DOI: 10.1007/s11099-016-0651-6 PHOTOSYNTHETICA 55 (2): 368-377, 2017

Response of stem sap flow and leaf photosynthesis in *Tamarix chinensis* to soil moisture in the Yellow River Delta, China

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Abstract

Soil moisture is the main limiting factor for vegetation growth at shell ridges in the Yellow River Delta of China. The objective of this study was to explore the soil moisture response of photosynthetic parameters and transpiration in *Tamarix chinensis* Lour., a dominant species of shell ridges. Leaf photosynthetic light-response parameters and sap flow were measured across a gradient of relative soil water content (RWC), from drought (23%) to waterlogging (92%) conditions. Leaf photosynthetic efficiency and stem sap flow of *T. chinensis* showed a clear threshold response to soil moisture changes. Leaf net photosynthetic rate, water-use efficiency (WUE), light-saturation point, apparent quantum yield, maximum net photosynthetic rate, and dark respiration rate peaked at moderately high RWC, decreasing towards high and low values of RWC. However, peak or bottom RWC values substantially differed for various parameters. Excessively high or low RWC caused a significant reduction in the leaf photosynthetic capacity and WUE, while the high photosynthetic capacity and high WUE was obtained at RWC of 73%. With increasing waterlogging or drought stress, *T. chinensis* delayed the starting time for stem sap flow in the early morning and ended sap flow activity earlier during the day time in order to shorten a daily transpiration period and reduce the daily water consumption. The leaf photosynthetic capacity and WUE of *T. chinensis* were higher under drought stress than under waterlogging stress. Nevertheless, drought stress caused a larger reduction of daily water consumption compared to waterlogging, which was consistent with a higher drought tolerance and a poor tolerance to waterlogging in this species. This species was characterized by the low photosynthetic capacity and low WUE in the range of RWC between 44 and 92%. The RWC of 49–63% was the appropriate range of soil moisture for plant growth and efficient physiological water use of *T. chinensis* seedlings.

Additional key words: drought; gas exchange; light-use efficiency; water consumption; waterlogging.

Introduction

Photosynthetic parameters belong to major indicators reflecting a response of physiological processes to water stress conditions in plants (Jin *et al.* 2011, Lang *et al.* 2013). Each plant has its own optimal soil water conditions, light intensity range, and other environmental needs for photosynthesis (Lang *et al.* 2013, Zhang *et al.* 2014). A study on the response of photosynthetic characteristics to soil moisture helps clarify the physiological responses of plants to environmental changes (Lang *et al.* 2013). Plant photosynthesis is not only related to leaf structure and physiological function as determined by the inherent genetic characteristics and phenotypic plasticity of species (Hsiao 1973), but it is also affected by various ecological factors, such as light, temperature, CO_2 concentration, and soil moisture (Sofo *et al.* 2009, Zhang *et al.* 2014). Soil moisture is an important ecological factor that affects the physiological process (Muller *et al.* 2011, Zong *et al.* 2014), and it exerts a profound impact on plant photosynthesis and water and light use (Zhang *et al.* 2010, Soares *et al.* 2015). In arid habitats, plants can optimize stomatal regulation (Farquhar and Sharkey 1982), regulate leaf movement (Du *et al.* 2010), reduce leaf area, and

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Received 15 September 2015, *accepted* 29 June 2016, *published as online-first* 23 August 2016.

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Abbreviations: AQY – apparent quantum yield; DSF – daily cumulative sap flow; *E* – transpiration rate; LCP – light-compensation point; LSP – light-saturation point; P_N – net photosynthetic rate; P_{Nmax} – light-saturated net photosynthetic rate; R_D – dark respiration rate; RWC – relative soil water content; SWC – soil water content; WUE – water-use efficiency.

Acknowledgements: This study was supported by the National Natural Science Foundation of China (NO.31370702), the Key Project of Natural Science Foundation of Shandong Province (NO. ZR2015JL014), the Science and Technolgy Projects of Shandong Province (No. 2014GSF117022; 2015GNC111022), and Natural Science Foundation of Shandong Province (NO. ZR2014CL032).

increase the depth of root systems (Maseda and Fernández 2006) through morphological and physiological pathways in order to maximize carbon assimilation for a given amount of water (Mitchell *et al.* 2008, Gao *et al.* 2010, Gardian *et al.* 2011), ultimately improving the WUE.

Studies have shown that the leaf photosynthetic parameters of plants, such as *Malus pumila* cv. Goldspur (Zhang *et al.* 2010) and *Campsis radicans* (L.) Seem (Xia *et al.* 2011b), do not follow a simple linear relationship with soil moisture but exhibit a critical effect of soil moisture. In recent years, some research has been conducted on drought resistance of different afforestation tree species (Du *et al.* 2010). Relevant studies concerned changes in plant anatomic structures and physio-biochemical factors under different degrees of water deficit and their characteristics and mechanisms of adaptation to water stress (Farooq *et al.* 2009, Jin *et al.* 2011, Talaat *et al.* 2015). However, most of the studies are limited to polyethylene glycol (PEG) treatments or simple pot simulations, not under field conditions, and their experimental designs mainly include three to four levels of water treatment, such as mild, moderate, and severe drought stress. Responses of photosynthesis to soil moisture may be complex and cannot be captured by such a simple design. Thus, little is known about the response of plant photosynthesis to the full range of soil moisture conditions. Meanwhile, the photosynthetic productivity dependence on soil moisture and suitable moisture conditions for tree growth in their actual habitat are not fully understood, and the research can present guidance for afforestation of tree species.

