

Photosynthesis and growth adaptation of *Pterocarya stenoptera* and *Pinus elliottii* seedlings to submergence and drought

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Abstract

To uncover adaptation capacities of two flooding-tolerant plant species, *Pterocarya stenoptera* (a native species) and *Pinus elliottii* (an exotic species from southeastern USA), to alternating submergence and drought, we investigated their physiological and growth responses to water stress. Water treatments, including control, continuous flooding (CF), and periodic flooding and drought (PF), were applied to seedlings in order to simulate water level fluctuation in the hydro-fluctuation zone of the Three Gorges Reservoir Region. Results showed that net photosynthetic rate (P_N), stomatal conductance, and intrinsic water-use efficiency of both plant species were negatively affected under CF and PF compared with the corresponding controls. The P_N of both species under PF was comparable to that under CF. At the end of the experiment, the ratio of intercellular to ambient CO_2 concentration was not statistically different between water treatments, while that of *P. elliottii* was significantly higher than that of *P. stenoptera*. Although *P. stenoptera* formed lenticels under flooding conditions, *P. elliottii* seedlings allocated more mass to leaves and increased the relative growth rate of height to enhance the photosynthetic efficiency. Our results illustrated that *P. stenoptera* and *P. elliottii* seedlings developed different adaptive strategies in response to flooding, both CF and PF. Therefore, both *P. stenoptera* and *P. elliottii* are promising candidates for the vegetation reconstruction of the riparian zones in the Three Gorges Reservoir Region.

Additional key words: chinese wingnut; gas exchange; pine; soil redox potential; stomatal limitation.

Introduction

The Three Gorges Dam on the Yangtze River is the largest dam ever built in China (Wu *et al.* 2004). It has created a large reservoir surrounded by a new 400 km² riparian region containing about 2,000 km of shoreline. This new riparian region experiences large fluctuations in soil water content as a result of annual fluctuations in 30 m water level in the reservoir and its associated water table (Chen and Xie 2007). These extreme fluctuations have led to the formation of different water regimes including flood, drought, and alternations of flood and drought. In these altered habitats, prior dam vegetation has failed to flourish, causing a decline in species richness and diversity (New

and Xie 2008, Zhang *et al.* 2013). This has led to considerable erosion, geological disasters (*e.g.*, landslides) in the uplands, reduction in types of ecosystems, environmental pollution, and algal blooms in the aquatic environment (Ye *et al.* 2007, Fu *et al.* 2010). Thus, reforestation and vegetation reconstruction have become top priorities for the authorities restoring these newly-formed riparian zones of the Three Gorges Reservoir Region (Lu *et al.* 2010). However, the greatest obstacle preventing total ecosystem restoration is that few species are expected to survive in an aquatic-terrestrial environment with an annual cycle

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Abbreviations: C – control; CF – continuous flooding; C_i/C_a – the ratio of intercellular to ambient CO_2 concentration; E_h – soil redox potential; g_s – stomatal conductance; PF – periodic flooding and drought; P_N – net photosynthetic rate; RGR – relative growth rate; WUE_i – intrinsic water-use efficiency.

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of inundation as deep as 30 m (Tan *et al.* 2010). Therefore, the process of revegetation in the Three Gorges Reservoir Region hinges on the task of selecting species that can readily adapt to this habitat. Understanding plant responses and tolerance, and their underlying mechanisms, to flooding and drought regimes is critical in selecting these potential species.

Investigating the physiological response of species to flooding and drought is a crucial step in the selection of pioneer species for vegetation restoration of a degraded ecosystem (Chen *et al.* 2012). Water stress impacts survival, growth, and physiologically or ecologically adaptive characteristics of existing vegetation in riparian zones (Issarakraisila *et al.* 2007). Because the interactions between stress factors and various molecular, biochemical, and physiological characteristics are very intricate in plants, their mechanisms for tolerating water stress are complex (Chaves *et al.* 2009, Krasensky and Jonak 2012). In general, we would expect that a sensitive plant reduces its stomatal conductance, and thereby decreases its net photosynthetic rate and lowers biomass accumulation, and shows adaptive metabolic changes under water stress. The impact of flooding on plants is closely related to alterations in soil chemical properties, including redox status and nutrient availability (Pezeshki 2001). Many wetland plants form aerenchyma and shallow root systems, or enhance alcohol dehydrogenase activity to enhance oxygen transport to roots (Benz *et al.* 2007). However, water deficits adversely affect plant growth, reduce the synthesis of photosynthetic pigments (Jaleel *et al.* 2009), and may increase the production of superoxides or hydrogen peroxide (Taylor *et al.* 2004). Other water stress-induced characteristics include photosynthesis and transpiration changes. For example, stomata reduce their degree of openness in order to prevent desiccation under drought conditions (Flexas and Medrano 2002). Subsequently, photosynthesis is affected by internal water deficiency. Net photosynthesis is unavoidably reduced due to limited CO₂ availability at chloroplast level. In some plant species, nonstomatal factors reduce mesophyll photosynthesis capacity (Signarbieux and Feller 2011, Zhou *et al.* 2013). Therefore, the mechanism for water stress tolerance should be explored in plants through measurements including net photosynthetic rate (P_N), stomatal conductance (g_s), intercellular CO₂ concentration (C_i), and water-use efficiency.

