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ORIGINAL PAPER

Physiological mechanism for the reduction in soil water in poplar (*Populus deltoides*) plantations in Dongting Lake wetlands

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Abstract The use of large-scale tree plantations has provoked increasing concern regarding the negative effects on local environments in different ecosystems. However, the physiological mechanism underlying the reduction in soil water by tree plantations in wetlands is not clear. The aims of this study were to investigate the effects of poplar (*Populus deltoides*) plantations on soil water content and to elucidate the underlying physiological mechanisms. To this end, we conducted a 1-year fixed-plot investigation of soil water content (SWC), plant photosynthetic rate (Pn), stomatal conductance (Gs), transpiration rate (Tr), and water-use efficiency (WUE) of individual leaves of 11- and 5-year-old poplars and of reed (*Triarrherca sacchariflora*, a native herbaceous plant) in the Dongting Lake wetlands, China. SWC was highest in reed, intermediate in 11-year-old poplar, and lowest in 5-year-old poplar, suggesting that poplar plantations produce a lower soil water content in wetlands. From May to July, Pn was significantly higher in reed than in the two poplar stands, but did not differ between the different-aged poplars. As a whole, Gs and Tr were higher, but WUE was lower, in the poplar stands than in reed during the growing season, indicating that Gs and Tr are the key physiological mechanisms associated with the lower soil water in poplar stands. Relationships among Pn, Gs, and Tr showed positive correlations ($P < 0.01$) for each type of vegetation. These data suggest that poplar plantations may cause the transformation of wetlands into dry land due to a lower WUE leading to a massive water loss from soil. This, in turn, would have an influence on community composition and ecosystem function after establishment of the plantations.

Keywords Soil water content · Photosynthetic rate · Stomatal conductance · Transpiration rate · Water-use efficiency

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Introduction

The use of fast-growing tree plantations has been increasing throughout the world to satisfy demands for industrial timber and pulp, to mitigate climatic changes (Richards et al. 2007), and to produce biofuels

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(IEA 2004). Tree species used in plantations include eucalyptus (Gerber 2011), rubber (Tan et al. 2011), pines (Licata et al. 2008), and poplars (Perry et al. 2001). Fast-growing trees are generally planted in monocultures, and these species have obvious advantages over native plants in competing for light, nutrients, and water resources. These factors have led to increasing concerns regarding the negative effects of large-scale tree plantations on local environments, including nutrition depletion (Onyekwelu et al. 2006), reduced biodiversity (Morris et al. 2008), water-table decline (Almeida et al. 2007), and outbreaks of pests and diseases (Kelty 2006).

The water-pumping effects of fast-growing tree plantations have been clarified in different ecosystems, such as in semiarid areas (Wilske et al. 2009; Tan et al. 2011) and wetlands (Le Maitre et al. 2002; Hernández-Santana et al. 2008; Migliavacca et al. 2009). For example, poplar plantations have the potential to extract groundwater and to reduce the water table in wetland ecosystems (Migliavacca et al. 2009). Excessive loss of soil water caused by tree plantations would influence community structure and ecosystem function (Gaitán et al. 2011). However, compared to groundwater, soil moisture content can more closely reflect the water status of the rhizosphere of tree plantations, which is more important in terms of regulating species distribution, community composition, and biodiversity (Engelbrecht et al. 2007; Gaitán et al. 2011). To date, the effects of tree plantations on soil water status have remained far from clear.

The mechanisms underlying the effects of tree plantations on soil water status are complex. Studies have shown that plant transpiration accounts for over 60 % of evapotranspiration (Almeida et al. 2007) and for approximately 50 % of total rainfall (Huang et al. 2011). Tree plantations usually have higher rates of transpiration than native vegetation (Granier et al. 2000; Schiller et al. 2007; Licata et al. 2008), due to higher stomatal conductance, which leads to greater water loss (Wallace and McJannet 2010; Chen et al. 2011). In addition, photosynthetic rate is closely linked to transpiration rate and has been suggested to provide a direct indication of water consumption because higher photosynthesis is usually associated with higher utilization efficiency of water resources (Licata et al. 2008; Wallace and McJannet 2010). It therefore appears that the physiological mechanism for high water loss in fast-growing tree plantations is closely related to the high rates of photosynthesis, transpiration, and stomatal activity in these systems.

