EFFECTS OF GROUNDWATER DEPTH ON PHOTOCHEMICAL PERFORMANCE OF POPULUS EUPHRATICA IN ARID REGIONS OF CHINA

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Abstract

This study has surveyed three plots with different groundwater depth (GWD) along the lower reaches of Tarim River in Northwest China. Chlorophyll fluorescence of *Populus euphratica* (*P. euphratica*) was investigated to understand the effects of increasing GWD on its photochemical efficiency and activity. Our results showed that the actual photochemical efficiency of photosystem II (PSII) in light-adapted leaves, the electron transportation rate, and the fractions of absorbed light energy used in PSII photochemistry rose first but declined thereafter with the increase in GWD, which was accompanied by an initial declining and then increasing of non-photochemical quenching. However, the maximum efficiency of PSII in dark-adapted leaves is maintained at optimal values. The photochemical activity in moderately drought-stressed *P. euphratica* is slightly higher than that in relatively well-watered one and significantly declines, with an elevated excess excitation energy, the photosystem can still maintain a normal function. These data suggest that decline in photochemical efficiency and activity due to decreased water availability may not play an important role in the degeneration of *P. euphratica* at the lower reaches of Tarim River.

Abbreviations: E_{max}: maximal electron transportation rate; ETR: electron transportation rate; F_m: maximum fluorescence of dark-adapted leaves; Fo: minimal fluorescence of dark-adapted leaves; Fs: actual fluorescence of special time in light-adapted leaves; Fm': maximum fluorescence of light-adapted leaves; Fo': minimal fluorescence of light-adapted leaves; F_v/F_m: maximum photochemical efficiency of PSII in the darkadapted leaves; F_v/F_o : potential activity of photosystem II; GWD: groundwater depth; Ik: semi-saturation light intensity; LWP: leaf water potential; NPQ: nonphotochemical quenching; PAR: photosynthetically active radiation; PSII: photosystem II; q_P: photochemical quenching coefficient; P% : fractions of the excitation energy absorbed by the PSII allocated to PSII photochemistry; D%: fractions of the excitation energy absorbed by the PSII allocated to thermal dissipation; X%: fractions of excess excitation energy in the excitation energy absorbed by the PSII; SWC: soil water content; Φ_{PSII} : actual photochemical efficiency of photosystem II in light-adapted leaves.

Introduction

In arid environment, water is the major limiting factor of plant growth, and the ecophysiological characteristics of vegetation are therefore largely determined by water availability (Elmore *et al.*, 2006; Baghalian *et al.*, 2010). Groundwater is a critical water source and important factor for the succession of plants in arid regions (Allen-Diaz, 1991; Stromberg *et al.*, 1996; Thomas *et al.*, 2006; Pang *et al.*, 2010). In the Tarim River Basin of Northwest China, the increasing consumption of water resources has tremendously changed the hydrologic process of inland river in the area and resulted in an obvious increase in groundwater depth (GWD) (Hao *et al.*, 2010). The increasing GWD has influenced the ecological and physiological performance

of plants in the desert riparian forest (Chen et al., 2004, 2006; Westermann et al., 2008) and imposed more water stresses on those perennial plants relying on groundwater (Fu et al., 2006). It is well established that water stress impairs numerous metabolic and physiological processes and even damages the organs of plants (Zhang et al., 2011). Most of the damaging effects of environmental stress are associated with the photosynthetic process of plant (Lambers et al., 1998; Guerfel et al., 2009, Perveen et al., 2010, Raziuddin et al., 2011). Studies have demonstrated that PSII is highly drought-resistant (Yordanov et al., 2000), but the photosynthetic electron transport through PSII is inhibited (Chakir & Jensen, 1999). Several in vivo studies have shown that water deficit results in damages to the PSII oxygen-evolving complex (Skotnica et al., 2000). PSII is also accepted as the most vulnerable part of the photosynthetic apparatus to light-induced damage and photo-oxidative stress under environmental stress (Maxwell & Johnson, 2000; Huang et al., 2010a, Kanwal et al., 2011). Study of the photochemical performance of plants under stress is helpful to better understand the physiological process and adaptive strategy in stressed plants.