The shell ridge is mainly formed by biological shells living in an intertidal zone and their debris transported by waves and accumulated near a high-tide line. Two shell ridges, roughly parallel with the coast, are located in the Yellow River Delta of China. These shell ridges are of high elevations, and the shell sand soil shows large porosity, high coarse sand content, and poor rainwater storage capacity. Moreover, this region lacks freshwater resources, together with an uneven distribution of seasonal precipitation and a high evaporation-to-precipitation ratio. Consequently, soil moisture is the main limiting factor for vegetation growth on the shell ridges in this area. Existing research has investigated the physiology and ecology of plants grown on the shell ridges in this region and focused on physiological parameters of photosynthesis in major shrub species, such as *Periploca sepium* (Wang *et al.* 2013) and *Ziziphus jujuba* (Zhang *et al.* 2014), under a few drought gradients of simulated shell sand habitats. *Tamarix chinensis* Lour. has a strong capacity for wind break and sand fixation, as well as soil and water conservation. It is the major tree species used for vegetation restoration and ecological reconstruction of shell ridges in the Yellow River Delta, but its physiological response to water availability in this habitat has not been thoroughly studied. This situation has substantially limited research-based and knowledgeable decisions on tree species selection and planting management at shell ridges.

In this study, we selected *T. chinensis*, the dominant species on the shell ridges in the Yellow River Delta, as the experimental material. Serial moisture gradients were simulated and designed under field conditions. Photosynthetic light-response parameters and stem sap flow characteristics of *T. chinensis* were measured under gradient moisture conditions. The aims of our study were to elucidate the soil moisture response of photosynthetic parameters and characteristics of water consumption in *T. chinensis*, and to clarify suitable moisture conditions for plant growth of *T. chinensis* at the shell ridges. Furthermore, we established the grading of soil moisture availability and productivity evaluation based on photosynthetic parameters and stem sap flow characteristics of *T. chinensis* in order to provide a theoretical basis and technical reference for a site selection and water management of *T. chinensis* at shell ridges. We hypothesized that leaf photosynthesis and stem sap flow parameters of *T. chinensis* grown on shell ridges did not follow a simple linear relationship with soil moisture but show a clear threshold effect.

Materials and methods

Site description: Field experiments were performed in Jijiabuzi-Wangzidao, which is located at the central and eastern coastal lowlands of the Wudi County, Binzhou City, Shandong Province, China. The experimental site is located in the buffer zone of the Binzhou National Shell Ridge Island and Wetland Nature Reserve (N38°13′–38°14′, E117°52′–117°56′). This area belongs to the East Asian monsoon semi-humid continental climate zone in the warm temperate region. It has an average annual sunshine of 2,849 h, average annual rainfall of 550 mm, average annual evaporation of 2,431 mm, and average annual temperature of 12.4°C. The shell ridge island has a flat terrain. The thickness of shell sand is 1.0–2.5 m on average and reaches up to 3.0–4.0 m in local areas. Shell ridge soil has the following properties: shell sand content > 90%, pH 7.40, soil salt content < 0.3%, soil moisture at field capacity 21%, and bulk density 1.25 g cm^{-3}. The major vegetation types are xeric herbs and shrubs. Dominant shrub species include *T. chinensis*, *P. sepium*, and *Z. jujuba*.

Experimental material and design: Three-year-old *T. chinensis* seedlings with a mean height of 1.36 m and a mean root diameter of 0.86 cm were selected. Six plots of 100 cm (length) × 80 cm (width) × 60 cm (depth) each were dug near a sparse area of *T. chinensis* shrub communities on shell ridges in the Yellow River Delta. The bottom of the plot was covered with an impermeable film. Separating ditches were dug around each plot, and ridges were built up using an impermeable film to prevent water exchange with groundwater and external soil water. One plant was grown in each plot from 20 March, 2015. The experimental plants were allowed to grow for 90 d under normal irrigation. Irrigation was performed once every 10 d, with 5 L of water applied each time. From 22 June, the gradient moisture was established by a combination of artificial water supply and natural water consumption. First, the soil was irrigated to reach saturated soil moisture. After 2 d of equilibrium, the initial gravimetric soil water content (SWC) and relative soil water content (RWC) reached 20% and 92%, respectively. Soil samples were collected from the main root distribution layer at a 10–30 cm depth, using a 1.5 cm diameter soil borer in each plot. Gravimetric SWC was determined by oven drying method, the SWC at field capacity was measured by ring shear testing in laboratory (Tika and Hutchinson 1999), and RWC was calculated as the ratio of gravimetric SWC to soil moisture at the field capacity. Then, the soil surface was covered with a plastic film to reduce evaporation. Thereafter, soil moisture was reduced mainly through natural physiological water consumption by *T. chinensis*. The SWC was measured in each group every 1–2 d, and the measurement lasted until the leaf net photosynthetic rate (P_N) of *T. chinensis* became zero. In order to maintain the continuum of soil moisture, eleven typical levels of SWC were selected according to the differences of RWC and D-optimum law (Kiefer and Wolfowitz 1952).

Series of soil moisture content. All the values are means of three replications. GSWC – gravimetric soil water content; RWC – relative soil water content. Means ± SE, *n* = 3.

