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Vertical distribution characteristics of photosynthetic parameters for *Phragmites australis* in Liaohe River Delta wetland, China

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ABSTRACT

A field experiment was undertaken to measure diurnal variation in photosynthetic and light-response parameters of leaves of *Phragmites australis* growing in the Liaohe River Delta wetland, China. Four developmental stages (leaf-expansion, jointing, heading, and mature stages) and three (upper, middle, and lower layers) or five vertical layers (top, upper, middle, lower, and bottom layers) were delimited. Diurnal variations in net photosynthetic rate, stomatal conductance, and transpiration rate showed single-peak or double-peak curves that were lower in the morning and evening and higher at noon. The diurnal variation in intercellular CO₂ concentration showed the opposite pattern, with higher values in the morning and evening and lower values at noon. Midday depression was observed under strong light, in the top, upper, and middle layers but not under weak light or in the lower and bottom layers. The net photosynthetic rate, stomatal conductance, and transpiration rate were higher in the upper layer, and gradually decreased in value and in diurnal variability below the middle layer with increasing proximity to the plant base. Leaves showed a strong photosynthetic ability at the leaf-expansion stage, with the maximum net photosynthetic rate in the middle layer and the minimum net photosynthetic rate in the lower layer. Photosynthetic ability increased at the jointing and heading stages. The maximum net photosynthetic rate was in the upper or middle layers and the minimum in the bottom layer. Photosynthetic ability was weak at the mature stage. The light compensation point in leaves was 27.1–38.2, 24.6–29.5, 27.7–72.6, and 15.4–31.0 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at the leaf-expansion, jointing, heading, and mature stages, respectively. The developmental stages of *P. australis* leaves were ranked, from highest ability to use weak light to lowest, as follows: mature stage > jointing stage > leaf-expansion stage > heading stage.

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Wetland; photosynthetic parameters; light response; simulation; *Phragmites australis*

Introduction

Phragmites australis is a large perennial grass that is one of the most widespread plants in wetlands in temperate and tropical regions worldwide (Tarun and Narine 2004; Brix et al. 2014; Nada et al. 2015). This species shows high productivity under diverse climatic conditions (Srivastava et al. 2014). Its typical habitats are fresh or brackish water in swamps, riversides, and lakesides (Gorai et al. 2011). Given its high photosynthetic rate and transpiration rate, *P. australis* plays an important role in water–carbon exchange between wetland vegetation and the atmosphere (Zhou et al. 2006). Reed wetlands are characterized by their broad adaptability and strong resistance to abiotic stresses,

and are important for the maintenance of water balance, regulation of climatic and environmental conditions, and protection of biodiversity (Tian et al. 2016). The Liaohe River Delta in Northeastern China covers an area of 756 km² and is believed to be the largest reed wetland in Asia (Chen et al. 2017). *Phragmites australis* is widely distributed in North China (Liang et al. 2016) and is the dominant plant species in the Liaohe Delta. *Phragmites australis* is highly productive and its photosynthetic ability is highly sensitive to environmental factors. Thus, changes in photosynthetic activity directly affect the ecological structure and function of the wetland ecosystem (Qi et al. 2016).

Photosynthesis is a complex biochemical process that converts light energy into chemical energy and organic compounds. Thus, it is the most important metabolic process in plants (Wang et al. 2017). Leaf photosynthetic capacity is the basis and the direct driving force for the formation of plant yield (Huang et al. 2011). Previous studies on photosynthesis in *P. australis* have compared photosynthetic parameters among different habitats (Ding et al. 2015; Nada et al. 2015), evaluated the adaptability of photosynthetic physiological parameters under stress (Chen et al. 2005; Caudle and Maricle 2015), monitored the photosynthetic responses to environmental factors (Madrid et al. 2012; Herrera 2013; Han et al. 2014) and assessed its photosynthetic ability under various light conditions (Ye and Yu 2008; Groenendijk et al. 2011).