P. euphratica is a temperate deciduous arbor of *Salicaceae* family. In the Tarim River Basin, *P. euphratica* forests are important habitats with a high biodiversity of plants and animal lives (Thevs, 2005) and play an important role in maintaining the ecosystem and protecting oases from sandstorms (Thomas *et al.*, 2006). However, the communities in the middle and lower reaches of Tarim River have severely degenerated in the last five decades, since the stream flow has been disrupted for about forty years, and GWD has increased sharply. Much attentions to the status of *P. euphratica* under increasing GWD in Tarim River Basin have been focused on its growth, water relation (Gries *et al.*, 2006), biochemical characteristics, and photosynthetic gas exchange (Chen *et al.*).

al., 2006; Zhuang et al., 2006; Zhou et al., 2010). However, the effects of increasing GWD on photochemical performance of PSII in *P. euphratica* remain unclear. Therefore, more attentions need to be paid on the photochemical efficiency, the status of PSII, and the extent of excess excitation energy in PSII reaction centers. Comprehensive analysis of the responses of photochemical process is still needed for a better understanding of the fate of local vegetation in response to the changing environment. Therefore, the present work has investigated the changes of chlorophyll fluorescence of *P. euphratica* under different GWD, aiming to reveal the effects of declined groundwater level on photosynthetic activity of *P. euphratica*.

Materials and Methods

Study areas: The study areas were located in the lower reaches of Tarim River (Latitude $39^{\circ}8'-41^{\circ}45'$ N; Longitude $85^{\circ}42'-89^{\circ}17'$ E) between Taklamakan and Kuruk Deserts. The selected three survey plots with GWD at 5.15 m, 6.46 m, and 8.42 m, respectively, were located in the respective upper, middle, and lower sectors at the lower reaches of Tarim River (Fig. 1). The study area had a hyper-arid desert climate with fragile and unstable ecosystems. The annual precipitation was greater than 2,700 mm. The weather was predominantly dry and windy. Since 1970s, the stream flow at the lower reaches (321 km from Qiala station to Taitema Lake) was completely

cut off, resulting in a significant drop in groundwater level and degeneration of the desert riparian forest ecosystem.

Plant materials and design of experiment: *P. euphratica* within 20 m around the monitoring well were selected as survey samples for the analysis of chlorophyll fluorescence at each survey plot. All trees used in this study were about fifty years old, 8–10 m in height, healthy, and free from infections. Only the grown and well-lit leaves were collected for further studies. The experiments were conducted during the most sweltering and dry season from July 8th to 15th, 2011. It was the season for seed production and the time frame when *P. euphratica* was sensitive to environmental stress.

Soil water content and leaf water potential measurement: Soil water content (SWC) of 0–200 cm in each survey plot was obtained by a drying method, using aluminum sample boxes containing certain specific soil layers from three soil investigation sections. The samples were dried for 24 h in an oven under 105 °C after weighing. The leaf water potential (LWP) of *P. euphratica* was measured with a Dew Point Microvolt-meter (HR-33, Wescor, USA) at predawn. Healthy and grown leaves from the well-lit portion of the canopy were picked, immediately sliced, and placed in the C-52 sample chamber of the apparatus to obtain the μ_v value. The LWP was calculated by $\mu_v/-7.5$.



Fig. 1. The locations of study area and survey plots.