Pterocarya stenoptera, a widely distributed native species in subtropical regions of China (22–40°N, 100–122°E), especially downstream of the Yangtze River (Jiang *et al.* 2005), grows quickly in July, and can create a forest within 10 to 15 years (Li *et al.* 2001). It is highly valued for its tolerance to flooding (Li *et al.* 2010, Yang *et al.* 2013), resistance to pests, and utilization in medicine and as pesticide (Wang *et al.* 2006). *Pinus elliotii*, a fast-growing

exotic species introduced from the southeastern coast of North America, is one of the most important timber trees among southern pine species. Since its introduction to China, *P. elliotii* has been planted in more than 12 Chinese provinces, especially, where it is humid with an annual average temperature of 15.4–21.8°C. It experiences its fastest growth period in April (Gholz and Fisher 1982, Ma *et al.* 2008). *P. elliotii* exhibits a strong hardiness resistance and tolerance to flooding, drought, and low soil fertility (Ford and Brooks 2003, Kominoski *et al.* 2013). Both *P. stenoptera* and *P. elliotii* have demonstrated the capacity to withstand flooding as well as drought (Li *et al.* 2010, Wang *et al.* 2012, Yang *et al.* 2013). However, how plants respond to water stress, it is based on their genetically determined traits and life cycles. Different species can respond differently to variations in flooding duration (Kozłowski 1984, Lu *et al.* 2010). Currently, there is scarce literature available concerning responses of *P. stenoptera* and *P. elliotii* to different water regimes. Therefore, a detailed understanding of their comparative photosynthetic and growth characteristics is necessary for the species selection in the restoration process of the Three Gorges Reservoir Region.

In this study, we designed a 60-d garden experiment focusing on species-specific responses to different soil water conditions by simulating periodic flooding-drought events in the Three Gorges Reservoir Region of the Yangtze River. The plants selected were one-year-old *P. stenoptera* and *P. elliotii* seedlings. The purpose of this study was: (1) to evaluate the impact of water treatment on the photosynthetic capabilities and growth of the exotic and native species, and understand their adaptive mechanisms for tolerating water stress, specifically, alternating submergence and drought; and (2) to compare the differences between the abilities of the exotic and native species to adapt to different water treatments. We hypothesized that: (1) *P. stenoptera*, the native species, which shows a high survival rate in the Three Gorges Reservoir Region, demonstrates reduced g_s , consequently reduced P_N and biomass accumulation under both continuous flooding and periodic flooding-drought compared with those growing in control conditions; (2) both *P. stenoptera* and *P. elliotii* are tolerant to these flooding or periodic flooding-drought conditions, and can maintain g_s and P_N at the control level; and (3) *P. stenoptera* is a more suitable species for vegetation restoration in the hydro-fluctuation zone compared to *P. elliotii* due to its generally greater total biomass and biomass allocation to leaves in each individual; it might benefit from greater carbon storage and having a stronger photosynthetic carbon sink in response to water stress than that of *P. elliotii* plants at the same age.

Materials and methods

Plants and growing site: Purple soils (Regosols in FAO Taxonomy or Entisols in USDA Taxonomy) collected from the riparian region of the Three Gorges Reservoir

were homogenized and placed in 180 identical pots, 23 cm of the inner diameter and 24 cm in height. Each pot was filled with about 5 kg of soil, with composition as follows:

pH value	Organic matter [g kg ⁻¹]	Total N [g kg ⁻¹]	Total P [g kg ⁻¹]	Total K [g kg ⁻¹]	Alkali hydrolysable N [mg kg ⁻¹]	Available P [mg kg ⁻¹]	Available K [mg kg ⁻¹]
7.94 ± 0.03	8.13 ± 0.28	0.53 ± 0.01	0.30 ± 0.01	48.85 ± 0.71	50.74 ± 1.26	5.99 ± 0.27	78.55 ± 3.49

In May 2010, 90 one-year-old seedlings of each *P. stenoptera* and *P. elliotii* were transplanted into the pots. Each pot contained one of the seedlings, uniform in size, age, and height. All of the pots were then transported to a shelter with a transparent roof, which was open at four sides. It was located in Southwest University Experimental Zone of Ecology (29°49'13"N, 106°25'21"E, 249 m a.s.l., about 30 km from the Yangtze River). After the 6-week period of acclimation under well-watered and well-drained standard conditions, water treatments started on July 23, 2010. The initial average heights of *P. stenoptera* and *P. elliotii* seedlings were 21.50 ± 1.96 and 9.38 ± 0.21 cm, respectively.

Experimental design: For both species, the pots containing plants were randomly divided into three groups, each with 30 seedlings. Each group was treated with a different water treatment: control (C), continuous flooding (CF), or periodic flooding-drought (PF). Seedlings in the C group were grown in soil with a moisture content of 60–63% of field capacity, which was determined by field investigation in the water-fluctuation zone of the Three Gorges Reservoir Region, where the plants commonly grow. For the CF treatment, pots were placed in a plastic basin of 72 cm in diameter and 30 cm in height, which was filled with water 5 cm above the soil surface. The soils remained continuously submerged for 60 d. For the PF condition, a 12-d water treatment period consisting of alternating flooding and drought (6 d each) was used for a total of 60 d according to the literature (Anderson and Pezeshki 2000, Li *et al.* 2005, Brown and Pezeshki 2007). Drought conditions were created by siphoning water out of the plastic basin containing the growing plants. The plants entered a state of mild drought after two days, with the predawn leaf water potential lower than -0.5 MPa, resulting primarily from an average daily high temperature near 35–40°C during the experimental period.

Once the treatment began, photosynthesis and growth parameters of the seedlings were measured every 12 d. Five random seedlings served as replicates during each measuring period. Soil redox potential (E_h) and predawn leaf water potential (Fig. 1) were measured to ensure the accuracy of the experimental design and the reliability of the experimental treatment. These measurements were obtained from the *DW-I* oxidation-reduction potential

(ORP) (*Jiangfen Electroanalytical Instrument*, Jiangsu, China) and *PSYPRO* water potential systems (*Wescor, Inc.*, Logan, Utah, USA), respectively.