Most of the previous studies on the photosynthetic mechanisms involved in adaptation of *P. australis* to different stress conditions have been conducted on leaves at a single vertical position on the plant. For example, the photosynthetic physiological indices of *P. australis* and other plants were compared by measuring the third or fourth leaf from the top of the plant (Zhang et al. 2014). The effects of flooding, salt, or drought on photosynthetic physiological indices of *P. australis* were determined for the second or third leaves from the top of the plant (Xie et al. 2009a; Deng et al. 2012; Liu et al. 2014). The photosynthetic characteristics of *P. australis* were measured for the second or third leaf from the top of the plant when studying the effects of different freshwater-saline environments or soil types (Xie et al. 2009b; Xia et al. 2014; Ding et al. 2015). In another study, stomatal conductance of *P. australis* was measured in the top, middle, and base leaves of the plant (Zhou et al. 2006).

Some studies have reported that the leaves in the middle layer of the plant have the best photosynthetic function because their cell and tissue structures are fully developed, while photosynthesis is weaker in the top leaves (Wang and Hu. 1986, Han et al. 2012). Photosynthetic pigment contents were shown to be higher in middle leaves of *P. australis* than in the uppermost (still developing) and lowest leaves (already senescent), which was determined by nitrogen availability (Lippert et al. 2001). However, other reports have drawn different conclusions about the vertical distribution of photosynthetic capacity in *P. australis*. Hirtreiter and Potts (2012) measured the vertical gradient of photosynthetically active radiation (PAR) at 30-cm increments from the top of the *P. australis* canopy to the base, and found that, because of the horizontally oriented leaves in *P. australis*, light was attenuated more rapidly than in *Typha latifolia*. Hirtreiter and Potts (2012) expected that nitrogen would be concentrated in the upper-most leaves where light is most available, and found that nitrogen content and photosynthetic capacity were consistent throughout the canopy of *P. australis*.

To clarify the vertical distribution of the photosynthetic capacity of *P. australis* in the Liaohe Delta wetland, we conducted field experiments to measure diurnal variation in photosynthetic parameters and light-response processes of *P. australis* leaves at four developmental stages (leaf-expansion, jointing, heading, and mature stages) and three (upper, middle, and lower layer) and five vertical layers (top, upper, middle, lower, and bottom layer). We analyzed the diurnal dynamics of photosynthetic parameters (net photosynthetic rate, leaf conductance, transpiration rate, and intercellular CO₂ concentration), and simulated the light-response curve to calculate the maximum net photosynthetic rate, quantum efficiency, dark respiration rate, and light compensation point. These analyses were conducted for *P. australis* leaves in each developmental stage and vertical layer. The objective of this research was to reveal the physiological and ecological characteristics and light-response characteristics of *P. australis* in coastal wetlands, and to increase our understanding of the photosynthetic mechanisms of *P. australis*.

Methods

Study site

The study was conducted at the Panjin Wetland Ecosystem Research Station ($40^{\circ}56'N$, $121^{\circ}57'E$), which belongs to the Institute of Atmospheric Environment, China Meteorological Administration, Shenyang (Figure 1). The station is located in the natural wetland reserve of the Liaohe Delta ($40^{\circ}41' - 41^{\circ}27'N$, $121^{\circ}30' - 122^{\circ}41'E$), China. The delta is situated in the warm temperate zone, and has a continental semi-humid monsoon climate with four distinct seasons. The annual mean temperature is $8.6^{\circ}C$, and the air temperature is higher in summer (June to August) and lower in winter (December to February) (Figure 2). The mean annual precipitation is 631 mm, which is concentrated from July to September (Zhou et al. 2009; Jia et al. 2016). The main water source of reed wetlands in the study area is river water from the Daling and Shuangtaizi Rivers (Wang et al. 2016). The mean growing season and flood time of *P. australis* is from April to October, and the annual mean water salt content in the growing season is 0.23 g/L (Figure 3). The *P. australis* reedbeds in the