Chlorophyll fluorescence measurement: Chlorophyll fluorescence was measured with a portable modulated fluorometer (Mini-PAM, Walz, Germany). Red light (<0.1 μ mol m⁻² s⁻¹ PAR) was taken as measure-light, and saturation light pulse of 800 ms duration (>10000 µmol m⁻² s⁻¹ PAR) was supplied by the inner haloid-lamp. Measures of 50 randomly-selected healthy and mature leaves from five trees were taken on clear days from 08:00 to 20:00 with 2 h intervals to obtain the actual fluorescence at specific time in light-adapted leaves (F_s) and maximum fluorescence in light-adapted leaves (F_m'). The initial fluorescence (F_o) and maximum fluorescence (F_m) of darkadapted leaves were measured before dawn and at midday after shading with a black cloth for 20 min. The minimal fluorescence of light-adapted leaves (F_0) , actual photochemical efficiency of PSII in light-adapted leaves (Φ_{PSII}) , electron transportation rate (ETR), maximum photochemical efficiency of PSII in dark-adapted leaves (F_v/F_m) , photochemical quenching coefficient (q_P) , nonphotochemical quenching (NPQ) were calculated using the following formulas, respectively:

$$F_{o}' = \frac{F_{o}}{\left(\frac{F_{v}}{F_{m}} + \frac{F_{o}}{F_{m}'}\right)}$$
(Oxborough *et al.*, 1997); (1)

$$\Phi_{PSII} = \frac{\left(F_{m}' - F_{s}\right)}{F_{m}'} \quad (Genty \ et \ al., 1989); \quad (2)$$

$$ETR = \frac{\left(F_{m}'-F_{s}'\right)}{F_{m}'} \times PAR \times 0.5 \times 0.84$$
; (3)

$$\frac{F_{\rm v}}{F_{\rm m}} = \frac{\left(F_{\rm m} - F_o\right)}{F_m}; \qquad (4)$$

$$q_{\rm P} = \frac{\left(F_{\rm m}' - F_{\rm s}\right)}{\left(F_{\rm m}' - F_{\rm o}'\right)} \quad \text{(Schreiber et al., 1986);} \quad (5)$$

NPQ =
$$\frac{F_{\rm m}}{F_{\rm m}} - 1$$
 (Bilger & Björkman, 1991); (6)

The fractions of the light energy absorbed by the PSII allocated to PSII photochemistry (P%), thermal dissipation (D%), and excess excitation energy (X%) were estimated with the following formulas, respectively:

$$P\% = \frac{F_{v}'}{F_{m}'} \times q_{P} \times 100$$
 (Adams *et al.*, 1996); (7)

$$D\% = 1 - \frac{F_{v}'}{F_{m}'} \times 100$$
(8)

$$X\% = \frac{F_{v}'}{F_{m}'} \times (1 - q_{P}) \times 100$$
; (9)

Statistical analysis and fit curves: Statistic analysis was conducted using SPSS 13.0. ANOVA, LSD multi-compare, and Pearson correlation coefficient were used to analyze the differences among survey plots and the correlation among factors. Data-processing and map-making were implemented using Excel 2003 and Sigmaplot 9.0. The relationship among Φ_{PSII} , q_P and PAR were fitted by three parameters single exponential decay function, and the relationship among ETR, NPQ and PAR was fitted by three parameters single exponential rise function.

Results

SWC and LWP at different groundwater depths: The results of SWC in 0–200 cm soil layer at survey plots with different GWD indicate that the average SWC obviously decreases with the increase of GWD (Fig. 2). While the SWC in 0–200 cm soil layer at all three survey plots was low, the predawn LWP of *P. euphratica* also presented a downtrend with the increase of GWD. Average predawn LWP of trees at GWD 5.15, 6.46, and 8.42 m were -1.53 ± 0.12 , -1.57 ± 0.08 , and -2.60 ± 0.14 MPa, respectively, indicating a declining water availability with the increase of GWD.

The maximum photochemical efficiency ($\mathbf{F}_v/\mathbf{F}_m$) and potential activity ($\mathbf{F}_v/\mathbf{F}_o$) of PSII: Although a declining tendency of F_v/F_m with the increase of GWD is observed, the difference is not significant (p>0.05). The predawn values of F_v/F_m of *P. euphratica* at all three survey plots are maintained at optimal values (0.84–0.85), but the midday values of F_v/F_m , compared with that of predawn values, decrease more at that survey plot with deeper GWD. The decrease of F_v/F_m , from predawn to midday, is accompanied by a significant decline in F_m , but little changes and slight increase are observed in F_o at GWD 5.15, 6.46, and 8.42 m, respectively. The potential activities (F_v/F_o) of PSII decrease with the increase of GWD, which becomes significant only when the data collected on midday (Table 1).