Photosynthesis and growth determination: Five randomly selected seedlings served as replicates for each measuring period. Photosynthesis measurements, including net photosynthetic rate (P_N), stomatal conductance (g_s), and the ratio of intercellular to ambient CO₂ concentration (C_i/C_a), were taken on the third or fourth upper leaf from each seedling from each treatment on days 12, 24, 36, 48, and 60 after initiation of the treatments (DAT). All of the measurements were performed between 9:00–12:00 h on sunny days using a *LI-6400 Portable Operation System* (*Li-Cor, Inc.*, Lincoln, USA) at a fixed CO₂ concentration (C_a) of 400 $\mu\text{mol mol}^{-1}$ and leaf temperature of 25°C, after the seedlings were saturated at a light intensity (red/blue light source) of 1,000 $\mu\text{mol}(\text{photon}) \text{m}^{-2} \text{s}^{-1}$ and 1,200 $\mu\text{mol}(\text{photon}) \text{m}^{-2} \text{s}^{-1}$ for *P. stenoptera* and *P. elliotii* seedlings, respectively. This PPFD was chosen according to previous determination of the light-saturation curve, which indicated that seedlings were light-saturated at this level. The light-saturation curves of the two species were measured at different light intensities starting with the highest intensity [2,000; 1,600; 1,200; 1,000; 750; 500; 250; 100; 50; 25, and 0 $\mu\text{mol}(\text{photon}) \text{m}^{-2} \text{s}^{-1}$]. Leaves in the chamber were acclimated for at least 7 min until steady rates of assimilation were observed. The leaves also required about 5 min to attain a stable CO₂ exchange rate. Leaf area was determined by tracing the portion of the leaf enclosed by the *Li-Cor LI-6400* cuvette onto paper, then passing it through a *Li-Cor 3100* leaf area meter. The paper area was divided by two to correct for spaces between the individual needles on the leaf. A comparison of this procedure to the direct measurement with the *Li-Cor 3100* leaf area meter showed less than 3% error between the two measurement methods. Following Medavilla *et al.* (2002), the ratio of P_N to g_s was taken as an estimate of intrinsic water-use efficiency (WUE_i).

When determining a plant height and base diameter, the same plants, which were used for measuring photosynthesis, were taken. These growth traits were evaluated by a tape measure and vernier calipers, respectively. Every 12 d from the beginning of the water treatment, the same individuals for which height and diameter measurements

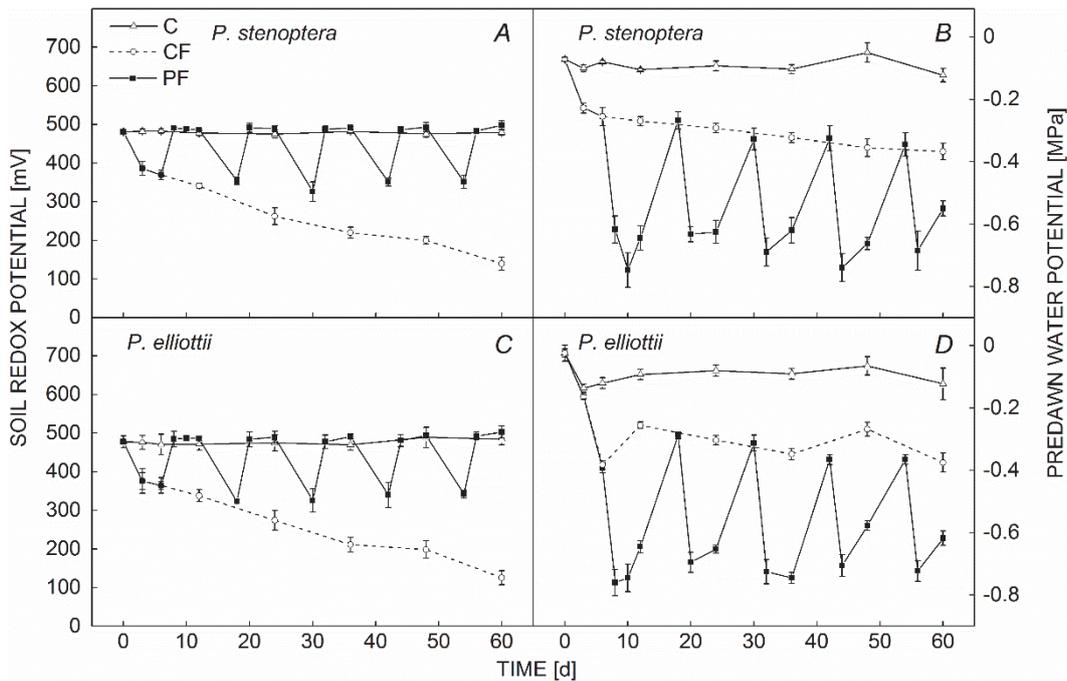


Fig. 1. Changes in soil redox potential of *Pterocarya stenoptera* seedlings (A) and their predawn leaf water potential (B), and the soil redox potential of *Pinus elliottii* seedlings (C) and their predawn leaf water potential (D) under control (C), continuous flooding (CF), and periodic flooding (PF) treatment (mean \pm SE, $n = 5$).

had been made, were harvested; the roots, stems, and leaves of each plant were sampled separately. Plant samples were washed thoroughly and subsequently dried in an oven at 80°C until constant mass. Total biomass was calculated as the sum of the root, stem, and leaf biomasses. The percentage of each plant organ to the plant total biomass was expressed as the mass fraction of the plant roots, stem, and leaves.

Relative growth rate (RGR) of plant biomass was calculated as the difference between the natural logarithm of total biomass per plant at the sampling date ($\ln\text{Mass}$) and the mean logged mass at the former sampling day ($\ln\text{Mass}_{\text{former}}$), divided by 12 d (the duration between the two measurements) (Hoffmann and Poorter 2002). Similarly, RGR of plant height was calculated, replacing biomass with plant height, as seen below (Meyer 1998).

$$\text{RGR in plant biomass} = \frac{\ln\text{Mass} - \ln\text{Mass}_{\text{former}}}{12}$$

Results

Photosynthetic physiological responses: P_N was not significantly different in both species, nor it was significantly affected by the interactions between species and water treatments, while a significant difference in P_N was observed between the different water treatments (Table 1S, *supplement available online*). For *P. stenoptera*, the P_N in the C group kept stable, while the seedlings under CF and

$$\text{RGR of plant height} = \frac{\ln\text{Height} - \ln\text{Height}_{\text{former}}}{12}$$

Data analysis: Analysis of the data employed GLM procedures (*SPSS 13.0 Version*) to determine any significant differences between treatments for each plant species. Multiple pair-wise comparisons (*Duncan's method*) were used to determine significant differences at the 0.05 level between individual treatment groups. Cross-species comparisons were made with a two-way analysis of variance (*ANOVA*) with independent variables species (two levels) and water treatment (three levels). The normality and equality of variances were tested prior to all of the analyses. *Pearson's correlation* was used to analyze the relationships between photosynthetic parameters, predawn leaf water potential, and soil redox potential of *P. stenoptera* and *P. elliottii* seedlings.