Poplar (*Populus deltoides*), a fast-growing tree, is the dominant species in broadleaf forests in China (Fang et al. 2005). In 2003, poplar accounted for 13.5 % of total forest plantation area in China (CFS 2003). In 1970, the alien *P. deltoides* was introduced into the Yangtze River basin for schistosome control. For example, the area in the Dongting Lake wetlands covered by tree plantations increased from 87 km^2 in 1983 to 640 km^2 in 2007 (approximately 26 % of the wetland area), replacing the habitat of native herbaceous species, which were the dominant vegetation in the Dongting Lake wetlands (Xie and Chen 2008). These poplar plantations have provoked serious concern regarding increases in soil desiccation and a reduction in biodiversity (Chang et al. 2006; Liang et al. 2006; Migliavacca et al. 2009; Wilske et al. 2009; Yang et al. 2009). In the semiarid Loess Plateau, water consumption of poplar decreases with reductions in soil water content (Liang et al. 2006), suggesting that soil water loss may also be higher in wetlands due to the saturated conditions in these areas. In the research presented here, we conducted a 1-year fixed-plot study of 11- and 5-year-old poplar plantations, and of reed (*Triarrherca sacchariflora*, a native herbaceous perennial), to test the following hypotheses: first, the soil water content will be lower in poplar than in reed areas; second, photosynthetic rate, transpiration rate, and stomatal conductance will be higher in poplars than in reeds.

Materials and methods

Study sites

The Yangtze River is connected to Dongting Lake through 3 inlets (Songzikou, Taipingkou, Ouchikou) and 1 outlet (Chenglingji). Dongting Lake is the second largest freshwater lake in China and covers an area of 2,625 km^2 (28°38′–29°45′N, 111°40′–113°10′E). The lake is characterized by a subtropical monsoon climate, with an average annual temperature of 16.2–17.8 °C and 259–277 frost-free days per year. Mean annual precipitation ranges from 1,200 to 1,415 mm, with the rainy season from April to August; average humidity is 80 %, and average evaporation is 1,270 mm (Cui et al. 2012). The annual mean wind speed is 2.0–3.0 m s^{-1} and the elevation is 28–35 m above sea level (a.s.l). Poplars have been planted extensively for industrial pulp since 1970, and have become the dominant vegetation in the Dongting Lake area.

Our study site was located on the beach of the Yangtze River, Guangxingzhou Town (29°32′N, 112°55′E), Yueyang City, Hunan Province, China. The site is approximately 15 km from the Chenglingji outlet and belongs to the Dongting Lake area. The elevation is approximately 30 m a.s.l. Three vegetated areas were chosen for study: 2 areas of poplar—one planted in 2000 (11-year poplar) and one planted in 2006 (5-year poplar)—and one of reed (planted in 2000 and harvested annually for paper making in November or December). Before establishment of the plantation using cuttings, the plant community in the study site comprised common herbaceous wetland plants, including *Carex brevicuspis, T. sacchariflora*, and *Phragmites australis*. The area covered by 11- and 5-year poplar was approximately 3 ha, and the area of reed was approximately 8 ha. The 3 vegetated areas were adjacent to one another, each separated by approximately 30–40 m. Soils in all the study areas were of the same origin, and were deposited by flooding. Soil physical and chemical properties are similar among the 3 vegetated areas ($P > 0.05$). Mean soil pH at a depth of 0–60 cm is 8.01–8.22. Total carbon, total nitrogen, total phosphorus, and total potassium are 21.59–25.25, 1.43–1.51, 0.70–0.73, and 19.35–22.51 g kg^{-1}, respectively.

