2-mm sieve. Then, three soil samples (each sample was 50 g) were taken from the mixed soil. Filtered soil leachate (50 mL) that was a solution of soil sample and water mixed in a ratio of 1:5 and was filtered after a 3-min oscillation, was placed in a dried pan, where the filtered soil leachate was dried in a thermostat water bath. The drying residue was then dried at 105°C for at least 4 h, until its weight was stabilized. Total soluble salt (SS) content in soil was calculated by the following equation:  $SS=(m_t-m_p)\times d\times 1000/m$ , where SS was the total soluble salt content in soil (g/kg);  $m$  was the soil sample weight (g);  $m_t$  was the weight of dried residue and pan (g);  $m_p$  was the weight of the dried pan (g); and  $d$  was the extraction times from the soil leachates. The amount of salt that a plant absorbed from the soil in the PVC pipes was calculated according to the following equations:

$$M_{\text{absorb}}=M_{\text{initial}}+M_{\text{irrigation}}-M_{\text{measure}}, \quad (1)$$

$$M_{\text{initial}}=c_1\times m, \quad (2)$$

$$M_{\text{irrigation}}=c_2\times d\times t, \quad (3)$$

$$M_{\text{measure}}=(c_3+c_4)/2\times m, \quad (4)$$

where  $M_{\text{absorb}}$  was the salt amount that plant absorbed from soil (g);  $M_{\text{initial}}$  was the initial salt amount of soil (g);  $M_{\text{irrigation}}$  was the salt amount brought from the saline irrigation water (g);  $M_{\text{measure}}$  was the salt amount of soil at the end of the experiment (g);  $c_1$  was the soil soluble salt content before transplant (g), and the value of  $c_1$  was 0.69 g/kg in this study;  $c_2$  was the saline concentration of irrigation water (g/kg);  $d$  was the amount of irrigation water every time (L), and in this study the value of  $d$  was 2 L;  $t$  was the times of irrigation;  $c_3$  and  $c_4$  were the soil soluble salt contents in the 0–30 and 30–60 cm soil layers at the end of the experiment, respectively (g/kg); and  $m$  was the soil weight in each pipe (kg), and in this study the value of  $m$  was 60 kg. Because the irrigation water was from drinking water under the control treatment, the salt amount in the drinking water was negligible during the experimental period.

## 2.7 Statistical analyses

Pearson's correlation, one-way analysis of variance (ANOVA), least-significant difference (LSD) and Tukey multiple comparisons were conducted using the SPSS statistical package (SPSS 13.0, Chicago, IL, USA) in this study for statistical analysis. Plots were made using Sigmaplot 12.5 software (Systat Software, San Jose, CA, USA).

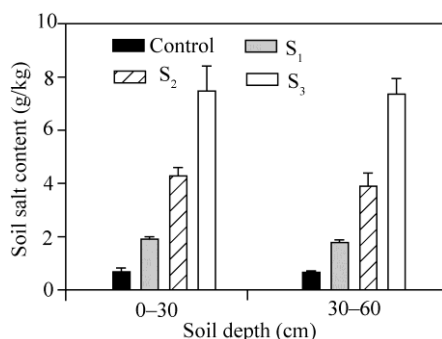
## 3 Results

### 3.1 Soil salt content and salt absorbed by *P. euphratica* saplings

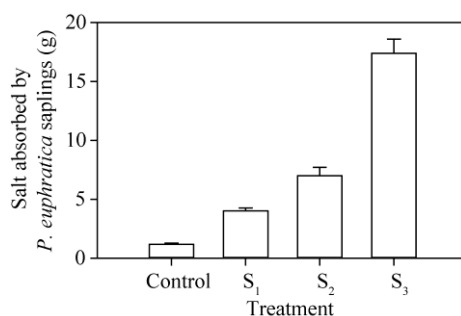
Soil salt contents were similar in the beginning, and their differences appeared after several months of continuous exposure to different saline water irrigation treatments. The differences of soil salt contents were apparent in the 0–30 and 30–60 cm soil layers (Fig. 2). Soil salt contents under saline water irrigation treatments significantly increased compared with control treatment ( $P<0.05$ ). Soil salt content at the 0–30 cm soil layer was higher than that in the 30–60 cm soil layer (Fig. 2), indicating that surface soil might had a stronger accumulation of salinity due to the intense evaporation, and plant roots tended to absorb soil salinity in the 30–60 cm soil layer where root system may have been mainly distributed. For control treatment, soil salt content was lower in the 30–60 cm soil layer than in the 0–30 cm soil layer (0.69 g/kg), demonstrating that *P. euphratica* saplings absorbed salt from soil. Moreover, the amount of salt absorbed by *P. euphratica* saplings increased with the increase in saline water concentration (Fig. 3).

