

Photosynthesis of *Populus euphratica* in relation to groundwater depths and high temperature in arid environment, northwest China

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Abstract

The photosynthetic characterization of *Populus euphratica* and their response to increasing groundwater depth and temperature were analyzed based on net photosynthetic rate (P_N), stomatal conductance (g_s), intercellular CO_2 concentration (C_i), transpiration rate (E), water use efficiency (WUE) and stomatal limitation (L_s) measured by a portable gas-exchange system (LI-6400) in the lower reaches of the Tarim River. Light-response curves were constructed to obtain light-compensation and light-saturation points (LCP and LSP), maximum photosynthetic rates (P_{max}), quantum yields (AQY), and dark respiration rates (R_D). The growth condition of *P. euphratica*, soil moisture, and groundwater depth in the plots were analyzed by field investigation. The results showed that the growth condition and photosynthetic characterization of *P. euphratica* were closely related to groundwater depth. The rational groundwater depth for the normal growth and photosynthesis was 3–5 m, the stress groundwater depth for mild drought was more than 5 m, for moderate drought was more than 6 m, for severe drought was more than 7 m. However, *P. euphratica* could keep normal growth through a strong drought resistance depended on the stomatal limitation and osmotic adjustment when it faced mild or moderate drought stress, respectively, at a normal temperature (25°C). High temperature (40°C) significantly reduced P_N and drought stress exacerbated the damage of high temperature to the photosynthesis. Moreover, *P. euphratica* would prioritize the resistance of high temperature when it encountered the interaction between heat shock and water deficit through the stomata open unequally to improve the transpiration of leaves to dissipate overheating at the cost of low WUE, and then resist water stress through the osmotic adjustment or the stomatal limitation.

Additional key words: environmental stress; groundwater depth; net photosynthetic rate; stomatal limitation.

Introduction

Photosynthesis is sensitive to several stresses, including excess irradiance, water stress, high or low temperature, elevated CO_2 , soil nutrient supply, air pollution, and others (Lambers *et al.* 1998). Two of the most studied stresses are high temperature and water stress, which induce severe damage in the photosynthetic apparatus (Vu 2005).

Photosynthesis is known to be one of the most heat-sensitive processes and it can be completely inhibited by high temperature before other symptoms of stress are detected (Berry and Björkman 1980). High temperatures affect photosynthesis through damage to chloroplasts and effects on the biofilm and photosynthetic electron

transport (Taub *et al.* 2000). It had been reported that the inhibition of photosystem II (PSII) activity, which has been shown to be the most thermally labile component of the electron transport chain, could result in the decrease of photosynthesis (Havaux *et al.* 1996). Calvin cycle activity is also sensitive to rapid heat-stress treatments (Bilger *et al.* 1987). There is an evidence that inactivation of Rubisco is an early event in the inhibition of photosynthesis by high temperature (Feller *et al.* 1998). Damaged membrane also relates to the decrease of photosynthesis by high temperature, since membrane disintegration is a primary symptom of heat injury (Blum and Ebercon 1981).

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Abbreviations: AQY – quantum yield; C_i – intercellular CO_2 concentration; D – plant diameter; E – transpiration rate; GD – groundwater depth; g_s – stomatal conductance; LCP – light compensation; LSP – light saturation points; L_s – stomatal limitation; PC – plant coverage; PD – plant density; PH – plant height; PPFD – photosynthetic photon flux density; P_{max} – maximum photosynthetic rate; P_N – net photosynthetic rate; RH – air relative humidity; R_D – dark respiration rate; SM – soil moisture; T_a – air temperature; T_l – leaf temperature; WUE – water use efficiency; Φ – apparent quantum efficiency; θ – convexity.

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Generally, high temperatures occur accompanied by drought stress (Xu and Zhou 2005). These two environmental stresses primarily cause a decrease in the photosynthetic activity which has been attributed, among other physiological changes, to the closure of stomata (Kramer 1983, Franks *et al.* 2001, Centritto *et al.* 2003), to a high resistance to CO₂ flow from the mesophyll cells to the chloroplast stroma (Parry *et al.* 1993) and to alterations in the photochemical processes of the thylakoid membranes (Kim and Portis 2005). Thus, water deficit and heat shock can affect the light-harvesting systems, the flow through the electron transport chain, NADPH and ATP synthesis, photosynthetic carbon reduction cycle in the chloroplast, and the utilization of assimilates (Delatorre *et al.* 2008). Not all physiological processes are equally affected under water stress. For some plants, such as sugar beet and cotton, noncyclic electron flow in the chloroplasts becomes affected when severe drought conditions reduce leaf water potential falls by more than 50% (Hsiao 1973, 2000). Both the photosystems and the electron transport flow in the thylakoid membrane are less sensitive to changes in cellular water balance (Keck and Boyer 1974, James *et al.* 2002), as expected for physiological processes occurring in a nonaqueous medium, such as the lipid membranes. Therefore, water deficit may cause direct damage to the manganese–enzyme complex (Parry *et al.* 1993) also affecting the biosynthesis of Rubisco (Weiss and Berry 1987, Yamasaki *et al.* 2002).

P. euphratica is a member of the *Salicaceae* family of trees found in the semiarid and hyper-arid regions of midwestern Asia, North Africa, and southern Europe (30°–50°N) (Chen *et al.* 2006a). In these regions,

P. euphratica is subjected to extreme environmental conditions such as high solar radiation, extreme temperatures, high salinity, and high water stress (Chen *et al.* 2006a,b). China has the largest range and number of *P. euphratica* in the world (Su *et al.* 2003), and the Tarim River, one of the longest arid inland rivers in the world running between the Taklimakan Desert and the Kuluke Desert, has the largest range and number of *P. euphratica* in China. Over recent decades, as a result of human activities and natural factors, the stream flow of the lower reaches of the Tarim River has sharply decreased, resulting in a significant increase in the groundwater depth along the lower river with a concurrent decline in natural forestry (Liu *et al.* 2005, Chen *et al.* 2006c). Additionally, the temperature of the Tarim Basin experienced a significant monotonic increase at the speed of 5%, nearly a 1°C rise over the past years (Chen and Xu 2005). These disturbances will exacerbate the environmental stresses of *P. euphratica* growth.