GSWC [%]	20 ± 1.6	17 ± 1.7	15 ± 1.5	13 ± 1.2	12 ± 1.5	10 ± 1.1	9 ± 1.2	8 ± 0.7	7 ± 0.8	6 ± 0.6	5 ± 0.5
RWC [%]	92 ± 4.3	82 ± 5.1	73 ± 4.2	63 ± 3.7	54 ± 3.8	49 ± 4.1	44 ± 3.7	39 ± 3.1	35 ± 3.3	29 ± 2.5	23 ± 2.4

Photosynthetic light-response parameters: From 24 June, leaf photosynthetic light-response parameters of *T. chinensis* were measured in each group every 1–2 d using an artificial light source. Measurements were made at 09:00–11:00 h and ended on 6 July. In order to avoid a systematic bias in physiological parameter changes introduced by temporal differences, we measured leaf photosynthetic parameters using an alternate model of different leaves in different plants, which could further ensure the comparability and accuracy of the measured data among different treatments. At each moisture gradient, we randomly selected three plants (one plant per plot) as sample plants for fixed observation. P_N-light responses were measured in 2–3 healthy, mature, sun-exposed in the mid–upper canopy of each plant. The leaf P_N light-response process was measured using the *LI-6400 XT* photosynthesis system (*LI-COR Inc.*, Lincoln, NE, USA). PAR was controlled at 11 gradient levels [1,200–20 μmol(photon) m^{-2} s^{-1}] using artificial light (*LI-COR Inc.*, Lincoln, USA). At each PAR, the measurement was controlled for 120 s; a CO_2 controller was used to maintain a CO_2 concentration of 370 μmol mol^{-1}, the relative air humidity was 55%, and the atmospheric temperature was 28°C. Leaf areas were calculated from photographs obtained from the leaf scans taken using *CI-400CIAS s*oftware (*Computer Imaging Analysis Software, CID Co.*, Logan, UT, USA). The light response of major leaf photosynthetic parameters was measured, including P_N, transpiration rate (E), and WUE = P_N/E (Prior *et al.* 2010). In addition, the leaf gas exchange parameters of P_N and WUE were analyzed at a PAR of 1,200 μmol(photon) m^{-2} s^{-1}.

Stem sap flow was measured on the same three plants as on which the photosynthetic parameters measurements were carried out. The measurements were made using the heat-balance packaged stem sap flow measuring system (*Stem Heat Balance*, *Dynamax*, AUS), which automatically and continuously recorded the instantaneous rate and daily flux of stem sap flow. A packaged *SGA5* probe was installed at a 0.4-m height (stem diameter of 0.61 ± 0.06 cm) of each sample plant on the sunny side. Installation of the probe strictly followed the instructions of *Dynamax*, mainly including selection and pre-treatment of the stem, installation of the probe, and installation of the O-ring and radiation projection shield. The data transmission cable of the probe was connected to the corresponding interface on the data collector (*Delta-T 80 Logger*). Stem sap flow was monitored continuously for 24 h per day, and the data were collected at 30-min intervals.

Data analysis: The modified rectangular hyperbolic model was used to simulate the leaf P_N light-response curve as follows (Ye 2007):

$$P(\mathrm{I}) = \alpha \frac{1-\beta I}{1+\gamma I}(I - I_C)$$

where P(I) is net photosynthetic rate (P_N); I is photosynthetically active radiation (PAR); α, β, and γ are coefficients that are independent of I; and I_C is the light compensation point (LCP). According to the above model expression, nonlinear regression analysis was performed using *SPSS 12.0*. Light-response parameters under different soil moisture conditions were obtained by derivative conversion (Ye 2007): quantum yield parameters (α, β, and γ), I_m is light saturation point (LSP), $P(I_m)$ is light-saturated net photosynthetic rate (P_{Nmax}), and dark respiration rate (R_D). The apparent quantum yield (AQY) was calculated using the linear regression method of the P_N-PAR curve under PAR ≤ 200 μmol(photon) m^{-2} s^{-1}.

Microsoft Excel 2010 and *SPSS 12.0* were used for data processing and analysis. The photosynthetic and water consumption parameters were analyzed by one-way analysis of variance (*ANOVA*) at different RWC. Significant levels of differences between means were determined by using Least-significant difference (LSD) tests at the 0.05 or 0.01 significant levels. Cluster analysis was performed on 11 soil moisture points according to P_N, daily cumulative sap flow (DSF) and WUE, and the cluster method was between-group linkage according the measure of Euclidean distance.

Results

Leaf P_N light response under different moisture conditions: Leaf P_N of *T. chinensis* increased rapidly with the enhancement of light intensity at a PAR of less than 200 μmol(photon) m^{-2} s^{-1} (Fig. 1) under different soil moisture conditions. However, P_N decreased significantly with continuous enhancement of the light intensity at above the saturation intensity except for RWC of 92 and 73%. The leaf P_N of *T. chinensis* peaked at moderately high RWC, decreasing towards high and low values of RWC. The highest photosynthetic capacity was obtained at RWC of 73%, when the optimum irradiance was in the range of 800–1,200 μmol(photon) m^{-2} s^{-1}. P_N was maintained relatively high at RWC of 49–63%, when the optimum PAR was in the range of 600–800 μmol(photon) m^{-2} s^{-1}. The leaf P_N was relatively low under moderate drought stress (RWC of 29–44%) and mild waterlogging stress (RWC of 82%), with a suitable PAR of 400–1,000 μmol(photon) m^{-2} s^{-1}. The leaf P_N decreased significantly under severe waterlogging stress (RWC of 92%) and severe drought stress (RWC of 23%), when the optimum was within the range of 800–1,200 and 400–800 μmol(photon) m^{-2} s^{-1}, respectively.