PF were stabilized after 36 DAT. In contrast, the seedlings of *P. elliottii* in CF and PF were stabilized after 36 and 24 DAT, respectively (Table 1). During the final measurement, *P. stenoptera* seedlings significantly reduced their P_N by 61.2 and 55.9% under CF and PF, respectively, as compared with their C group. The trend was the same for *P. elliottii*, but with larger declines. However, for each

Table 1. Time course of photosynthetic physiological responses of *Pterocarya stenoptera* and *Pinus elliottii* seedlings under control (C), continuous flooding (CF), and periodic flooding-drought (PF) treatment (mean \pm SE, $n = 5$). Different uppercase letters indicate significant differences between different measurement time points within the same treatment group ($p < 0.05$), while different lowercase letters indicate significant differences between different experimental groups at the same measurement time ($p < 0.05$), as tested using one-way ANOVA followed by a post hoc Duncan's pair-wise comparison.

Parameter	Time [d]	<i>Pterocarya stenoptera</i>			<i>Pinus elliottii</i>		
		C	CF	PF	C	CF	PF
P_N [$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$]	12	10.09 \pm 0.20 ^{Aa}	7.70 \pm 0.43 ^{Ab}	7.26 \pm 0.39 ^{Ab}	10.11 \pm 0.51 ^{ABa}	5.70 \pm 0.14 ^{Ab}	6.00 \pm 0.21 ^{Ab}
	24	10.42 \pm 0.67 ^{Aa}	5.50 \pm 0.16 ^{Bb}	4.33 \pm 0.06 ^{Cc}	10.98 \pm 0.50 ^{Aa}	5.70 \pm 0.35 ^{ABb}	5.03 \pm 0.24 ^{Bb}
	36	11.28 \pm 0.43 ^{Aa}	5.72 \pm 0.33 ^{Bb}	4.50 \pm 0.28 ^{BCb}	10.14 \pm 0.09 ^{ABa}	4.37 \pm 0.17 ^{Bb}	4.25 \pm 0.33 ^{Bb}
	48	10.26 \pm 0.44 ^{Aa}	5.92 \pm 0.23 ^{Bb}	5.05 \pm 0.22 ^{BCb}	9.29 \pm 0.21 ^{Ba}	4.91 \pm 0.27 ^{Bb}	5.08 \pm 0.18 ^{Bb}
	60	9.99 \pm 0.10 ^{Aa}	6.20 \pm 0.08 ^{Bb}	6.41 \pm 0.11 ^{Bb}	9.66 \pm 0.16 ^{Ba}	4.10 \pm 0.08 ^{Bb}	4.14 \pm 0.06 ^{Bb}
g_s [$\text{mol m}^{-2} \text{ s}^{-1}$]	12	0.19 \pm 0.00 ^{Aa}	0.15 \pm 0.01 ^{Ab}	0.14 \pm 0.00 ^{Bb}	0.18 \pm 0.00 ^{Aa}	0.15 \pm 0.00 ^{Ab}	0.14 \pm 0.01 ^{Ab}
	24	0.19 \pm 0.01 ^{Aa}	0.09 \pm 0.00 ^{Cb}	0.10 \pm 0.00 ^{Db}	0.16 \pm 0.00 ^{Ba}	0.12 \pm 0.01 ^{Bb}	0.06 \pm 0.00 ^{Bc}
	36	0.20 \pm 0.00 ^{Aa}	0.08 \pm 0.00 ^{Dc}	0.10 \pm 0.01 ^{Db}	0.16 \pm 0.00 ^{Ba}	0.11 \pm 0.00 ^{Bb}	0.06 \pm 0.00 ^{Bc}
	48	0.21 \pm 0.00 ^{Aa}	0.12 \pm 0.00 ^{Bb}	0.13 \pm 0.00 ^{Cb}	0.14 \pm 0.00 ^{Ca}	0.09 \pm 0.00 ^{Cb}	0.06 \pm 0.00 ^{Bc}
	60	0.20 \pm 0.00 ^{Aa}	0.14 \pm 0.00 ^{Ac}	0.17 \pm 0.00 ^{Ab}	0.13 \pm 0.01 ^{Ca}	0.10 \pm 0.00 ^{Cb}	0.06 \pm 0.01 ^{Bc}
C_i/C_a	12	0.77 \pm 0.01 ^{Aa}	0.79 \pm 0.01 ^{Ba}	0.77 \pm 0.02 ^{Ca}	0.90 \pm 0.01 ^{Ac}	0.99 \pm 0.01 ^{Aa}	0.97 \pm 0.01 ^{Ab}
	24	0.75 \pm 0.02 ^{Ac}	0.85 \pm 0.03 ^{ABb}	0.91 \pm 0.01 ^{Aa}	0.90 \pm 0.00 ^{Ab}	0.99 \pm 0.00 ^{Aa}	0.94 \pm 0.01 ^{ABb}
	36	0.74 \pm 0.03 ^{Ac}	0.90 \pm 0.02 ^{Aa}	0.85 \pm 0.02 ^{Bb}	0.92 \pm 0.01 ^{Ab}	0.98 \pm 0.00 ^{Aa}	0.94 \pm 0.01 ^{ABb}
	48	0.76 \pm 0.02 ^{Ac}	0.83 \pm 0.03 ^{Ba}	0.81 \pm 0.02 ^{BCb}	0.87 \pm 0.03 ^{Ab}	0.99 \pm 0.01 ^{Aa}	0.93 \pm 0.02 ^{ABb}
	60	0.75 \pm 0.03 ^{Ab}	0.81 \pm 0.02 ^{Ba}	0.80 \pm 0.00 ^{BCa}	0.94 \pm 0.02 ^{Ab}	0.99 \pm 0.00 ^{Aa}	0.95 \pm 0.00 ^{ABb}
WUE_i [$\mu\text{mol mol}^{-1}$]	12	52.28 \pm 1.47 ^{Aa}	52.56 \pm 1.35 ^{Ba}	50.12 \pm 1.43 ^{Aa}	55.76 \pm 2.40 ^{Ca}	37.94 \pm 1.04 ^{Bb}	43.95 \pm 3.57 ^{Bb}
	24	54.35 \pm 2.53 ^{Aa}	57.94 \pm 1.23 ^{Aa}	42.69 \pm 1.20 ^{Bb}	67.00 \pm 3.72 ^{ABb}	48.65 \pm 3.06 ^{Ac}	80.41 \pm 4.86 ^{Aa}
	36	50.23 \pm 2.02 ^{Aa}	50.13 \pm 5.95 ^{Ba}	45.32 \pm 1.08 ^{Bb}	62.95 \pm 0.61 ^{BCa}	38.17 \pm 1.67 ^{Bb}	72.40 \pm 5.37 ^{Aa}
	48	48.78 \pm 1.69 ^{Aa}	48.81 \pm 1.01 ^{Ba}	38.60 \pm 1.55 ^{Cb}	66.12 \pm 1.59 ^{ABb}	53.26 \pm 2.20 ^{Ab}	89.23 \pm 7.26 ^{Aa}
	60	49.23 \pm 0.85 ^{Aa}	44.16 \pm 0.55 ^{Cb}	37.99 \pm 0.68 ^{Cc}	72.50 \pm 3.79 ^{Aa}	41.67 \pm 0.79 ^{Bb}	90.84 \pm 3.07 ^{Ac}