In this study, the photosynthesis of *P. euphratica* grown at different groundwater depths in the lower Tarim River was assessed at both ideal and high-temperature conditions. Our objective was to study the acclimation mechanism of *P. euphratica* to drought and temperature stress. We tested the following hypothesis: “The interaction between heat shock and water deficit has a more severe effect on the photosynthesis of *P. euphratica* than each of these stress conditions experienced individually.” In addition, we attempted to understand the rational groundwater depth for *P. euphratica* growth to provide scientific information for protecting and restoring the damaged riparian ecosystem in arid and semi-arid regions.

Materials and methods

General situation of the study area: The lower reaches of the Tarim River stretch from Qiala in Yuli County to Taitema Lake in Ruqiang County. The ground surface is remarkably flat, and the elevation decreases from north to south. Water seeps from streams into the alluvial fans, which can recharge shallow aquifers. The region is classified as an extremely arid warm temperate zone. The annual precipitation varies in the range 17.4–42.0 mm, and the total annual potential evaporation is approximately 2,500–3,000 mm. Total solar radiation varies between 5,692 and 6,360 MJ m⁻² per year, with cumulative daylight hours ranging from 2,780 to 2,980 h. Annual cumulative temperature ≥10°C varies between 4,100 and 4,300°C, with the average diurnal temperature ranging from 13 to 17°C. Strong winds blow frequently in the region. The construction of the Daxihaizi Reservoir in 1972 dried up a length of 321 km in the lower reaches of the Tarim River. The groundwater level fell greatly as a result of the lack of recharging through surface runoff. The soil has been seriously desertified and plant life has seriously degenerated in the region.

Plants: In 2000, nine study sections were established in conjunction with the advent of an ecological emergency water supply from Bosten Lake to the lower reaches of the Tarim River for the purpose of restoring riparian vegetation. Forty groundwater monitoring wells of 15 m in depth and 44 plant plots were established to allow measurement of the groundwater depth and vegetation responses to the ecological emergency water supply. In this study, experiments were conducted in Yhepumahan along the lower reaches of Tarim River (Fig. 1). A plant plot of 50 × 50 m was established around a groundwater monitoring well, in all, 4 plots were placed at transects of 50, 150, 250, and 350 m from the riverbank. The plot was further divided into four 25 × 25 m sample fields, where plant species composition and abundance, coverage, height, and the diameter at breast height of trees were measured. Within each transect, groundwater depth was monitored by the electrical conduction method. Within the center of the plot, three soil profiles were excavated. In all, 12 soil profiles were excavated in the four plots. Soil samples were collected from soil profiles in each

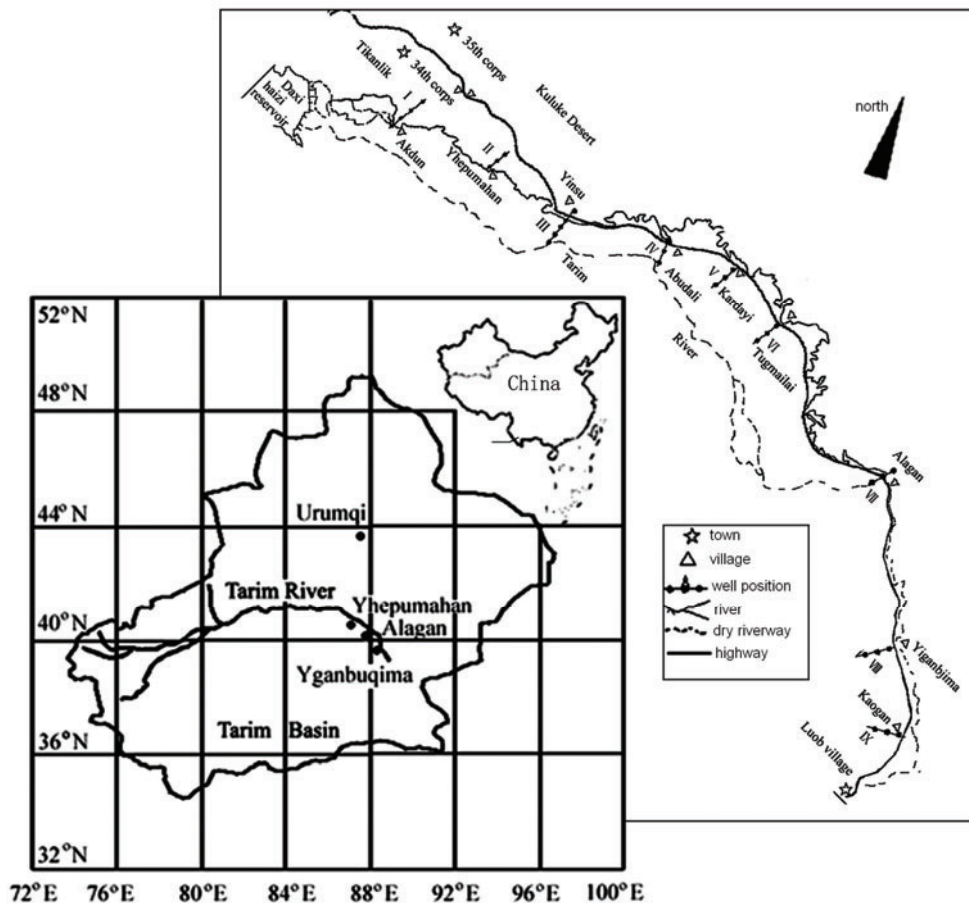


Fig. 1. Sketch of the study area.

plot with a shovel in depths of 0–20, 20–50, 50–100, 100–160, and 160–220 cm, respectively. Each sample was a soil composite comprising three different soil profiles in the same layer. The composite soil sample was collected in an aluminum box and weighed using an electric balance as soon as possible, and later were dried at 105°C for 6 h using an oven (101-E, Beijing, China) and weighed after cooling in a desiccator. Soil moisture was calculated by the standard formula.

Leaf gas exchange measurements: About 8–10 big trees (*P. euphratica*), more than 10 m tall, were in each plot, three of them with the similar diameter at breast height (about 50 cm), 12–15 m in height, about (300–350) × (320–410) cm in crown canopy, healthy, otherwise free of diseases and pest damage were studied. Three fully expanded, healthy, mature, and sunny leaves (exposed to full radiation) in the middle parts of a tree crown were selected for measurement.