Response of leaf P_N and WUE to soil moisture: Fig. 2*A* shows that at PAR of 1,200 μmol(photon) m^{-2} s^{-1}, the leaf P_N and WUE peaked at moderately high RWC, decreasing towards high and low values of RWC. Both parameters reached the highest values (3.18 and 1.47 μmol m^{-2} s^{-1}, respectively) at RWC of 73%, following a typical unimodal curve. As the soil moisture decreased (RWC < 73%), there was a significant decline in P_N and a slow reduction in WUE, suggesting that the sensitivity of leaf P_N to soil moisture was significantly higher than that of WUE. At RWC of 35–63%, P_N was maintained relatively high; the mean P_N was 1.28 μmol(CO_2) m^{-2} s^{-1}, which decreased by 60% compared with the maximum value. The corresponding WUE was also maintained relatively high; the mean WUE was 0.82 μmol $mmol^{-1}$, which was reduced by 44% compared with the maximum value. Under low moisture conditions (RWC of 29% and 23%), P_N and WUE both showed significant differences compared with the respective maximum values. P_N was reduced by 83% and 98%, and WUE was reduced by 67% and 97%, respectively. Significant differences were also found in P_N and WUE under high moisture conditions (RWC of 92% and 82%); compared with the respective maximum values, P_N was reduced by 88% and 80%, and WUE was reduced by 80% and 84%, respectively.

Response of leaf photosynthetic light-response parameters to soil moisture

LCP and LSP: As shown in Fig. 2*B*, the leaf LCP of *T. chinensis* declined to a minimum at RWC of 54% and then rose with RWC decreasing. Relatively low LCP (72–78 μmol m^{-2} s^{-1}) appeared at RWC of 44–73%. The leaf LSP of *T. chinensis* peaked at moderately high RWC, decreasing towards high and low values of RWC. A relatively high LSP (934–1,013 μmol m^{-2} s^{-1}) was found at a RWC of 35–73%, and the highest value appeared at RWC of 49%.

AQY and P_{Nmax}: Fig. 2*C* shows that the leaf AQY and P_{Nmax} of *T. chinensis* both reached a peak at moderately high RWC and then declined towards high and low values of RWC. AQY reached the maximum value of 0.025 at RWC of 73% and then slowly decreased with decreasing RWC. AQY was maintained at relatively high levels of 0.018–0.025 with RWC in the range of 35–92%. AQY was significantly lower at RWC < 35%. The reduction in AQY

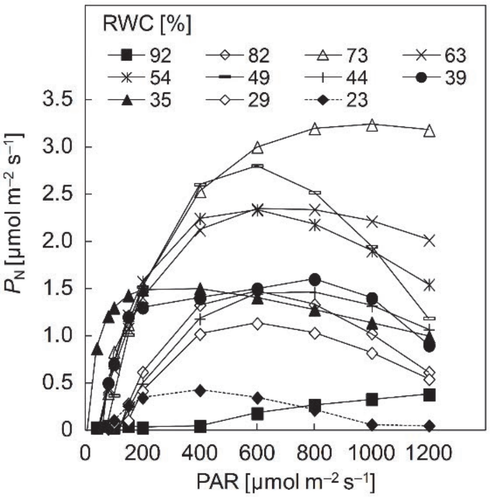

Fig. 1. Leaf photosynthetic light-response curves of *Tamarix chinensis* under different soil moisture conditions. PAR – photosynthetically active radiation; P_N – net photosynthetic rate; RWC – relative soil water content.