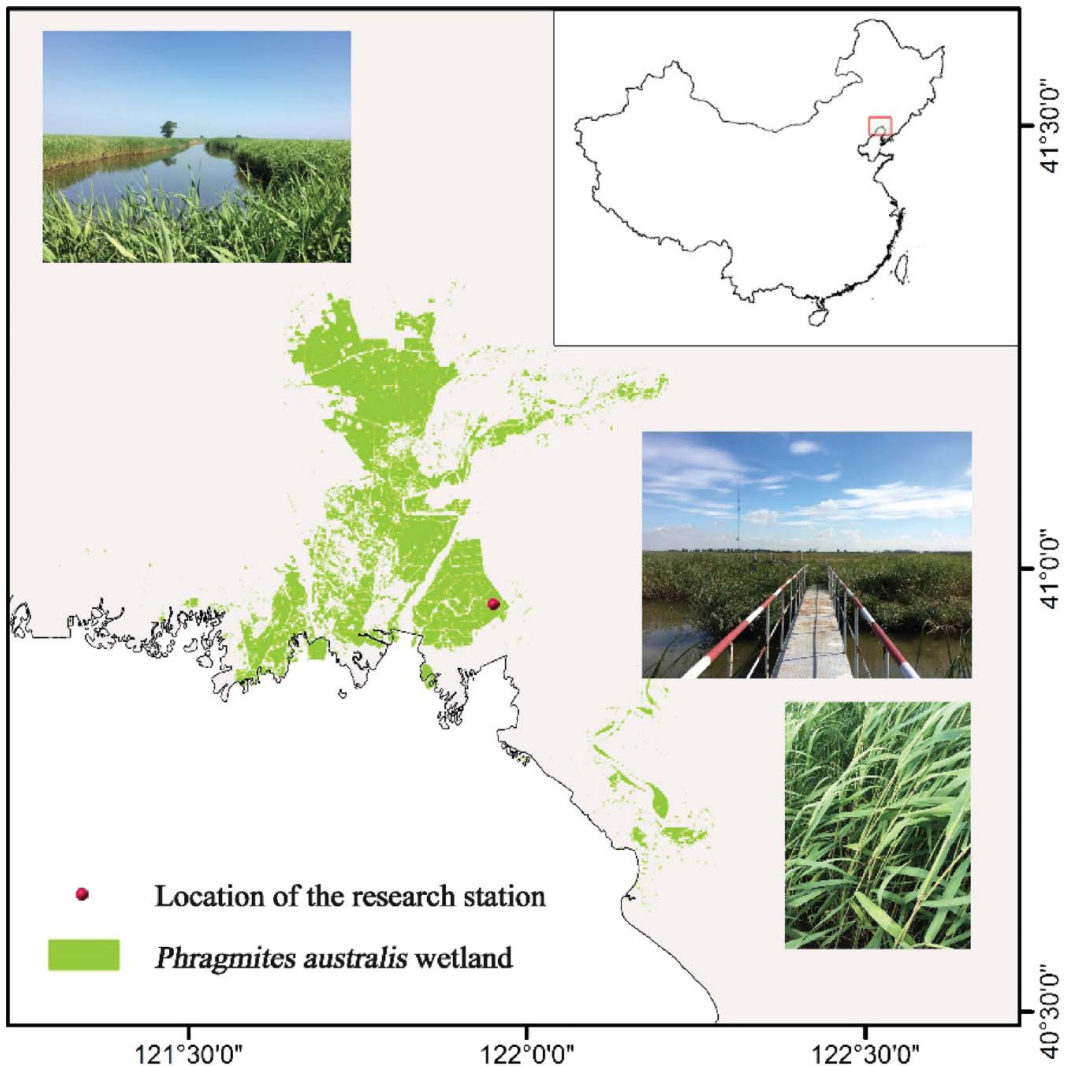


Figure 1. Locations of the study area and experimental sites in the Liaohe River Delta wetland, China.

