

Full Length Research Paper

## Effects of salt and water stress on plant biomass and photosynthetic characteristics of Tamarisk (*Tamarix chinensis* Lour.) seedlings

Wei Wang<sup>1,2</sup>, Renqing Wang<sup>1,2</sup>, Yifu Yuan<sup>1,2</sup>, Ning Du<sup>1,2</sup> and Weihua Guo<sup>1,2\*</sup>

<sup>1</sup>Institute of Ecology and Biodiversity, School of Life Sciences, Shandong University, Jinan 250100, P. R. China.  
<sup>2</sup>Shandong Provincial Engineering and Technology Research Center for Vegetation Ecology, Shandong University, Jinan 250100, P. R. China.

Accepted 31 October, 2011

*Tamarix chinensis* Lour. (Tamarisk) is regarded as a potential shrub that improves the marginal lands, and is conversely considered as an invasive species in many areas. This study conducted controlled experiments to investigate the biomass accumulation, allocation and photosynthetic responses of *T. chinensis* seedlings to different salt and water conditions. The results showed that *T. chinensis* seedlings died when soil salt content attained 16 to 20 g kg<sup>-1</sup>; total biomass, root biomass, shoot biomass and leaf biomass decreased by 63.3, 56.3, 70.6 and 62.4% respectively, from 0 to 16 g kg<sup>-1</sup> (added NaCl content), and decrease by 37.9, 25.3, 48.4 and 37.9%, respectively, from 60 to 20% field capacity (FC, soil moisture). Water deficit led to earlier peaks of net photosynthetic rate (P<sub>N</sub>) during the day. Relative rate of electron transport (ETR) decreased, but optimal quantum yield of photosystem II (F<sub>v</sub>/F<sub>m</sub>) showed no significant difference (P<0.05) with water deficit (from 60 to 20% FC); soil salt significantly decreased P<sub>N</sub> and transpiration rate (E), and also decreased ETR and F<sub>v</sub>/F<sub>m</sub> when soil moistures was 40 or 20% FC. Increased soil salt content had no significant effect (p>0.05) on biomass allocation of *T. chinensis* seedlings, while water deficit significantly favoured root biomass accumulation. *T. chinensis* seedlings were able to maintain high leaf gas exchange rates under 20% FC, but water use efficiency (WUE) decreased and sufficient water supply may increase the ability of *T. chinensis* to survive in higher soil salinity conditions.

**Keywords:** Salt cedar, biomass allocation, gas-exchange, fluorescence, photosystem II.

### INTRODUCTION

Study of relationships between plants and their environmental conditions is one of the most popular subjects in ecological studies, and these studies are helpful in understanding the responses to changing environmental conditions. Among variety of environmental factors, soil drought and salinization are two worldwide problems that limit plant growth (Munns, 2002). Although, plant responses to salt and water stress have much in common, salinity leads to many metabolic changes identical to those caused by water stress, and there are still salt-

specific effects, for example Na<sup>+</sup> accumulation in leaves which results in necrosis and premature leaf senescence (Munns, 2002), and may disrupt enzymatic processes dependent on K<sup>+</sup>, due to the increasing Na<sup>+</sup>/K<sup>+</sup> ratio (Ehling et al., 2007). Nowadays, with the improvement of portable open gas-exchange systems, the measurements of leaf and canopy photosynthetic rate has become more accurate and convenient (Long and Bernacchi, 2003). As compared to the external parameters by gas-exchange measurement, the measurement of chlorophyll fluorescence has been proven to be a unique indicator of photosynthesis, and pulse-amplitude-modulation (PAM) fluorometry in conjunction with the saturation pulse method which have been widely applied (Ralph and Gademann, 2005). Such techniques have been proven to

\*Corresponding author. E-mail: guo\_wh@yahoo.com. Fax: +86 0531-88363573.

**Table 1.** Schedule for the addition NaCl solution using salt treatments design.

2008	30 June	5 July	10 July	15 July	20 July
S1	—	—	—	—	+
S2	—	—	—	+	+
S3	—	—	+	+	+
S4	—	+	+	+	+
S5	+	+	+	+	+

2009	21 June	24 June	27 June	30 June
S2	—	+	—	+
S4	+	+	+	+

S0, 0 g kg<sup>-1</sup>; S1, 4 g kg<sup>-1</sup>; S2, 8 g kg<sup>-1</sup>; S3, 12 g kg<sup>-1</sup>; S4, 16 g kg<sup>-1</sup>; S5, 20 g kg<sup>-1</sup>. The experiment was arranged for five soil salt treatments by gram of salt per kilogram of soil. '+' means 0.68 l NaCl solution (1 mol l<sup>-1</sup>) was added, and '−' means not added.

be valuable to study the effects of salt and water stress on plant growth (Bongi and Loreto, 1989; Wu, 2008; Zhang et al., 2009). As an old world genus occurring in ancient Mediterranean region, *Tamarix* exists in habitats varying from drought areas to humid areas (Cui et al., 2010). *Tamarix* invasions are reported from riparian zones in western America (Shafrroth and Briggs, 2008) and Australia (Griffin et al., 1989).

These invasions resulted in many ecological problems, such as considerable water consumption and replacement of native species; and lots of money have been spent to control and eradicate them in these areas. Due to the wide range of adaptability to different ecological environment and high endurance of adversity, *Tamarix* is reported in China to be an excellent sand-fixing shrub (Zhang et al., 2002).

It also serves as a windbreak for preventing desertification and erosion in arid areas (Li et al., 2004) and potential bio-energy resources for marginal land utilization (Li et al., 2010).

Furthermore, it is reported that *Tamarix chinensis* is a useful species in preventing sea water intrusion in coastal areas of northern China, and the distribution of *T. chinensis* is influenced significantly by ground water, soil salinity (Cui et al., 2010) and fire (Stromberg and Rychener, 2010). In China, *T. chinensis* is mainly distributed in Yellow River Delta (Gaskin and Schaal, 2002); an area that is well known for its frequent water-salinity perturbations (Weng, 2006).

The objectives of this study were to quantify the effects of varied soil salt and water conditions on biomass accumulation and allocation of *T. chinensis* seedlings; to investigate the physiological responses of *T. chinensis* seedlings to varied salt and water conditions by gas exchange and chlorophyll fluorescence measurements; and to discuss the interactions between salt and water on plant growth.

## MATERIALS AND METHODS

### Study site

The controlled experiment was conducted in a ventilative greenhouse in order to exclude the influence of precipitation; other environmental conditions were coherent with local environment. The experiment was conducted at Fanggan Research Station of Shandong University, Shandong Province, China (36°26'N, 117°27'E). The area has a warm temperate monsoon climate, with an average temperature of 13 ± 1°C, and an average annual precipitation of 700 ± 100 mm, most of which falls during the summer (Xu et al., 2009).