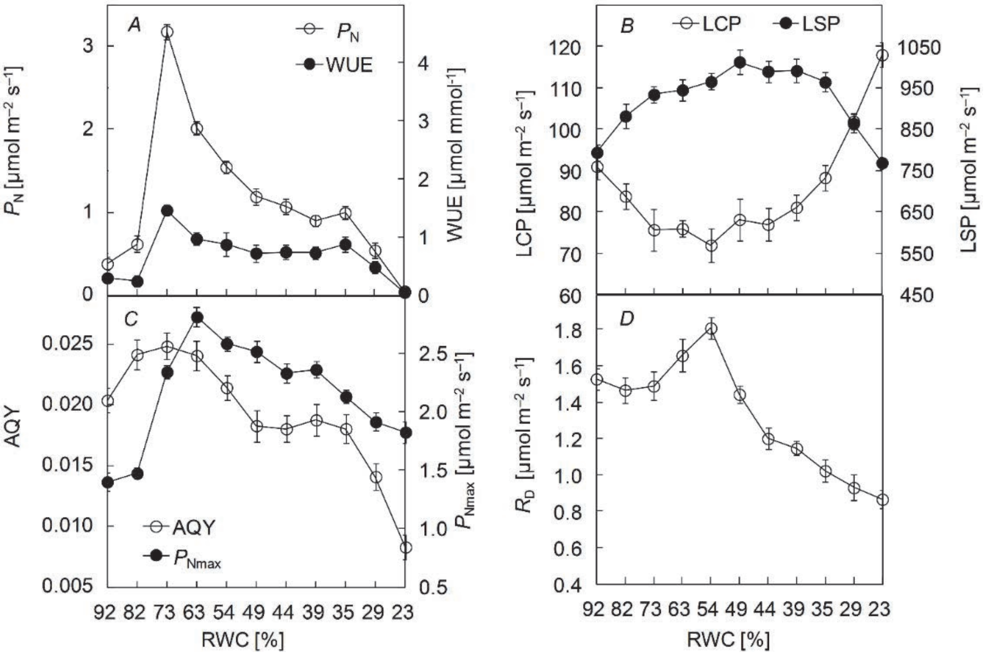

Fig. 2. Leaf net photosynthetic rate and water use efficiency at a PAR of 1,200 µmol m^{-2} s^{-1} (*A*), leaf light compensation point and light saturation point (*B*), leaf apparent quantum yield and maximum net photosynthetic rate (*C*), and leaf dark respiration rate (*D*) of *Tamarix chinensis* under different soil moisture conditions. The values represent the means of 3 replications and the bars represent SE. P_N – net photosynthetic rate; RWC – relative soil water content; WUE – water-use efficiency; LCP – light-compensation point; LSP – light-saturation point; AQY – apparent quantum yield; P_{Nmax} – light-saturated net photosynthetic rate; R_D – dark respiration rate.

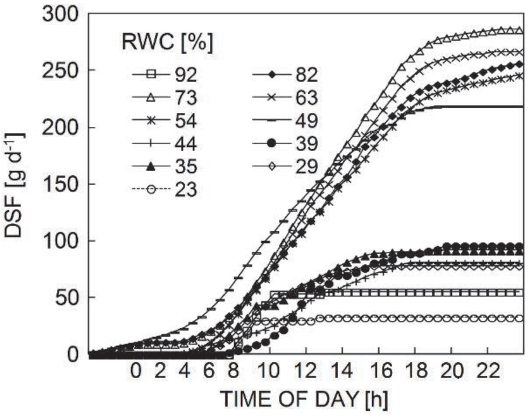

Fig. 3. Daily cumulative sap flow of *Tamarix chinensis* stems under different soil moisture conditions. DSF – daily cumulative sap flow; RWC – relative soil water content.

relative to the maximum value was 68%, and the low-light use capacity was markedly reduced at RWC of 23%. P_{Nmax} reached the highest value of 2.81 µmol(CO$_2$) m^{-2} s^{-1} at RWC of 63% and then declined significantly with decreasing RWC. Leaf photosynthetic capacity was significantly reduced at RWC > 82% and RWC < 39%; the reduction in P_{Nmax} relative to the maximum value was 50% and 35% at RWC values of 92% and 23%, respectively. The analysis showed that the leaf light-use efficiency of *T. chinensis* was significantly higher under high water contents (RWC > 54%) than under drought stress; however, the photosynthetic capacity appeared to be significantly higher under severe drought stress (RWC < 35%) than that under waterlogging stress (RWC > 82%), indicating the water adaptability of *T. chinensis*, namely to drought stress in contrast to waterlogging.

R_D: Fig. 2*D* shows that the leaf R_D of *T. chinensis* peaked at moderately high RWC, decreasing towards high and low values of RWC. Relatively high values of R_D (1.44–1.66 µmol m^{-2} s^{-1}) were maintained at RWC > 49% and the maximum value (1.81 µmol m^{-2} s^{-1}) appeared at RWC of 54%. Furthermore, R_D significantly declined with decreasing RWC. The minimum value of 0.87 µmol m^{-2} s^{-1} appeared under severe drought stress (RWC of 23%). On balance, the leaf R_D was significantly higher under high water conditions (RWC > 49%) than that under low water conditions (RWC < 44%).

Daily cumulative sap flow (DSF): As shown in Fig. 3, under different soil moisture conditions, DSF in the stems of *T. chinensis* followed similar trends in an "S" pattern, with highly significant variations between day and night. Under waterlogging stress (RWC of 92%) and severe drought stress (RWC of 23%), *T. chinensis* exhibited no sap flow activities from 13:00 to 07:30 in the next morning (18 h), indicating that the excessively high or low water content inhibited water use by *T. chinensis*. The DSF showed highly significant differences with RWC change. The DSF reached a peak at a RWC of 73% and then declined greatly with increasing drought stress. At RWC of 49–82%, *T. chinensis* maintained relatively high DSF at 219–286 g d^{-1}. Under RWC of 29–44%, DSF reached 79–96 g d^{-1}. At a RWC of 92% and 23%, the DSF markedly dropped to 55 and 32 g d^{-1}, respectively. The analysis showed that under suitable moisture conditions, *T. chinensis* could maintain stem sap flow activities for a long time, even at night, and DSF was maintained at higher levels. The results showed that increasing drought stress inhibited to some extent a water loss of *T. chinensis*, reflecting the survival strategy of this species as adaption to drought stress. Drought resulted in a decline in stem sap flow velocities of *T. chinensis* more easily than did waterlogging stress.

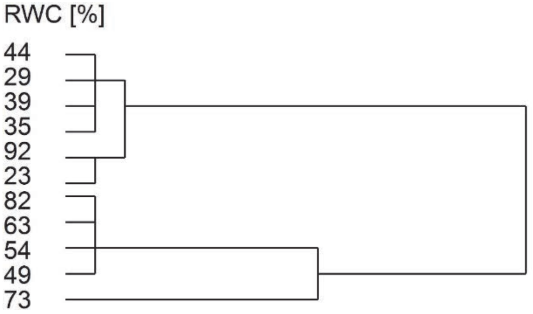

Fig. 4. Cluster analysis of soil moisture for *Tamarix chinensis* seedlings. RWC – relative soil water content.

