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# Photosynthesis of *Populus euphratica* and its response to elevated $CO_2$ concentration in an arid environment

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**Abstract**

The photosynthetic characterization of *Populus euphratica* and its response to the elevated carbon dioxide concentration ([$CO_2$]) were analyzed based on its net photosynthetic rate ($P_n$), stomatal conductance ($g_s$), intercellular $CO_2$ concentration ($C_i$), transpiration rate ($T_r$), and water use efficiency (WUE) at different groundwater depths measured by a portable gas exchange system (LI-6400) in the lower reaches of the Tarim River. The results showed that the elevation of [$CO_2$] decreased the $g_s$, and increased the $P_n$, $C_i$ and WUE of *P. euphratica.* However, the effects of the elevated [$CO_2$] on $g_s$, $P_n$, $C_i$ and WUE varied considerably with groundwater depth. The response of photosynthesis to rising [$CO_2$] was stronger at the greater groundwater depth (more than 6 m) than that at the shallower groundwater depth (less than 6 m). The critical groundwater depth required to maintain the normal survival of *P. euphratica* was less than 6 m. When the groundwater depth increased to more than 6 m, *P. euphratica* encountered moderate water stress, and the plant suffered severe water stress when the groundwater depth increased to more than 7 m.


*Keywords:* Photosynthesis; *Populus euphratica*; Groundwater depth; $CO_2$ concentration; The lower reaches of the Tarim River

## 1. Introduction

Photosynthesis is a very complicated physiological process, affected by the combined effects of the intrinsic properties of plants and environmental factors [1], of which light, water, carbon dioxide concentration and temperature are important variables [1,2]. Some studies show that the atmospheric $CO_2$ has increased by 1.5 ppm per year [3]. The IPPC IS92a emission scenario predicts that the atmospheric $CO_2$ will increase to 750 ppm by 2100 [4]. Therefore, plants will face a higher $CO_2$ environment. It is expected to alter the photosynthetic function of plants [5,6], especially those that grow in arid environments. The relationship between plant photosynthesis and environmental factors has been well characterized [7–11], yet the photosynthetic stimulation observed in the elevated [$CO_2$] experiments does not always match theoretical expectations [12,13]. Especially, the impact of the elevated $CO_2$ on photosynthesis in *Populus euphratica* in an arid environment has not been well characterized.

*Populus euphratica* is the oldest tree species of desert riparian forest, and is distributed widely in arid desert regions of 30°–50°N, e.g. midwestern Asia, North Africa and southern Europe. China has the largest range and number of *P. euphratica* in the world [14]. *P. euphratica* is a dominant tree species of the green corridor around the lower reaches of the Tarim River in China [15].

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The Tarim River is one of the longest arid inland rivers in the world. Its main stream is 1321 km in length and runs between the Taklimakan Desert and the Kuluke Desert. This is an extremely arid region with a continental warm temperate climate, dry and sandy soils, low annual rainfall and strong annual evaporation. Over recent decades, as a result of human activities and natural factors, the eco-environment of the lower reaches of the Tarim River has deteriorated markedly; the river flow has decreased rapidly and the groundwater depth has deepened sharply, which has exacerbated the water stress level in the environment of *P. euphratica* [16]. As a result of global warming, *P. euphratica* is bound to face multiple stresses, including high temperature, drought stress and high $CO_2$ concentrations. In order to understand the mechanism that underlies the response of photosynthesis in *P. euphratica* to the elevated $CO_2$, as well as to improve our ability to predict the effect of global climate change on the growth of *P. euphratica*, the alteration in photosynthesis in *P. euphratica* grown at different groundwater depths in response to rising $CO_2$ in the arid environment of the lower reaches of the Tarim River was analyzed. Additionally, our study was designed to provide scientific information to use as the basis for protecting and restoring the damaged ecosystem of the lower reaches of the Tarim River.

## 2. General situation of the study area

The lower reaches of the Tarim River stretch from Qiala in Yuli County to Taitema Lake in Ruoqiang County. The channel bed stretches from east to south on alluvial fans along the Taklimakan and Kuluk deserts. 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 2500–3000 mm. Total solar radiation varies between 5692 and 6360 MJ/m$^2$ per year, with cumulative daylight hours ranging from 2780 to 2980 h. Annual cumulative temperature $\geqslant$10 °C varies between 4100 and 4300 °C, with an average diurnal temperature ranging from 13 to 17 °C. Strong winds blow frequently in the region. The construction of the Daxihaizi Reservoir in 1972 reduced the water flow into the Tarim River and dried up a length of 321 km in its lower reaches. The groundwater level fell greatly, to a depth of 8–12 m, 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.