### 3.2 Photosynthesis, WUE and chlorophyll fluorescence

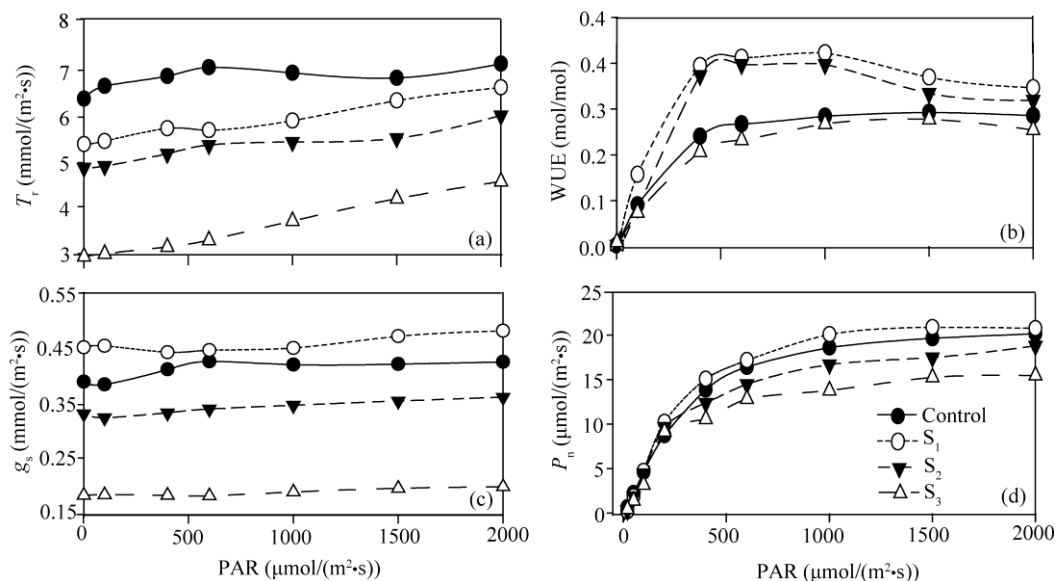
Figure 4 showed the results of photosynthesis and WUE in the leaves of *P. euphratica* under different saline water irrigation treatments.  $P_n$  increased in  $S_1$ -treated *P. euphratica* saplings compared with control plants, but decreased in  $S_2$ -treated and  $S_3$ -treated plants (Fig. 4d). An ANOVA revealed that  $P_n$  did not significantly differ among  $S_1$ -treated,  $S_2$ -treated and control plants ( $P>0.05$ ). However, it decreased by 22.83% in  $S_3$ -treated plants compared with control



**Fig. 2** Soil salt contents in the 0–30 and 30–60 cm soil layers under different saline water irrigations. Control, 0.00 g/L NaCl; S<sub>1</sub>, 2.93 g/L NaCl; S<sub>2</sub>, 8.78 g/L NaCl; S<sub>3</sub>, 17.55 g/L NaCl. Bars indicate standard errors;  $n=15$ .



**Fig. 3** Salt absorbed by *P. euphratica* saplings under different saline water irrigations. Control, 0.00 g/L NaCl; S<sub>1</sub>, 2.93 g/L NaCl; S<sub>2</sub>, 8.78 g/L NaCl; S<sub>3</sub>, 17.55 g/L NaCl. Bars indicate standard errors;  $n=15$ .