Measurement of vegetation parameters and soil water content

In each of the 3 vegetated areas, 3 fixed plots (20 m × 30 m) with equal spacing were established as replicates. Stand density, height of vegetation, and diameter at breast height (DBH) of poplars were measured in October 2011. Multiple comparisons showed that the density of reed (148,000 plants ha^{-1}) was significantly higher than that of 11-year poplar (833 trees ha^{-1}, in rows spaced 3 m × 4 m) and 5-year poplar (1,666 trees ha^{-1}, in rows spaced 2 m × 4 m). The average height of vegetation in each of the 3 areas was 20.1, 10.5, and 3.7 m for 11-year poplar, 5-year poplar, and reed, respectively. The average DBH of 11- and 5-year poplar was 18.4 and 11.1 cm, respectively. The average crown diameter of 11- and 5-year poplar was 3.95 and 3.08 m, respectively.

Soil samples were collected from October 2011 to September 2012. In each plot, soil was sampled from 3 layers (0–15, 15–40, and 40–70 cm) using a soil sampler, according to the 5-point sampling method (Pobel et al. 2011). The latitude and longitude of each soil sampling point was recorded using a global positioning system. Soils within vegetated areas were mixed by soil layer, and stored in a bag for measurement of soil water content (SWC) using the classical method of drying and weighing (Dobriyal et al. 2012). Precipitation data from the meteorological station of the Dongting Lake Station for Wetland Ecosystem Research, located approximately 6 km from the study site, were used in this study.

Measurement of photosynthesis, stomatal conductance, and transpiration

On one cloudless day of each month during the 2012 growing season (May to September), a Li-6400 portable photosynthesis system (LI-COR, Inc., USA) was used to measure photosynthetic rate (Pn, μmol m^{-2} s^{-1}), stomatal conductance (Gs, mol m^{-2} s^{-1}), and transpiration rate (Tr, mmol m^{-2} s^{-1}). In poplar stands, 6 trees of average height and DBH were chosen as samples for 6 replicates. Ten fully expanded leaves from the north, south, east, and west parts of each sampled tree were selected and measurement were taken from approximately 50–60 leaves. In the reed area, 12 plants of average height were chosen as samples for 12 replicates. Four fully expanded leaves from the north, south, east, and west at the top of each sample were selected, and measurements were taken from a total of 48 leaves. All measurements were performed between 9:00 and 11:00 am. In May, June, and September, measurements were conducted during the middle 10 days of the month. However, measurements were conducted during the first 10 days of July and the last 10 days of August because parts of the plots were submerged by a flood from mid-July to mid-August. The water-use efficiency (WUE) of individual leaves was calculated as the ratio of Pn to Tr (Liang et al. 2006).

Statistical analysis

Multiple comparisons of density, height, DBH, and crown diameter in each of the 3 vegetated areas were analyzed by LSD at the 0.05 significance level, and monthly mean Pn, Gs, Tr, and WUE were analyzed by Tukey's test at the 0.05 significance level. Homogeneity of variances was tested using Levene's test, and data were $\log_{10}$-transformed when necessary to reduce the heterogeneity of variances. Correlation analyses among GS, Pn, and Tr were performed using bivariate correlations with two-tailed tests. Relationships among Pn, Gs, and Tr in the 3 vegetated areas were determined by curve regression (linear, power, logarithmic, or polynomial equations) on the basis of R^2 and *P* values. All statistical analyses were performed using SPSS v17.0 (SPSS Inc., USA).

Results

Precipitation and soil water content (SWC)

Monthly precipitation exceeded 100 mm from March to June, which was higher relative to that of other months (Fig. 1). During the investigation period, precipitation decreased from 60 mm in October to 7.1 mm in December, then increased to 205 mm in June and decreased to 51.0 mm in July, and finally increased to 92.4 mm in September.