Photosynthetic light-response curves were measured at ideal and high temperatures (25°C and 40°C) on a clear day on August 10–13th, 15–18th, 20–23th 2006 using a portable gas-exchange system (Li-6400, LiCor, Lincoln, NE, USA). Every tree was measured for one day with three repetitions, and the repetition interval was about 0.5 h. The used light source (6400-02B LED) was set to

0, 20, 50, 100, 400, 600, 800, 1,000; 1,200; 1,500; and 2,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively. The ambient carbon dioxide concentration ($375 \mu\text{mol mol}^{-1}$) was controlled by the LI-6400 CO₂ injecting system. The measurement sequence varied from 25 to 40°C and induced photosynthesis within 5–8 min before measurement was taken at each temperature. Each leaf was measured three times. Meanwhile, P_N , g_s , C_i , air CO₂ concentration (C_a), E , photosynthetically active radiation (PAR), leaf temperature (T_l), air temperature (T_a) and air relative humidity (RH) were automatically recorded by the portable gas-exchange system. WUE was calculated from the ratio P_N/E , and stomatal limitation (L_s) was calculated as $1 - C_i/C_a$.

A protocol commonly used in photosynthetic light-response curves was as follows (Chen *et al.* 2006d):

Firstly, photosynthetic photon flux density (PPFD) was set at $1,000 \mu\text{mol m}^{-2} \text{s}^{-1}$ to induce photosynthesis because the saturating PPFD of C₃ plants generally was about $1,000 \mu\text{mol m}^{-2} \text{s}^{-1}$ until P_N was steady-state, where P_N showed no systematic decrease or increase ($\pm 2\%$) over a 5-min period. Values of photosynthesis parameters were then recorded and PPFD was increased to $1,200 \mu\text{mol m}^{-2} \text{s}^{-1}$. The intensities of PPFD were applied for 2–3 min in order to stabilize the response of the plant, and then photosynthesis parameters were recorded. This

procedure was repeated for PPFD values of 1,200; 1,500; and 2,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Upon completion of the measurement at a PPFD of 2,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, the PPFD was returned to 1,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ to check if the original P_N could be restored. If this was achieved then the PPFD was decreased stepwise to 800, 600, 400, 100, 50, 20, and 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The intensities of PPFD were applied for 2–3 min in order to stabilize the response of the plant at each step.

Models: AQY, $P_{\max}$, R_D , LCP, and LSP were obtained using light-response curves. The light-response curve of photosynthesis was fitted with a nonrectangular hyperbola (Farquhar *et al.* 1980):

$$P_N = \frac{\Phi I + P_{\max} - \sqrt{(\Phi I + P_{\max})^2 - 4\Phi I P_{\max}}}{2\theta} - R_D$$

where Φ is the apparent quantum efficiency, I is the

Results

Growth: *P. euphratica* was a constructive species of the desert riverbank forest. As groundwater depth increased, the environment became degraded from riverway to both banks of the river and *P. euphratica* growth condition changed. In the shallower groundwater depth (3.37 m), average *P. euphratica* height was 302.04 cm, significantly shorter than those grown in groundwater depths of 5.08, 6.12, and 7.47 m ($p < 0.05$). However, there was no significant difference in the plant heights among those grown at 5.08, 6.12, and 7.47 m groundwater depths (Fig. 2). Similarly, the average diameter at breast height at a groundwater depth of 3.37 m was the shortest, and it gradually increased as groundwater depth increased. However, the average diameter at breast height of *P. euphratica* at different groundwater depths did not show significant differences, with the exception of that at 7.47 m (Fig. 2).

Contrary to the findings for height and diameter, the

PPFD, and θ is the convexity. Firstly, Φ , R_D , LSP, and LCP were obtained from the slope and Y-intercept of the linear regression of the photosynthetic rate on PPFD at 0–200 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively. Then, a nonrectangular hyperbola was fitted to the whole curve using the Φ and R_D values to obtain $P_{\max}$, θ , and the coefficient (R^2) for determining the linear equation that represented the best fit.

Statistical analysis: All data obtained in this study were analyzed by SPSS 13.0 (SPSS, Inc., USA), correlation analysis between groundwater depths, soil moisture, and growth condition of *P. euphratica* was used by *t*-test, and differences of P_N , g_s , E , WUE, C_i , and growth condition of *P. euphratica* at different groundwater depths and temperatures were determined using the one-way ANOVA or multiple comparison (LSD test). The graphs were produced with SigmaPlot 9.0 (SPSS, Inc., USA).

density and coverage of *P. euphratica* growing much nearer to the river were significantly higher than for those growing away from the river. Compared with *P. euphratica* at groundwater depths of 3.37 and 5.08 m, the densities at 6.12 and 7.47 m were significantly reduced by 77.11% and 90.36% (at 3.37 m) and by 65.77% and 85.59% (at 5.08 m), respectively, and the coverage was significantly reduced by 65.61% and 75.64% (at 3.37 m) and by 65.40% and 75.58% (at 5.08 m), respectively ($p < 0.05$; Fig. 3). Through the field investigation, there were many saplings when the groundwater depths were 3.37 and 5.08 m, especially at 3.37 m, which suggested it was beneficial to growth and propagation when the groundwater depth was less than 6 m. In contrary, the quantity of *P. euphratica* was less when the groundwater increased to 6.12 and 7.47 m, however, most of them were tall and adult trees with big diameter. Therefore, there were lower heights and

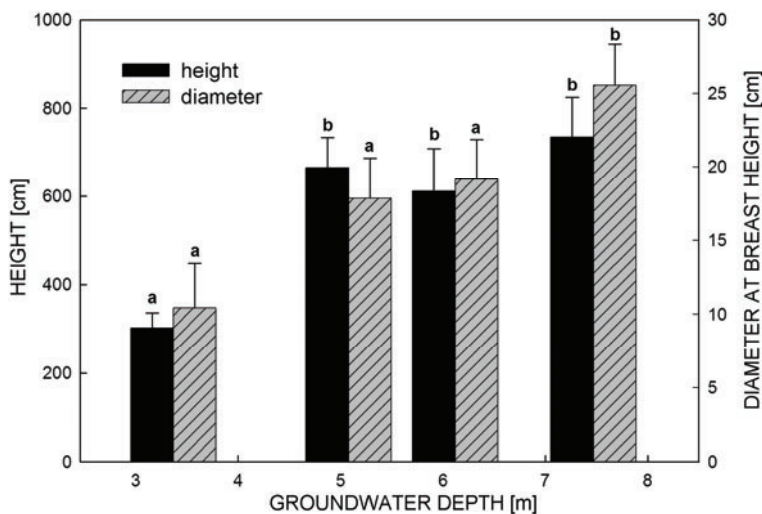


Fig. 2. Height and diameter of *P. euphratica* at different groundwater depths. Each data point is the average obtained from plant investigation, $n = 18-54$ ($\pm$ SE), LSD test of one-way ANOVA indicated statistically significant differences caused by groundwater depths. The same letter, not significant; the different letter, significant at 0.05 level.