Fig. 2 The upper-layer soil water content of survey plots at different groundwater depths. Triangle (Δ) represent survey plot at 5.15 m GWD; circle (\circ) represent survey plot at 6.46 m GWD; crosshair (×) represent survey plot at 8.42 m GWD.

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Survey plots with different groundwater depths	time	Fo	$\mathbf{F}_{\mathbf{m}}$	F_v/F_m	F _v /F _o		
5.15 m	predawn	304.28±3.19 ^a	2077.64±26.43 ^a	$0.85{\pm}0.002^{a}$	5.83±0.08 ^a		
	midday	299.33±4.63 ^a	1848.33 ± 17.33^{b}	$0.83{\pm}0.004^{a}$	5.17±0.15 ^a		
6.46 m	predawn	293.73±2.80 ^a	1929.45±32.61 ^b	$0.84{\pm}0.003^{a}$	5.57±0.11 ^a		
	midday	301.50±3.50 ^a	1528.25±12.15 ^c	$0.80{\pm}0.008^{a}$	4.07±0.18 ^b		
8.42 m	predawn	275.20±4.27 ^b	1699.65±30.54 ^c	$0.84{\pm}0.003^{a}$	5.19±0.12 ^a		
	midday	292.80±4.75 ^a	1398.60±39.37 ^d	$0.79{\pm}0.004^{a}$	3.77 ± 0.09^{b}		

Table 1. The maximum efficiency (F_v/F_m) and potential activity (F_v/F_o) of PSII in *P. euphratica* at different groundwater depths.

Data are means \pm SE of ten replicates (n = 10), and data followed by the same lowercase letter indicate no significant (P>0.05) differences between different periods of time of surveys and survey plots with different groundwater depths

The actual photochemical efficiency (Φ_{PSII}) and electron transportation rate (ETR): Contrary to expectation, the relationship between Φ_{PSII} , ETR, and GWD is not simply linear. The Φ_{PSII} first rises then declines with the increase of GWD, and the highest Φ_{PSII} is found in *P. euphratica* at GWD 6.46 m not at GWD 5.15 m (Fig. 3A). Similarly, the ETR goes up first and then decrease (Fig. 3B) with the increase of GWD. The *P. euphratica* at GWD 6.46 m has the highest maximal electron transportation rate (E_{max}) and the highest semisaturation light intensity (I_k). The Φ_{PSII} of *P. euphratica* at GWD 8.46 m decreases by 13.18% and 28.84% compared with those at GWD 5.15 and 6.46 m respectively. The differences in Φ_{PSII} among trees at different GWD become significant (p<0.05) only under a high light intensity (>1000 µmol m⁻² s⁻¹). The minimum E_{max} and I_k are found in the trees at GWD 8.46 m that show decrease in ETR by 8.14% and 18.65% compared with those at GWD 5.15 and 6.46 m respectively.



Fig. 3. The relationship between PAR and $\Phi_{PSII}(A)$, ETR (*B*) of *P. euphratica* at different groundwater depths. Measures were taken at each survey plot from 08:00 to 20:00 at 2 h intervals, and each measurement has twenty replicates on each measure-time. The triangle (Δ) and dash line represent the *P. euphratica* at GWD 5.15m; the circle (\circ) and dash-dot line represent the *P. euphratica* at GWD 6.46m; the crosshair (×) and solid line represent *P. euphratica* at GWD 8.42m. ETR: Electron transportation rate; E_{max} : Maximal electron transport rate; I_k : Semi-saturation light intensity; PAR: photosynthetically active radiation; Φ_{PSII} : actual photochemical efficiency of PSII in the light.