One-year-old *T. chinensis* seedlings were collected from a nursery in the Forestry Bureau of Dongying City (37°24'37"N, 118°40'46"E) in April 2008 and April 2009. In order to normalize the individual divergences, diameters and weights of branch cuttings were measured as group basis. Then each selected branch cutting of *T. chinensis* (5 cm long) were planted in plastic pots (32 × 29 cm, height × diameter) on 21 April 2008 and 15 April 2009. Soils were air-dried to constant weight. The chemical composition of air-dried soil was organic matter (16.40 g kg<sup>-1</sup>), total N (1.11 g kg<sup>-1</sup>), total P (1.12 g kg<sup>-1</sup>) and total K (23.08 g kg<sup>-1</sup>). Air-dried sandy loam soils were filtered by sieve (diameter 3 mm mesh), and then put into lab-graded plastic pots. Each pot contained 10 kg of air-dried soil.

### Treatments design

The controlled experiment was made to run for two years (2008 and 2009). In 2008, the effects of salt stress on plant biomass and dry matter allocation were tested. The experiment was arranged for five soil salt treatments by gram of salt per kilogram of soil [0 (S0), 4 (S1), 8 (S2), 12 (S3), 16 (S4), 20 (S5) g kg<sup>-1</sup>]. 0.68 l NaCl solution (1 mol l<sup>-1</sup>) was added every five days from 30 June, 2008 (Table 1). Each pot was weighed at 18:00 every day to keep the soil moisture stable [60% field capacity (FC)]. Each pot had a plastic plate on the bottom to collect exuded salt, which would be added in the pots again. All the treatments got to requirement simultaneously on 20 July, 2008, and then lasted for six weeks.

In 2009, the effects of salt and water stress on plant biomass and photosynthetic characteristics were measured. The experiment was arranged for two soil salt levels [0 (S0), eight (S2), 16 (S4) g kg<sup>-1</sup>], and three water supply levels [60 (W1), 40 (W2) and 20% (W3)]

**Table 2.** Survival ratio of *T. chinensis* L. seedlings under different soil salt and water conditions.

Year	Treatment	S0 (%)	S1 (%)	S2 (%)	S3 (%)	S4 (%)	S5 (%)
2008	W1	100	100	100	100	100	All dead
2009	W1	100	-	100	-	16.7	-
2009	W2	100	-	100	-	All dead	-
2009	W3	100	-	100	-	All dead	-

Soil NaCl content: S0, 0 g/kg<sup>-1</sup>; S1, 4 g/kg<sup>-1</sup>; S2, 8 g/kg<sup>-1</sup>; S3, 12 g/kg<sup>-1</sup>; S4, 16 g/kg<sup>-1</sup>; S5, 20 g kg<sup>-1</sup>; W1, 0%; W2, 40%; W3, 20% of field capacity.

FC]. Thus, the treatments were arranged for 9 treatments: S0W1, S0W2, S0W3, S2W1, S2W2, S2W3, S4W1, S4W2 and S4W3. 0.68 M NaCl solution (1 mol l<sup>-1</sup>) was added every three days from 21 June (Table 2); soil moisture was controlled by weighing pots at 18:00 every day. The treatments got to requirement till 30 June, and then lasted for eight weeks. Each treatment had six pots, and four pots were harvested for biomass measurement at last.

#### Measurements and calculations

Diurnal variation of *T. chinensis* gas-exchange characteristics were measured with a portable leaf gas exchange system (CI-340, CID inc., WA98607, USA), on 12 August 2009, a sunny day. Leaflets of terminal branches at middle layer (classified by height) were measured at 3:00, 6:00, 8:00, 10:00, 12:00, 14:00, 16:00, 18:00, 21:00 and 24:00 (24 h) and four clusters of leaflets were measured for each treatment. Net photosynthetic rate ( $P_N$ ), transpiration rate (E), stomata conductance ( $g_s$ ) and water use efficiency (WUE) were calculated. Chlorophyll fluorescence measurements (rapid light curves of chlorophyll fluorescence) were carried out using a pulse amplitude modulation chlorophyll fluorometer (Mini-PAM, Walz GmbH, Effeltrich, Germany). Leaves were adapted to the dark for more than 30 min by dark leaf-clips (DLC-8, Walz GmbH, Effeltrich, Germany) to ensure complete relaxation of all light reaction centers. The minimum chlorophyll fluorescence ( $F_0$ ), actual fluorescence intensity (F) and maximum chlorophyll fluorescence ( $F_m$ ) were recorded. Maximum quantum yield of photosystem II was calculated: (PS II) [ $F_v / F_m = (F_m - F_0) / F_m$ ] (Maxwell and Johnson, 2000), effective quantum yield (Yield) and relative rate of electron transport (ETR), photochemical quenching ( $qP$ ) and non-photochemical quenching (NPQ) (Schreiber et al., 1986).

The biomass were measured in September; four individuals per treatment were harvested, all the plant parts were dried at 85°C for 48 h, after that root biomass (RB), stem biomass (SB) and leaf biomass (LB) were measured by electronic balance, total biomass (TB = RB+SB+LB), root to shoot ratio (R/S = RB/SB), root dry mass ratio (RB/TB = RB/TB), stem dry mass ratio (SB/TB = SB/TB), leaf dry mass ratio (LB/TB = LB/TB) which were then calculated.

#### Statistical analysis

Analysis of variance (ANOVA) and Tukey's method for multiple comparisons (Godfrey, 1985) at P≤0.05 were performed in order to determine the significance of the variations in the groups under different treatments. All the statistical analyses were performed using the SPSS 13.0 software package (SPSS Inc., Illinois, USA).