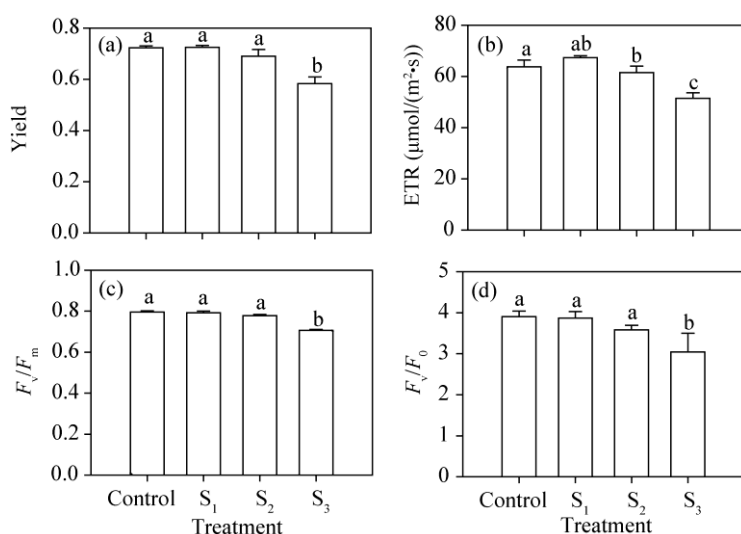
**Fig. 4** Transpiration rate ( $T_r$ ; a), water use efficiency (WUE; b), stomatal conductivity ( $g_s$ ; c) and net photosynthetic rate ( $P_n$ ; d) of *P. euphratica* saplings under different saline water irrigations and different photosynthetically active radiation (PAR) levels. Control, 0.00 g/L NaCl; S<sub>1</sub>, 2.93 g/L NaCl; S<sub>2</sub>, 8.78 g/L NaCl; S<sub>3</sub>, 17.55 g/L NaCl.

plants ( $P<0.05$ ). Moreover,  $g_s$  in S<sub>3</sub>-treated plants significantly decreased by 55.64% compared with control plants ( $P<0.05$ ; Fig. 4c), which suggested that more than 50.00% of the stomata were closed or stomatal aperture decreased when the saline concentration was increased to 17.55 g/L. Salinity also decreased  $T_r$  of *P. euphratica* saplings, but a significant difference was only observed in S<sub>3</sub>-treated plants, i.e., 48.54% decreases compared with control plants ( $P<0.05$ ; Fig. 4a). WUE

significantly increased in  $S_1$ -treated and  $S_2$ -treated plants compared with control plants ( $P<0.05$ ; Fig. 4b). However, it decreased sharply when the concentration of saline was increased to 17.55 g/L ( $P<0.05$ ).

Similarly, photochemical quantum PS II yield (Yield), maximum photochemical PS II efficiency ( $F_v/F_m$ ) and potential PS II activity ( $F_v/F_0$ ) in  $S_1$ -treated and  $S_2$ -treated plants did not differ significantly from those of control plants, but a significant decrease in  $S_3$ -treated plants was observed ( $P<0.05$ ; Fig. 5). In addition, ETR increased in  $S_1$ -treated plants and decreased in  $S_3$ -treated plants compared with control plants, but no significant differences were observed between 2.93 and 8.78 g/L saline water irrigation treatments.

Saline water irrigation significantly increased Y(NPQ) compared with control plants, but Y(NPQ) significantly decreased when saline water concentration was increased from 8.78 to 17.55 g/L (Table 1). Increased salinity also enlarged Y(NO), but a significant difference was only observed when concentration of saline irrigation water was increased to 17.55 g/L (Table 1). Y(NPQ)/Y(NO) ratio was higher in control plants than those of in salt-treated plants.



**Fig. 5** (a) Photochemical quantum yield of PS II (Yield); (b) electron transport rate (ETR); (c) maximal photochemical efficiency of PS II ( $F_v/F_m$ ); and (d) potential activity of PS II ( $F_v/F_0$ ) of *P. euphratica* saplings under different saline water irrigations. Control, 0.00 g/L NaCl;  $S_1$ , 2.93 g/L NaCl;  $S_2$ , 8.78 g/L NaCl;  $S_3$ , 17.55 g/L NaCl. Bars indicate standard errors;  $n=15$ . Different lowercase letters indicate significance among different saline water irrigations at  $P<0.05$  level.

**Table 1** Quantum yield of regulated energy loss (Y(NPQ)), quantum yield of non-regulated energy loss (Y(NO)) and Y(NPQ)/Y(NO) ratio of *P. euphratica* saplings under different saline water irrigations

Treatment	Y(NPQ)	Y(NO)	Y(NPQ)/Y(NO) ratio
Control	0.180±0.076 <sup>a</sup>	0.084±0.011 <sup>a</sup>	2.143±0.017 <sup>a</sup>
$S_1$	0.269±0.090 <sup>bc</sup>	0.162±0.069 <sup>a</sup>	1.661±0.051 <sup>a</sup>
$S_2$	0.386±0.156 <sup>b</sup>	0.203±0.100 <sup>a</sup>	1.901±0.095 <sup>a</sup>
$S_3$	0.293±0.087 <sup>c</sup>	0.379±0.132 <sup>b</sup>	0.773±0.090 <sup>b</sup>