species, there was no significant difference in P_N between CF and PF (Fig. 2A). The P_N of *P. elliottii* was significantly lower than that of *P. stenoptera* only when they were subjected to CF or PF (Fig. 2A).

The g_s was significantly influenced by species and water treatment and their interactions (Table 1S). In *P. stenoptera*, the g_s in the C group remained stable throughout

the entire testing period, while the seedlings under both CF and PF experienced a decrease followed by an increase after 36 DAT. In *P. elliottii* seedlings, all treatments exhibited an overall decrease throughout the testing period, except for PF, which initially decreased but then stabilized after 24 DAT (Table 1S). At the end of the experiment, the g_s in C was larger than that of both water treatments for each

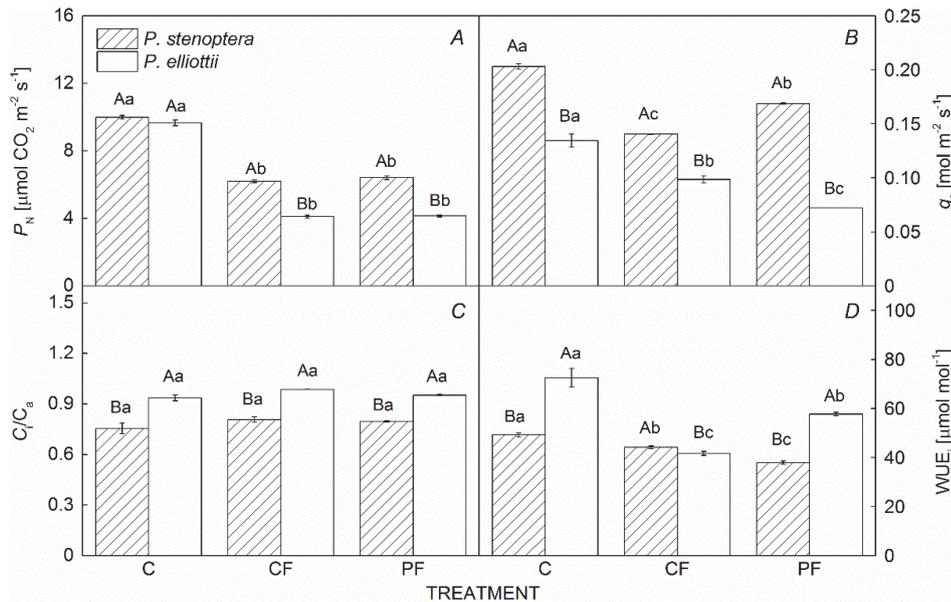


Fig. 2. Final measurements of net photosynthetic rate (P_N) (A), stomatal conductance (g_s) (B), ratio of intercellular to ambient CO_2 concentration (C_i/C_a) (C), and intrinsic water-use efficiency (WUE_i) (D) of *Pterocarya stenoptera* and *Pinus elliottii* seedlings under control (C), continuous flooding (CF), and periodic flooding (PF) treatment. Value in each column stands for mean \pm SE of five samples at the 60 days. Different uppercase letters indicate significant differences between the values of the two species in each treatment ($p < 0.05$), while different lowercase letters indicate significant differences between experimental groups for each species ($p < 0.05$).

plant type, while g_s under CF was significantly lower than that under PF for *P. stenoptera*, but significantly larger than that under PF in *P. elliottii* (Fig. 2B). For each treatment group, the g_s of *P. stenoptera* seedlings was significantly greater than that of *P. elliottii* seedlings (Fig. 2B).