## 3. Materials and methods

### 3.1. Materials

In conjunction with the establishment of an ecological emergency water supply in 2000 from Bosten Lake to the lower reaches of the Tarim River to restore the riparian vegetation, nine study sections were established. Forty groundwater monitoring wells of 15 m depth and 44 plant plots were established to allow the measurement of the groundwater depth and vegetation responses to the ecological emergency water supply (Fig. 1). In this study, experiments were conducted in Yhepumahan along the lower reaches of the Tarim River. Plant plots of 50 × 50 m were established at different groundwater depths, and were placed at transects of 50, 150, and 250 m from the riverbank. The ground-surface of the plots was remarkably flat with the elevation having little change. In each plot, five trees (*P. euphratica*) of about 50–55 years old, 8–10 m in height, healthy and free of diseases and pest damage were studied. Within each transect, a 15 m deep well was installed for monitoring the groundwater depth by the method of electrical conduction.

### 3.2. Measurements of the response of photosynthesis in P. euphratica to [$CO_2$]

Four fully expanded, healthy and mature leaves in the middle parts of a tree crown were selected for measurement from each tree. Photosynthetic light-response curves were measured on clear days in June 2006 using a portable gas exchange system (Li-6400, LiCOR, Lincoln, NE, USA) at different [$CO_2$] (360 ppm and 720 ppm) controlled by a $CO_2$ injecting system. The light source used was a 6400-02B LED, and was set to 0, 20, 50, 100, 400, 600, 800, 1000, 1200, 1500, and 2000 μmol m$^{-2}$ s$^{-1}$, individually. Each leaf was measured three replications, and the mean was used. Meanwhile, net photosynthetic rate ($P_n$), stomatal conductance ($g_s$), intercellular $CO_2$ concentration ($C_i$), air $CO_2$ concentration ($C_a$), transpiration rate ($T_r$), 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. Water use efficiency (WUE) was calculated from the ratio $P_n/T_r$.

### 3.3. Models

The light-response curve of photosynthesis was fitted with a non-rectangular hyperbola [17]:

$$P_n = \frac{\phi I + P_{max} - \sqrt{(\phi I + P_{max})^2 - 4\phi\theta I P_{max}}}{2\theta} - R_d$$

where $P_n$ is the photosynthetic rate; $\phi$, the initial slope of the curve; $I$, photosynthetic photon flux density (PPFD); $P_{max}$, the light-saturated rate of photosynthesis; $\theta$, the convexity and $R_d$, the dark respiratory rate. First, from the linear regression of the photosynthetic rate on PPFD at 0–200 mmol.m$^{-2}$ s$^{-1}$, $\phi$, $R_d$, light saturation point (LSP) and light compensation point (LCP) were obtained from the slope and $Y$-intercept, respectively. Then, a non-rectangular hyperbola was fitted to the whole curve using the $\phi$

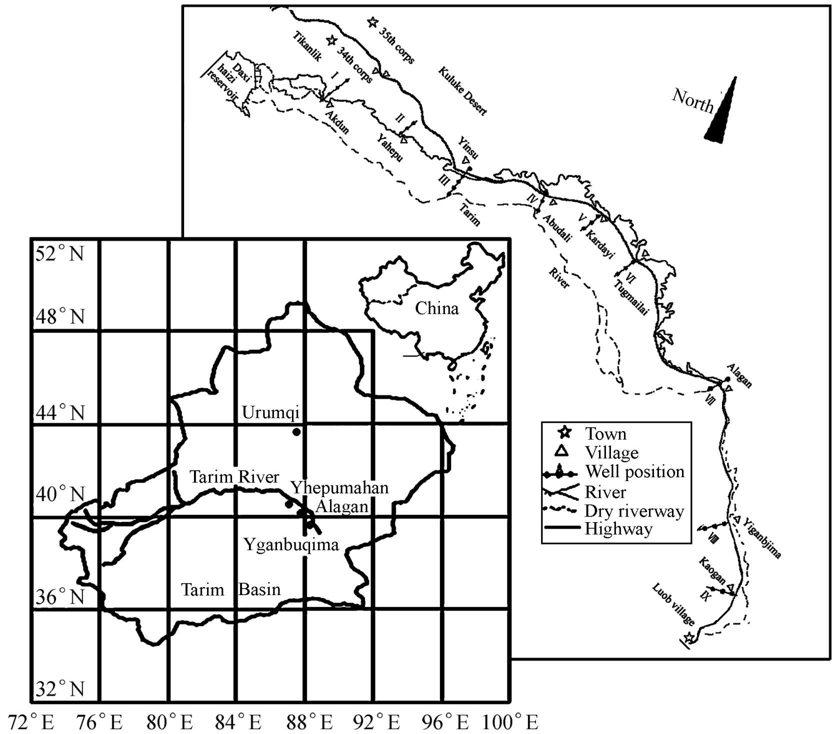


Fig. 1. Sketch map of study area.

and $R_d$ values to obtain $P_{max}$, $\theta$ and the coefficient of the determination of the fitting equation ($R^2$).