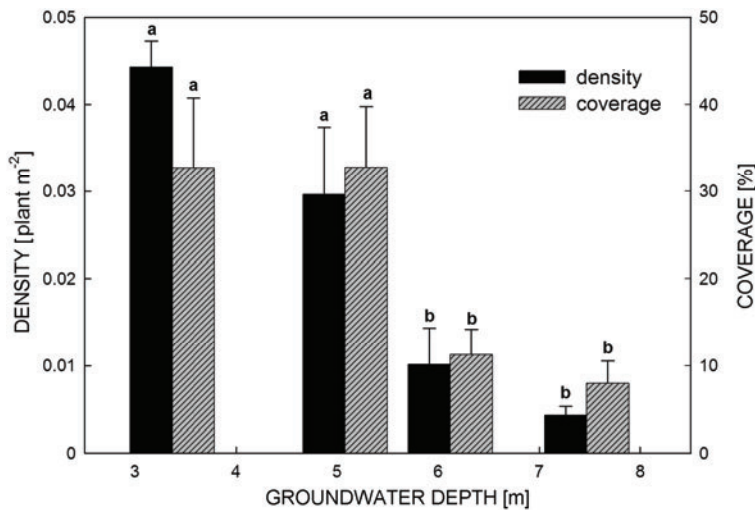


Fig. 3. Density and coverage of *P. euphratica* at different groundwater depths. Each data point is the average obtained from plant fields, $n = 4$ ($\pm$ SE), LSD test of one-way ANOVA indicated statistically significant differences caused by groundwater depths. The same letter, not significant; the different letter, significant at 0.05 level.

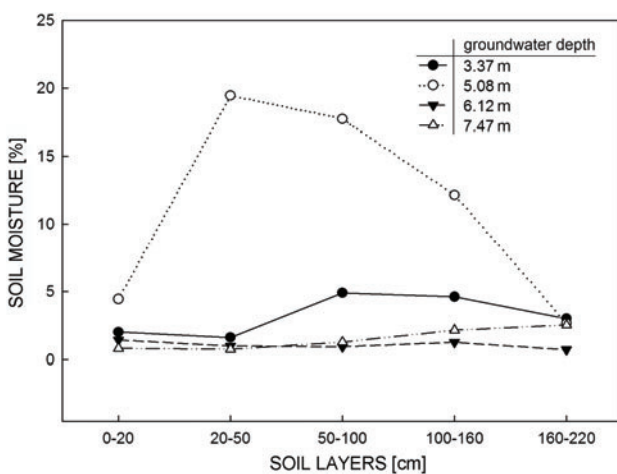


Fig. 4. Soil moisture at 0–220 cm layers.

diameters along with higher densities and coverage across the shallower groundwater depths.

Soil moisture: The water source for plant photosynthesis was primarily from surface water, soil moisture and

groundwater. Because the study area was extremely dry and scare of rainfall resulted in surface runoff was seldom formed, water for *P. euphratica* existence and development was mainly from soil moisture and groundwater. The soil moisture changed with the variation of groundwater depths (Fig. 4), moreover, the soil moisture at 5.08 m groundwater depth was higher than those at the others, which might be caused by soil texture difference. However, there was no significant correlation between soil moisture and groundwater depths in the study area ($p > 0.05$, Table 1). Similarly, no significant correlations were found between soil moisture and plant height (PH), plant density (PD), plant coverage (PC) and plant diameter (D), respectively ($p > 0.05$, Table 1).

P_N : The photosynthetic light-response curves obtained at different groundwater depths and temperatures showed that the photosynthetic rates changed as temperature and water deficit increased (Fig. 5). At 25°C, although the P_N of *P. euphratica* changed with the ingcreasing groundwater depth, the analysis of variance showed that there were no significant differences among the P_N obtained at different groundwater depths ($p > 0.05$), except for that at

Table 1. The correlation analysis (R) between groundwater depths, soil moisture and *P. euphratica* growth condition. * $p < 0.05$; ** $p < 0.01$. GD – groundwater depth; SM – soil moisture; PH – plant height; PD – plant density; PC – plant coverage; D – plant diameter.

	GD [m]	SM [%] 0–20 cm	20–50 cm	50–100 cm	100–160 cm	160–220 cm	PH [cm]	PD [plant m ⁻²]	PC [%]	D [cm]
GD	1									
SM		1								
0–20 cm	-0.453	1								
20–50 cm	-0.205	0.963*	1							
50–100 cm	-0.367	0.984*	0.982*	1						
100–160 cm	-0.393	0.973*	0.967*	0.997**	1					
160–220 cm	-0.414	0.314	0.287	0.421	0.489	1				
PH	0.889	0.008	0.266	0.093	0.058	0.315	1			
PD	-0.987*	0.531	0.311	0.480	0.516	0.591	-0.824	1		
PC	-0.976*	0.777	0.608	0.743	0.769	0.604	-0.594	0.944	1	
D	0.964*	-0.344	-0.081	-0.239	-0.259	-0.289	0.927	-0.930	-0.801	1

6.12 m ($p<0.05$; Fig. 5A). At the higher temperature (40°C), the P_N of *P. euphratica* decreased with the increasing groundwater depth, and the magnitude of the decrease increased with a rise in PAR (Fig. 5B), moreover, there was a significant difference in P_N at 7.47 m compared to that at 3.37, 5.08, and 7.47 m, respectively ($p<0.05$).

High temperature significantly reduced the P_N of *P. euphratica* ($p<0.01$; Fig. 5). However, the magnitude of the decrease in average P_N varied with the change of groundwater depth. The average P_N at groundwater depths of 3.37, 5.08, 6.12, and 7.47 m was reduced by 22.3, 20.70, 40.95, and 55.06%, respectively, with temperatures rising from 25°C to 40°C, which suggested the restraint of high temperature on photosynthesis of *P. euphratica* in deeper groundwater depth was more obvious than that in shallower groundwater depth.