The ratio of C_i/C_a was significantly affected by the species and water treatment (Table 1S). In *P. stenoptera*, the C_i/C_a of C experienced little variation throughout the experiment, while it peaked at 36 and 24 DAT under CF and PF, increasing by 22.6 and 21.0%, respectively, as compared with that of the C group. In *P. elliottii*, the C_i/C_a did not change significantly by any treatments throughout the entire testing period (Table 1). Interestingly, no significant differences were found between any groups during the final measurement of C_i/C_a , while this ratio was significantly lower in *P. stenoptera* than that of *P. elliottii* in each group (Fig. 2C).

Similarly, WUE_i was significantly affected by the plant species, water regime, and their interactions (Table 1S). Throughout the experiment, the WUE_i of *P. stenoptera* seedlings in the C group remained stable, while there was an initial significant increase followed by a decrease in WUE_i in CF; the PF treatment caused an overall decrease in WUE_i . However, the WUE_i of *P. elliottii* under CF constantly fluctuated, and the seedlings under PF initially increased and then stabilized (Table 1). At the end of the experiment, the water treatment significantly impacted the WUE_i of both species and followed the sequence of $C > CF > PF$ for *P. stenoptera*, and $C > PF > CF$ for *P. elliottii*. The WUE_i of *P. stenoptera* in both the C and CF group was significantly lower than that in the *P. elliottii* seedlings under the same treatments, but it was

significantly higher under CF (Fig. 2D).

Plant biomass: Mass fractions of plant roots, stem, and leaves were significantly affected by species and species by water regime interaction, but not by the water treatment (Table 1S). In *P. stenoptera* seedlings, the root mass fraction experienced little variation under CF and PF throughout the experiment, while the stem fraction kept increasing in CF and decreased significantly after 48 DAT in the PF group (Fig. 3B,C). Unlike the *P. stenoptera* seedlings, *P. elliottii* had the highest leaf mass fraction among their organs in all the treatments (Fig. 3D–F). The mass of the root fraction in *P. elliottii* was higher than that of the stem, except for the C group at 36 and 48 DAT, and for CF at 24 DAT. Compared to the decline in the stem and root fractions under CF after 24 DAT, the root and stem mass fractions of the entire plant under PF were stable after 24 DAT (Fig. 3D–F).

Variances of RGR in plant biomass were only significantly affected by the water treatment when considering the entire course of the experiment (Table 1S). However, there was no significant difference between treatments for either plant species at the end of the experiment (Fig. 4). In contrast, the RGR in biomass for *P. stenoptera* was significantly higher than that of *P. elliottii* for each water regime on the same day (Fig. 4). These facts indicated a greater RGR of the native species in the later stage of the experiment under any water treatment.

RGR of plant height and base diameter was significantly affected by the water treatment, but not by species and species by treatment interaction (Table 1S). There was no

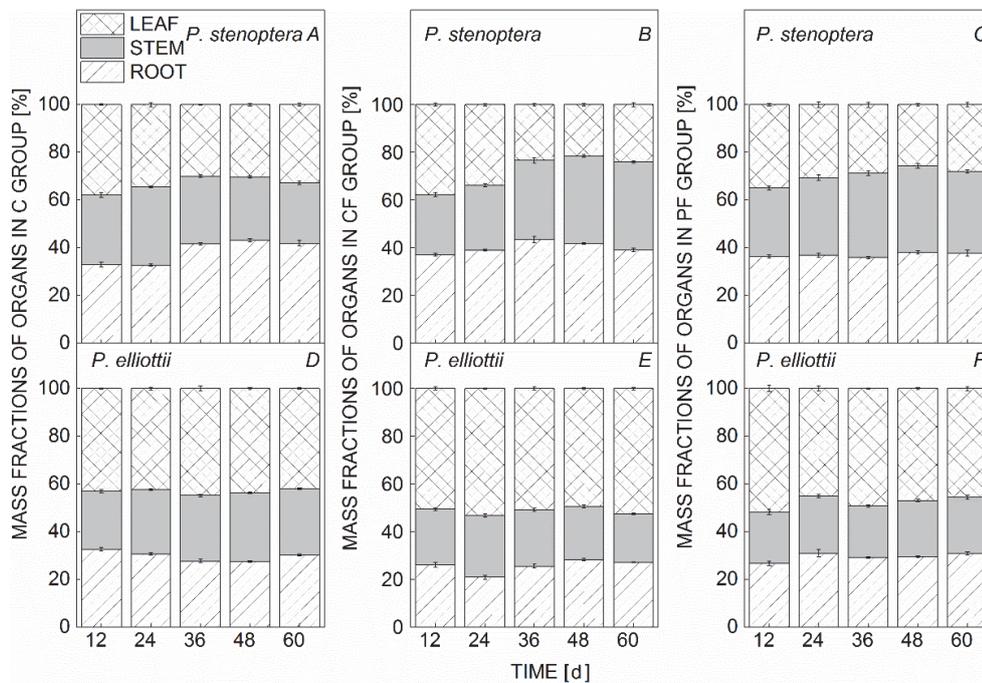


Fig. 3. The change in mass fraction of plant organs in *Pterocarya stenoptera* and *Pinus elliottii* seedlings under control (C), continuous flooding (CF), and periodic flooding (PF) treatment during the experiment (mean \pm SE, $n = 5$).