### 3.4. Statistical analysis

All the data were analyzed by Excel and Spss 13.0 software, including the model simulation of the light–response curve, analysis of variance, independent-samples *t*-test.

## 4. Results

### 4.1. Response of the parameters of photosynthetic rate of P. euphratica to [$CO_2$]

The photosynthetic light–response curve of *P. euphratica* at different [$CO_2$] is presented in Fig. 2. The $P_n$ value of *P. euphratica* was different at different [$CO_2$] and groundwater depths. At the same [$CO_2$], the highest photosynthetic rate of *P. euphratica* was recorded in a suitable environment, namely with a groundwater depth of 3.37 m, and it gradually decreased with an increase in groundwater depth. The magnitude of the decrease increased with increasing PAR, e.g. at a $CO_2$ concentration of 360 ppm, the $P_n$ of *P. euphratica* at groundwater depths of 5.08, 6.12 and 7.47 m, respectively, decreased by 2.44%, 2.79% and 6.04% compared with that at 3.37 m when PAR was 200 μmol $m^{-2}$ $s^{-1}$, but it decreased by 6.99%, 11.29% and 19.89%, respectively, when the PAR was 1000 μmol $m^{-2}$ $s^{-1}$. Analysis of variance showed that there were significant differences among the $P_n$ values obtained at different groundwater depths under the same [$CO_2$] supply ($P < 0.05$), except between 3.37 and 5.08 m. The $P_n$ was significantly increased when [$CO_2$] increased from 360 to 720 ppm, but the magnitude of the increase varied with groundwater depth. At 720 ppm, the $P_n$ of *P. euphratica* growing at 3.37, 5.08, 6.12 and 7.47 m groundwater depth increased by 31.09%, 35.58%, 44.70% and 32.87%, respectively. An independent-samples *t*-test showed that there were significant differences in the $P_n$ values of *P. euphratica* growing among different groundwater depths, except those at groundwater depths of 3.37 and 5.08 m.

Results from the investigation of the response of $P_n$ of *P. euphratica* at different [$CO_2$] and groundwater depths to PAR simulated by the non-rectangular hyperbola showed that the maximum net photosynthetic rate ($P_{max}$) of *P. euphratica* decreased with an increase of groundwater depth at the same [$CO_2$] (Table 1). The $P_{max}$ of *P. euphratica* was greatest at 3.37 m of groundwater depth. At a [$CO_2$] of 360 or 720 ppm, $P_{max}$ was reduced by 4.76%, 22.44%, and 27.62%, or 42%, 24.62%, and 28.90% at groundwater depths of 5.08, 6.12 and 7.47 m, respectively, compared with the $P_{max}$ at a groundwater depth of 3.37 m. The $P_{max}$ of *P. euphratica* increased with a rise in [$CO_2$] from 360 ppm to 720 ppm, but the magnitude of the increase varied with groundwater depths. The $P_{max}$ of *P. euphratica* at groundwater depths of 3.37, 5.08, 6.12 and 7.47 m increased by 43.72%, 39.69%, 58.20%, and 41.16% at the elevated [$CO_2$], respectively.

Apparent quantum yield (AQY) is an index that reflects the light use efficiency of a plant [18]. At the same [$CO_2$], the AQY of *P. euphratica* was greatest, i.e., the light use efficiency was highest, when the groundwater depth was