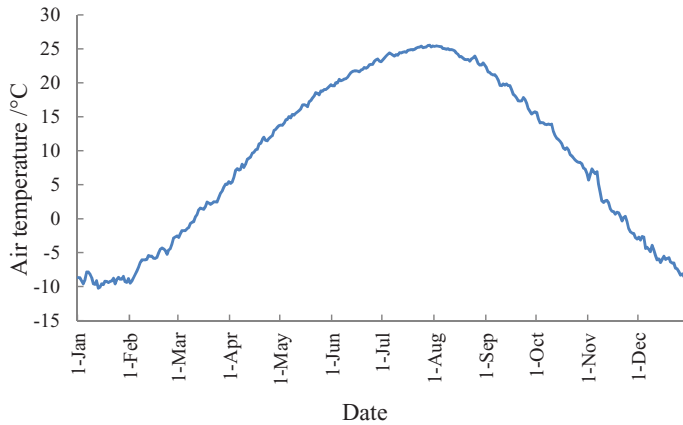


Figure 2. Seasonal changes in daily mean temperature from 1961 to 2010 at the research station.

research station were well preserved and were representative of the vegetation cover in the Liaohe Delta wetland.

Measurement of photosynthetic parameters

The growing season of *P. australis* was divided into five stages: seedling stage (21 April–10 May), leaf-expansion stage (11 May–10 June), jointing stage (11 June–31 July), heading stage (1 August–20 September), and mature stage (21 September–31 October). Experimental measurements were conducted on sunny days during the growing season from May to September in 2015 and 2016. The diurnal dynamics of photosynthetic parameters and light-response curves of *P. australis* leaves were measured at the leaf-expansion stage, jointing stage, heading stage and mature stage. The diurnal dynamics of photosynthesis were monitored from 08:00 to 18:00 at 1–2 h intervals; the light-response curve was observed from 09:00 to 15:00. For each individual plant three or five vertical layers were delimited, measured from the top to the base of the stem (i.e. at ground or water-surface level), with a height of 60 cm per layer (Figure 4). Plants at the leaf-expansion stage were delimited into upper (A1), middle (A2) and lower (A3) layers (height ranges 120–180, 60–120, and 0–60 cm, respectively). Plants at the jointing, heading and mature stages were delimited into top (A1), upper (A2), middle (A3), lower (A4) and bottom (A5) layers (height ranges 240–300, 180–240, 120–180,

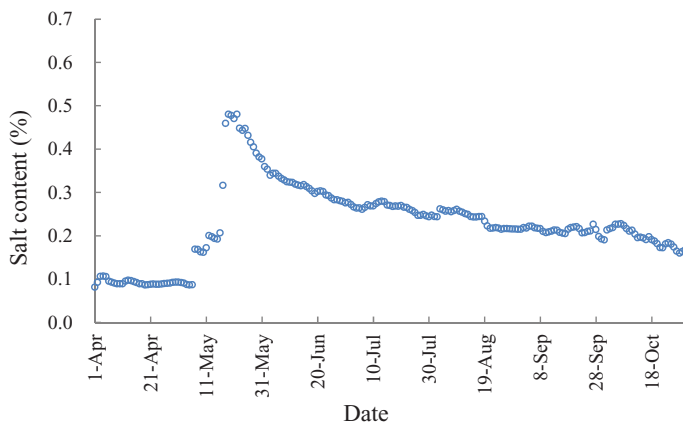


Figure 3. Annual mean water salt content during the growing season from 2013 to 2015.