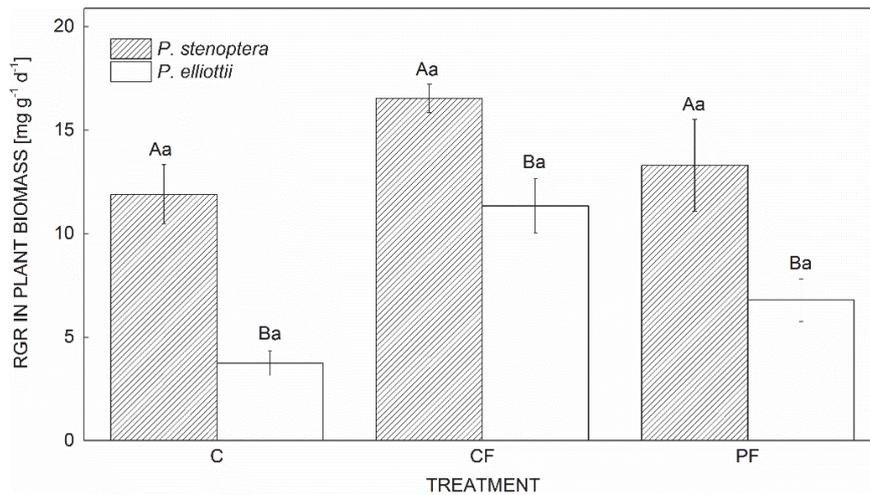


Fig. 4. Final measurement of relative growth rate (RGR) in biomass of *Pterocarya stenoptera* and *Pinus eliottii* seedlings under control (C), continuous flooding (CF), and periodic flooding (PF) treatment. Value in each column stands for mean \pm SE of five samples after 60 days. Different uppercase letters indicate significant differences between the values of the two species in each treatment ($p < 0.05$), while different lowercase letters indicate significant differences between experimental groups for each species ($p < 0.05$).

significant difference in RGR of plant height between treatments for either species at the end of the experiment (Fig. 5A). However, compared to *P. stenoptera*, *P. eliottii* showed significantly greater RGR of plant height in both the C and CF treatment at the end of the study, in contrast to a comparable RGR of plant height in the PF treatment (Fig. 5A).

The base diameters of the plants were found to be significantly influenced by the species, treatment, and their interactions (Table 1S). At the end of the experiment, the average base diameter of *P. stenoptera* seedlings in CF significantly increased by 23.2 and 23.8% as compared to that under the C and PF treatment, respectively. In contrast, the base diameter of *P. eliottii* seedlings demonstrated a

significant decline following the sequence of C > CF > PF (Fig. 5B). In conclusion, the base diameters of the one-year-old *P. stenoptera* seedlings were significantly greater than those of *P. eliottii* under any water treatment at the end of the experiment (Fig. 5B).

For *P. stenoptera* seedlings, there were significant positive correlations between photosynthetic parameters and predawn leaf water potential, and soil redox potential (E_h). However, there was no significant correlation between WUE_i and E_h . In contrast, *P. eliottii* seedlings displayed significant positive correlations in all parameters except for the relations between g_s and E_h , and between WUE_i and predawn leaf water potential (Table 2).

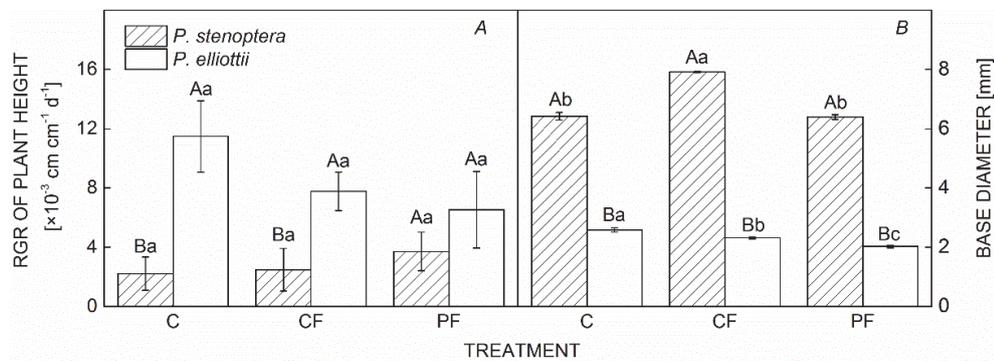


Fig. 5. Final measurement of relative growth rate (RGR) of plant height (A) and base diameter (B) of *Pterocarya stenoptera* and *Pinus eliottii* seedlings under control (C), continuous flooding (CF), and periodic flooding (PF) treatment. Value in each column stands for mean \pm SE of five samples after 60 days. Different uppercase letters indicate significant differences between the values of the two species in each treatment ($p < 0.05$), while different lowercase letters indicate significant differences between experimental groups for each species ($p < 0.05$).

Discussion

After the construction of the Three Gorges Reservoir, the region exposed to very high fluctuations of water level was formed. For identifying revegetation candidates in this region, water stress capacities of one-year-old

P. stenoptera, a native species, and *P. eliottii*, an exotic species, were compared. Each species showed a decline in g_s , presumably as a protective measure, at expense of the photosynthetic rate, and different growth performances

Table 2. Pearson's correlation coefficient of photosynthetic parameters, predawn leaf water potential and soil redox potential of *Pterocarya stenoptera* and *Pinus elliottii* seedlings. Data used were stable in the whole experimental period. ** – significant at $p < 0.01$ for correlations. P_N – net photosynthetic rate; g_s – stomatal conductance; WUE_i – intrinsic water-use efficiency.

	P_N	g_s	WUE_i
<i>P. stenoptera</i>			
Predawn leaf water potential	0.787**	0.617**	0.569**
Soil redox potential	0.332**	0.469**	-0.169
<i>P. elliottii</i>			
Predawn leaf water potential	0.685**	0.746**	-0.186
Soil redox potential	0.342**	-0.058	0.686**

in response to stressful water regime. Our results indicated that both species are sensitive to the water treatments. However, only *P. stenoptera* exhibited later enhanced g_s and P_N after their initial declines; it proved a tolerance to water stress. The ability to develop such characteristics determines species as suitable candidates to reconstruct riparian zones, as they can withstand different water regimes (Mulia and Dupraz 2006).