SWC displayed similar seasonal dynamics to precipitation, and was relatively higher from March to September except in July (Fig. 2). For a given vegetated area, mean SWC during the study period was higher in the 0–15 cm soil layer than in the 15–40 and 40–70 cm layers. The reed area had higher SWC than the 11-year poplar in the 0–15 cm soil layer, and 11-year poplar had a higher SWC than the 5-year poplar except in December. In the 15–40 cm soil layer, SWC was higher in reed than in 11-year poplar except in August, and was higher in 11-year poplar than in 5-year poplar except in November and February. In the 40–70 cm soil layer, the SWC of reed was higher than that of 11-year poplar except in April and August, and the SWC of 11-year poplar was higher than that of 5-year poplar except in December and February. On the whole, SWC was highest in reed, intermediate in 11-year poplar, and lowest in 5-year poplar. For example, mean SWC in the 0–15 cm soil layer was 32.6, 28.6, and 25.3 % in reed, 11- and 5-year poplar, respectively. Therefore, it was clear that poplar plantations resulted in a lower SWC.

Photosynthetic rate (Pn)

The Pn of the 3 vegetated areas varied during the growing season, with different patterns (Fig. 3). In 11-year poplar, Pn decreased from 16.25 μmol m^{-2} s^{-1} in May to 10.84 μmol m^{-2} s^{-1} in July, but increased to 17.58 μmol m^{-2} s^{-1} in September. In 5-year poplar, Pn decreased from 16.47 μmol m^{-2} s^{-1} in May to 9.98 μmol m^{-2} s^{-1} in July, but increased to 16.59 μmol m^{-2} s^{-1} in August, and decreased to 13.55 μmol m^{-2} s^{-1} in September. In reed, Pn increased from 23.24 μmol m^{-2} s^{-1} in May to 28.34 μmol m^{-2} s^{-1} in July, but decreased to 16.05 μmol m^{-2} s^{-1} in September.

From May through July, Pn was significantly higher in reed than in the two poplar stands, and did not differ between the different-aged poplars. In August, the Pn of 11-year poplar (13.79 μmol m^{-2} s^{-1}) was lower

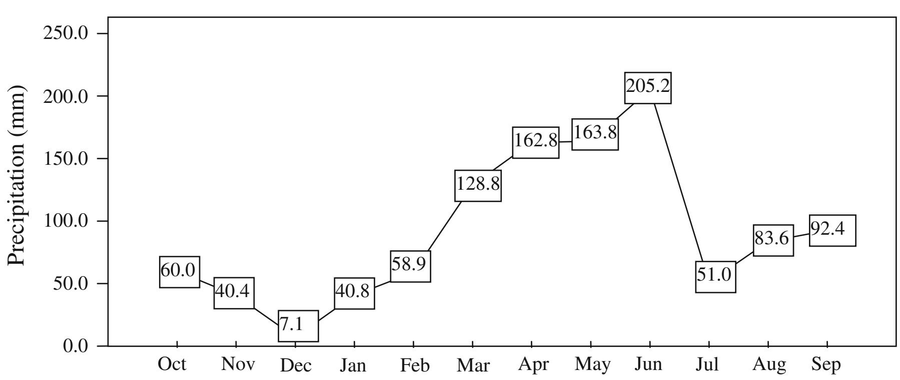

Fig. 1 Monthly precipitation during the study period (October 2011–September 2012)

