

Morphological, physiological, and biochemical responses of *Populus euphratica* to soil flooding

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Abstract

The riparian forests along the Tarim River, habitats for *Populus euphratica* establishment, are subjected to frequent flooding. To elucidate adaptive strategies that enable this species to occupy the riparian ecosystem subjected to seasonal or permanent water-logging, we examined functional characteristics of plant growth, xylem water relations, leaf gas exchange, chlorophyll (Chl) content and fluorescence, soluble sugar and malondialdehyde (MDA) content in *P. euphratica* seedlings flooded for 50 d. Although flooded seedlings kept absorbing carbon throughout the experiment, their shoot and root growth rates were lower than in non-flooded seedlings. The reduced leaf gas exchange and quantum efficiency of PSII of flooded seedlings resulted possibly from the reduction in total Chl content. Content of soluble sugar and malondialdehyde in leaves were higher in flooded than in control seedlings. Soil flooding induced hypertrophy of lenticels and increased a stem diameter. These responses were responsible for species survival as well as its success in this seasonally flooded riparian zone. Our results indicate that *P. euphratica* is relatively flood-tolerant due to a combination of morphological, physiological, and biochemical adjustments, which may support its dominance in the Tarim riparian forest.

Additional key words: chlorophyll fluorescence; flooding tolerance; leaf soluble sugar; poplar.

Introduction

Riparian zones in floodplains are occasionally or periodically disturbed by flood events (Amlin and Rood 2001). This disturbance, of which the timing, frequency, intensity, and duration are determined by a flow regime, greatly influences reproduction, survival, growth, community structure, and even patterns of riparian vegetation (Friedman and Lee 2002, Corenblit *et al.* 2009, Stromberg *et al.* 2010). Flooding and subsequent submergence are common in riparian ecosystems (Fernández 2006), thus riparian plants are expected to adapt to soil flooding.

Under flooding conditions, the soil environment becomes deficient in oxygen because of reduced gas-exchange rates with the atmosphere at the soil surface. Soil anoxia in rhizosphere of plants affects water and mineral nutrient uptake and changes plant metabolism (Crawford

and Braendle 1996, Pezeshki 2001). Soil flooding usually induced a significant reduction in the photosynthetic rate of many plant species (Pezeshki *et al.* 1996a, Gravatt and Kirby 1998), particularly of flood-intolerant species. The decline in photosynthesis under flooding is related to various responses in plants, including stomatal closure (Bradford 1983, Waldhoff *et al.* 1998, Armbrüster *et al.* 2004), decline in leaf Chl content (Bradford 1983), ethylene production (Pallas and Kays 1982), reduced sink demand (Wample and Thornton 1984), and disruption in photosynthate transport (Sij and Swanson 1973). For flood-intolerant species, photosynthesis reduction is generally accompanied by the accumulation of nonstructural carbohydrates during inundation (Vu and Yelenosky 1991, Gravatt and Kirby 1998). Some studies

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Abbreviations: C_i – intercellular CO₂ concentration; Chl – chlorophyll; E – transpiration rate; F_m – maximal fluorescence in dark adapted state; F_m' – maximal fluorescence in light-adapted state; F_s – steady-state fluorescence yield; F_v/F_m – maximal quantum yield of PSII photochemistry; F_v/F_m' – energy harvesting efficiency of PSII; F_0 – minimal fluorescence in dark-adapted state; F_0' – minimal fluorescence in light-adapted state; FM – fresh mass; g_s – stomatal conductance; MDA – malondialdehyde; P_N – net photosynthetic rate; q_P – photochemical quenching coefficient; Φ_{PSII} – effective quantum yield of PSII photochemistry; Ψ_{md} – midday xylem water potential. **Acknowledgements:** This study was supported by the National Natural Science Foundation (41171095, 41101100, and 41171037), the National Project (No. 2013BAC10B01) of China.

suggested that Chl *a* fluorescence, a tool that measures the efficiency of the photosynthetic apparatus (Maxwell and Johnson 2000), may decrease during inundation (Waldhoff *et al.* 2002, Rengifo *et al.* 2005). Flooding response may also induce changes in biomass allocation, allometric traits, and leaf shedding (Schöngart *et al.* 2002, Mommer and Visser 2005).