## RESULTS

#### Survival ratio

The intervals of adding NaCl solution were five days in

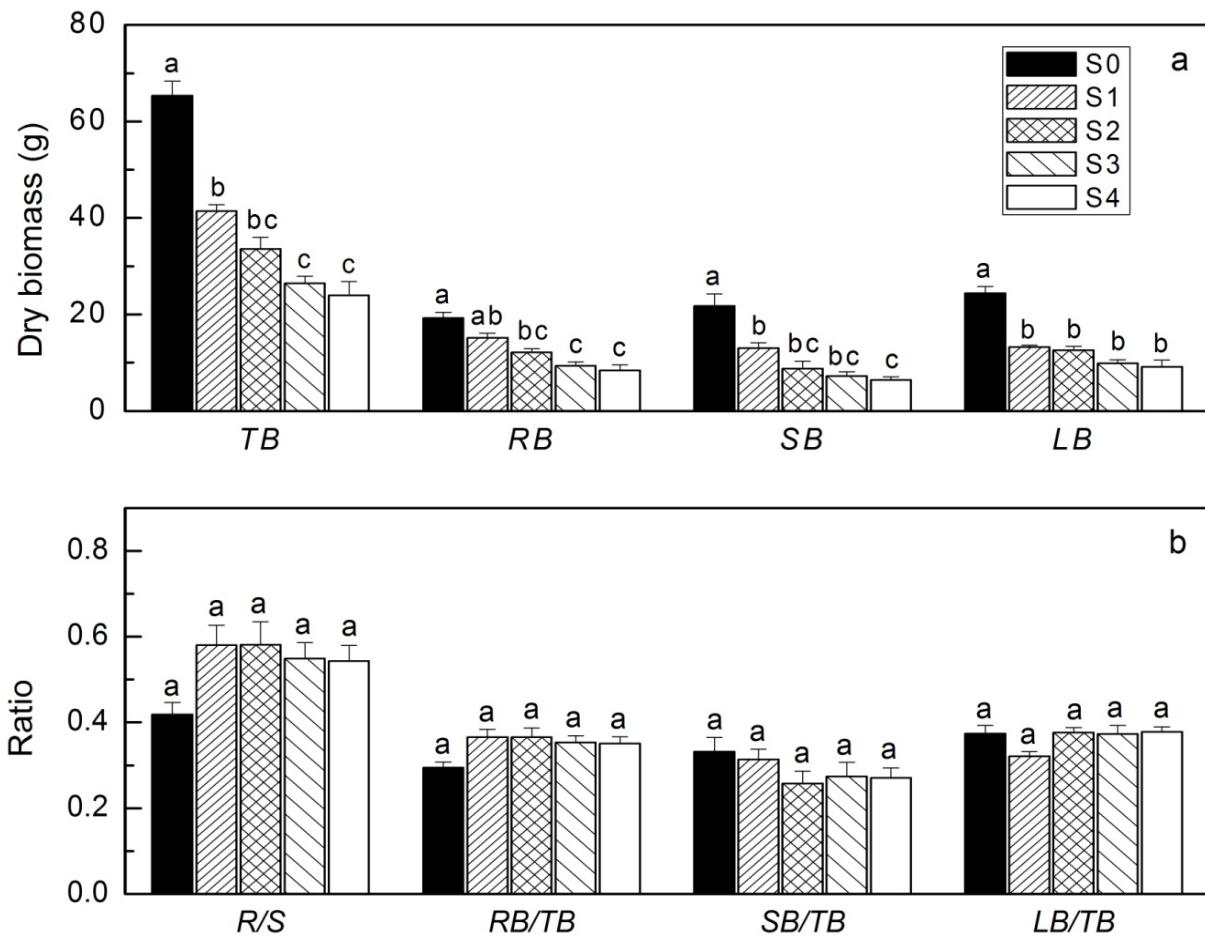
2008 and three days in 2009 (Table 1). The *T. chinensis* seedlings died at S5 in 2008 and S4 in 2009. Some seedlings (16.7%) survived at S4W1, but all died at S4W2 and S4W3 in 2009 (Table 2).

#### Plant biomass and biomass allocation

In 2008, with soil moisture of 60% FC, the total biomass, root biomass and shoot biomass decreased significantly (P≤0.05) with the increased soil salt content until S2, while no significant differences were tested between S2, S3 and S4. Leaf biomass of salt-treatments decreased significantly (P≤0.05) as compared to treatments without salt in soil, but leaf biomass had no remarkable decrease with increased soil salt content; as compared to S0, total biomass, root biomass, shoot biomass and leaf biomass of S4 decreased by 63.3, 56.3, 70.6 and 62.4%, respectively (Figure 1a). No significant effect of soil salt content was seen on the biomass allocation (P>0.05) (Figure 1b).

In 2009, total biomass, shoot biomass, leaf biomass decreased significantly with the water severity (S0W1>S0W2>S0W3, P≤0.05), root biomass of S0W2, S0W3 were not significantly different (P>0.05); as compared to S0W1, total biomass, root biomass, shoot biomass and leaf biomass of S0W3 decreased by 37.9, 25.3, 48.4 and 37.9%, respectively. Root biomass of salt treatments (S2W1, S2W2 and S2W3) were tested with no significant difference between each other (P>0.05), which were obviously lower than that of the three no-salt treatments (Figure 2a). Root to shoot ratio and root dry mass ratio of S0W1, S0W2, S0W3, S2W1 and S2W2 were not significantly different (P>0.05), while S2W3 was significantly higher (P≤0.05); shoot dry mass ratio of the six treatments had no significant difference (P>0.05); leaf dry mass ratio of S2W3 was significantly lower (P≤0.05) (Figure 2b).

Effects of water-salinity regimes on biomass of *T. chinensis* seedlings by two-way ANOVA indicated that salt had significant (P<0.001) influence on plant biomass, including all parts, but it had no significant effects (P>0.05) on biomass allocation. Water had significant influence on plant biomass (P<0.001) and root dry mass ratio (P<0.05), but had no significant effect on stem dry mass ratio (P=0.091) and leaf dry mass ratio (P=0.506).



**Figure 1.** Dry mass production (a) and biomass allocation (b) of *T. chinensis* Lour. seedlings under different salt supplies. S0, 0 g/kg<sup>-1</sup>; S1, 4 gkg<sup>-1</sup>; S2, 8 gkg<sup>-1</sup>; S3, 12 gkg<sup>-1</sup>; S4, 16 gkg<sup>-1</sup>, soil moisture 60% field capacity. The data in the figure are means  $\pm$  SE ( $n = 4$ ). Significant differences between different supplies tested by the Tukey's method were marked with letters on top of the error bars. TB, total biomass; RB, root biomass; SB, stem biomass; LB, leaf biomass; R/S, root to shoot ratio; RB/TB, root dry mass ratio; SB/TB, stem dry mass ratio; LB/TB, leaf dry mass ratio.