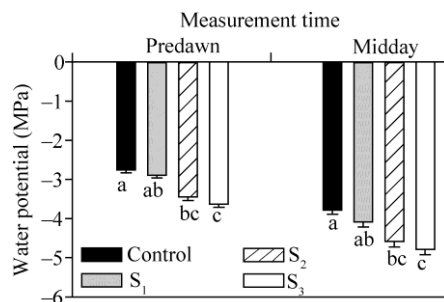
Note: Different lowercase letters indicate significance among different saline water irrigations at  $P<0.05$  level. Control, 0.00 g/L NaCl;  $S_1$ , 2.93 g/L NaCl;  $S_2$ , 8.78 g/L NaCl;  $S_3$ , 17.55 g/L NaCl. Mean±SE;  $n=15$ .

### 3.3 Water potential ( $\Psi$ ) and relative water content (RWC)

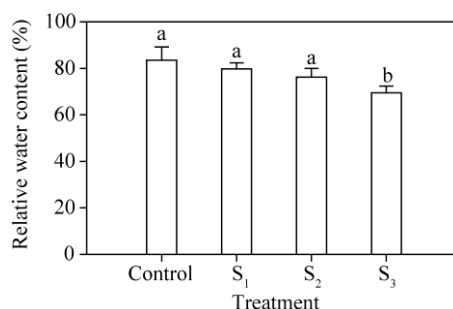
Saline water irrigation decreased the values of  $\Psi$  in leaves of *P. euphratica* saplings at predawn and midday compared with control plants, and significant decreases in  $\Psi$  were observed in  $S_2$ -treated and  $S_3$ -treated plants (Fig. 6). Moreover, the values of  $\Psi$  in leaves of *P. euphratica* sapling under all treatments at midday were significantly lower than at predawn ( $P<0.05$ ; Fig. 6). Generally,  $\Psi$  in leaves at predawn substantially represented the soil  $\Psi$ . This result implied that a

high concentration of saline irrigation water (8.78 and 17.55 g/L) reduced soil  $\Psi$ , under which plant could not absorb water from soil or even caused water seepage from the plant.

Usually, the higher RWC of leaves means a higher resistance to environmental stresses. Saline water irrigation decreased the RWC in leaves of *P. euphratica* saplings compare with control plants, and a significant decrease in RWC was observed in  $S_3$ -treated plants (Fig. 7) indicating that *P. euphratica* saplings experienced a severe salt stress under 17.55 g/L saline concentration.



**Fig. 6** Water potential in leaves of *P. euphratica* saplings at predawn and midday under different saline water irrigations. Control, 0.00 g/L NaCl;  $S_1$ , 2.93 g/L NaCl;  $S_2$ , 8.78 g/L NaCl;  $S_3$ , 17.55g/L NaCl. Bars indicate standard errors;  $n=15$ . Different lowercase letters indicate significance among different saline water irrigations at the same measurement time at  $P<0.05$  level.



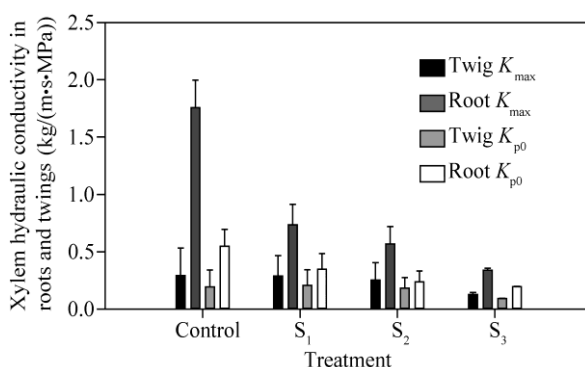
**Fig. 7** Relative water content in leaves of *P. euphratica* saplings under different saline water irrigations. Control, 0.00 g/L NaCl;  $S_1$ , 2.93 g/L NaCl;  $S_2$ , 8.78 g/L NaCl;  $S_3$ , 17.55g/L NaCl. Bars indicate standard errors;  $n=15$ . Different lowercase letters indicate significance among different saline water irrigations at  $P<0.05$  level.