For survival and growth under the anaerobic soil environment, created by continuous flooding, a variety of morphological, physiological, and metabolic adaptations contribute to flood-tolerance in plants (Blom and Voesenek 1996). The major adaptations include: (1) Production of hypertrophied lenticels in submerged parts of stems to reduce hypoxic stress, to facilitate downward diffusion of O₂, and/or help release phytotoxic byproducts of anaerobic metabolism (such as acetaldehyde, ethanol, and ethylene) (Kozłowski and Pallardy 2002, Mielke *et al.* 2003, Folzer *et al.* 2006); (2) Development of aerenchyma in roots with large intercellular spaces to facilitate O₂ diffusion (Evans 2003, Voesenek *et al.* 2006); (3) Formation of adventitious roots on the submerged portions of stems to increase water uptake (Jackson and Drew 1984, Tsukahara and Kozłowski 1985) and to supply minerals (Gibberd *et al.* 2001); and (4) Maintaining glucose supply and avoiding accumulation of toxic compounds to enhance the capacity to survive soil flooding (Kozłowski 2002).

Material and methods

Plant material and experiment setting: Experiments were conducted at the Aksu Water Balance Station, Chinese Academy of Sciences (40°27'N, 80°45' E, hereafter Aksu Station) in 2012. Aksu Station is approximately 30 km north of the source of the Tarim River. The station has an annual average rainfall of 45.7 mm and an evaporation potential of 2,500 mm. Average annual sunshine duration and incoming solar radiation were 2,940 h and 6,000 MJ m⁻², respectively. During the experiment, the daily mean temperature was 24°C (the highest was 37°C and the lowest 21°C).

Two years old *P. euphratica* Oliv. seedlings were collected at a floodplain site close to the Tarim River (40°28'N, 80°51'E). In April, the seedlings were transferred to pots of 1.2 m in height and 0.3 m in diameter. The pots were randomly placed in outdoor troughs at Aksu Station. Each pot was filled with loamy (sand:silt:clay, 20:75:5) and loosely structured soil collected from the riparian site where *P. euphratica* seedlings were present. Two treatments were designed: (1) control (C), pots were irrigated every 3 d; each time water was added and allowed to leak from the pot bottom; and (2) flood (FL), where the water level was maintained about 10 cm above the soil surface. Each treatment consisted of 10 replicates, thus, 20 pots in total. After transplanting (in May and July), all seedlings were well watered to promote their establishment. On July 25, the experimental treatments were initiated and lasted for 50 d.

Populus euphratica Oliv. is the dominant species that forms natural riparian forests along the Tarim River, the longest inland river located in the Tarim Basin, the most arid region in China. Commonly, *P. euphratica* seedlings become established on bare, moist, and newly deposited floodplain sediment after flood recession. The floodplains are subjected to summer flooding greatly induced by snowmelt and rainstorm from mountain areas. Flood events result in substrate saturation and partial or complete plant submergence. Plants capable to tolerate better flooding can thrive near the river channel where flooding is frequent. Therefore, it is important to understand how *P. euphratica* seedlings survive soil flooding, which is necessary for the success of ongoing restoration programmes of the Tarim riparian forest.

The aim of this work was to evaluate the tolerance and ecophysiological responses of *P. euphratica* seedlings to soil flooding. We exposed *P. euphratica* seedlings in pots to soil inundation for 50 d. During that period, physiological, morphological, biochemical, and growth parameters related to flood tolerance were examined. Specifically, we expected that soil flooding stress would reduce photosynthesis, and thus the growth of *P. euphratica* seedlings. We also expected that *P. euphratica* seedlings would exhibit morphological and/or physiological adjustments in response to flooding.

Growth parameters: The heights and stem diameters of all seedlings were measured at the end of the experimental period. We also measured the leaf, stem, and root dry mass of each seedling by destructive harvesting. Dry mass (DM) of all parts was determined by weighing after drying at 65°C for 48 h. Additionally, the root length of each seedling was measured before drying.