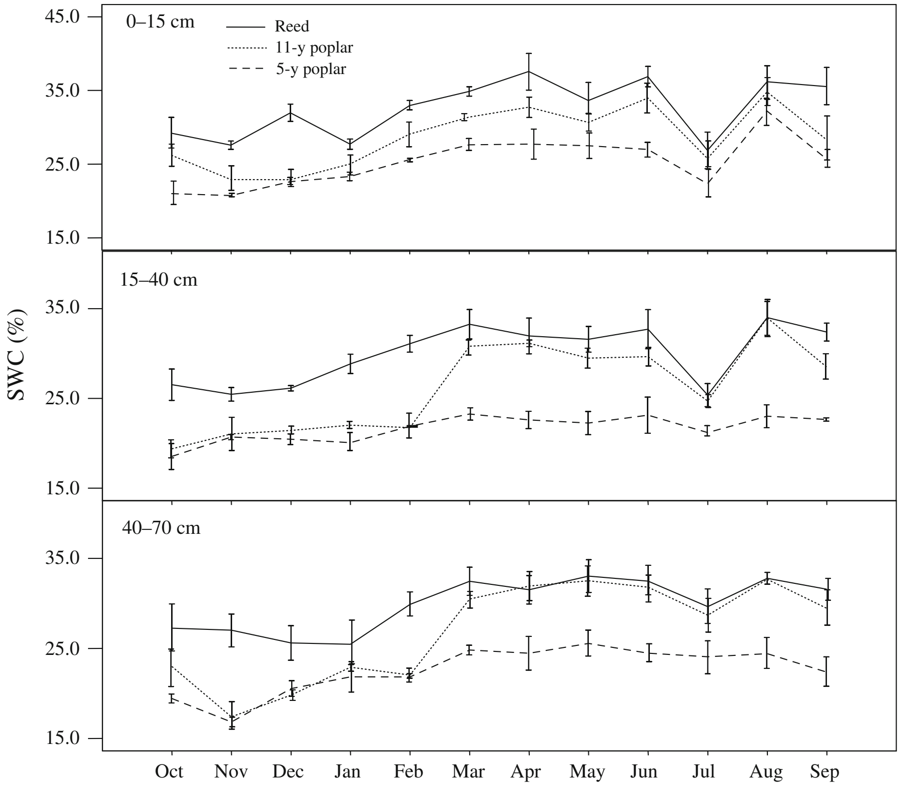

Fig. 2 Soil water content (SWC, mean ± SE, $n = 3$) of the 3 vegetated areas examined during the study period (October 2011–September 2012)

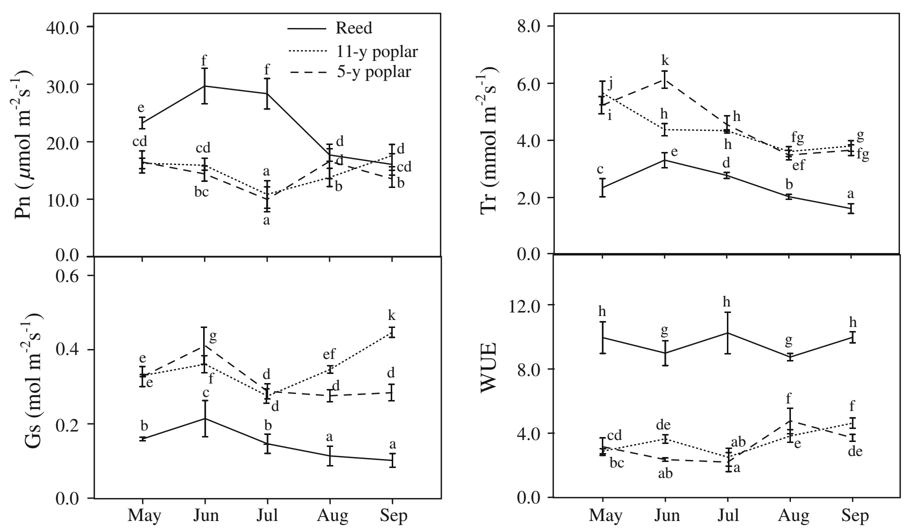

Fig. 3 Photosynthetic rate (Pn), stomatal conductance (Gs), transpiration rate (Tr), water-use efficiency (WUE) (mean ± SE, $n = 6$, 12) of the 3 types of vegetation during the 2012 growing season. Different letters indicate significant differences at $\alpha = 0.05$

than that of 5-year poplar (16.59 μmol m^{-2} s^{-1}) and reed (17.69 μmol m^{-2} s^{-1}). In September, the Pn of 5-year poplar was lower than that of 11-year poplar or reed. On the whole, mean Pn in reed was approximately 1.6 times higher than that of 11- and 5-year poplars, respectively.