 Table 2. The fractions of the energy absorbed by the PSII used in photochemistry (P %), thermal dissipation (D%) and fractions of excess excitation energy (X%) in the energy absorbed by the PSII in *P. euphratica* at different groundwater depths

Survey plots with different groundwater depths	P%	D%	X%
5.15 m	53.07 ± 2.24 ^a	29.11 ± 1.64 ^a	17.82 ± 1.47 ^a
6.46 m	62.07 ± 2.73 ^b	21.50 ± 1.35 ^b	16.43 ± 2.22 ^a
8.42 m	49.38 ± 3.95 °	31.10 ± 2.40^{a}	19.52 ± 2.04 ^b
		1	

P%, D% and X% were calculated, respectively, using empirical formulas according to chlorophyll fluorescence parameters, which were measured from 08:00 to 20:00 at 2 h intervals. Data in the table are means \pm SE of seven independent measurements, each measurement has twenty replicates (n = 140). Data followed by the same lowercase letter indicate no significant at P=0.05 according to ANOVA. P%: fractions of the excitation energy absorbed by the PSII allocated to PSII photochemistry; D%: fractions of the excitation energy in the excitation energy absorbed by the PSII allocated to thermal dissipation; X%: fractions of excess excitation energy in the excitation energy absorbed by the PSII

Photochemical quenching (q_P), non-photochemical quenching (NPQ), and excitation energy dissipation: *P. euphratica* at GWD 6.46 m also shows the highest q_P and fractions of the energy absorbed by the PSII used in photochemistry (P %), which is accompanied by the lowest NPQ, fractions of the energy absorbed by the PSII used in thermal dissipation (D%) and fractions of excess excitation energy (X%, Fig. 4, Table 2). The q_P, P%, NPQ, D%, and X% present a variation tendency of first rise then decline and first decline then rise with the increase of GWD, respectively.

Discussion

Studies have shown that most roots of P. euphratica in the desert riparian forest mainly distribute in the 0-150 cm soil layer (Si et al., 2008), thus the SWC of upper soil layer is important for P. euphratica. The SWC of desert riparian forest ecosystem in the lower reaches of Tarim River is primarily recharged by groundwater due to the < 50 mm annual precipitation and completely dried stream flow since the 1970s. In this study, the low SWC in 0-200 cm soil layer of survey plots and obvious downtrend of SWC with increasing GWD indicate that groundwater exerts little effects on SWC of upper soil layer when its level constantly declines to > 4 m. The decreased hydraulic contact between upper soil and groundwater due to increasing GWD have resulted in a reduction in water availability, leading to the difficulties in water uptake and imposing greater water deficit on P. euphratica, as demonstrated by decreased predawn LWP.

All of changes about F_v/F_m and F_v/F_o suggest that PSII in *P. euphratica* has not been irreversibly damaged by light-inhibition, though the potential activity of PSII in plants at GWD 6.46 and 8.42 m has significantly decreased at midday. The observed reduction of F_v/F_m at midday compared with that in predawn is due to the photoprotection process not the photoinhibition damage. The phenomenon that the highest E_{max} , I_k , Φ_{PSII} of PSII in trees appear on the survey plots with 6.46 m GWD may indicate an additional electron sink, such as higher proportion of photorespiration in moderately waterstressed trees (Massacci et al., 2008). The higher rate of photorespiration or other alternative electron sinks in P. euphratica during the onset of water stress due to increasing GWD would remove the excess electron pressure and make the PSII working with a higher efficiency. When the GWD increases to about 8 m, more water stress induced by the reduced water availability and increased difficulty of water uptake by P. euphratica cause significant reductions of ETR and Φ_{PSII} . This change can be attributed to the restriction of the supply of both material and energy in photosynthesis caused by increasing water stress. The decrease of electrons from photosynthetic water splitting reduces the continuity of electron transportation chains and ETR, consequently reducing the photosynthetic rate due to the shortage of energy supply (Pelzer et al., 2002; Bellot et al., 2004). The central factors involved in photosynthesis (H₂O, CO₂) are also in short supply with an increased GWD, which is resulted from the decreased water availability and increased diffusion resistance of CO₂ from air to leaf caused by stomatal control. These restrictions would eventually reduce the photosynthetic activity and photosynthesis of P. euphratica. Additionally, decreased water availability caused by increased GWD inevitably affected the absorption and transportation of nutrient substances, such as Nitrogen, Phosphorus and the others, which play a important role in the reduction of photosynthetic activity of stressed plant (Ozbucak et al., 2011).