Leaf gas exchange and Chl fluorescence have been widely used in the research of flood adaptation for riparian tree species (Gravatt and Kirby 1998, Pezeshki 2001, Qiu *et al.* 2003). Leaf gas exchange was measured on clear days in September, using a LI-6400 portable photosynthesis system (LI-COR, Lincoln, NE, USA). The measurements were made on fully expanded leaves between 10:00 and 14:00 h local time under natural solar irradiance, dark-adapted and light-adapted Chl fluorescence was measured on fully expanded leaves of each seedling, using a pulse amplitude modulated leaf chamber fluorometer (LI-6400, LI-COR, Lincoln, NE, USA). Dark-adapted Chl fluorescence was measured in leaves dark-adapted for at least 30 min, using dark-adapting leaf clips, while light-adapted Chl fluorescence was measured under natural light conditions. For each seedling, dark-adapted and light-adapted Chl fluorescence was measured on the same day. Maximum quantum efficiency of PSII (F_v/F_m) was calculated as $F_v/F_m = (F_m - F_0)/F_m$, where F_0 and F_m were obtained from the dark-adapted leaves. The energy

harvesting efficiency of PSII (F_v'/F_m') in a light-adapted leaf was calculated as $F_v'/F_m' = (F_m' - F_0')/F_m'$, where F_0' is the minimal fluorescence in the light-adapted state, and F_m' is the maximal value when all reaction centers were closed through a pulse of saturating light. Using these fluorescence parameters, we also calculated effective quantum yield of PSII (Φ_{PSII}) as $\Phi_{PSII} = (F_m' - F_s)/F_m'$, and photochemical quenching coefficient (q_p) as $q_p = (F_m' - F_s)/(F_m' - F_0')$ (Genty *et al.* 1989, Schreiber *et al.* 1994).

Midday xylem water potential (ψ_{md}): The plant capacity to maintain xylem water potential can be considered a discrimination factor for flooding tolerance (Gravatt and Kirby 1998). Plant water status was determined by measuring ψ_{md} with a *PMS 1000* (PMS Instrument Co., Albany, OR, USA) pressure chamber. The ψ_{md} was measured at solar noon. Because suitable branches for water potential measurements were lacking at the beginning of the treatments, we only measured plant water status twice (20 and 50 d after treatment initiation, respectively) during the experimental period. For each time, six randomly selected seedlings were sampled for each treatment.

Chl content: Flooding usually causes a reduction in leaf Chl concentration (Vu and Yelenosky 1991). Leaves used for gas-exchange measurements were collected, immediately frozen on ice, and transported to the laboratory. The leaf samples were wiped up, and the edge and midrib removed, and 0.2 g of leaf was cut and homogenized in a flask with 25 ml ethanol:acetone (1:1, v/v). The flasks were sealed with plastic wrap and placed in the dark. Leaf fragments were completely white after overnight extraction; absorbance of the extracted liquid was recorded at 645 and 663 nm against the miscible liquids (Wang 2006). The calculation of Chl *a*, Chl *b*, and Chl (*a+b*) contents [$\text{mg g}^{-1}(\text{FM})$] were performed based on the following equations (Arnon 1949):

$$\text{Chl } a = [(12.7A_{663} - 2.69A_{645}) \times V]/(1000 \times W) \quad (1)$$

$$\text{Chl } b = [(22.9A_{645} - 4.68A_{663}) \times V]/(1000 \times W) \quad (2)$$

$$\text{Chl } (a+b) = \text{Chl } a + \text{Chl } b \quad (3)$$

where A_λ is the absorbance at wavelength λ nm, V is the volume of extracted liquid, W is the mass of sample.

Leaf soluble sugar content: Soluble sugars play an important role in maintaining osmotic stress balance under flooding stress. The content of soluble sugars in leaves at the end of our experiment was determined by the anthrone colorimetric method (Wang 2006). From each seedling,

0.3 g of fresh leaves were cut and homogenized in 10 ml of distilled water in test tubes. The test tubes were sealed with plastic wrap and extracted in a boiling water bath for 30 min (the extraction was repeated twice). After cooling, the extract was filtered into volumetric flask and set the volume to 25 ml with distilled water. Then 0.5 ml of the solution was extracted into a 20-ml test tube, 1.5 ml of distilled water was added, and followed by 0.5 ml of anthrone reagent and 5 ml of concentrated sulphuric acid. The tubes were immediately incubated in a boiling water bath for 1 min after which they were thoroughly shaken. After that, the test tubes were cooled to the room temperature to allow color development. The absorbance of the extracted liquid was measured at 620 nm against a blank. Content of soluble sugar [%] was calculated as $[(C \times V_T \times N)/(W \times V_S \times 10^6)] \times 100$, where C is the glucose content obtained by referring to the standard curve [μg], V_T is the total volume of the extracted solution [ml], N is the dilution multiple, W is the mass of sample [g], V_S is the volume of sample solution for color development [ml].