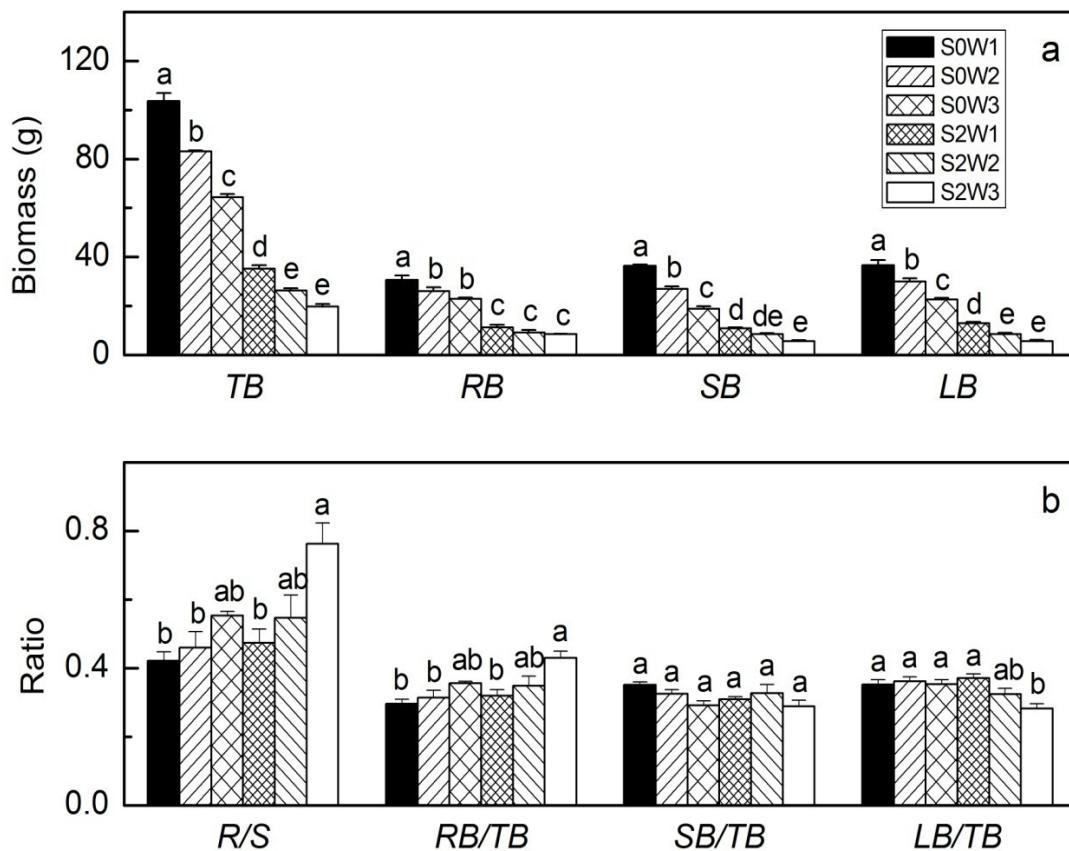
Salt and water had interactive effects on plant biomass ( $P < 0.001$ ), but no effect on biomass allocation ( $P > 0.05$ ) (Table 3).

#### Photosynthetic characteristics

$P_N$ , E and WUE of salt treatments (S2W1, S2W2 and S2W3) were similar, and significantly lower than S0 treatments ( $P \leq 0.05$ ).  $P_N$  of S0W2 was about half of S0W1, but S0W2 had lower E and  $g_s$  to maintain similar WUE (S0W1  $4.21 \pm 0.38^a$  and S0W2  $4.24 \pm 0.39^a$  mmol mol<sup>-1</sup>) (Table 4). Optimal quantum yield of photosystem II ( $F_v/F_m$ ) were compared, S0W1, S0W2 and S0W3 were not significantly different from one another ( $P > 0.05$ ), but were all higher than 0.84 (Table 4). S2W1 decreased slightly ( $0.837 \pm 0.01$ ) and was not significantly different from the S0 treatments ( $P > 0.05$ ).  $F_v/F_m$  of S2W2 and S2W3 were below 0.8, and significantly lower than the

others ( $P \leq 0.05$ ) (Table 4).

Diurnal  $P_N$  and E under different water and salt treatments (Figure 3) showed that  $P_N$  of S0 presented typical bimodal curves, while  $P_N$  of S2 presented single-peaked curves (Figures 3a and b).  $P_N$  peak of S0W1 occurred at 10:00 ( $11.68 \pm 1.34$   $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), while S0W2, S0W3, S2W1 and S2W2 occurred at 8:00 ( $8.05 \pm 0.30$ ,  $6.08 \pm 0.21$ ,  $5.15 \pm 0.15$  and  $3.55 \pm 0.10$   $\mu\text{mol m}^{-2} \text{s}^{-1}$  respectively), S0W3 occurred at 6:00 ( $3.57 \pm 0.28$   $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). E of S0W3 showed a single-peaked curve, while the other 5 treatments presented typical bimodal curves (Figures 3c and d). S0W3 had higher  $P_N$  and E than S0W2 during 12:00 to 16:00 of the day, but S2W3 had no such appearance when compared with S2W2 (Figure 3). Tendency of WUE were similar with water severity, while WUE of S0W1, S0W2 and S0W3 reached peak at 8:00 ( $9.64 \pm 0.64$ ,  $9.19 \pm 0.27$  and  $7.08 \pm 0.20$  mmol mol<sup>-1</sup> respectively), and WUE of S2W1, S2W2 and S2W3 were highest at 6:00 ( $7.14 \pm 0.69$ ,  $4.97 \pm 0.29$  and  $5.26 \pm 0.27$



**Figure 2.** Dry mass production (a) and biomass allocation (b) of *T. chinensis* Lour. seedlings under different soil salt and water treatments. S0, 0 g/kg<sup>-1</sup>; S2, 8 gkg<sup>-1</sup>; W1, 60%; W2, 40% and W3, 20% of field capacity. The data in the figure are means  $\pm$  SE ( $n = 4$ ). Significant differences between different regimes tested by the Tukey's method were marked with letters on top of the error bars. TB, RB, SB, LB, R/S, RB/TB, SB/TB, LB/TB are same with that in Figure 1.

**Table 3.** Effects of varied soil salt and water conditions on biomass characteristics of *T. chinensis* Lour. seedlings by two-way analysis of variance (ANOVA).

Factor	Salt		Water		Salt*water	
	F	P	F	P	F	P
TB	233.90	<0.001	62.67	<0.001	25.67	<0.001
RB	89.59	<0.001	13.41	<0.001	9.34	0.001
SB	118.17	<0.001	46.29	<0.001	17.82	<0.001
LB	118.31	<0.001	31.80	<0.001	10.03	<0.001
R/S	2.01	0.114	4.94	0.013	1.30	0.285
RB/TB	1.916	0.128	5.06	0.011	1.07	0.354
SB/TB	1.06	0.390	2.56	0.091	0.54	0.589
LB/TB	2.09	0.102	0.69	0.506	1.61	0.214

Salt\*water indicates the interactive effect between NaCl and water. The effects are significant at the level of  $P < 0.05$ . TB, total biomass; RB, root biomass; SB, stem biomass; LB, leaf biomass; R/S, root to shoot ratio; RB/TB, root dry mass ratio; SB/TB, stem dry mass ratio; LB/TB, leaf dry mass ratio. F is the result of F-test in analysis of variance(ANOVA),F = between-group variability/within-group variability. P is statistical significance.