Fig. 4 The relationship between PAR and $q_P(A)$, NPQ (*B*) of *P. euphratica* at different groundwater depths (n = 140). Measures were taken at each survey plot from 08:00 to 20:00 at 2 h intervals, and each measurement has twenty replicates on each measure-time. The triangle (Δ) and dash line represent the *P. euphratica* at *GWD* 5.15m; the circle (\circ) and dash-dot line represent the *P. euphratica* at *GWD* 6.46m; the crosshair (\times) and solid line represent *P. euphratica* at *GWD* 8.42m. NPQ: non-photochemical quenching; PAR: photosynthetically active radiation; q_P : photochemical quenching coefficient.

As discussed above, higher photochemical efficiency and photosynthetic activity under moderate water stress lead to relatively higher qP, P% of PSII in P. euphratica. With the increasing GWD, more serious water stress caused by durative declining water availability would affect the activity of certain key enzymes, thus reduce the assimilation rate of CO₂ and anabolism of photosynthetic production, and further restrict the Calvin-cycle (Tezara et al., 1999; Herting et al., 2002; Hamerlynck et al., 2009). The decreasing energy demands of photochemical reaction in P. euphratica under water stress would feed back to PSII, resulting in the reduction of light-trapping and the enhancement of heat dissipation. These changes have finally reduced the photochemical activity and efficiency of light energy utilization, as demonstrated by lower E_{max} , I_k , Φ_{PSII} , q_P and higher NPQ, D%, and X% at GWD 8.42 m. Although the photochemical efficiency and P% are declined, and the excess excitation energy is increased when GWD increased to about 8 m (Fig. 3, Table 2), significantly increased NPQ at highlight conditions and significantly negative correlation between P% and D% suggest that P. euphratica at different GWD can dissipate most of the unnecessary absorbed energy through non-photochemical quenching. The regression analysis also shows that most (more than 50%) of unnecessary excitation energy can dissipate as heat when the fraction of absorbed energy utilized in PSII photochemistry was inhibited (Fig. 5). The well predawn values of F_v/F_m also suggest that the effects of water stress and excess excitation energy on PSII can be effectively repaired in the night, which is considered as a proof of safely keeping the normal function of photosystem of plants under drought stress (Siam et al., 2008). In this process, non-photochemical quenching and thermal dissipation of excess excitation energy involved in xanthophyll cycle play an important role (Bilger et al., 1995; Goss et al., 1998; Huang et al., 2010b).



Fig. 5 The relationship between the fractions of energy absorbed by PSII in *P. euphratica* used in photochemistry (P%) and thermal dissipation (D%). P% and D% were calculated, respectively, using empirical formulas according to chlorophyll fluorescence parameters, which were measured from 08:00 to 20:00 at 2 h intervals. Each measurement has twenty replicates on each measure-time at each survey plot. P%: fractions of the excitation energy absorbed by the PSII allocated to PSII photochemistry; D%: fractions of the excitation energy absorbed by the PSII allocated to thermal dissipation.

Conclusion

This study has investigated the effects of increased GWD on photochemical efficiency and activity of PSII in P. euphratica in the lower reaches of Tarim River. The photochemical activity raises first, declines then with the increase of GWD, and is slightly higher under moderate drought stress than that under relatively well-watered condition. With the continuous increase in GWD, the photochemical activity of PSII declines significantly, resulting in a significantly decreased capability of using light energy and an increase in excess excitation energy. However, the function of photosystem remains normal because of a series of photo-protective mechanisms. All these data suggest that declined photochemical activity of PSII due to reduced water availability may not play an important role in the degeneration of P. euphratica at the lower reaches of Tarim River in China.

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