The photosynthetic parameters of *P. euphratica* at different groundwater depths and normal (25°C) and high (40°C) temperatures were calculated using the non-rectangular hyperbola, presented in Table 2, and all the R^2 were above 0.9, which meant the predicted curve and observed curve fitted well using the models. At 25°C, $P_{\max}$ at different groundwater depths were not significantly different. When the temperature rose to 40°C, $P_{\max}$ significantly decreased compared that at the same groundwater depth, and the value at 7.47 m significantly

decreased than that at 3.37, 5.08, and 6.12 m, respectively ($p<0.05$, Table 2).

Apparent quantum yield (AQY) is an index reflecting the light-use efficiency of a plant (Xu 2002). The AQY at different groundwater depths ranged from 0.05–0.075 when temperature was 25°C, from 0.058–0.082 when temperature was 40°C. However, all of them did not show significant differences ($p>0.05$). With the rise in the temperature from 25°C to 40°C, AQY at groundwater depths of 3.37, 5.08, and 6.12 m significantly increased ($p<0.05$), i.e., the light-conversion efficiency increased with the rising temperature. However, AQY at a groundwater depth of 7.47 m sharply decreased ($p<0.05$; Table 2).

Light saturation point (LSP) and light compensation point (LCP), which reflect the ability of a plant to use the highest and lowest light levels, are upper and limit indices that measure the relationship between light and photosynthesis (Chang *et al.* 2006). At 25°C, LSP significantly decreased as groundwater depth increased from 3.37 to 5.08 m, however, it significantly increased when the groundwater depths increased beyond 5.08 m to 6.12 and 7.47 m. At 40°C, the change trend of LSP was similar to that at 25°C when the groundwater depth was less than 7 m, however, the LSP at groundwater depths of 7.47 m sharply decreased compared with those at 3.37, 5.08, and 6.12 m ($p<0.05$). In contrast, LCP increased

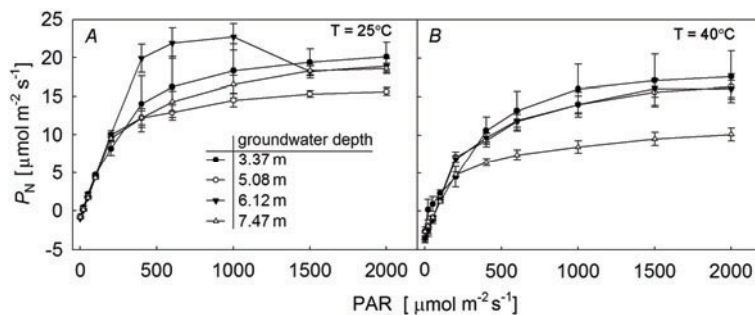


Fig. 5. Response of net photosynthetic rate (P_N) to photosynthetic photon flux density in leaves of *P. euphratica* to different groundwater depths at 25°C (A) and 40°C (B) ($n = 27$, $\pm$ SE).

Table 2. Response of parameters of photosynthetic rate in *P. euphratica* to light intensity at different temperatures and different groundwater depths. The values of parameters of photosynthetic rate are the statistical mean values ($n = 27$) under the temperature of 25 and 40°C, respectively. $P_{\max}$ – the light-saturated rate of photosynthesis; AQY – the apparent quantum efficiency; LSP – light saturation point; LCP – light compensation point; R_D – the dark respiratory rate; θ – the convexity; R^2 – the determining coefficient. LSD test was conducted to indicate statistically significant differences between photosynthetic parameters at the same temperature and groundwater depths, as well as between photosynthetic parameters at the same groundwater depth and temperature. The same letter, not significant; the different letter, significant at 0.05 level.

Groundwater depth [m]	Temperature [°C]	$P_{\max}$ [$\mu\text{mol m}^{-2} \text{s}^{-1}$]	AQY [$\mu\text{mol}(\text{CO}_2)$ $\mu\text{mol}^{-1}(\text{photon})$]	LSP [$\mu\text{mol m}^{-2} \text{s}^{-1}$]	LCP [$\mu\text{mol m}^{-2} \text{s}^{-1}$]	R_D [$\mu\text{mol m}^{-2} \text{s}^{-1}$]	θ	R^2
3.37	25	22.608 ^a	0.056 ^a	503.905 ^a	8.072 ^a	0.639 ^a	0.699	0.999
	40	20.243 ^b	0.066 ^b	692.822 ^d	39.825 ^d	0.816 ^a	0.819	0.994
5.08	25	22.015 ^a	0.073 ^a	331.249 ^b	15.972 ^b	1.156 ^b	0.704	0.994
	40	17.056 ^b	0.082 ^b	488.098 ^e	68.819 ^e	1.395 ^b	0.176	0.995
6.12	25	21.428 ^a	0.05 ^a	403.652 ^c	19.638 ^c	1.031 ^b	0.999	0.982
	40	16.161 ^b	0.073 ^b	495.054 ^f	68.885 ^e	1.102 ^b	0.331	0.996
7.47	25	19.006 ^a	0.075 ^a	440.518 ^c	18.083 ^c	1.237 ^c	0.281	0.996
	40	13.708 ^c	0.058 ^c	435.069 ^e	89.349 ^f	1.335 ^c	0.372	0.994