Stomatal conductance (Gs) and transpiration rate (Tr)

Over the growing season, the Gs of 5-year poplar and reed increased from May to June, but decreased in September (Fig. 3). However, the Gs of 11-year poplar increased from May to June, but decreased in July, and then increased in September. Gs was significantly higher in the poplars than in reed. Mean Gs in 11- and 5-year poplar was 2.39 and 2.16 times higher than that of reed, respectively. In June, Gs was higher in 5-year than in 11-year poplar, while in August and September, Gs was higher in 11-year than in 5-year poplar.

The Tr of 5-year poplar and reed increased from May to June, but decreased in September (Fig. 3). However, the Tr of 11-year poplar decreased from May to September. Tr was significantly higher in the poplars than in reed. Mean Tr in 11- and 5-year poplar was 1.81 and 1.91 times higher than that of reed, respectively. In May, Tr was higher in 11-year poplar than in 5-year poplar. In June, Tr was higher in 5-year poplar than in 11-year poplar. From July through September, Tr did not differ between the two poplar stands.

Water-use efficiency (WUE) of individual leaves

WUE differed significantly among months and vegetation types (Fig. 3). In 11-year poplar, WUE, in order from lowest to highest, was July $\leq$ May $<$ Jun $\leq$ August $<$ September. In 5-year poplar, WUE from lowest to highest was July $\leq$ June $<$ May $\leq$ September $<$ August. In reed, WUE was higher in May, July, and September than in June and August.

During the growing season, mean WUE in reed was 2.7 and 3.0 times higher than that of 11- and 5-year poplars ($P < 0.001$), respectively. In June and September, WUE was higher in 11-year (3.63 and 4.62) than in 5-year poplar (2.35 and 3.71). In August, WUE was higher in 5-year (4.76) than in 11-year poplar (3.82). In May and July, WUE did not differ between the two poplar stands.

Relationships among Pn, Gs, and Tr

Correlation analyses showed that Gs was positively correlated with Pn and Tr in the 3 vegetation types ($P < 0.001$). Pn was also positively correlated with Tr ($P < 0.01$). Relationships between Pn and Gs were linear in 11-year poplar ($P < 0.001$) and were described by power functions in 5-year poplar and reed ($P < 0.001$, Fig. 4). Relationships between Tr and Gs were described by power functions in 11- and 5-year poplar ($P < 0.001$), and were linear in reed ($P < 0.001$). The relationships between Tr and Pn fitted a cubic function in 11-year poplar ($P < 0.01$), a quadratic function in 5-year poplar ($P < 0.05$), and a power function in reed ($P < 0.001$). Therefore, there was a stronger relationship among Pn, Tr, and Gs in reed than in the poplars.

Discussion

Soil water conditions reflect a balance between water influx and efflux. Rainfall is the most direct source of soil water, particularly for the ground surface (Grassini et al. 2010). In wetlands, soil water is also affected by flooding due to the high groundwater level (Xie et al. 2011). This may be the main explanation for similar seasonal changes in SWC and precipitation from January to August, and for the relatively higher SWC during the flood period (April to August). SWC was significantly lower in poplar stands than in reed, which is consistent with our first hypothesis. Previous studies have shown that poplar plantations can reduce the water table and desiccate soil in arid and semiarid areas (Chang et al. 2006; Wilske et al. 2009). Our study clearly showed that poplar plantations also reduced soil water content in wetlands.