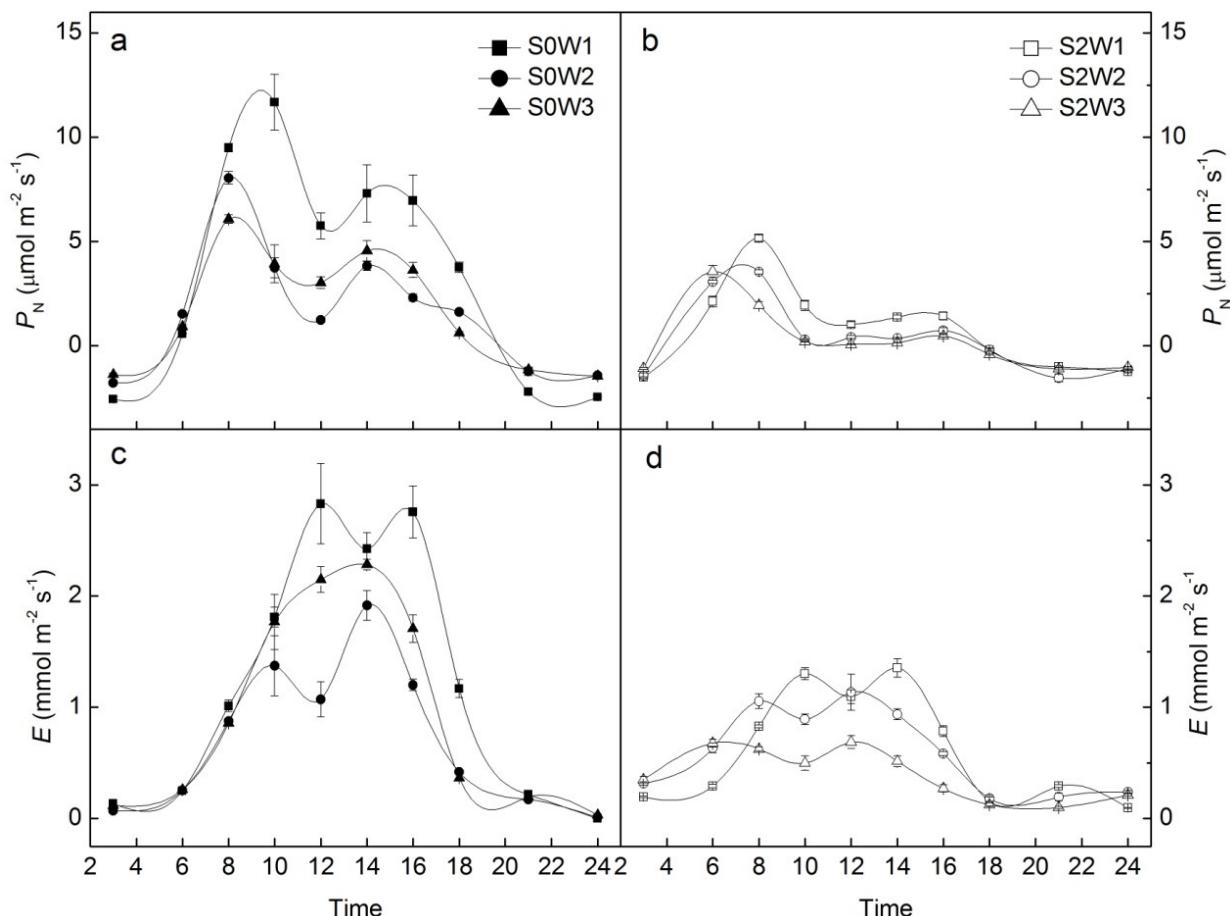
mmol mol<sup>-1</sup> respectively) (Figures 4a and b). The  $g_s$  of S0W3 showed a single-peaked curve, and maintained

high level from 10:00 to 16:00, which was highest at 14:00 ( $82.51 \pm 2.97$  mmol m<sup>-2</sup> s<sup>-1</sup>); the  $g_s$  of S0W1 and

**Table 4.** Photosynthetic characteristics of *T. chinensis* L. seedlings at different soil salt and water treatments.

Parameter	S0W1	S0W2	S0W3	S2W1	S2W2	S2W3
$P_N$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$6.50 \pm 0.54^a$	$3.18 \pm 0.29^b$	$3.25 \pm 0.28^b$	$1.83 \pm 0.20^c$	$1.17 \pm 0.18^c$	$0.85 \pm 0.17^c$
$E$ ( $\text{mmol m}^{-2} \text{s}^{-1}$ )	$1.75 \pm 0.13^a$	$1.02 \pm 0.08^{bc}$	$1.34 \pm 0.11^b$	$0.83 \pm 0.06^{cd}$	$0.77 \pm 0.05^{cd}$	$0.50 \pm 0.03^d$
WUE ( $\text{mmol mol}^{-1}$ )	$4.21 \pm 0.38^a$	$4.24 \pm 0.39^a$	$2.88 \pm 0.25^{ab}$	$2.64 \pm 0.38^{bc}$	$1.30 \pm 0.28^c$	$1.37 \pm 0.37^c$
$g_s$ ( $\text{mmol m}^{-2} \text{s}^{-1}$ )	$52.24 \pm 5.45^a$	$28.36 \pm 2.30^b$	$43.84 \pm 3.87^a$	$22.63 \pm 1.46^{bc}$	$19.34 \pm 1.20^{bc}$	$12.06 \pm 0.75^c$
$F_v/F_m$	$0.846 \pm 0.004^a$	$0.849 \pm 0.001^a$	$0.853 \pm 0.001^a$	$0.837 \pm 0.01^a$	$0.798 \pm 0.019^b$	$0.796 \pm 0.01^b$

The data in the figure are means  $\pm$  SE. Soil NaCl content [S0, 0 g kg<sup>-1</sup>; S2, 8 g kg<sup>-1</sup>]; soil moisture [W1, 60%; W2, 40% and W3, 20% of field capacity].  $P_N$ , Net photosynthetic rate; E, transpiration rate; WUE, water use efficiency;  $g_s$ , stomatal conductance;  $F_v/F_m$ , optimal quantum yield of photosystem II. Mean of  $P_N$ , E, WUE and  $g_s$  were calculated using data from 6:00 to 18:00.