Table 1. Grading criterion of soil water productivity for *Tamarix chinensis* Lour using cluster analysis. All the values are means of three replications. Means ± SE, *n* = 3. *Different lowercase letters* indicate significant differences (P<0.05). DSF – daily cumulative sap flow; P_N – net photosynthetic rate; WUE – water-use efficiency.

Cluster	Grading of soil water productivity	Cluster mean±SE P_N [μmol m^{-2} s^{-1}]	WUE [μmol $mmol^{-1}$]	DSF [g d^{-1}]
I	High photosynthetic capacity and high WUE	3.18 ± 0.59^a	1.46 ± 0.43^a	286 ± 26^a
II	Medium photosynthetic capacity and medium WUE	1.34 ± 0.43^b	0.70 ± 0.39^b	247 ± 22^b
III	Low photosynthetic capacity and low WUE	0.55 ± 0.15^c	0.44 ± 0.21^c	65 ± 17^c

Grading of the soil moisture productivity: Cluster analysis was performed on 11 soil moisture points according to P_N, DSF, and WUE. When the number of soil moisture clusters was 3 using cluster analysis, the results are summarized in Fig. 4 and Table 1. The physiological significance of different soil moisture was clarified in order to establish the grading of soil moisture availability and evaluation criteria for *T. chinensis* seedlings, based on the response of the plant photosynthesis process and water consumption capacity to soil moisture (Figs. 2*A*, 3). According to the cluster means, the soil moisture productivity and availability for *T. chinensis* seedlings were divided. Cluster I: RWC was ranked to a high P_N, DSF, and WUE type. In this cluster, all three parameters reached the highest values at RWC of 73%. Despite high water consumption, the *T. chinensis* seedlings showed the highest production efficiency, called high photosynthetic capacity and high WUE. Cluster II: RWC was ranked to the medium P_N, DSF, and WUE type; RWC was in the range of 49–63% and 82%, called medium photosynthetic capacity and medium WUE. Cluster III: RWC was ranked to the low P_N, DSF, and WUE type; RWC ≤ 44% or ≥ 92%, called low photosynthetic capacity and low WUE. The cluster means of high and medium photosynthetic capacity of P_N were 5.8 and 2.4 times, respectively, that of low P_N. The cluster means of DSF under high water consumption and medium water consumption were 4.4 and 3.8 times, respectively, that of DSF under low water consumption. The cluster means of high-efficiency and medium-efficiency WUE were 3.3 and 1.6 times, respectively, that of low-efficiency WUE. The analysis of variance results revealed that the above division of soil moisture had a great impact on the P_N, DSF, and WUE of *T. chinensis*, showing significant differences. Thus, different soil moisture conditions significantly affected the photosynthetic characteristics and water consumption of *T. chinensis* seedlings.

Discussion

Photosynthetic light-response parameters: With increasing RWC, the leaf AQY, LSP, P_{Nmax}, and R_D of *T. chinensis* reached a peak at moderately high RWC and then declined towards high and low values of RWC, while LCP followed the opposite trend. However, the critical water point for peak or bottom values of these parameters showed certain differences. A similar phenomenon has been found in photosynthetic light-response parameters of shrubs *Z. jujuba* (Xia *et al.* 2014), *Prunus sibirica* (Xia *et al.* 2011a), *Hippophae rhamnoides* L., and *Pinus tabulaeformis* Carr. (Lang *et al.* 2013), as well as in *Campsis radicans* (Xia *et al.* 2011b). Under different soil moisture conditions, the leaf LCP of *T. chinensis* was in the range of 72–118 μmol m^{-2} s^{-1}, and LSP was in the range of 769–1,013 μmol m^{-2} s^{-1}, being characteristic of heliophytes (Meng 2000). AQY was between 0.008 and 0.025, lower than the range (0.03–0.05) of AQY in most plant species under suitable growth conditions, and it showed that the capability of *T. chinensis* for using low light was low. The leaf LCP showed significant variations under drought stress and waterlogging stress. The lowest LCP of 72 μmol m^{-2} s^{-1} appeared at RWC of 54%, the corresponding AQY was 0.021, indicating a relatively strong low-light use capacity of leaves of *T. chinensis* under this moisture condition (RWC of 54%).

The leaf AQY and R_D of *T. chinensis* seedlings were both markedly higher under waterlogging stress than under drought stress. However, P_{Nmax} and LCP followed the opposite trend, higher namely under drought than under waterlogging stress. These results indicated that *T. chinensis* maintained a better photosynthetic potential under drought than under waterlogging stress. This species can adapt to drought stress by the strategy of increasing LCP, weakening low-light use, and reducing respiratory consumption. The leaf LSP of *T. chinensis* seedlings showed no significant variations under drought and waterlogging stress. The parameter of LSP was maintained at low values of 769–794 μmol m^{-2} s^{-1}, indicating that under drought and waterlogging stress, the leaves of *T. chinensis* can easily reach light saturation, while the excessive absorption of light quanta may be dissipated through fluorescence and heat dissipation (Gardian *et al.* 2011, Ye and Kang 2012), showing the adaptability of *T. chinensis* to withstand high-light intensity. This mechanism may be a survival strategy for *T. chinensis* in order to protect photosynthetic organs from high-intensity light damage under extreme drought or waterlogging stress. The highest LSP was found in leaves of *T. chinensis* at RWC of 49%; under such a moisture condition, the light inhibition was relatively weak, and the light-use efficiency was the highest, showing an optimum photosynthetic performance. The highest P_{Nmax} in the *T. chinensis* leaves appeared at RWC of 63%; under this moisture condition, the enhancement of leaf photosynthetic capacity might be associated with an increase in stomatal conductance, improvement in the plant water status, and enhancement of inorganic ion uptake and transport capacity (Gardian *et al.* 2011, Wang *et al.* 2012). Leaf P_{Nmax} values of *T. chinensis* were markedly higher under drought stress than under waterlogging stress (Fig. 2*C*). Indeed, *T. chinensis* retained a certain photosynthetic capacity under drought habitats, exhibiting its water adaptability with strong drought tolerance and no waterlogging tolerance.