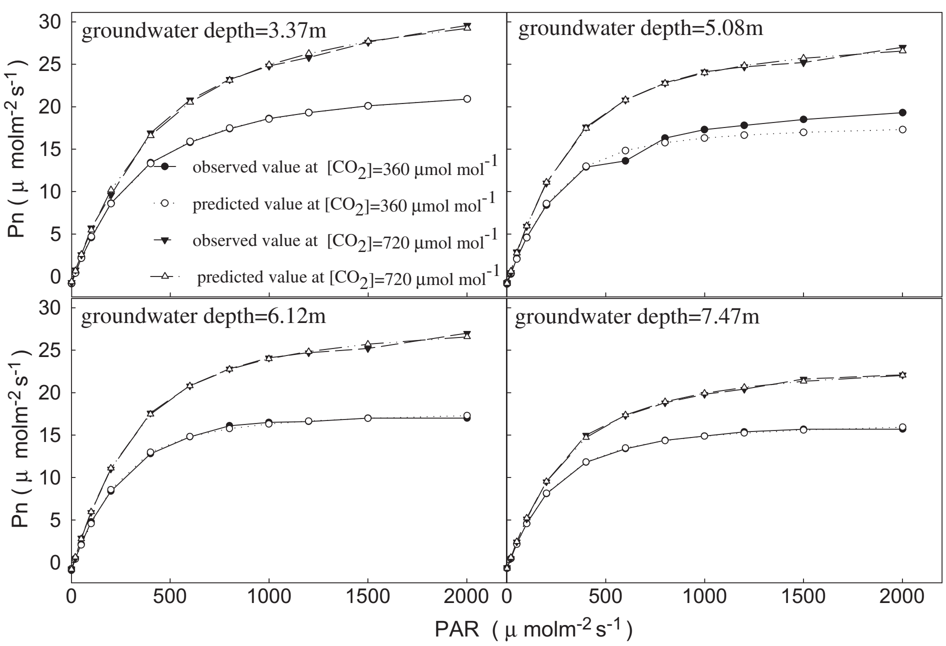


Fig. 2. Response of net photosynthetic rate ($P_n$) to photosynthetic photon flux density in the leaves of *P. euphratica* under different [$CO_2$], at different groundwater depths.

3.37 m. AQY decreased with increasing groundwater depths, which led to a more evident photoinhibition. For example, when the [$CO_2$] was 360 ppm, compared with the AQY of *P. euphratica* at a groundwater depth of 3.37 m, the AQY decreased by 12.00%, 17.33%, and 21.33% at groundwater depths of 5.08, 6.12, and 7.47 m, respectively. When the [$CO_2$] was 720 ppm, the AQY of *P. euphratica* decreased by 10.26%, 11.54%, and 7.69%, respectively, at groundwater depths of 5.08, 6.12, and 7.47 m compared with that at 3.37 m. The AQY of *P. euphratica* increased with a rise in [$CO_2$] from 360 ppm to 720 ppm, and it increased more at greater groundwater depths. At 720 ppm [$CO_2$], the AQY of *P. euphratica* at groundwater depths of 5.08, 6.12, and 7.47 m increased by 6.06%, 11.29%, and 22.03% compared with that at 360 ppm [$CO_2$], respectively (Table 1).

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 [19]. The LSP of *P. euphratica* was highest at a groundwater depth of 3.37 m at the same [$CO_2$], but it gradually decreased with greater groundwater depth. At 360 or 720 ppm [$CO_2$], the LSP of *P. euphratica* at groundwater depths of 5.08, 6.12, and 7.47 m was reduced by 14.99, 111.04, and 120.58 or 80.60, 174.68, and 195.12 $\mu$mol $m^{-2}$ $s^{-1}$ compared with that at 3.37 m, respectively. As the [$CO_2$] rose from 360 ppm to 720 ppm, the LSP of *P. euphratica* increased in the same groundwater, and the magnitude of the increase in LSP increased with greater groundwater depth, e.g. the LSP at groundwater depths of 3.37, 5.08, 6.12, and 7.47 m was increased by 15.21%, 17.99%, 22.52%, and 20.54%, respectively. There was a little variation in the LCP of *P. euphratica* with groundwater depth at 3.37 and 5.08 m at 360 ppm [$CO_2$]; however, the LCP was gradually reduced when the groundwater depth increased. The LCP at a groundwater depth of 3.37 m rapidly reduced to 4.35 $\mu$mol $m^{-2}$ $s^{-1}$ when the [$CO_2$] rose to 720 ppm, i.e. a decrease of 58.41%, and at groundwater depths of 5.08, 6.12, and 7.47 m it was reduced by 24.19%, 21.04%, and 9.66%, respectively (Table 1).

### 4.2. Response of transpiration rate ($T_r$) to [$CO_2$]

The $T_r$ of *P. euphratica* increased with increasing light at 360 ppm and 720 ppm [$CO_2$]; however, the magnitude of the increase in $T_r$ varied with groundwater depth. When groundwater depth was less than 7 m, the $T_r$ of *P. euphratica* was reduced with increasing groundwater depth; in contrast, it started to increase when the groundwater depth was more than 7 m (Fig. 3a and b). When the [$CO_2$] was 360 ppm and 720 ppm, the $T_r$ of *P. euphratica* at a groundwater depth of 5.08 m was reduced by 6.35% and 7.93%, respectively, compared with that at 3.37 m. However, neither of the differences in $T_r$ were statistically significant ($P > 0.05$). The $T_r$ of *P. euphratica* at a groundwater depth of 6.12 m was reduced by 29.74% and 24.98%, and 35.23% and 29.65%, respectively, compared with that at 3.37 m and 5.08 m when the [$CO_2$] was 360 ppm and 720 ppm; these differences in $T_r$ were statistically significant ($P < 0.05$). The $T_r$ of *P. euphratica* at a groundwater depth of 7.47 m increased by 23.06% and 29.20% compared with that at 6.12 m when the [$CO_2$] was 360 ppm and 720 ppm,

Table 1
Response of the parameters of photosynthetic rate to light intensity of *P. euphratica* under different [$CO_2$] at different groundwater depths.