### 3.4 Xylem hydraulic conductivity ( $K$ ) and anatomical structure of xylem vessels

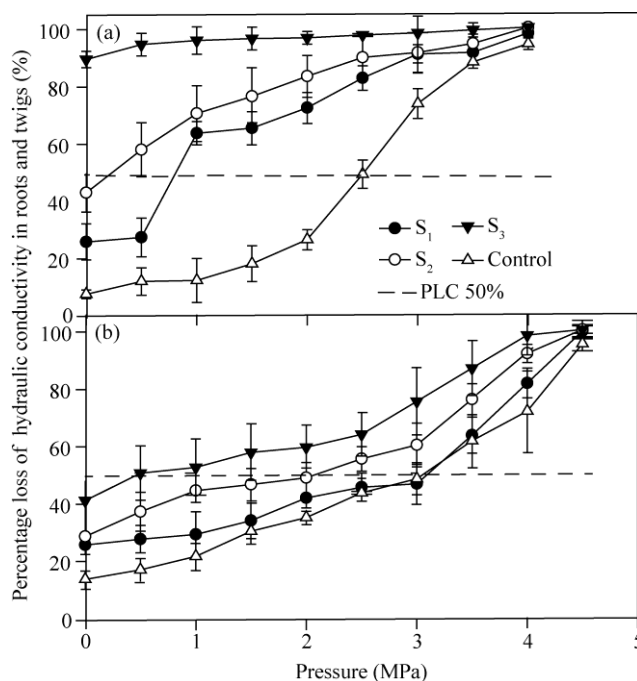
$K_{\max}$  was significantly higher than  $K_{p0}$  under all treatments ( $P<0.05$ ; Fig. 8), which suggested that the xylem of *P. euphratica* saplings could adjust  $K$  over a broad range. The values of  $K_{\max}$  in twigs of *P. euphratica* saplings under control,  $S_1$ ,  $S_2$  and  $S_3$  treatments were 1.51, 1.39, 1.38 and 1.36 times those of  $K_{p0}$ , respectively, and they were 3.21, 2.11, 2.38 and 1.73 times those of  $K_{p0}$  in roots of *P. euphratica* saplings, respectively. These results suggested that the adjustment range of  $K$  in twigs and roots of *P. euphratica* saplings gradually decreased as the concentration of saline increased. Moreover, the values of  $K_{p0}$  and  $K_{\max}$  in roots of *P. euphratica* saplings were significantly higher than those in twigs under both control and salinity treatments (Fig. 8), indicating that water transportation in roots was stronger than that in twigs.

Compared with control plants, the values of  $K_{p0}$  in roots of *P. euphratica* saplings under  $S_1$ ,  $S_2$  and  $S_3$  treatments significantly decreased by 36.40%, 56.98% and 52.35%, respectively, and the values of  $K_{\max}$  significantly decreased by 58.23%, 67.71% and 80.74%, respectively ( $P<0.05$ ; Fig. 8). These results showed that saline water irrigation significantly restrained the water transport in roots of *P. euphratica* saplings. However, compared with control plants, both the  $K_{p0}$  and  $K_{\max}$  in twigs of *P. euphratica* saplings under  $S_1$  and  $S_2$  treatments exhibited no significant differences, but they significantly decreased by 56.75% and 52.35%, respectively under  $S_3$  treatment ( $P<0.05$ ; Fig. 8), suggesting that severe salt stress restrained water transport in twigs of *P. euphratica* saplings.

For xylem vulnerability to cavitation, approximately 50% PLC was recorded in roots and twigs of control plants under 2.5 and 3.0 MPa pressures; and greater than 95% PLC was found in roots and twigs of control plants under 4.0 and 4.5 MPa pressures (Fig. 9). Under  $S_1$  treatment, greater than 50% PLC was found in roots and twigs under 1.0 and 3.0 MPa pressures. Approximately 98% and 100% PLC were found in roots and twigs under 4.0 MPa pressure, respectively, thus completely inhibiting the water transport in xylem. Under  $S_2$  treatment, greater than 50% PLC was observed in roots under 0.5 MPa pressure, and more than 95% PLC in roots and twigs was record under 3.5 and 4.0 MPa pressures. Under  $S_3$  treatment, 88% PLC were recorded in roots even under 0.0 MPa pressure and 95% PLC under 1.0 MPa pressure, which was significantly higher than those of twigs, indicating the xylem vulnerability to cavitation in roots was significantly higher than in twigs under severe salt stress.