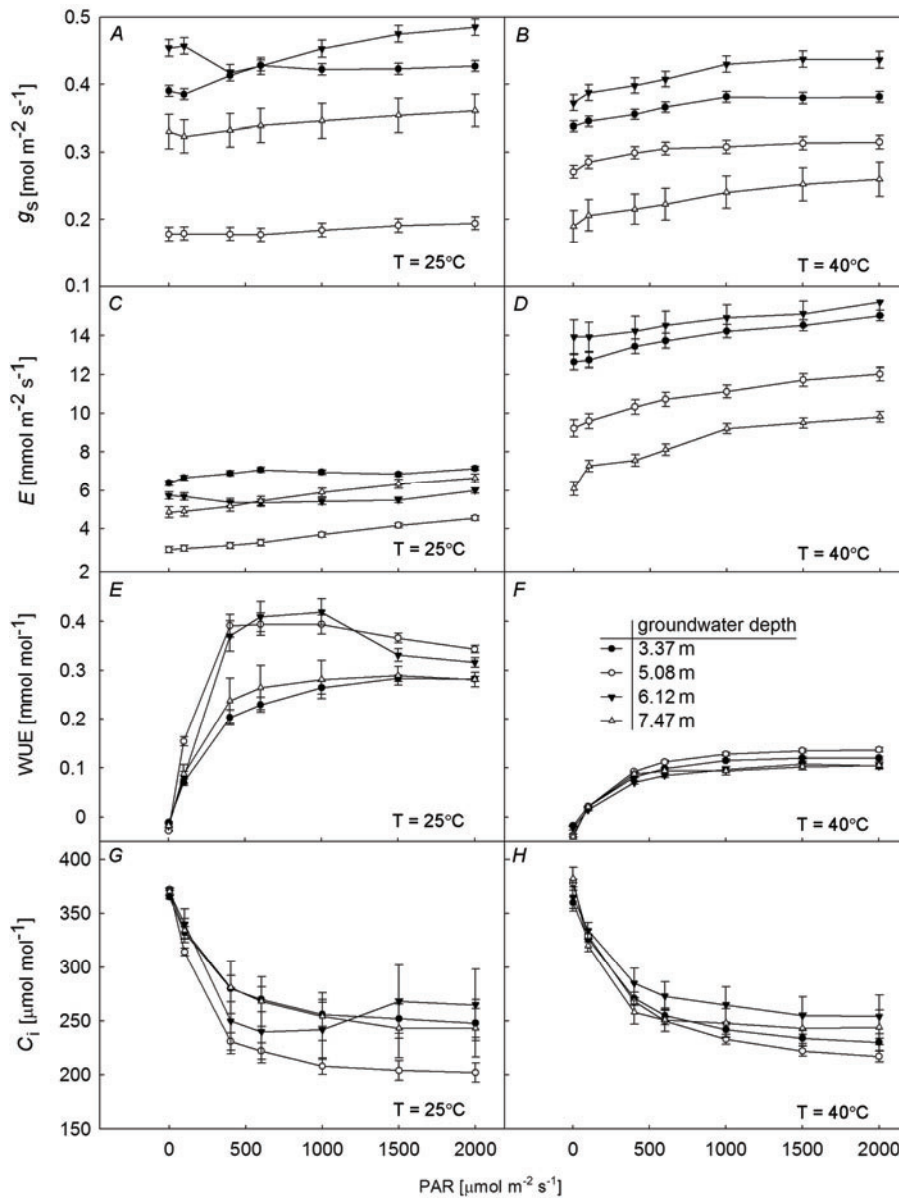


Fig. 6. Response of stomatal conductance (g_s) (A,B), transpiration rate (E) (C,D), intercellular CO_2 concentration (C_i) (E,F), and water use efficiency (WUE) (G,H) of *P. euphratica* to different temperatures and different groundwater depths ($n = 27$, $\pm\text{SE}$).

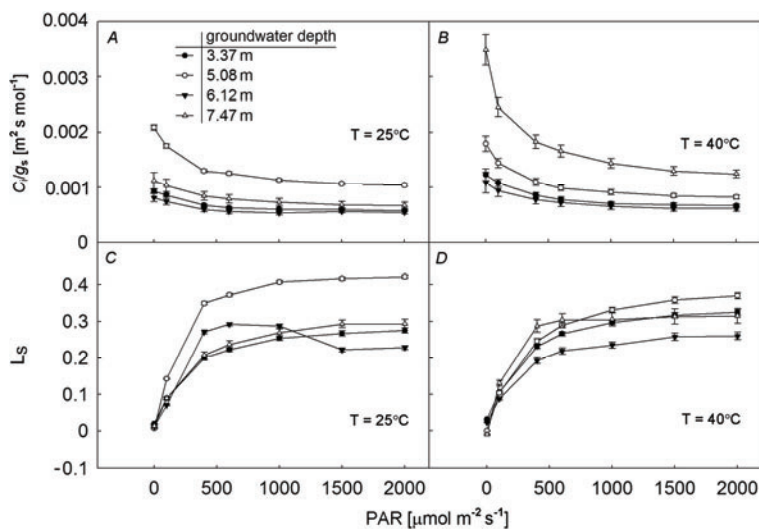


Fig. 7. Response of C_i/g_s values (A,B) and stomatal limitation (L_s) (C,D) of *P. euphratica* to different temperatures and different groundwater depths ($n = 27$, $\pm\text{SE}$). C_i – intercellular CO_2 concentration; g_s – stomatal conductance.

along with the increase of groundwater depths from 3.37 to 6.12 m under the temperature of 25°C. This suggested that water stress increased the efficient use of stronger light but reduced the efficient use of weaker light at normal temperatures. With the temperature rising from 25°C to 40°C, both the LSP and LCP significantly increased when the groundwater depth was less than 7 m. However, rising temperature not only stimulated a further increase in LCP but also stimulated the LSP to decline when the groundwater depth reached 7.47 m (Table 2). This suggested that rising temperature could enhance the light use efficiency of stronger light and reduce the light use efficiency of weaker light at groundwater depths of less than 7 m, but it reduced the usage efficiency of both stronger and weaker light and narrowed the scope of adaptation to light, which severely limited the photosynthetic capacity of *P. euphratica* when the groundwater depth was more than 7 m.

g_s : A significant difference in the g_s of *P. euphratica* presented at different groundwater depths ($p < 0.05$). The highest average g_s were recorded at a groundwater depth of 6.12 m, both at 25 and 40°C, and the lowest value was recorded at 5.08 and 7.47 m, at 25 and 40°C, respectively. g_s increased with the increasing light, however, the magnitude of the increase at 3.37 and 6.12 m were more than those found at 5.08 and 7.47 m ($p < 0.05$). With a rise in temperature from 25 to 40°C, g_s significantly reduced ($p < 0.05$), and the magnitude of the decrease rose with the increasing groundwater depth (Fig. 6A,B), except for that at 5.08 m.

E : At 25°C, the average E of *P. euphratica* was in

sequence of $3.37 > 7.47 > 6.12 > 5.08$ m, and it was significantly different with groundwater depth at 5.08 m compared with each of those found at 3.37, 6.12, and 7.47 m. However, the average E at 40°C was in a sequence of $6.12 > 3.37 > 5.08 > 7.47$ m, which was consistent with the changes in g_s with groundwater depth at 5.08 and 7.47 m. With a rise in temperature from 25 to 40°C, the E of *P. euphratica* grown at different groundwater depths increased significantly ($p < 0.05$; Fig. 6C,D). Strong transpiration could accelerate the dissipation of heat from the leaves to prevent high temperature stress.