| Groundwater depth (m) | [$CO_2$] (ppm) | $P_{max}$ [μmol $m^{-2}$ $s^{-1}$] | AQY [μmol $CO_2$ $\mu mol^{-1}$ photons] | LSP [μmol $m^{-2}$ $s^{-1}$] | LCP [μmol $m^{-2}$ $s^{-1}$] | $R_d$ [μmol $m^{-2}$ $s^{-1}$] | $K$ | $R^2$ $n = 11$ |
|---|---|---|---|---|---|---|---|---|
| 3.37 | 360 | 24.50 | 0.075 | 533.99 | 10.46 | 0.898 | 0.375 | 1.000 |
| | 720 | 35.21 | 0.078 | 693.43 | 4.35 | 0.713 | 0.354 | 0.999 |
| 5.08 | 360 | 23.34 | 0.066 | 519.00 | 11.72 | 1.080 | 0.098 | 0.998 |
| | 720 | 32.60 | 0.070 | 612.84 | 8.05 | 0.884 | 0.306 | 1.000 |
| 6.12 | 360 | 19.00 | 0.062 | 422.95 | 9.84 | 0.805 | 0.725 | 0.999 |
| | 720 | 28.06 | 0.069 | 518.18 | 7.77 | 0.904 | 0.562 | 1.000 |
| 7.47 | 360 | 17.73 | 0.059 | 413.41 | 7.60 | 0.760 | 0.601 | 1.000 |
| | 720 | 25.03 | 0.072 | 498.31 | 6.86 | 0.800 | 0.514 | 1.000 |

and those differences in $T_r$ were also statistically significant ($P < 0.05$). However, the differences in $T_r$ at the same groundwater depth resulting from the rise in [$CO_2$] were not statistically significant ($P > 0.05$).

### 4.3. Response of stomatal conductance ($g_s$) to [$CO_2$]

At the same [$CO_2$] supply, the $g_s$ of *P. euphratica* at different groundwater depths increased with higher light levels. However, the magnitude of the increase in $g_s$ varied with groundwater depth (Fig. 3c and d). For example, when the [$CO_2$] was 360 ppm, although the average $g_s$ of *P. euphratica* at a groundwater depth of 5.08 m was increased by 2.50% compared with that at 3.37 m, the difference was not statistically significant ($P > 0.05$). The average $g_s$ of *P. euphratica* at a groundwater depth of 6.12 m increased by 45% and 47.5% compared with that at 3.37 m and 5.08 m, respectively, which was statistically significant ($P < 0.05$). The average $g_s$ of *P. euphratica* at a groundwater depth of 7.47 m was increased compared with that at 6.12 m; this difference was also statistically significant ($P < 0.05$). As the [$CO_2$] rose to 720 ppm, the $g_s$ of *P. euphratica* was reduced at the same groundwater depth, and the magnitude of the decrease in $g_s$ increased as the groundwater depth increased. The average $g_s$ of *P. euphratica* at groundwater depths of 3.37, 5.08, 6.12, and 7.47 m was reduced, respectively, by 7.92%, 8.35%, 16.47%, and 15.88% compared with that at 360 ppm [$CO_2$]; the decreases at groundwater depths of 6.12 and 7.47 m were statistically significant. In addition, rising [$CO_2$] increased the magnitude of the variation in the $g_s$ of *P. euphratica* at different groundwater depths. Although the average $g_s$ of *P. euphratica* at a groundwater depth of 5.08 m increased by 5.41% over that at 3.37 m at the elevated [$CO_2$], the difference was not statistically significant ($P > 0.05$). The average $g_s$ decreased sharply when groundwater depth increased to 6.12 m, and was reduced by 48.65% and 53.16% compared with those at groundwater depths of 3.37 and 5.08 m, respectively; the differences were statistically significant ($P < 0.05$). The average $g_s$ of *P. euphratica* at a groundwater depth of 7.47 m was increased significantly by 89.4% compared with that at 6.12 m ($P < 0.05$).

### 4.4. Response of intercellular $CO_2$ concentration ($C_i$) to [$CO_2$]

The $C_i$ of *P. euphratica* varied with groundwater depths at the same [$CO_2$], and the variability increased with higher light levels (Fig. 3e and f). At 360 and 720 ppm [$CO_2$], the difference in $C_i$ of *P. euphratica* between groundwater depths of 3.37 and 5.08 m was not significant ($P > 0.05$). The average $C_i$ value of *P. euphratica* at a groundwater depth of 6.12 m decreased by 9.56% and 12.29%, and 9.98% and 11.51%, respectively, compared with those at 3.37 and 5.08 m, and the differences were statistically significant ($P < 0.05$). The average $C_i$ value at 7.47 m increased by 5.59%, 2.41%, and 16.76%, and 3.11%, 1.36%, and 14.55%, respectively, compared with those at 3.37, 5.08 and 6.12 m, of which the difference in $C_i$ between groundwater depths of 61.2 and 7.47 m was also statistically significant ($P < 0.05$). The average $C_i$ value of *P. euphratica* increased with rising air [$CO_2$]; however, the magnitude of the increase in $C_i$ value decreased with greater groundwater depth. As the [$CO_2$] rose from 360 to 720 ppm, the magnitude of the increase in $C_i$ of *P. euphratica* grown in the more suitable environment was maximal, increased by 114.38%, and the $C_i$ of *P. euphratica* at the groundwater depths of 5.08, 6.12, and 7.47 m increased by 111.51%, 113.39%, and 109.34%, respectively; all the differences were statistically significant ($P < 0.05$).