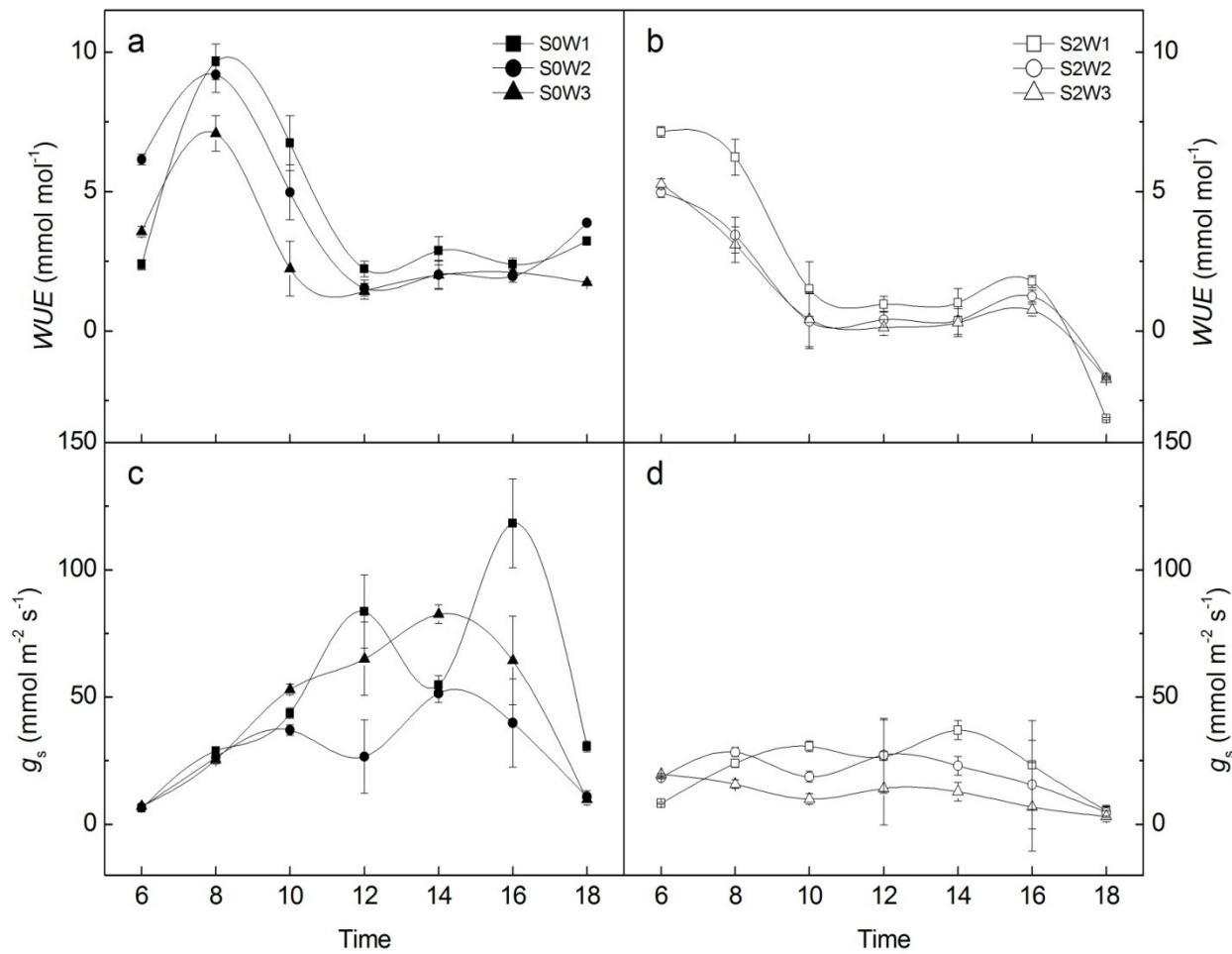


**Figure 3.** Diurnal variances of gas exchange parameters of *T. chinensis* Lour. seedlings under different soil salt and water treatments. ■, S0W1; ●, S0W2; ▲, S0W3; □, S2W1; ○, S2W2; △, S2W3. S0, 0 g/kg<sup>-1</sup>; S2, 8 gkg<sup>-1</sup>; W1, 60%; W2, 40% and W3, 20% of field capacity. The data in the figure are means  $\pm$  SE ( $n = 9$ ).  $P_N$ , Net photosynthetic rate ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ); E, transpiration rate ( $\text{mmol m}^{-2} \text{s}^{-1}$ ).

S0W2 presented typical bimodal curves, and decreased significantly at 14:00 ( $54.65 \pm 3.71 \text{ mmol m}^{-2} \text{ s}^{-1}$ ) and 12:00 ( $26.50 \pm 4.05 \text{ mmol m}^{-2} \text{ s}^{-1}$ ), respectively, indicating stomatal closure at noon (Figure 4c). The  $g_s$  of S2W1 showed bimodal curve, and was highest at 14:00 ( $36.92 \pm 2.97 \text{ mmol m}^{-2} \text{ s}^{-1}$ ), and that of S2W2 and S2W3 were highest at 8:00 ( $28.36 \pm 1.86 \text{ mmol m}^{-2} \text{ s}^{-1}$ ) and 6:00

( $19.56 \pm 1.04 \text{ mmol m}^{-2} \text{ s}^{-1}$ ), respectively (Figure 4d).

Rapid light curves of chlorophyll fluorescence under different water-salinity treatments were given (Figure 5). Similar tendencies between 6 treatments were seen. ETR, Yield and qP decreased with water severity (S0W1>S0W2>S0W3, S2W1>S2W2>S2W3). At 850  $\mu\text{mol m}^{-2} \text{ s}^{-1}$  (PAR), ETR of S0W1, S0W2, S0W3, S2W1,



**Figure 4.** Diurnal variances of water use efficiency (WUE) and stomatal conductance ( $g_s$ ) of *T. chinensis* Lour. seedlings under different water-salinity treatments. ■, S0W1; ●, S0W2; ▲, S0W3; □, S2W1; ○, S2W2; △, S2W3. S0, 0 g/kg<sup>-1</sup>; S2, 8 gkg<sup>-1</sup>; W1, 60%; W2, 40% and W3, 20% of field capacity. The data in the figure are means  $\pm$  SE (n = 9).

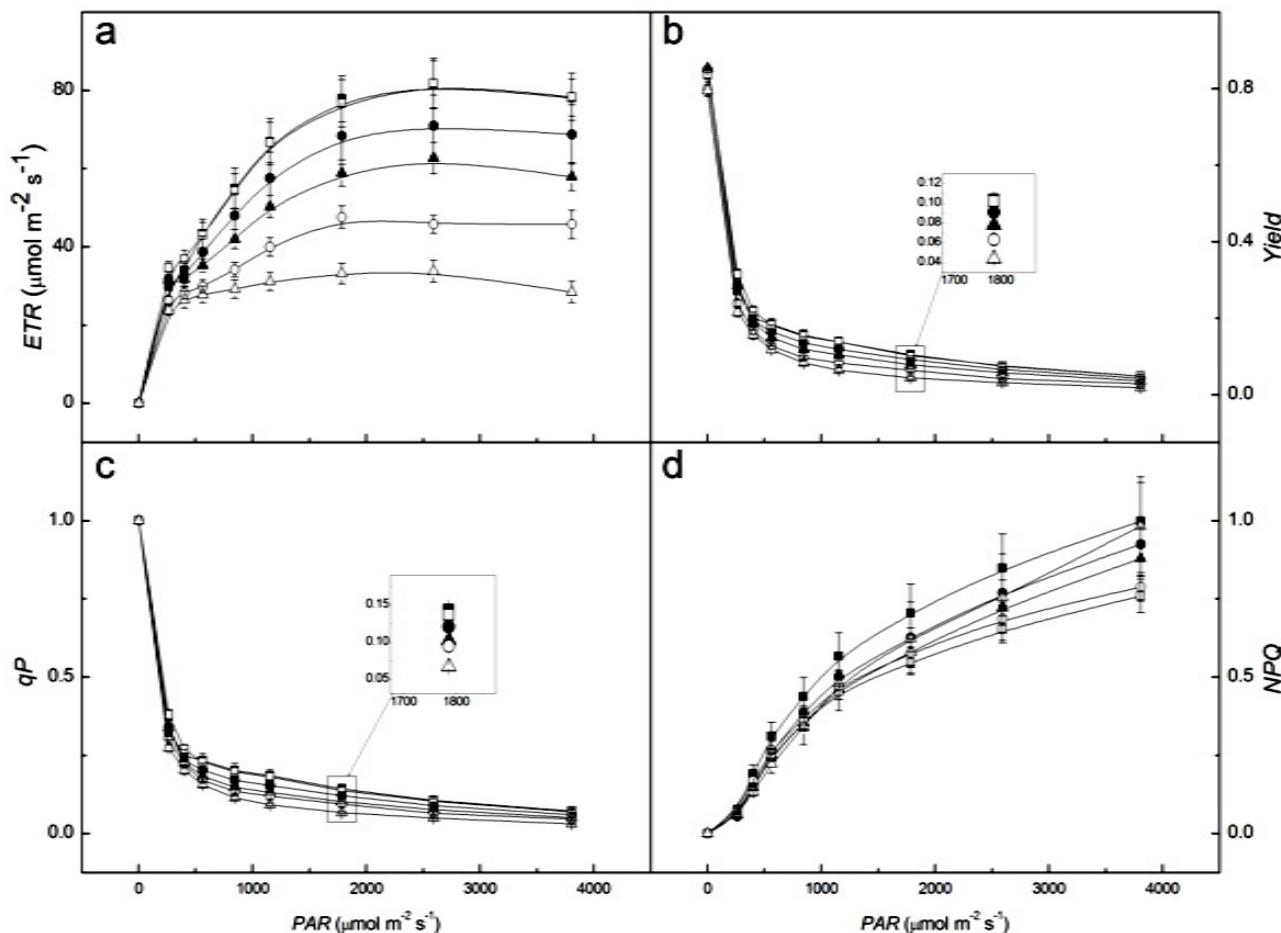
S2W2 and S2W3 were  $54.88 \pm 5.25$ ,  $47.94 \pm 5.70$ ,  $41.92 \pm 2.45$ ,  $54.24 \pm 4.42$ ,  $34.13 \pm 1.85$  and  $29.17 \pm 2.32$   $\mu\text{mol m}^{-2} \text{s}^{-1}$  (Figures 5a, b and c). NPQ of S2W3 had a sharp increase after  $850 \mu\text{mol m}^{-2} \text{s}^{-1}$ , when PAR increased from  $850$  to  $1800 \mu\text{mol m}^{-2} \text{s}^{-1}$ . NPQ of S2W1, S2W2 and S2W3 increased (54.8, 57.0 and 83.4%) (Figure 5d).