Leaf MDA content: MDA has been used as a parameter to assess the capability of flood tolerance (Arbona *et al.* 2008). After 50 d of flood treatment, MDA content was measured by the method of Wang (2006). From each seedling 0.5 g of fresh leaf sample was homogenized in 5 ml of a solution containing 5% trichloroacetic acid and centrifuged at $3,000 \times g$ for 10 min. The supernatant (2 ml) was mixed with 2 ml of 0.67% thiobarbituric acid. The mixtures in the test tubes were allowed to react in a water bath at 100°C for 30 min and then quickly cooled. After cooling and centrifugation (at $3000 \times g$ for 10 min), absorbance of the supernatant was recorded at 450, 532, and 600 nm against a blank. MDA content was calculated based on the following formulas (Heath and Packer 1968):

$$\text{MDA } [\mu\text{mol l}^{-1}] = 6.45(A_{532} - A_{600}) - 0.56 A_{450} \quad (4)$$

$$\text{MDA } [\mu\text{mol g}^{-1}(\text{FM})] = \text{MDA } [\mu\text{mol l}^{-1}] \times V/W \quad (5)$$

where A_λ is the absorbance at wavelength λ nm, V is the volume of extracted liquid, W is the mass of sample.

Statistical analysis: One-way analysis of variance (ANOVA) with the least significant differences (LSD) was used to test the flooding effects on the ecophysiological performance of *P. euphratica* seedlings. Significant differences between control and treatment were determined for all morphological, physiological, and biochemical parameters at $p < 0.05$. All statistical tests were performed using SPSS 13.0 (SPSS, Chicago, USA).

Results

Morphological and growth responses: All FL seedlings survived under flooding for 50 d. Development of adventitious roots, as a typical response symptom to flooding, was not observed in *P. euphratica* seedlings. However, they

developed hypertrophied lenticels on the submerged stems after 10 d of flooding. Though surviving, FL seedlings exhibited symptoms of stress, such as significant reductions in the shoot height, root length (Fig. 1), and total DM

(Fig. 2). FL seedlings increased their stem diameter, and showed a different pattern in DM allocation during the experimental period, with a decreased root DM and increased stem and leaf DM (Fig. 2).

Water potential: ψ_{md} was significantly affected by soil flooding (Fig. 3). On both sampling dates (20 and 50 d), FL seedlings exhibited less negative ψ_{md} than that in C seedlings. The ψ_{md} difference between the treatments appeared to increase over time.

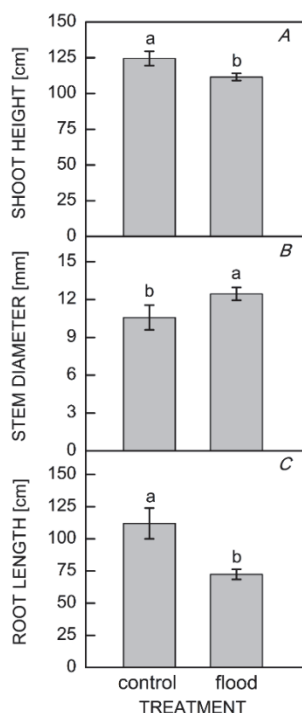


Fig. 1. Shoot height, stem diameter, and root length of the *Populus euphratica* seedlings under control and soil flooding conditions for 50 d. Vertical bars represent the mean standard error (mean $\pm$ SE; $n = 10$). Means followed by different letters indicate significant differences at $p < 0.05$ according to LSD test.

Discussion

Overall, while *P. euphratica* seedlings exhibited some indications of flooding stress, typical symptoms described for flood-intolerant species, such as leaf senescence, necrosis, and abscission (Pezeshki 1994, Kozłowski 1997) were not observed. All *P. euphratica* seedlings survived the 50-d soil flooding. After about 10 d of flooding, presence of abundant lenticels was observed at the stem bases. Formation of hypertrophied lenticels at stem bases of woody plants under soil flooding is usually associated with flood tolerance (Kozłowski 1997). According to this criterion, a plant that can survive more than 50 d under flooding condition is considered as an extremely flood-tolerant species (Loucks and Keen 1973). Therefore, our results indicate that *P. euphratica* appears to be a flood-tolerant species, similarly to other flood-tolerant poplars (Kreuzwieser *et al.* 2004).