Leaf P_N and WUE: Different results have been obtained with respect to the response relationship of the leaf P_N and WUE in plants to soil moisture, depending on the numbers of simulated moisture gradients. Suitable soil moisture can significantly increase the photosynthetic capacity of plants at community and leaf levels. An increase or decrease in the soil moisture to some extent inhibits photosynthesis in plants. For example, it has been found that the physiological parameters of photosynthesis in plant species, such as *Malus pumila* cv. Goldspur (Zhang *et al.* 2010), *C. radicans* (Xia *et al.* 2011b), and *Z. jujuba* (Xia *et al.* 2014), follow a certain threshold response relationship with soil moisture. The leaf photosynthetic efficiency parameters of *T. chinensis* grown at shell ridges also showed a similar threshold effect of soil moisture. Studies have revealed different soil moisture critical values for the highest P_N values of different plant species (Table 2). These findings indicate that the critical value of soil moisture for the highest P_N is substantially different with varying plant types and habitat conditions.

In this study, the maximum leaf WUE of *T. chinensis* grown on shell ridges appeared at RWC of 73%; however, the WUE values were relatively low at RWC ≥ 82% and RWC ≤ 29%. This result indicates that excessively high or low moisture can significantly inhibit the efficient use of water by *T. chinensis*. The reason is that the normal physiological metabolism of the plant roots is inhibited or that plants maintain a limited water consumption in order to obtain carbon for growth, making the leaves obtain the maximum CO_2 assimilation by limited water loss. Leaves exhibit stomatal optimization behavior (Farquhar and Sharkey 1982), resulting in gradual stomatal closure in order to reduce transpiration loss. Although stomatal closure reduces the absorption of CO_2 and the associated photosynthetic capacity is decreased, photosynthesis is limited by various factors, namely at its limiting process that is a carboxylation reaction (Jin *et al.* 2011). Therefore, under drought stress, the leaves of *T. chinensis* reduce transpiration, stomatal conductance, and intercellular CO_2 concentrations to reduce water loss and meanwhile enhance CO_2 assimilation (Xia *et al.* 2014), resulting in a higher WUE under drought stress (RWC of 29%) than that under waterlogging stress (RWC of 82–92%) (Fig. 2*A*). This finding is similar to conclusions of other studies regarding the strategy through which a water deficit increases the plant WUE to adapt to a drought habitat in the early stages of mild drought or drought (Gao *et al.* 2010, Zhang *et al.* 2010). The leaf WUE of *T. chinensis*

Table 2. The different soil moisture critical values for the highest P_N values of different plant species. P_N – net photosynthetic rate; RWC – relative soil water content.

Functional types	Plant species	The highest P_N values at RWC [%]	Reference
Shrub	*H. Ammodendron*	50	Gao *et al.* 2010
Shrub	*P. sibirica*	68	Xia *et al.* 2011a
Liana	*C. radicans*	71	Xia *et al.* 2011b
Shrub	*T. chinensis*	73	In this study
Tree	*M. pumila cv. Goldspur*	76	Zhang *et al.* 2010

exhibited great differences following changes in RWC, mainly because P_N and *E* showed an asynchronous response to soil moisture and an inconsistent sensitivity to moisture changes. Under water stress, the leaf P_N and *E* of *T. chinensis* both followed a downward trend; however, P_N showed a more sensitive response to RWC under waterlogging stress (Fig. 1). The reduction in the leaf P_N was far greater than that in the leaf *E* of *T. chinensis*, accounting for the relatively low WUE. The opposite trend was found under drought stress. Thus, waterlogging stress can lead more easily to a reduction in the leaf photosynthetic capacity and WUE of *T. chinensis* compared to drought stress. This finding suggests that *T. chinensis* possesses weak waterlogging tolerance but prefers a certain drought environment. In summary, the leaf photosynthetic efficiency parameters (*e.g.*, P_N and WUE) of *T. chinensis* did not follow a single linear relationship with soil moisture. *T. chinensis* seedlings did not show the highest P_N and WUE under saturated moisture conditions (Figs. 1, 2*A*), possibly because the short-term waterlogging stress led to root anoxia and water imbalance, causing leaf stomatal closure and increased CO_2 diffusion resistance (Gautam *et al.* 2015).