## DISCUSSION

Water table depth and soil salinity are two major factors that influence growth and distribution of *T. chinensis* (Cui et al., 2010). In this study, we investigated the effects of soil water supply and salt content on biomass accumulation, biomass allocation and leaf photosynthetic characteristics of *T. chinensis* seedlings. The results indicate that water supply and soil salt content has interactive effects on biomass of *T. chinensis* seedlings, while interactive effects did not occur in biomass allocation. Biomass allocation was mainly affected by

water supply, which implied that the balance between soil water availability and atmospheric evaporative demand determined the biomass allocation pattern. Some studies indicated that water supply almost had no effect on biomass partitioning in *Prunus dulcis* (Heilmeier et al., 2001) and *Eucalyptus globulus* seedlings (Osório et al., 1998), but water deficits were important in delaying plant growth. Conversely, many studies on woody species showed increased partitioning of root biomass under water limit (Sands and Mulligan, 1990; Ericsson et al., 1996). Heilmeier et al. (2001) also mentioned that high transpiration rates and low soil water availability required a dense rooting system for effective water uptake in balance with water loss. In our study, when soil moisture decreased to 20% FC, *T. chinensis* seedlings maintained high transpiration rate due to high leaf conductance, and consequently root growth was obviously favoured.

Plant responses to soil salt and water stress were identical in many aspects, while discriminations also exist. Salinity has both osmotic and salt-specific effects



**Figure 5.** Rapid light curves of chlorophyll fluorescence of *T. chinensis* Lour. seedlings under different soil salt and water treatments. ■, S0W1; ●, S0W2; ▲, S0W3; □, S2W1; ○, S2W2; Δ, S2W3. S0, 0 g/kg<sup>-1</sup>; S2, 8 gkg<sup>-1</sup>, W1, 60%; W2, 40% and W3, 20% of field capacity. The data in the figure are means  $\pm$  SE ( $n = 4$ ). Yield, effective quantum yield; ETR, relative rate of electron transport; qP, photochemical quenching; NPQ, non-photochemical quenching.

on plant growth (Dionisio-Sese and Tobita, 2000). Saline environments can affect plant growth by decrease in water uptake, accumulation of ions to toxic levels and reduction of nutrient availability (Tunçtürk et al., 2010). Munns et al. (2002) reported that salt-specific effects mainly occur in old leaves where salt accumulates to salt-toxic level. In this study, effect of soil salt on biomass accumulation had an obvious boundary for *T. chinensis* seedlings, plant biomass accumulation was inhibited when soil NaCl content increased to 8 g kg<sup>-1</sup> (Figure 1a), and for salt treatments (S2W1, S2W2 and S2W3), we found that soil water had no significant effects on root biomass accumulation. Some researchers still noted that *T. chinensis* is often a "remarkable non-halophilous species" (Anderson, 1982). Salt stress may reduce the activity of PS II and the synthesis of chlorophylls (Allahverdiyev et al., 2011),  $F_v/F_m$  may decrease when coping with stress conditions. In our study, when water supply was sufficient (60%FC), although  $P_N$  of salt treatments decreased significantly, the  $F_v/F_m$  did not

decrease significantly, and damage to PS II by soil salt was obvious when FC was below 40% (Table 4). The varied water-salinity conditions have obvious effect on the distribution of *T. chinensis* individuals, this species were mainly distributed at modest water table depth and moderate soil salinity conditions, and sufficient water supply may increase the ability of *T. chinensis* to survive in higher soil salinity conditions (Cui et al., 2010).

Tamarisk is able to maintain high leaf gas exchange rates under extremely hot and dry conditions (high vapor pressure deficit, high temperature and low soil water availability) relative to native species (Horton et al., 2001). Results from this study support this point.  $P_N$  remained stable when soil moisture decreased from 40 to 20% FC (Figure 3a). Decreased  $P_N$  at noon was observed in the study. For S0W2,  $g_s$  varied simultaneously, implying that photosynthetic limitations were mainly contributed by stomatal closure; while for S0W3, non-stomatal limitations occurred (Figures 3a and 4c). *Tamarix* are typical salt-secreting plants, which secretes

actively even under low salt conditions, and the composition of the secretions is highly dependent on the composition of the root environment (Berry, 1970). Leaflets of *T. chinensis* had large amount of salt glands, which play an important role in regulating iron balance, maintaining osmotic pressure and improving salt endurance (Thomson et al., 1969). For S0W1 and S0W2, stomatal regulation were observed at noon, while for S0W3 it was not observed, implying that water deficit may influence the ability of countering high temperature and excessive heat at noon, and stomatal and salt glands cells might be damaged when soil moisture decreased to 20% FC. This might be why stoma did not close timely, so high transpiration rate and lower WUE were observed. Further anatomical studies may provide more information of the relationships between stomatal regulation and water deficit.