When soil is flooded, oxygen deprivation changes soil

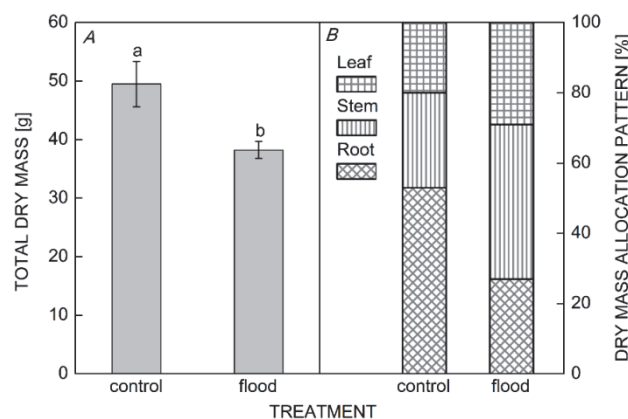


Fig. 2. Total dry mass and dry mass allocation pattern of *Populus euphratica* seedlings under control and soil flooding conditions for 50 d. Vertical bars represent the mean standard error (mean $\pm$ SE; $n = 10$). Means followed by different letters indicate significant differences at $p < 0.05$ according to LSD test.

Leaf gas exchange and Chl fluorescence: Seedlings grown in flooded soil showed net photosynthetic rate (P_N) about 50% lower than those of the C seedlings, and highly reduced stomatal conductance (g_s) and transpiration rate (E). FL seedlings showed a tendency for reduction of intercellular CO_2 concentration (C_i) (Fig. 4). This pattern also occurred in the F_v/F_m , F_v'/F_m' , Φ_{PSII} , and q_P parameters. The values for FL seedlings were 20% lower compared with C seedlings (Fig. 5).

Biochemical properties: After 50 d of flooding, the content of Chl *a*, *b* and total Chl decreased significantly in FL seedlings (Fig. 6). Leaf-soluble sugar and MDA content were significantly higher in FL than in C seedlings (Fig. 7).

physicochemical properties, reduces the soil redox potential (Eh) and changes overall plant metabolism (Kozłowski 1997, Pezeshki 2001). Prolonged flooding caused predominantly the reduction in growth and decreased the root/shoot ratio compared to non-flooded plants (Figs. 1, 2). The results indicate that flooding conditions impaired growth of *P. euphratica*, although all plants survived. Decreased DM allocation to roots in flooded plants has been observed in many flood-tolerant tree species (Kozłowski 1997). In response to soil flooding, the DM allocation pattern and the shallow distribution of roots in *P. euphratica* could be considered as an adaptive mechanism to soil flooding. The reduction of DM allocation to roots diminishes the metabolic requirement of stressed roots for oxygen, water, and nutrient uptake (Naidoo and Naidoo 1992, Joly 1994).

Increase in ψ_{md} of *P. euphratica* under soil flooding

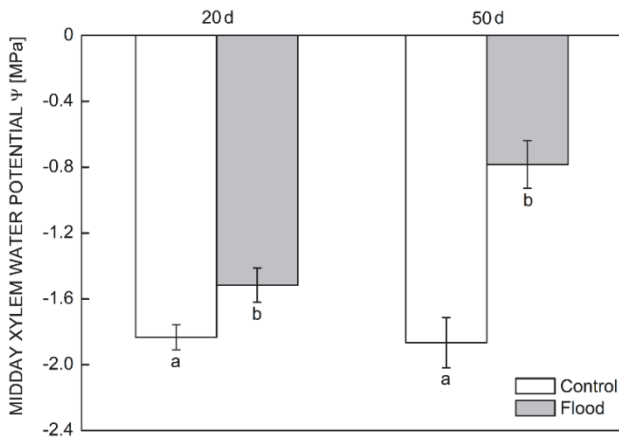


Fig. 3. Midday xylem water potential (ψ_{md}) of *Populus euphratica* seedlings at 20 and 50 d of control and soil flooding treatments. Vertical bars represent the mean standard error (mean $\pm$ SE; $n = 10$). Means followed by different letters indicate significant differences at $p < 0.05$ according to LSD test.