Li *et al.* (2004) demonstrated that plants exhibit certain adaptations under flooding to maintain their photosynthetic capacity. The change in P_N is one of the most important indicators of a photosynthetic physiological response (Wertin *et al.* 2010, Pattison *et al.* 2011). In our study, the fact that the P_N of both *P. stenoptera* and *P. elliottii* seedlings was significantly lower than that of the respective C groups under CF and PF conditions was in agreement with most water stress studies (Jackson and Colmer 2005). However, the stabilized P_N after the initial decline under these two conditions suggested an innate ability of the plants to adapt their photosynthetic capacities to flooding (Pezeshki *et al.* 2007). Schulze (1986) believed that a decrease in P_N not only depends on stomatal factors, but also on nonstomatal factors. A decline in P_N due to stomatal limitation is determined by a concordant drop in CO_2 concentration in the substomatal cavity. However, if the decreasing P_N is caused by nonstomatal limitations, there is an increase or no change in the intracellular CO_2 concentration. (Tang and Kozłowski 1983, Martínez *et al.* 2007). We found that under water stresses (CF and PF), g_s of the two plant species decreased, while C_i/C_a increased as compared to the corresponding C groups. This suggested the reduced P_N was largely caused by nonstomatal factors. Reduced g_s indicated that plants at first tried to avoid flooding and drought by closing their stomata. It is also not surprising that P_N and g_s were closely linked, which has been documented for riparian species (Li *et al.* 2011). Meanwhile, in *P. stenoptera* seedlings, the significantly lower WUE_i under PF compared with CF was likely due to the larger decline of P_N compared to g_s . These results indicated that *P. stenoptera* seedlings were tolerant to flooding but sensitive to drought (Besset *et al.* 2001,

Hessini *et al.* 2009). Along with directly measuring photosynthetic capacity, we can examine biomass accumulation and allocation of a plant to offer insights into its responses to growing environment (Wilson and Keddy 1988, Niinemets 2010). Biomass allocation of different plant organs reflects the adaptive strategy of plants to various environments (Poorter and Nagel 2000). One of the basic tenets of plant ecophysiology is the trade-off between the capacity of a genotype to grow when resources are abundant and the plant's capacity to tolerate resource shortages (Chapin 1980). Our results indicated the seedlings of both plant species reduced their root mass fractions under both CF and PF when compared with their corresponding controls. This might help decrease the respiration by the root system (Visser *et al.* 2000). The increasing mass fractions of *P. stenoptera* stem under CF with stress duration indicated that the plants might escape from flooding through elongation growth. However, the leaves of *P. elliottii* seedlings were found to occupy higher percentages than their stems, and their leaf mass fractions overall increased under flooding conditions. Thus, it was possible that the broad-leaf species, *P. stenoptera*, increased its stem length to obtain more oxygen to survive the inundated conditions, while *P. elliottii* seedlings with needle leaves accumulated leaf mass to enhance the photosynthetic efficiency.

Although RGR in biomass of the native species *P. stenoptera* was always significantly higher than that of *P. elliottii* at the end of the experiment, the RGR was comparable in both species during the whole experiment as detected by ANOVA (Table 1S). This was not surprising because *P. stenoptera* has a later growing season than that of *P. elliottii*. In contrast to a previous study (Sánchez-Rodríguez *et al.* 2012), our study revealed slight increases in the RGR in biomass under both water treatments compared with the control. This might be explained by the different plant growth traits and various experimental conditions. Besides biomass RGR, the RGR of plant height for *P. elliottii* was significantly higher than that of *P. stenoptera* in any treatment at the final measurement, which further demonstrated that under water stresses, *P. elliottii* seedlings tended to elongate their growth rather than to accumulate biomass in order to capture light energy.

Plants under flooding conditions also exhibit certain morphological changes, such as the formation of adventitious roots, initiation of hypertrophied lenticels, or the establishment of aerenchyma (Pezeshki 2001). Given that *P. stenoptera* seedlings generated adventitious roots and lenticels under flooding conditions, their overall base diameter was larger under CF than that under the C conditions. In contrast to this, there was no obvious adventitious root or lenticel production in *P. elliottii* seedlings, nor was there any increase in the base diameter under water stresses compared with C.

For both the *P. stenoptera* and *P. elliottii* seedlings, the high positive correlation between the predawn leaf water potential and E_h with P_N indicated that both species were

able to effectively assimilate CO₂ and accumulate photosynthetic products when the predawn leaf water potential and E_h increased. The high predawn leaf water potential indicates lesser water stress in plants. *P. stenoptera* seedlings undergoing water stress reduced water consumption by decreasing g_s, which caused the decline in P_N and reduced the ability of the mesophyll cells to utilize CO₂. This accounted for the observed increase of C_i/C_a in *P. stenoptera*. In contrast, better soil permeability led to a higher E_h and a more sufficient plant root oxygen supply, both of which were conducive to plant photosynthesis. The significant positive correlation between g_s and predawn leaf water potential further illustrated the water content in plant leaves to be directly related to g_s.

Conclusion: After the Three Gorges Reservoir was constructed, a new hydro-fluctuation zone was formed along the Yangtze River ranging from 145 to 175 m. To uncover physiological and growth adaptation capacities of one-year-old *P. stenoptera*, a native species, and *P. elliotii*, an exotic species, to different water regimes, three water treatments including control (C), continuous flooding (CF),

and periodic flooding-drought (PF) were applied, simulating the water level change in these areas.

The study showed that both species were capable of adapting to various patterns of flooding in the riparian areas of the Three Gorges Reservoir Region. Although photosynthesis and growth of *P. stenoptera* and *P. elliotii* seedlings were negatively affected by the water treatments, the seedlings of both species showed adaptive characteristics to the different water stress scenarios. The two plant species survived continuous flooding or flooding and drought alternation through different strategies. Their reduced net photosynthetic rate was largely caused by nonstomatal factors. Under flooding condition, *P. stenoptera* increased stem biomass to escape the inundated environment, while *P. elliotii* seedlings allocated more mass to leaf and increased the RGR of height to enhance the photosynthetic efficiency. *P. stenoptera* formed lenticels under flooding treatment and had significantly greater base diameters than *P. elliotii* seedlings. Therefore, both *P. stenoptera* and *P. elliotii* are promising candidates for the vegetation reconstruction of the riparian zones in the Three Gorges Reservoir Region.

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