*T. chinensis* has a strong potential to be used as a sustainable bio-energy resource and will play a great role in the local natural ecosystems and economy in the future, especially in the Yellow River Delta, a fast growing delta of most saline habitats. Studying the effects of varied water-salinity conditions on plants will provide useful information for forest management in Yellow River Delta and similar coastal habitats.

## ACKNOWLEDGEMENTS

This work was supported by National Science Foundation of China (No. 30970166; 31140054), Ministry of Education on Doctorial Discipline (No. 20090131110066), Key Science and Technology Project of Shandong Province (No. 2009GG10002006; 2010GHZ0801) and Independent Innovation Project of Shandong University (No. 2010JC004).

## REFERENCES

- Allahverdiyev S, Atilla A, Ismail BS, Sahmurova A (2011). Response of photosystem II and photosynthetic pigments to salt and Baikal EM1 in tree seedlings. Afr. J. Biotechnol. 10(4): 535-538.
- Anderson JE (1982). Factors controlling transpiration and photosynthesis in *Tamarix chinensis* Lour. Ecology, 63(1): 48-56.
- Berry WL (1970). Characteristics of salts secreted by *Tamarix aphylla*. Am. J. Bot. 57(10): 1226-1230.
- Bongi G, Loreto F (1989). Gas-Exchange properties of salt-stressed Olive (*Olea europaea* L.) leaves. Plant Physiol. 90: 1408-1416.
- Cui BS, Yang QC, Zhang KJ, Zhao XS, You ZY (2010). Responses of saltcedar (*Tamarix chinensis*) to water table depth and soil salinity in the Yellow River Delta, China. Plant Ecol. 209: 279-290.
- Dionisio-Sese ML, Tobita S (2000). Effects of salinity on sodium content and photosynthetic responses of rice seedlings differing in salt tolerance. J. Plant Physiol. 157: 54-58.
- Ehling B, Dluzniewska P, Dietrich H, Selle A, Teuber M, H Nsch R, Nehls U, Polle A, Schnitzler JP, Rennenberg H, Gessler A (2007). Interaction of nitrogen nutrition and salinity in Grey poplar (*Populus tremula x alba*). Plant Cell Environ. 30: 796-811.
- Ericsson T, Ryttner L, Vapaavuori E (1996). Physiology of carbon allocation in trees. Biomass Bioenerg. 11: 115-127.
- Gaskin JF, Schaal BA (2002). Hybrid *Tamarix* widespread in U.S. invasion and undetected in native Asian range. P. Natl. Acad. Sci. 99: 11256-11259.
- Godfrey K (1985). Comparing the means of several groups. New Engl. J. Med. 313: 1450-1456.
- Griffin GF, Stafford SDM, Morton SR, Allan GE, Masters KA, Preece N (1989). Status and implications of the invasion of tamarisk (*Tamarix aphylla*) on the Finke River, Northern Territory, Australia. J. Environ. Manage. 29: 297-315.
- Heilmeier H, Erhard M, Wartinger A, Brinckmann E, Horn R, Schulze ED (2001). Biomass partitioning in response to soil drought: A pot experiment with *Prunus dulcis* trees during four years. Basic Appl. Ecol. 2: 165-175.
- Horton JL, Kolb TE, Hart SC (2001). Leaf gas exchange characteristics differ among Sonoran Desert riparian tree species. Tree Physio. 21: 233-241.
- Li X, Huang YM, Gong JR, Zhang XS (2010). A study of the development of bio-energy resources and the status of eco-society in China. Energy, 35: 4451-4456.
- Li XY, Zhang XM, He XY, Zeng FJ, Thomas FM, Foetzki A (2004). Drought stress and irrigation effects on water relations of *Tamarix ramosissima* in the Qira Oasis. Acta Phytoecologica Sinica Chinese, 28(5): 644-650.
- Long SP, Bernacchi CJ (2003). Gas exchange measurements, what can they tell us about the underlying, limitations to photosynthesis? Procedures and sources of error. J. Exp. Bot. 54: 2393-2401
- Maxwell K, Johnson GN (2000). Chlorophyll fluorescence - a practical guide. J. Exp Bot. 51: 659-668
- Munns R (2002). Comparative physiology of salt and water stress. Plant Cell Environ. 25: 239-250
- Osório J, Osório ML, Chaves MM, Pereira JS (1998). Water deficits are more important in delaying growth than in changing patterns of carbon allocation in *Eucalyptus globulus*. Tree Physiol. 18: 363-373
- Ralph PJ, Gademann R (2005). Rapid light curves: A powerful tool to assess photosynthetic activity. Aquat. Bot. 82: 222-237
- Sands R, Mulligan DR (1990). Water and nutrient dynamics and tree growth. Forest Ecol. Manage. 30: 91-111
- Schreiber U, Schliwa U, Bilger W (1986). Continuous recording of photochemical and non-photochemical chlorophyll fluorescence quenching with a new type of modulation fluorometer. Photosynth. Res. 10: 51-62
- Shafroth PB, Briggs MK (2008). Restoration ecology and invasive riparian plants: An introduction to the special section on *Tamarix* spp. in western North America. Restor. Ecol. 16: 94-96
- Stromberg JC, Rychener TJ (2010). Effects of fire on riparian forests along a free-flowing dryland river. Wetlands, 30: 75-86
- Tunçturk M, Tunçturk R, Yıldırım B, Çiftçi V (2010). Effect of salinity stress on plant fresh weight and nutrient composition of some Canola (*Brassica napus* L.) cultivars. Afr. J. Biotechnol. 10(10): 1827-1832
- Thomson WW, Berry WL, Liu LL (1969). Localization and secretion of salt by the salt glands of *Tamarix aphylla*. P. Natl. Acad. Sci. 63: 310-317
- Weng YL, Gong P (2006). Soil salinity measurements on the Yellow River Delta. Journal of Nanjing University (Natural Sciences). 42: 602-610. In chinense.
- Wu FZ, Bao WK, Li FL, Wu N (2008). Effects of water stress and nitrogen supply on leaf gas exchange and fluorescence parameters of *Sophora davidii* seedlings. Photosynthetica, 46(1): 40-48
- Xu F, Guo WH, Wang RQ, Xu WH, Du N, Wang YF (2009). Leaf movement and photosynthetic plasticity of black locust (*Robinia pseudoacacia*) alleviate stress under different light and water conditions. Acta Physiol. Plant. 31: 553-563
- Zhang DY, Yin LK, Pan BR (2002). Biological and ecological characteristics of *Tamarix* L. and its effect on the ecological environment. Sci. China Ser. D. 45: 18-22
- Zhang RH, Li J, Guo SR, Tezuka T (2009). Effects of exogenous putrescine on gas-exchange characteristics and chlorophyll fluorescence of NaCl-stressed cucumber seedlings. Photosynth. Res. 100: 155-162.