is consistent with the results that the ψ of flooded tree species increases with water column depth (Fernández *et al.* 1999), indicating that the maintenance of ψ was not subject to soil inundation in our experiment. Black (1984) also reported maintenance of high ψ values of *Quercus palustris* Muench. in experimentally flooded plants. A possible explanation is that the osmotic potential decreased (osmotic adjustment) as a metabolic response to flooding (Fernández *et al.* 1999).

Flooding significantly decreases P_N and g_s in many woody species of temperate (Sun *et al.* 1995, Gravatt and Kirby 1998, Cao and Conner 1999) and tropical forest ecosystems (Sena Gomes and Kozłowski 1988, Nuñez-Elisea *et al.* 1999). The decline in g_s would result in reduction of the transpiration under flooding condition

(Schaffer *et al.* 1992). Low g_s prevents excessive water loss by transpiration; flooding affects root metabolism and thus reduces water uptake capability to maintain a positive water balance (Kozłowski 1997, Pezeshki 2001). The decline in g_s would also reduce C_i , which contributes to a decline of P_N (Li *et al.* 2011). Under some circumstances, the values of g_s have a tendency to return to control levels in seedlings of flood-tolerant tree species (Sena Gomes and Kozłowski 1980, Pezeshki *et al.* 1996b, Gravatt and Kirby 1998). In the present study, in spite of appearance of hypertrophied lenticels in submerged stem bases of *P. euphratica*, we did not observe stomata reopening. Similar results have been found in studies on other tree species by Mielke *et al.* (2003, 2005). For flood-tolerant species, rapid closure of stomata should be considered a mechanism that enhances survival rate under soil-flooded conditions.

Decline in P_N of woody species subjected to flooding not only depends on stomatal factors but also on non-stomatal ones, such as enzyme activity associated with the Calvin cycle (Mielke *et al.* 2003) and electron transport activity of PSII (Pezeshki 2001). In our experiment, flooding resulted in the decreased F_v/F_m , an indicator of damage to the reaction centers of PSII. The decrease in PSII activity, accompanied by decreases in q_p and F_v'/F_m' was also observed throughout the experimental period. However, the small decrease in the F_v/F_m suggested that during flooding stress, *P. euphratica* plants can avoid photodamage. This adaptation occurs perhaps due to changes in the xanthophyll cycle matching reductions in photosynthesis (Qiu *et al.* 2003). The reductions in F_v/F_m could have been due to increased substomatal CO_2 concentration providing extra reducing power, which generated reactive oxygen species such as superoxide anions and H_2O_2 . These species can damage the