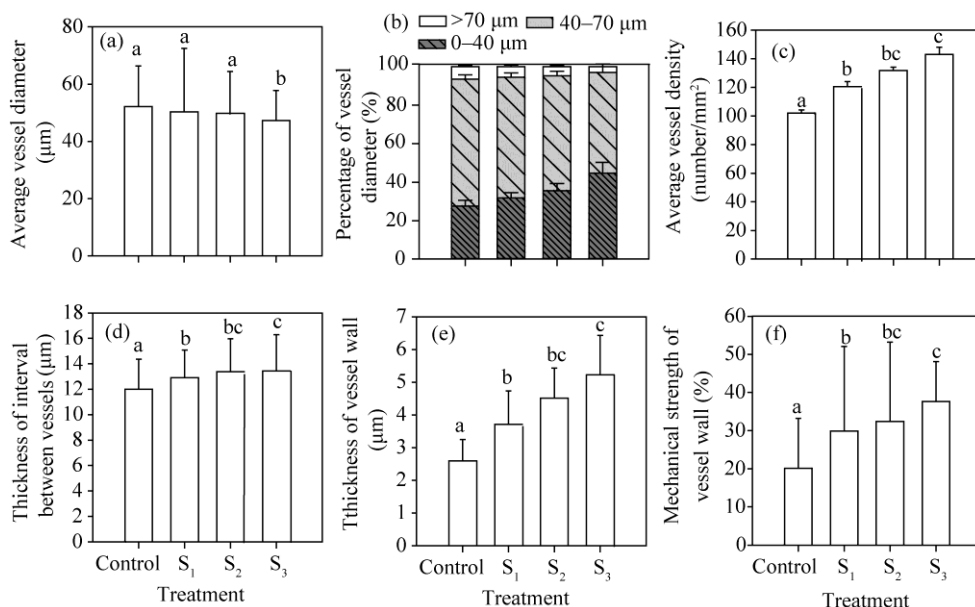


**Fig. 8** Xylem hydraulic conductivity in roots and twigs of *P. euphratica* saplings under different saline water irrigations.  $K_{p0}$ , initial xylem hydraulic conductivity;  $K_{max}$ , maximum xylem hydraulic conductivity; control, 0.00 g/L NaCl;  $S_1$ , 2.93 g/L NaCl;  $S_2$ , 8.78 g/L NaCl;  $S_3$ , 17.55 g/L NaCl. Bars indicate standard errors;  $n=15$ .



**Fig. 9** Percentage loss of hydraulic conductivity (PLC) in roots (a) and twigs (b) of *P. euphratica* saplings under different saline water irrigations. Bars indicate standard errors;  $n=15$ . Control, 0.00 g/L NaCl;  $S_1$ , 2.93 g/L NaCl;  $S_2$ , 8.78 g/L NaCl;  $S_3$ , 17.55 g/L NaCl. PLC 50%, 50% loss of hydraulic conductivity.

Average vessel diameters of *P. euphratica* saplings decreased in salt-treated plants compared with control plants, and a significant decrease was found in  $S_3$ -treated plants ( $P<0.05$ ; Fig. 10a). Similarly, saline water irrigation decreased the percentage of wide vessels (40–70 and  $>70\ \mu\text{m}$ ) and increased the percentage of narrow vessels (0–40  $\mu\text{m}$ ), and a significant decrease in the percentage vessel diameter was observed under  $S_3$  treatment ( $P<0.05$ ; Fig. 10b). Salt-treated plants significantly exhibited the increases in vessel density, vessel wall thickness, thickness of interval between vessels and mechanical strength of vessel wall ( $P<0.05$ ; Figs. 10c–f).



**Fig. 10** Anatomical characteristics of xylem vessels of *P. euphratica* saplings under different saline water irrigations. Control, 0.00 g/L NaCl;  $S_1$ , 2.93 g/L NaCl;  $S_2$ , 8.78 g/L NaCl;  $S_3$ , 17.55 g/L NaCl. Bars indicate standard errors;  $n=15$ . Different lowercase letters indicate significant differences among different saline water irrigations at  $P<0.05$  level.