WUE: When the temperature was 25°C, WUE at groundwater depths of 5.08 and 6.12 m was significantly higher than that found at 3.37 m ($p < 0.05$), especially for 500–1,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR, but it sharply declined at 7.47 m compared with those at 5.08 and 6.12 m ($p < 0.05$). WUE at different groundwater depths changed little when the temperature was 40°C. As the temperature rose from 25 to 40°C, WUE at different groundwater depths significantly decreased ($p < 0.05$), and the magnitude of the decrease rose with the increasing groundwater depth (Fig. 6E,F), which suggested that high temperature sharply reduced WUE, especially in deeper groundwater depths.

C_i : At temperatures of 25 and 40°C, C_i at different groundwater depths was in sequences of $3.37 > 6.12 > 7.47 > 5.08$ m and $6.12 > 3.37 > 7.47 > 5.08$ m, respectively, and C_i at 5.08 m was significantly lower at 25°C ($p < 0.05$). When the temperature rose from 25 to 40°C, C_i at 3.37 and 6.12 m slightly increased, but they slightly reduced at 5.08 and 7.47 m (Fig. 6G,H).

Discussion

The relationship between the groundwater depth and temperature: Fufezan *et al.* (2007) have indicated the photosynthetic rates at light saturation are greatly influenced by temperature. Low temperatures and high temperatures reduce the photosynthetic rates while moderate temperatures maintain the photosynthetic rate at a maximum. From the analysis on our experimentation, it was possible to conclude that high temperature (40°C) significantly reduced P_{max} , and this trend became more obvious for *P. euphratica* grown at deeper groundwater depths. Thus, the greater the water deficit, the greater the susceptibility to extreme temperature as well.

The greater reduction in P_N at the deeper groundwater depths, compared to those at the shallower groundwater depths when the temperature rose from 25 to 40°C, seemed to be corroborated by the data derived from the LCP. The LCP of *P. euphratica* showed an increase when the temperature rose from 25 to 40°C, moreover, this trend enhanced with the increasing groundwater depth. This increase in LCP found at high temperatures and water deficit required a greater photon flow to reach the

equilibrium between the O_2 liberated in photosynthesis and the O_2 absorbed by dark respiration (Delatorre *et al.* 2008). Since the dark respiration rate did not significantly increase with the increase in temperature (Table 2), we could conclude that photosynthesis provided more energy for *P. euphratica* than did dark respiration. One possible explanation for this could be that high temperatures reduced the capture of energy by the light-harvesting complex, or that the electron flux was partially interrupted at the PSII reaction center and, therefore, it required more photons to achieve water photolysis (Shirke and Pathre 2004, Delatorre *et al.* 2008), especially for deeper groundwater depths.

AQY showed no significant difference at 25°C, but it was significantly decreased at 7.47 m with an increase in temperature, indicating that water stress and high temperature had an additive effect on *P. euphratica*. It is known that heat shock disrupts the membrane-bound complexes of mitochondria, which in turn decrease the electron transport (Rizhsky *et al.* 2002). Similar to mitochondria, the membrane-bound complexes of

chloroplasts might be disrupted which a decrease of the electron transport between both photosystems (Delatorre *et al.* 2008). This, in turn, would increase the triplet state of chlorophyll *a* (Fufezan *et al.* 2007). As a consequence, there was an induction of oxidative stress with the formation of reactive oxygen species (ROS) since the electrons from water were not reducing the chlorophyll *a* of the reaction center. This might explain the great decrease of AQY grown at 7.47 m and 40°C.

Similarly, with the increase in the temperature, P_N and WUE sharply declined but the leaf transpiration significantly increased, and the changes were more obvious with the increasing groundwater depth. These results based on the above photosynthetic parameters confirmed our hypothesis that the interaction between high temperature and water deficit had a greater effect on photosynthesis than did each individual stress, which would obviously exacerbate the environmental stresses of the growth of *P. euphratica* in the future because of the significant monotonic increase of temperature in the Tarim Basin and water resource limitation resulted from the gradual reduction of water from the upper Tarim River (Chen and Xu 2005, Chen *et al.* 2005).

The relationship between photosynthesis and groundwater depth: The value of C_i/g_s has been used as an indicator to characterize mesophyll capacity under water stress (Sheshshayee *et al.* 1996), which depended on the activity of Rubisco and on the capacity of photosynthetic electron transport to regenerate Rubisco (Crafts-Brandner *et al.* 1997, Feller *et al.* 1998). Ramanjulu *et al.* (1998) had found the C_i/g_s value increased when the plant encountered water stress, especially for severe or moderate water stress. At both 25 and 40°C, C_i/g_s with groundwater depths at 5.08 and 7.47 m were significantly increased compared with those at 3.37 and 6.12 m in the study area ($p < 0.05$; Fig. 7A,B). So, it was possible to presume that *P. euphratica* had faced water deficit when the groundwater depth was more than 5 m.

Generally, mild water stress did not affect the P_N of trees, to the contrary, moderate water deficit might increase the P_N of trees (Chen *et al.* 2006a), and P_N sharply decreased when the tree faced severe water stress (Cregg and Zhang 2001). P_N with groundwater depth at 6.12 m was significantly higher than that at 5.08 m both at 25 and 40°C in the study area (Fig. 5), and it sharply decreased when the groundwater depth reached 7.47 m compared with that at 6.12 m, especially for that at 40°C. Hence we might suggest that *P. euphratica* was subjected to mild water deficit when the groundwater depth was more than 5 m, to moderate water deficit when the groundwater depth was more than 6 m, and to severe water stress when the groundwater depth was more than 7 m. The conclusion was further proved by the changes of WUE, which have been reported that the WUE of plants increased when they were subjected to mild and moderate water stress but it sharply decreased when they were

subjected to severe water stress (Wang *et al.* 2003, Su *et al.* 2005, Yang *et al.* 2004). So, it was reasonable to conclude that the ideal groundwater depth for the normal growth of *P. euphratica* was less than 5 m, the stress groundwater depth for mild water drought was more than 5 m, for moderate water drought it was more than 6 m, and for severe water stress more than 7 m.