### 4.5. Response of water use efficiency (WUE) to [$CO_2$]

The WUE of *P. euphratica* increased with greater light. However, there were differences in the WUE of *P. euphratica* at different groundwater depths, and the differences increased with higher light levels. At the same [$CO_2$], the WUE of *P. euphratica* increased with groundwater depth when the depth was less than 7 m. However, the WUE decreased rapidly when the groundwater depth was more than 7 m (Fig. 3g and h). At either 360 or 720 ppm [$CO_2$], there was no significant difference in the WUE of *P. euphratica* between 3.37 and 5.08 m, but the WUE at 6.12 m significantly increased compared with those at 3.37 and 5.08 m ($P < 0.05$). However, the WUE rapidly decreased when the groundwater depth increased to 7.47 m, and there was

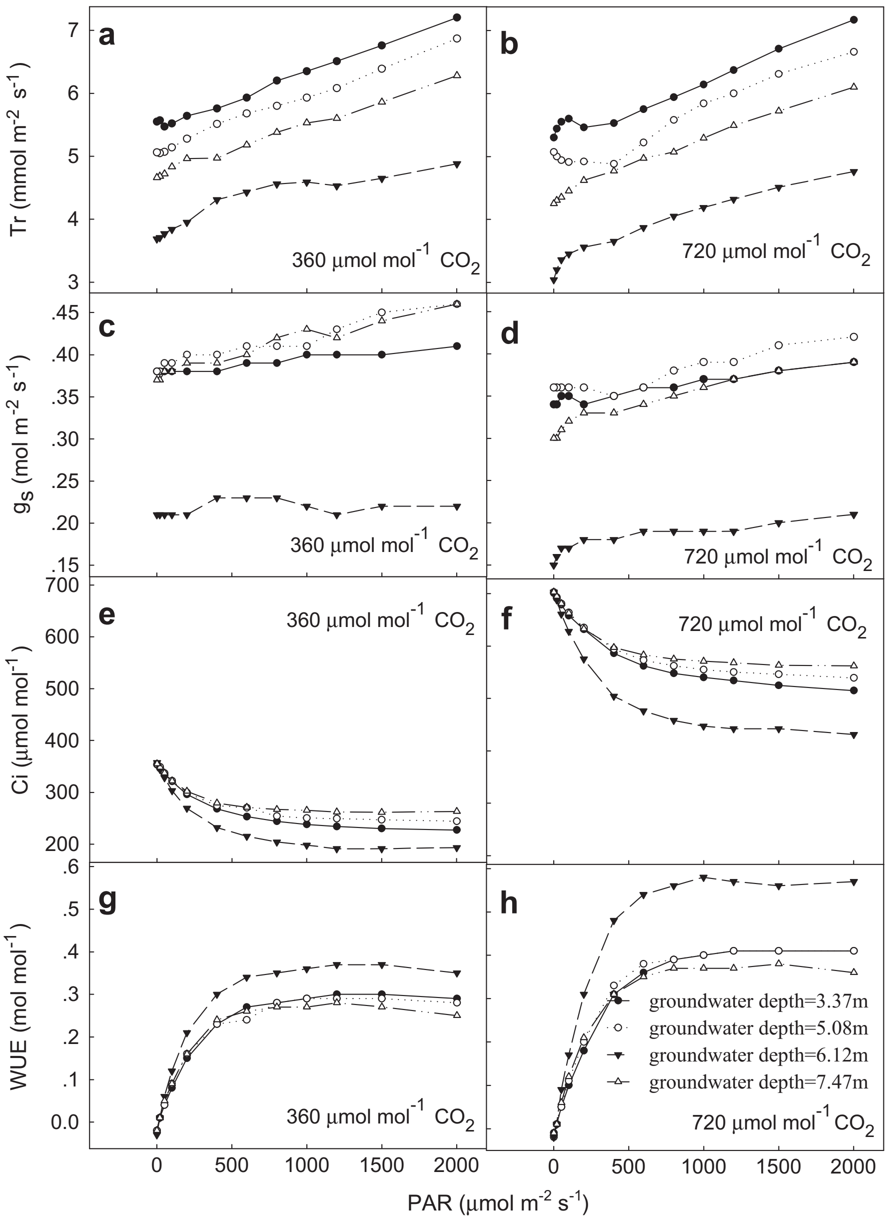


Fig. 3. Response of stomatal conductance ($g_s$), intercellular $CO_2$ concentration ($C_i$), transpiration rate ($T_r$), WUE to [$CO_2$] at different groundwater depths.