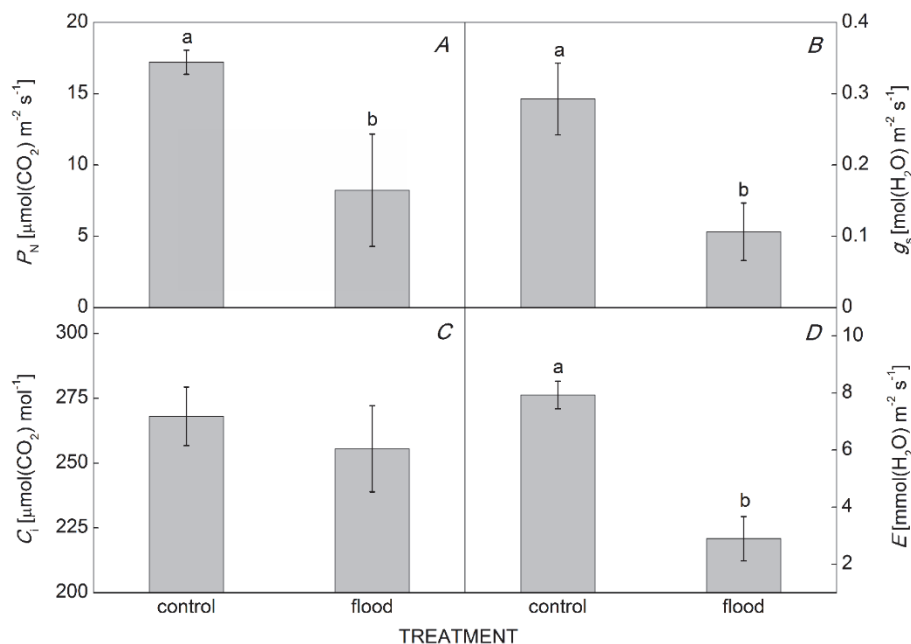


Fig. 4. Leaf net photosynthetic rate (P_N), stomatal conductance (g_s), intercellular CO_2 concentration (C_i) and transpiration rate (E) of *Populus euphratica* seedlings under control and soil flooding conditions for 50 d. Vertical bars represent the mean standard error (mean $\pm$ SE; $n = 10$). Means followed by different letters indicate significant differences at $p < 0.05$ according to LSD test.

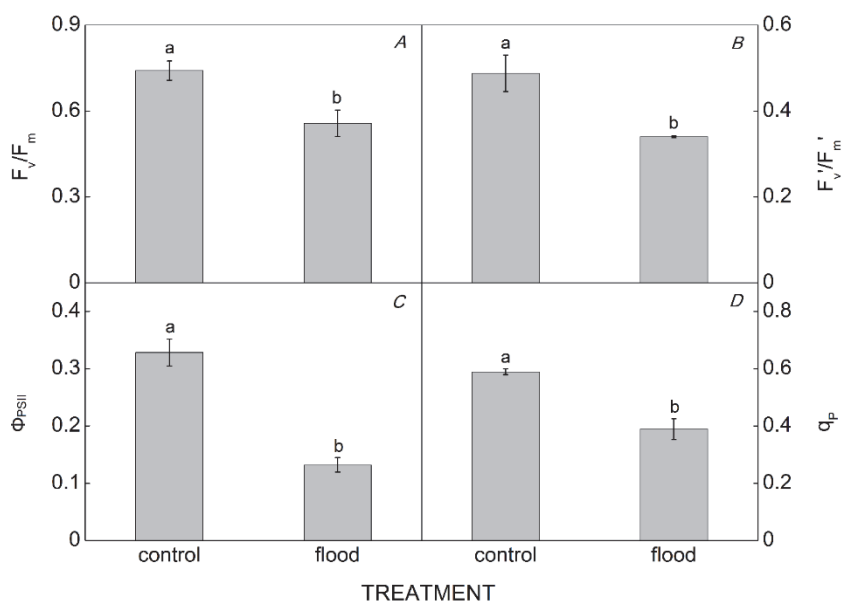


Fig. 5. The maximal quantum yield of PSII photochemistry (F_v/F_m), energy harvesting efficiency of PSII (F_v/F_m'), effective quantum yield of PSII photochemistry (Φ_{PSII}), and photochemical quenching coefficient (q_p) of *Populus euphratica* seedlings under control and soil flooding conditions for 50 d. Vertical bars represent the mean standard error (mean $\pm$ SE; $n = 10$). Means followed by different letters indicate significant differences at $p < 0.05$ according to LSD test.

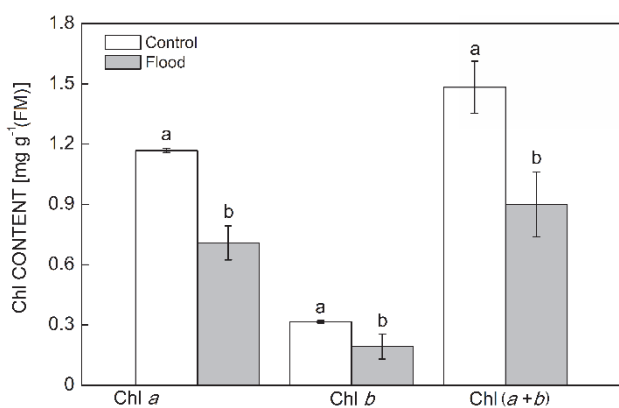


Fig. 6. Chlorophyll (Chl) *a*, Chl *b* and Chl (*a*+*b*) content of *Populus euphratica* seedlings under control and soil flooding conditions for 50 d. Vertical bars represent the mean standard error (mean $\pm$ SE; $n = 10$). Means followed by different letters indicate significant differences at $p < 0.05$ according to LSD test. FM – fresh mass.

chloroplast structure (Yordanova and Popova 2007).