The potential acclimation mechanism of *P. euphratica* to drought stress and high temperature: According to von Caemmerer and Farquhar (1981), as well as Calatayud *et al.* (2000), changes in P_N reflected alterations in both g_s and mesophyll capacity for photosynthesis. Researchers had pointed out that the reduction of P_N was the result of a decrease in g_s , but only if there was a reduction in C_i and an increase in L_s (Farquhar and Sharkey 1982, Xu 1997). In contrast, if a decrease in P_N accompanied an increase in C_i and a reduction of L_s as well, the main constraint of photosynthesis was the result of the nonstomatal limitation (von Caemmerer and Farquhar 1981, Su 2003). In this study, the reduction in P_N of *P. euphratica* at 25°C accompanied the reduction in g_s , C_i (Figs. 5, 6) and the increase of L_s (Fig. 7C,D) when the groundwater depth increased from 3.37 to 5.08 m. Therefore, the photosynthetic reduction at the normal temperature was attributed to the stomatal limitation when it was subjected to mild water stress, which is inconsistent with the result reported by Chen *et al.* (2006a). The reduction of g_s resulted from stomatal closure reduced the CO_2 assimilation rate, which finally resulted in the photosynthetic reduction. Moreover, the decrease of g_s could reduce the E , alleviate the evaporation of water from the leaves, accordingly improve the WUE, which effectively alleviated the water stress to maintain the normal growth of plants. This might explain why P_N , g_s , and E at 5.08 m were low, but WUE kept high at 25°C. These findings suggested that *P. euphratica* adapted to mild water stress through the improvement of WUE resulted from the reduction of g_s and the alleviation of evaporation of leaves at normal temperature (25°C). This was also the reason that there were higher density and coverage of *P. euphratica* when the groundwater depth was 5.08 m.

In contrast, the decrease in P_N at 5.08 m accompanied a slight increase in C_i when the temperature rose from 25 to 40°C. Therefore, the main constraint of photosynthesis of *P. euphratica* subjected to mild water stress was the result of the mesophyll capacity when it encountered high temperature stress, which was further proved by the increase of g_s and E , as well as the reduction of WUE (Fig. 6). The saturated light in the lower Tarim River was below $1,000 \mu\text{mol m}^{-2} \text{s}^{-1}$, while the light in the actual situation was more than that in summer, and the daylight hours were more than 12 h. Overheating stayed in leaves of *P. euphratica* would damage the leaves and reduce the photosynthesis if it could not be used or dissipated as soon as possible. So, when *P. euphratica* encountered the interaction between heat shock and mild water deficit, it

prioritized to keep some stomata open to accelerate the transpiration to dissipate the overheating and protect leaves against high-temperature damage. However, the stomata opening also reduced the WUE (Fig. 6), which might exacerbate the water stress. So, it might depend on other physiological mechanisms resisting the water stress. It has been reported the osmotic adjustment is done by accumulating proline, soluble sugars, superoxide dismutase, and ABA *etc.* in *P. euphratica* bodies (Chen *et al.* 2006c) when the plants encounter water stress. Additionally, *P. euphratica* could endure drought with a very low water potential to protect the main organs against damage, moreover, they also could transport water with the trunks and branches (Deng *et al.* 2002).

The photosynthetic parameters at 6.12 m suggested P_N and WUE were kept high when it was subjected to moderate water stress at 25°C, which was consistent with the conclusion that *P. euphratica* and grapevines could have maintained P_N as drought stress increased from mild to moderate levels, as reported by Chen *et al.* (2006a) and Guan *et al.* (2004), respectively. It has been reported that the maintenance of higher P_N and WUE in plants under drought stress depends on osmotic adjustment (Morgan *et al.* 1993, Rekika *et al.* 1998, Shangguan *et al.* 1999, Chen *et al.* 2006a). Therefore, we might speculate that the osmotic adjustment was done for maintaining higher P_N and WUE when *P. euphratica* encountered the moderate water stress at normal temperature in the lower reaches of the Tarim River.

When the temperature increased, P_N and C_i at 6.08 and 3.37 m decreased, but the L_s increased, suggested the photosynthetic reduction was attributed to the stomatal limitation. Generally, transpiration was positively related to g_s , however, the reduction of g_s did not result in the decrease of E (Fig. 6). We speculated this was caused by unequally opened stomata. Zheng *et al.* (2006) have observed that the densities of stomata on the adaxial and abaxial epidermis of the leaves of *P. euphratica* are similar, which means that both of them could photosynthesize, moreover, the stomata on the adaxial and abaxial epidermis of the same leaf open unequally when the leaf suffers from adverse environment. Indeed, the reduction of g_s resulted from two reasons, the first was

the degree of stomatal closure, and the other was the number of stomatal closure. E still could keep increasing if the high degree of closure presented few stomata and most stomata kept open or slight closure conducted by the stomata open unequally. Therefore, it was possible that *P. euphratica* would prioritize the resistance of high temperature when it encountered the interaction between heat shock and water deficit through the stomata open unequally to improve the transpiration of leaves to dissipate overheating at the cost of low WUE. then it resisted water stress through the osmotic adjustment or the stomatal limitation, which was further proved by the changes of photosynthetic parameters of *P. euphratica* at 7.47 m when the temperature rose from 25 to 40°C.

Conclusion: The results from analysis on the responses of the changes of photosynthetic parameters of *P. euphratica* to different groundwater depths and temperatures confirmed the hypothesis that the interaction between high temperature and water deficit had a greater effect on photosynthesis of *P. euphratica* in the lower Tarim River than did each individual stress.

The growth condition and photosynthetic characterization of *P. euphratica* were closely related to groundwater depth in the lower reaches of the Tarim River. The rational groundwater depth for the normal growth and photosynthesis of *P. euphratica* was 3–5 m. *P. euphratica* was subjected to mild water stress at a groundwater depth of more than 5 m, to moderate water stress at more than 6 m, and to severe water stress at more than 7 m.

It showed a strong drought resistance depended on the stomatal limitation and osmotic adjustment to maintain normal growth of *P. euphratica* faced mild or moderate drought stress, respectively, when the temperature was normal (25°C). However, it was possible that *P. euphratica* would prioritize the resistance of high temperature when it encountered the interaction between heat shock and water deficit through the stomata open unequally to improve the transpiration of leaves to dissipate overheating at the cost of low WUE.

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