a statistically significant difference in WUE between 6.12 and 7.47 m ($P < 0.05$). When the [$CO_2$] rose from 360 to 720 ppm, the WUE of *P. euphratica* was increased. However, the magnitude of the increase in WUE varied with the groundwater depth. The WUE at 3.37 and 5.08 m groundwater depth increased by 36.04% and 41.28%, respectively, with the rise in [$CO_2$], but neither of the differences were statistically significant ($P > 0.05$); the WUE at 6.12 m increased by 57.30% with the rise in [$CO_2$], and the difference was statistically significant ($P < 0.05$). In contrast, the difference in WUE of *P. euphratica* with groundwater depth at 7.47 m, which increased by 36.19% with a rise in [$CO_2$], was not statistically significant ($P > 0.05$).

## 5. Discussion and conclusions

Many mathematics' models were used to fit the light–response curve of photosynthesis, such as the quadratic polynomial model [20], the exponential model [21], the Michaelis–Menten equation [22], the rectangular hyperbola model [23] and the non-rectangular hyperbola model [17]. The results fitted by different models were different. In our study, the LSP of *P. euphratica* grown in 3.37 m were 533.99 and 693.43 µmol $m^{-2}$ $s^{-1}$, respectively, at 360 and 720 ppm [$CO_2$], which was consistent with the research results about adult *P. euphratica* in the Taklamakan Desert and sapling *P. euphratica* in the pot experiment test by

Deng et al. [24] and Wu et al. [25], respectively. Additionally, Hands and Peter found the LSP of most plants was between 500 and 1000 μmol $m^{-2}$ $s^{-1}$, and the LSP of the $C_3$ plant was only one fourth of the full sun [22]. Average full sun was about 2000 μmol $m^{-2}$ $s^{-1}$ in the lower reaches of the Tarim River, therefore, the results fitted with a non-rectangular hyperbola in our study was consistent with the conclusion. This suggested that the non-rectangular hyperbola was a proper model fitted to the light–response curve of the photosynthesis of *P. euphratica.*

The elevation of [$CO_2$] directly alters plant photosynthesis [5], but other environmental factors also affect the response of plant to the elevated [$CO_2$] [26]. We found that as the [$CO_2$] increased, the $P_n$ of *P. euphratica* increased, but the magnitude of the increase varied with the groundwater depth. At shallower groundwater depths (3.37 and 5.08 m), the average $P_n$ of *P. euphratica* increased, but the differences were not statistically significant. When the groundwater depths increased further to 6.12 and 7.47 m, the average $P_n$ of *P. euphratica* significantly increased at the elevated [$CO_2$]. The elevation of [$CO_2$] increased the LSP and AQY and decreased the LCP in the same groundwater depth suggesting that the elevation of [$CO_2$] enhanced the efficiency of the use of light and enlarged the usage scope for the light of *P. euphratica*, and that the stimulation of [$CO_2$] increased with the increasing groundwater depth. Therefore, the responses of the photosynthesis in *P. euphratica* to the rise in [$CO_2$] were different at different groundwater depths. The extent of the alteration in photosynthesis to the elevated [$CO_2$] at greater groundwater depths (more than 6 m) was larger than that at less than 6 m.

Su et al. found that there was little effect of rising [$CO_2$] on $T_r$ [14]. We found that the $T_r$ of *P. euphratica* at the same groundwater depth showed little change with the elevation of [$CO_2$], which was consistent with the research result mentioned above.

Zeiger found that the $g_s$ of plants was generally reduced by 40% when the [$CO_2$] doubled [27]. However, some studies have found that the response of $g_s$ to the elevated [$CO_2$] was not obvious [28]. In our study, the $g_s$ of *P. euphratica* was reduced with rising [$CO_2$]. When the groundwater depth was less than 6 m, the decreases in $g_s$ were not statistically significant. However, the $g_s$ significantly decreased when the groundwater depth was more than 6 m. The presumed cause was that a large amount of abscisic acid was synthesized in the root when the *P. euphratica* encountered drought stress [29], which was transported to leaves by transpiration current and finally reduced the $g_s$ of the leaves [30]. Therefore, groundwater depth was one of the key factors affecting the response of the $g_s$ of *P. euphratica* to the elevated [$CO_2$]. It would significantly reduce the stomatal movement of *P. euphratica* when the groundwater depth was more than 6 m.

