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 (PN), stomatal conductance (gs), intercellular CO₂ concentration (Ci), transpiration rate (E), water use efficiency (WUE) and stomatal limitation (Ls) 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 (Pmax), quantum yields (AQY), and dark respiration rates (Rd). 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 PN 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 CO₂, 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).

*Received* 16 October 2009, *accepted* 13 February 2010.

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**Abbreviations:** AQY – quantum yield; Ci – intercellular CO₂ concentration; D – plant diameter; E – transpiration rate; GD – groundwater depth; gs – stomatal conductance; LCP – light compensation; LSP – light saturation points; Ls – stomatal limitation; PC – plant coverage; PD – plant density; PH – plant height; PPFD – photosynthetic photon flux density; Pmax – maximum photosynthetic rate; PN – net photosynthetic rate; RH – air relative humidity; Rd – dark respiration rate; SM – soil moisture; Ta – air temperature; Tl – leaf temperature; WUE – water use efficiency; Φ – apparent quantum efficiency; θ – convexity.

**Acknowledgments:** This research was supported by the National Natural Science Foundation of China (No. 40901061, 40871059, 40701011), Light of the Western Training Program (XBBBS 200804).
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 \( \text{CO}_2 \) 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 (Weis 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 Ruoqiang 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