## 4 Discussion

### 4.1 Water transport of *P. euphratica* saplings under different saline water irrigation

Studies have reported that mild salt stress over a short-term (from a few minutes to 24 h or a few days) period could facilitate the activity or function of aquaporins (AQPs) or increase the accumulation of osmotic adjustments for increasing  $K$  (Guo et al., 2006; Horie et al., 2011; Muries et al., 2011; Sutka et al., 2011; Calvo-Polanco et al., 2014; Meng and Fricke, 2017). However, other studies demonstrated that high concentrations of NaCl in the cytoplasm decreased the activity or concentration of AQPs, leading to a large reduction in root  $K$  (Carvajal et al., 2000; Martínez-Ballesta et al., 2003, 2008; Nedjimi, 2009, 2014). Our study showed that saline water irrigation caused strong decreases in initial and maximum hydraulic conductivities, as well as cavitation resistance of roots (Fig. 7). This seemed that saline water irrigation might inhibit the activity/concentration of AQPs or osmotic adjustments in the root xylem cells of *P. euphratica* saplings. Increasing concentration of saline irrigation water also reduced  $K$  adjustment range in roots (Fig. 7); moreover,  $K$  and vulnerability to cavitation of *P. euphratica* saplings were more sensitive to salt stress in roots than in twigs. These results demonstrated that the capability of *P. euphratica* saplings to tolerate saline water irrigation might constitute a root-born process, in which it controlled NaCl ion loading into the xylem by decreasing  $K$  in roots (Chen et al., 2003; Sun et al., 2009).

Different from the roots, the high saline water concentration (17.55 g/L) instead of the mild (2.93 g/L) and moderate (8.78 g/L) salinities significantly reduced the hydraulic conductance in twigs of *P. euphratica* saplings. This indicated that xylem in twigs might possess an adjustment

mechanism for maintaining high hydraulic efficiency to adapt to mild and moderate salt stresses. Studies found that salt stress could regulate  $K$  by changing the anatomical structure of vessels (Ali et al., 1999; López-Perez et al., 2007; Navarro et al., 2007; Silva et al., 2008). According to the Hagen-Poiseuille relationship,  $K$  depended on the anatomic structure of xylem (Rajput et al., 2016). Typically, a larger vessel diameter and density were associated with higher  $K$  (Bass, 1982). However, larger vessel diameters were easier to be embolized, thus hindering water transport in xylem due to narrow vessel wall, low thickness between vessel walls and low mechanical strength of vessel wall (Zimmermann, 1983). An LSD or Tukey test indicated that, although vessel diameter in twigs of  $S_1$ -treated and  $S_2$ -treated plants decreased compared with control plants, the differences were not significant ( $P>0.05$ ). However, vessel density, vessel wall thickness, thickness between vessel walls and vessel wall mechanical strength in twigs in  $S_1$ -treated and  $S_2$ -treated plants significantly increased compared with control plants ( $P<0.05$ ). These results indicated that *P. euphratica* saplings could maintain  $K$  for the effective water transport in twigs under mild or moderate salt stress by increasing vessel density, vessel wall thickness, and vessel wall mechanical strength for compensating the negative effects of the reduction in vessel diameter. On the contrary, the vessel diameter significantly decreased by approximately 10% in  $S_3$ -treated plants compared with control plants ( $P<0.05$ ; Fig. 4), but the vessel density, vessel wall thickness, thickness between vessel walls and mechanical strength of vessel wall did not significantly increase ( $P>0.05$ ; Fig. 4). This result suggested that severe salt stress significantly increased xylem embolism and inhibited  $K$  that finally reduced the water transport in twigs.

#### 4.2 WUE of *P. euphratica* saplings under different saline water irrigation

Previous researches have suggested that salinity reduced plant photosynthesis (Sobrado, 2001; López-Berenguer et al., 2006; Navarro et al., 2007; Fernández-García et al., 2014; Baath et al., 2017). Moreover,  $g_s$  reduction was the initial and most profound cause of the decrease in photosynthetic rate (James et al., 2002). Compared with control plants, our data showed that the  $P_n$ ,  $g_s$  and WUE of *P. euphratica* sapling leaves increased with decreased  $T_r$  in  $S_1$ -treated plants, but WUE increased with decreases in  $P_n$ ,  $g_s$  and  $T_r$  in  $S_2$ -treated plants, while all of  $P_n$ ,  $g_s$ ,  $T_r$  and WUE decreased in  $S_3$ -treated plants. The findings indicated that leaves of *P. euphratica* sapling enduring mild, moderate and severe salt stresses utilized different adaptation mechanisms to maintain WUE.

In  $S_1$ -treated plants, *P. euphratica* sapling improved WUE by closing a part of stomata and selectively increasing the conductivity of those opened stomata. Significant decreases in water potential and RWC of *P. euphratica* leaves were also not observed when saline concentration increased from 0.00 to 2.93 g/L, which indicated that there was no obvious water-deficit in plants because the Yield, ETR,  $F_v/F_m$  and  $F_0/F_m$  in  $S_1$ -treated plants did not significantly decrease. Y(NPQ) significantly increased in  $S_1$ -treated plants, but Y(NO) did not significantly increase, indicating that  $S_1$ -treated plants dissipated excess PS II light energy via a non-photochemical quenching process. It was an important photo-protection mechanism that helped to maintain electron transportation chain and energy supply for photosynthesis to promote plant growth (Bellot et al., 2004; Zhu et al., 2014).