The maximal increase degree of the $C_i$ of *P. euphratica*, 114.38%, occurred at a groundwater depth of 3.37 m and resulted from a rise in [$CO_2$]. After that, the magnitude of the increase in $C_i$ was reduced with an increasing groundwater depth. This suggested that the elevation of [$CO_2$] significantly increased the $C_i$ of *P. euphratica*. However, the response of *P. euphratica* grown at shallower groundwater depths to the rise in [$CO_2$] was greater than that of those at greater groundwater depths.

Studies have found that the WUE of plants increased with the elevated [$CO_2$] [14,31]. In contrast, others have reported a decrease with the elevated [$CO_2$] [32]. In our study, the WUE of *P. euphratica* increased with the elevated [$CO_2$], but the magnitude of the increase was affected by groundwater depth. The difference in the WUE of *P. euphratica* resulting from rising [$CO_2$] was not statistically significant when the groundwater depth was less than 6 m. However, the WUE significantly increased at ambient [$CO_2$] versus elevated [$CO_2$] when the groundwater depth increased to 6.12 m. This suggested that the loss of water was reduced through stomatal closure when the *P. euphratica* survived in a limited water supply environment, which was good for *P. euphratica* maintaining the photosynthesis and strengthening the ability of drought-resistance of *P. euphratica* [33]. When the groundwater depth further increased to 7.47 m, there was no significant difference in the WUE of *P. euphratica* at the elevated [$CO_2$], which presumably indicated that the groundwater depth was insufficient to allow the roots of *P. euphratica* to drink, and that a strong $T_r$ accelerated the dissipation of water. As a result, the increase in the WUE of *P. euphratica* was slowed, which was consistent with the research results about *P. euphratica* under drought stress by Chen et al. [9].

Water for plant photosynthesis was primarily from surface water, soil moisture and groundwater [34,35]. Because the study area was extremely dry and due to scarcity of rainfall, surface runoff was seldom formed, and water for plant survival was mainly from soil moisture and groundwater. Results from Table 2 show that there is not a significant correlation between soil moisture and groundwater depth in the study area. Based on the analyses of the response of $P_n$, $g_s$, $C_i$, $T_r$ and WUE of *P. euphratica* to the elevation of [$CO_2$], it was obvious that there were differences in the response of photosynthesis in *P. euphratica* to rising [$CO_2$] at different groundwater depths. The response of photosynthesis to rising [$CO_2$] at the shallower groundwater depths was weaker than that at the greater groundwater depths. Therefore, groundwater depth was the critical factor controlling the response of photosynthesis in *P. euphratica* to rising [$CO_2$].

At the same [$CO_2$], there were no significant differences in $P_n$, $g_s$, $C_i$, $T_r$ and WUE of *P. euphratica* between groundwater depths of 3.37 and 5.08 m, and $P_{max}$, AQY, LSP and LCP also did not greatly change. However, when the groundwater depth arrived to 6 m, a reduction in $P_n$ was accompanied by a significant decrease in $g_s$ and $C_i$, which suggested that the main constraint of photosynthesis was the result of the stomatal factors, namely stomatal closure restraining the ambient [$CO_2$] from entering the intercellular space. The $T_r$ significantly decreased and the WUE sig-

Table 2
The correlation analysis between groundwater depths and soil moisture.

| | Groundwater depths (m) | 0–20 cm soil moisture | 20–50 cm soil moisture | 50–100 cm soil moisture | 100–160 cm soil moisture | 160–220 cm soil moisture |
|---|---|---|---|---|---|---|
| Groundwater depths | 1 | | | | | |
| 0–20 cm soil moisture | −0.453 | 1 | | | | |
| 20–50 cm soil moisture | −0.205 | 0.963* | 1 | | | |
| 50–100 cm soil moisture | −0.367 | 0.984* | 0.982* | 1 | | |
| 100–160 cm soil moisture | −0.393 | 0.973* | 0.967* | 0.997** | 1 | |
| 160–220 cm soil moisture | −0.414 | 0.314 | 0.287 | 0.421 | 0.489 | 1 |

* $p < 0.05$.
** $p < 0.01$.

nificantly increased at a groundwater depth of 6.12 m compared with those at 3.37 and 5.08 m. Romà and Josep [33], as well as Horton et al. [36], pointed out that the WUE of plants would increase when they encountered mild and moderate drought stress. Therefore, we concluded that 6 m was the critical groundwater depth for the normal survival of *P. euphratica*, and it would encounter drought stress when the groundwater depth was more than 6 m. In addition, when the groundwater depth was more than 7 m, the $P_n$ and WUE of *P. euphratica* sharply decreased, and the usage scope of light narrowed at the same [$CO_2$], which accompanied the rapid increase of $g_s$, $C_i$ and $T_r$. These findings suggested that the reduction in $P_n$ was not the result of the stomatal factor, but of water shortage, which resulted from strong $T_r$ and low WUE, and photoinhibition resulting from strong light. Therefore, we also concluded that *P. euphratica* encountered severe drought stress when the groundwater depth was more than 7 m.

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