Plant transpiration is the primary mechanism by which SWC is affected by the efflux of water from soil (Huang et al. 2011). Transpiration is positively correlated with Tr and leaf area index (Granier et al. 2000). In this study, Tr was higher in poplars than in reeds. Leaf area index is normally higher in trees than in herbaceous plants due to leaf stratification in trees (Wilske et al. 2009). Therefore, a higher Tr and a higher leaf area index might lead to the lower SWC in poplars compared to reed. Additionally, the Tr of poplars in Dongting Lake (4.49 mmol m^{-2} s^{-1}) was higher than that in other regions, such as 2.93 in 40 % field capacity reported in previous study (Liang et al. 2006). This higher Tr was largely due to the sufficient water supply for plant physiological requirements in wetlands. The higher Tr in poplar compared to reed is ascribed to the higher Gs in poplar due to the regulating role that leaf stomata play in water loss

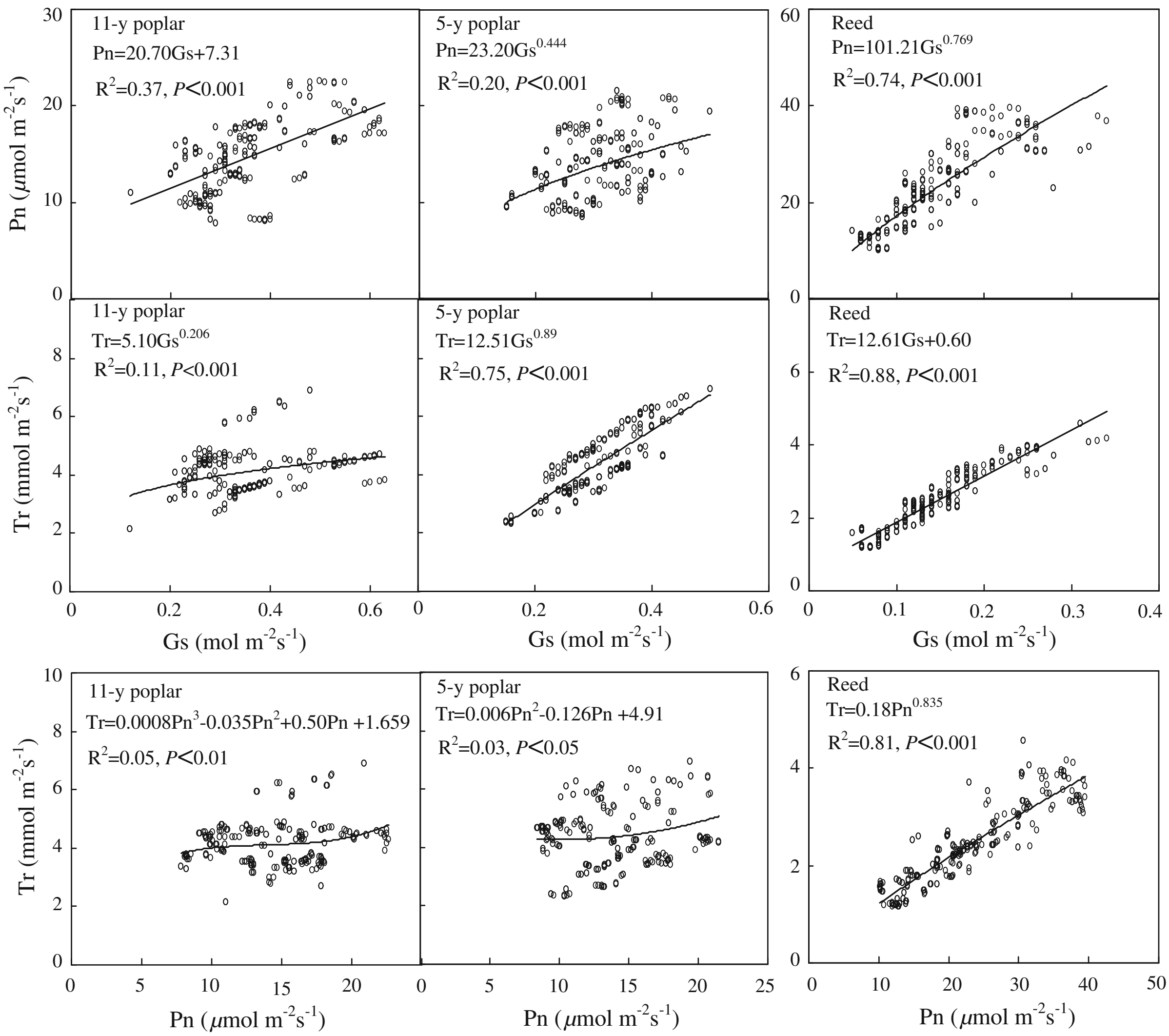

Fig. 4 Relationships among photosynthetic rate (Pn), stomatal conductance (Gs), and transpiration rate (Tr) in the 3 types of vegetation

(Huang et al. 2011), as supported by the positive relationship between Gs and Tr observed here and in previous studies (Chen et al. 2011). In this study, the Tr and Gs of the 3 vegetated areas did not exhibit seasonal changes similar to SWC, which is consistent with a majority of studies that have found little or no correlation between SWC and Tr (Fisher et al. 2008; Wallace and McJannet 2010). However, this finding differs from the dynamics observed in *Acacia mangium* stands and in a tropical mixed dipterocarp forest, where Gs was higher in wet than in dry conditions (Kumagai et al. 2004). This may be due to the high soil water availability in wetlands, or to the substantial rooting depths that are necessary to provide an adequate water supply during drier periods (Fisher et al. 2008). Therefore, the higher Tr and Gs in poplar compared to reed are the key physiological mechanisms underlying the reduction in soil water by poplar, consistent with our second hypothesis. However, the lower Pn observed in poplar compared to reed is contrary to the second hypothesis, but might be explained by the high productivity of reed (Heinsoo et al. 2011).