In  $S_2$ -treated plants, water potential of *P. euphratica* leaves significantly reduced, but RWC did not exhibit an obvious difference ( $P>0.05$ ) compared with control plants. Meanwhile, WUE increased with the decreases in  $P_n$ ,  $g_s$  and  $T_r$ . This indicated that, although the leaves of *P. euphratica* saplings had a water-deficit resulting from lower  $K$  in roots under 8.78 g/L saline concentration, they could maintain a high WUE by decreasing  $g_s$  and  $T_r$ . Results of fluorescence parameters also suggested that the decrease of photosynthesis in  $S_2$ -treated plants could be attributed the stomatal factors. Moreover, relative high  $K$  in twigs maintained RWC of leaves, thus avoiding osmotic stress in *P. euphratica* sapling in  $S_2$ -treated plants.

In  $S_3$ -treated plants, sharp decreases in  $P_n$ ,  $g_s$ ,  $T_r$ , WUE, water potential and RWC of leaves accompanied by sharp reductions in fluorescence parameters (Yield, ETR,  $F_v/F_m$  and  $F_0/F_m$ ) were found. Moreover, Y(NO) of *P. euphratica* leaves significantly increased. These results suggested that the decrease in photosynthesis and WUE in  $S_3$ -treated plants was due to the non-stomatal factors resulting from photo-damage in leaves, because *P. euphratica* saplings could not effectively alleviate and dissipate excess light energy when saline concentration was increased to

17.55 g/L. Therefore, leaves of *P. euphratica* saplings experienced a severe water-deficit under severe salt stress. Meanwhile, significant reductions of  $K$  in roots and twigs under severe salt stress aggravated the lack of water for *P. euphratica* saplings, which would finally inhibit the growth of *P. euphratica* saplings, or caused them to die.

### 4.3 Soil desalination by planting *P. euphratica*

Study found that *P. euphratica* was tolerant to salt stress by absorbing salt (Zhang, 2014). Our results validated that *P. euphratica* saplings did absorb salt from soil, and the absorbed salt increased with the increases in saline concentration (Figs. 2 and 3). He et al. (2012) found that the soil was desalted when *P. euphratica* was irrigated with 1.20–3.00 g/L saline water, and 1.20–12.00 g/L saline water irrigation did not seriously affect the growth of *P. euphratica*. In our study,  $P_n$ ,  $g_s$ ,  $T_r$ , WUE, yield,  $F_v/F_m$ ,  $F_v/F_0$ , ETR,  $Y(NPQ)$ ,  $Y(NO)$ ,  $Y(NPO)/Y(NO)$ ,  $\Psi$ , RWC and  $K$  in twigs of *P. euphratica* saplings did not show significant differences in  $S_1$ -treated and  $S_2$ -treated plants compared with control plants, however, they were significantly decreased or increased in  $S_3$ -treated plants (Figs. 3–8). These results indicated that *P. euphratica* saplings could tolerate saline water irrigation with low and moderate saline concentrations ( $\leq 8.78$  g/L). Usually, the concentration of NaCl in agricultural irrigation drainage ranged from 0.01–0.11 to 1.03–27.42 g/L (Liang, 2006) and the saline concentration of groundwater ranged from 3.00–10.00 g/L in Xinjiang (He et al., 2012). Thus, it is feasible to irrigate *P. euphratica* forest by using saline groundwater or agricultural irrigation drainage for improving the survival of *P. euphratica* saplings and vegetation restoration in arid and semi-arid areas of Xinjiang, China.

## 5 Conclusions

This study was conducted to test  $K$ , vessel anatomy, gas exchange, chlorophyll fluorescence,  $\Psi$  and RWC of *P. euphratica* saplings irrigated with different saline concentrations (0.00, 2.93, 8.78, and 17.55 g/L NaCl). Through the experiment, the following conclusions were made: (1)  $K$  and vulnerability to cavitation in roots of *P. euphratica* saplings were more sensitive than those of in twigs; and (2) *P. euphratica* could desalt from salinization soil and tolerate the saline water irrigation less than 8.78 g/L. However, overly high saline water irrigation (17.55 g/L) severely decreased water transport and WUE, and caused severe water-deficit, which finally led to lower growth or death of *P. euphratica* saplings.

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