Transpiration and water consumption capacity: The stem sap flow velocities of *T. chinensis* seedlings initially increased and then decreased with decreasing RWC. Only under fully saturated moisture conditions (RWC > 92%), *T. chinensis* grown on shell ridges limits its transpiration to some extent, while *T. chinensis* grown in the desert can take full advantage of water resources (Xu *et al.* 2007). The results indicated that *T. chinensis* grown on shell ridges was not well adapted to a high moisture environment, and Cui *et al.* (2010) reported that *T. chinensis* could not survive under waterlogging for a long period of time. Under drought stress, the stem sap flow velocities of *T. chinensis* seedlings followed a markedly decreasing trend with the decrease in RWC below 49%. This trend was similar to conclusions obtained from *S. superba* (Zhou *et al.* 2011) and *Z. jujuba* (Xia *et al.* 2014), possibly because increased soil-to-shoot hydraulic resistance and lower soil hydraulic conductance caused limited water uptake by plant roots (Irvine *et al.* 1998). It has been reported that different soil moisture conditions in wet and dry seasons yielded significant differences in the stem sap flow of *Schima superba*; the sap flow density decreased significantly with decreasing soil moisture (Zhou *et al.* 2011). In contrast, an increase in soil moisture markedly improved the sap flow velocity in *T. ramosissima* (Xu *et al.* 2007) and *Z. jujuba* (Xia *et al.* 2014). However, other studies (Pataki and Oren 2003, Otieno *et al.* 2005) have demonstrated that drought does not reduce the stem sap flow of certain deciduous tree species but it only causes leaf senescence and fall to occur earlier in the late growing season.

More than 99.8% of stem sap flow is used for transpiration (Yue *et al.* 2006), and the daily cumulative sap flow directly reflects the capacity of trees for daily water consumption by transpiration. The daily water consumption of *Haloxylon ammodendron* is significantly correlated with soil moisture, and its daily cumulative sap flow increases with increasing soil moisture (Li *et al.* 2012). In this study, the daily water consumption for the transpiration of *T. chinensis* seedlings grown on shell ridges showed a certain threshold effect of soil moisture; the maximum daily water consumption for transpiration occurred at RWC of 73%, rather than under saturated moisture conditions. The stem sap flow of *T. chinensis* was significantly reduced under severe drought stress. This phenomenon reflects that a soil moisture deficit affects water uptake by roots, leading to a significant reduction in the daily cumulative sap flow of *T. chinensis;* it is a water adaptation strategy for drought stress adaption. The daily cumulative sap flow of *T. chinensis* seedlings exhibited the "S" shaped pattern under different moisture conditions, with substantial variations between day and night. These trends are similar to the response of stem sap flow of *Z. jujuba* grown on shell ridges (Xia *et al.* 2014). The daily cumulative sap flow curve of *Haloxylon ammodendron* is different, as a linear trend under sufficient moisture conditions; however, a similar change process is found under moisture deficiency (Li *et al.* 2012).

Grading and evaluation of soil moisture availability: Cluster analysis was performed on series of soil moisture points measured, mainly using photosynthetic parameters, such as P_N, *E*, WUE, and light-use efficiency. The soil moisture threshold grading and evaluation were performed according to the cluster means in combination with the response of physiological parameters of plant photosynthesis to soil moisture (Xia *et al.* 2014, Zhang *et al.* 2014). Some studies (Zhang *et al.* 2010) used a constraint solving method or critical value classification method, which solve the critical moisture content for photosynthetic parameters and then divide the soil moisture availability. This method requires a significant quantitative relationship between photosynthetic parameters and soil moisture. In the present study, the soil moisture availability was graded using the cluster analysis. Taking into consideration the autocorrelation between WUE and *E*, we introduced the daily cumulative sap flow instead *E*, in order to improve further the accuracy of clustering results. Using this method, *T. chinensis* was classified as of the high photosynthetic capacity and high WUE for growth on shell ridges at RWC of 73%. This moisture condition maintained a relatively high photosynthetic capacity of *T. chinensis* and inhibited low-efficiency water consumption caused by transpiration, thereby ensuring efficient physiological water use in *T. chinensis* leaves. Cui *et al.* (2010) reported that sites with shallow water table depth (less than 1.5 m) and lower soil salinity (less than 30 practical salinity unit) were more suitable for the growth of *T. chinensis*. According to the soil water conditions, beach ridge zone is considered the suitable habitats for *T. chinensis* seedlings grown for restoration processes on shell ridges.

Conclusions: The leaf photosynthetic efficiency and stem sap flow parameters of *T. chinensis* showed a clear threshold response to soil moisture changes and this response was synchronous to a large extent. *T. chinensis* exhibited a complex variation of photosynthesis and water use parameters under contrasting water availability on shell ridges. Excessively high or low moisture markedly reduced the leaf photosynthetic efficiency of *T. chinensis*. *T. chinensis* seedlings exhibited a relatively high photosynthetic capacity and WUE under suitable moisture conditions, and high photosynthetic capacity and high WUE was obtained at RWC of 73%. Under drought stress, the leaf photosynthetic capacity and WUE were higher than those under waterlogging stress. Water stress significantly inhibited the daily water consumption of *T. chinensis* seedlings; however, drought stress caused a larger reduction in daily water consumption compared to waterlogging stress. With increasing waterlogging or drought stress, *T. chinensis* delayed the start time of stem sap flow in the morning and ended the sap flow activity earlier in the day time in order to shorten the daily transpiration period and reduce daily water consumption, thus showing a good capacity for regulating the water physiology under drought stress.

The most prominent ecological feature of shell ridges in the Yellow River Delta is drought and water shortage. Vegetation construction in such habitats should aim to improve effectively the water-use efficiency, but not to achieve the highest photosynthetic productivity with full supply of water. Therefore, we combined the actual water resources on shell ridges and began from the perspective of high photosynthetic productivity and high-efficiency water use of *T. chinensis* to determine suitable soil moistures for WUE. RWC of 49–63% was found as the suitable range of soil moisture for *T. chinensis* seedlings grown on shell ridges.

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