The Chl content is changed in plant leaves under flooding stress, often showing leaf chlorosis (Casanova and Brock 2000). In this study, Chl *a*, Chl *b*, and total Chl contents of *P. euphratica* leaves decreased under the flooding conditions, paralleled with the response of P_N . These results are consistent with previous studies, which reported that flooding usually causes a reduction in leaf Chl concentration (Vu and Yelenosky 1991, Dreyer 1994, Gravatt and Kirby 1998). It is possible that these reductions were caused by an increase in foliar carbohydrate concentration (Fig. 7). Reduction of photosynthetic pigments is considered a kind of protection mechanism for photosynthetic structures of flooded plants to reduce sunlight absorption and to avoid photooxidation (Du *et al.* 2012).

Under stress environment, plants can reduce the stress injury and maintain plant growth through their defense mechanisms. Among them, increase in soluble sugars can offer protection for flooded plants by improving cell osmotic potential, thus maintaining cell turgor pressure and stabilizing enzyme activity in the cell conformation. Increased sugar accumulation in woody species under flooding is attributed to reduced phloem transport of assimilates from shoots to roots (Kreuzwieser *et al.* 2004). This reduction results in a delay of growth and metabolism in roots, apparently caused by their decreased carbohydrate content (Wample and Davis 1983). Sugar accumulation in leaves may be a mechanism for trees to tolerate flooding (Rengifo *et al.* 2005).

MDA content has been used as a parameter to assess

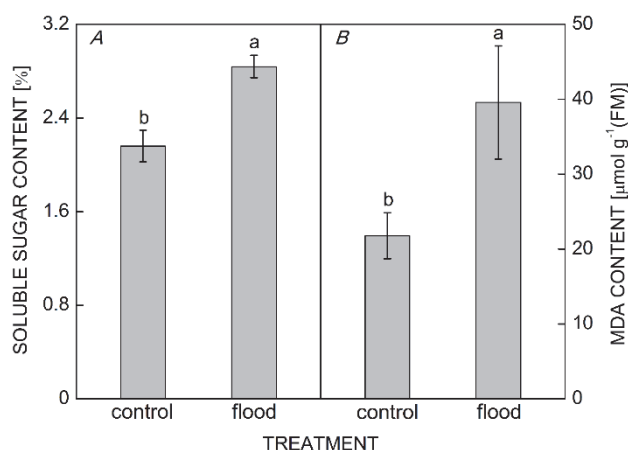


Fig. 7. Leaf soluble sugar and MDA content of *Populus euphratica* seedlings under control and soil flooding conditions for 50 d. Vertical bars represent the mean standard error (mean $\pm$ SE; $n = 10$). Means followed by different letters indicate significant differences at $p < 0.05$ according to LSD test. FM – fresh mass.

oxidative damage (Hossain *et al.* 2006, Arbona *et al.* 2008) and as an index of flood tolerance.

Under our experimental conditions, flooded plants showed significant changes in MDA content compared with the control seedlings at the end of the experimental period. Increased MDA content in leaves means increasing oxidative stress (Arbona *et al.* 2008), thus flooding was not beneficial for *P. euphratica* seedlings. MDA can also facilitate Chl degradation (Upham and Jahnke 1986) and thus reduce photosynthesis.

Flood-tolerant plants evolved two main strategies that include tolerance and escape from flood stress (Parolin 2002, Kreuzwieser *et al.* 2004). Our results indicate that *P. euphratica* adopted the tolerance strategy, as evidenced by high survivorship and maintaining carbon gain under

long-term soil flooding. This was accomplished through morphological adaptations, such as the development of hypertrophied lenticels, and the decline in physiological activities, such as reduction of photosynthesis limiting energy utilization. Based on these results, we concluded that *P. euphratica* is a flood-tolerant species that can adapt to relatively long periods of flooding. In Tarim River, the riparian zone is flooded every year from July to September. In this area, the flooding periods may last more than 60 d, during which most the floodplain plants are partially or completely submerged. The ability to grow and survive while flooded may lead to the dominance of *P. euphratica* in naturally flooded riparian zones along the Tarim River.

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