The higher SWC in 11-year poplars than in 5-year poplars suggests that transpiration may be lower in older poplar plantations. Two factors may contribute to this result. First, older stands might have a lower leaf area index (Almeida et al. 2007), which corresponds to lower stand transpiration (Delzon and Loustau 2005). Second, low stand density can result in low stand transpiration (Moreno and Cubera 2008). Therefore, both stand age and density may be important in regulating the reduction in soil water in poplar plantations.

The higher Pn in reed compared to poplar may indicate that reed has a better light-intercepting ability and a higher rate of dry matter accumulation than poplar. High productivity is dependent on high resource availability, such as that of water, solar radiation, and nutrients (Almeida et al. 2007; Fortier et al. 2010). The WUE of poplars in this study (3.36) was lower than that in other regions, such as 6.11 in 55 % field capacity reported in other studies, indicating that the consumed water producing dry matter per unit increased from drought condition to water saturation condition (Liang et al. 2006). The lower WUE of poplar compared to reed suggests that poplar plantations require larger water supplies to satisfy their physiological requirements. Therefore, the high soil water loss and low WUE of poplar plantations could cause the transformation of wetlands into dry land, which, in turn, would influence community composition and ecosystem function (Engelbrecht et al. 2007; Gaitán et al. 2011). An example of such an effect was observed in the Southern Dongting Lake wetlands, where a poplar plantation led to a significantly lower diversity of migratory birds (Deng et al. 2008). As a wetland of international importance, some measures, such as the rational planning of poplar planting and wetland restoration, should be applied to protect the habitats of migratory birds in the Dongting Lake region.

In conclusion, our study clearly showed that poplar plantations had negative effects on soil water condition, even in the water-saturated wetlands, via high rates of transpiration and stomatal conductance. The greater soil water loss and lower water-use efficiency of poplars causes large amounts of water to be lost from wetlands, resulting in the desiccation of areas in which poplar plantations are established.

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