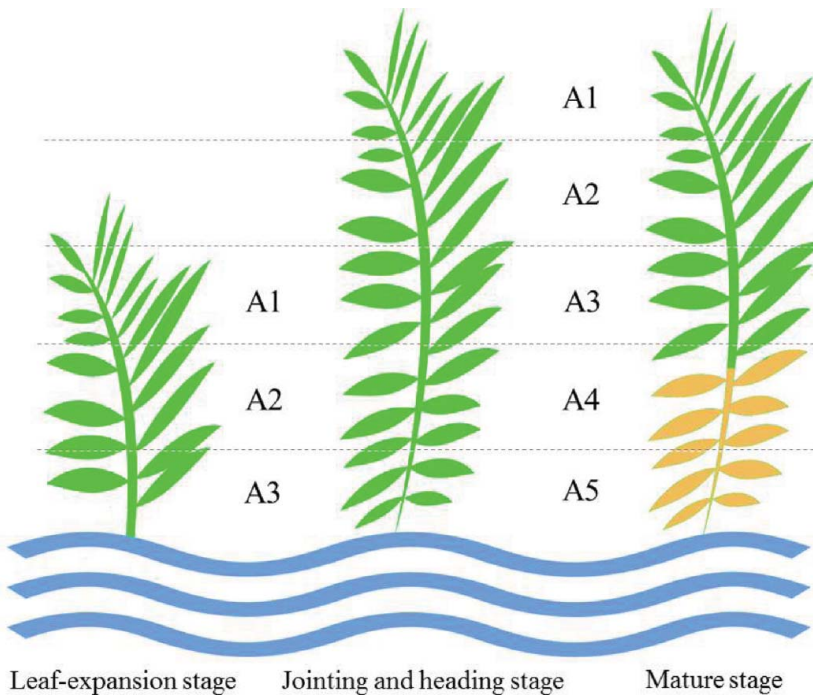


Figure 4. Delimitation of vertical layers of *Phragmites australis* plants at the leaf-expansion, jointing, heading, and mature stages of development.

60–120, and 0–60 cm, respectively). At the mature stage, the leaves in the lowermost layers of the plant were yellow and senescent, so only the top (A1), upper (A2), and middle (A3) layers were observed (Figure 4). The average height of *P. australis* at the leaf-expansion, jointing, heading, and mature stages was 1.8, 2.7, 2.8, and 2.9 m, respectively.

Three plants representative of the average growth of the *P. australis* community were selected to measure photosynthetic parameters. Net photosynthetic rate (P_n), stomatal conductance (G_s), intercellular CO_2 concentration (C_i), and transpiration rate (T_p) were measured simultaneously on leaves in each layer using a portable photosynthesis system (LI-COR 6400, Lincoln, NE, USA). We also measured PAR, atmospheric temperature (T_a), relative humidity (RH), saturated vapor pressure difference (VPD), and air CO_2 concentration. The light-response curve measurements were recorded at 14 levels of light intensity (2000, 1800, 1600, 1400, 1200, 1000, 800, 600, 400, 200, 100, 50, 20, and 0 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) in order from the highest to the lowest by adjusting the LI-64002B instrument. The CO_2 concentration was maintained at 380 $\mu\text{mol}\cdot\text{mol}^{-1}$.

Data analyses

The empirical formula to describe the light-response curve included a non-rectangular hyperbola model, a rectangular hyperbola model, and a quadratic model. Simulation of the light-response curve of the *P. australis* leaf is well represented by a non-rectangular hyperbola model (Zhou et al. 2006), and so we used this model to simulate the light-response curve of *P. australis* in the Liaohe Delta wetland. The coefficients of determination (R^2) of the simulated results were all >0.9 , indicative of high precision. Thus, the equations could be used to estimate the maximum net photosynthetic rate, quantum efficiency, dark respiration rate, light compensation point and other photosynthetic parameters.

The following equation is the non-rectangular hyperbola model (Lessmann et al. 2001):

$$P_n = \frac{\alpha I + P_{\max} - \sqrt{(\alpha I + P_{\max})^2 - 4kIP_{\max}}}{2k} - R_d, \tag{1}$$

where P_n is net photosynthetic rate, α is quantum efficiency, I is PAR, P_{\max} is maximum net photosynthetic rate, k is the angle of the non-rectangular hyperbola, the value range of k is from 0 to 1, and R_d is the dark respiration rate.

The light compensation point (I_c) was calculated as follows (Xie and Yang 2009b):

$$I_c = (R_d P_{\max} - k R_d^2) / [\alpha (P_{\max} - R_d)], \tag{2}$$

The data used were the averages of three repetitions of the three individuals sampled. The non-rectangular hyperbola model of the light-response curve and their parameters were estimated with SPSS 12 software (SPSS, Inc., Chicago, IL, USA).

Results

Diurnal variation in photosynthetically active radiation

The diurnal variation in PAR of *P. australis* leaves at four developmental stages and three or five vertical layers showed a vertical distribution, with higher PAR in upper layers and gradually decreasing PAR with increasing proximity to the plant base (Figure 5).

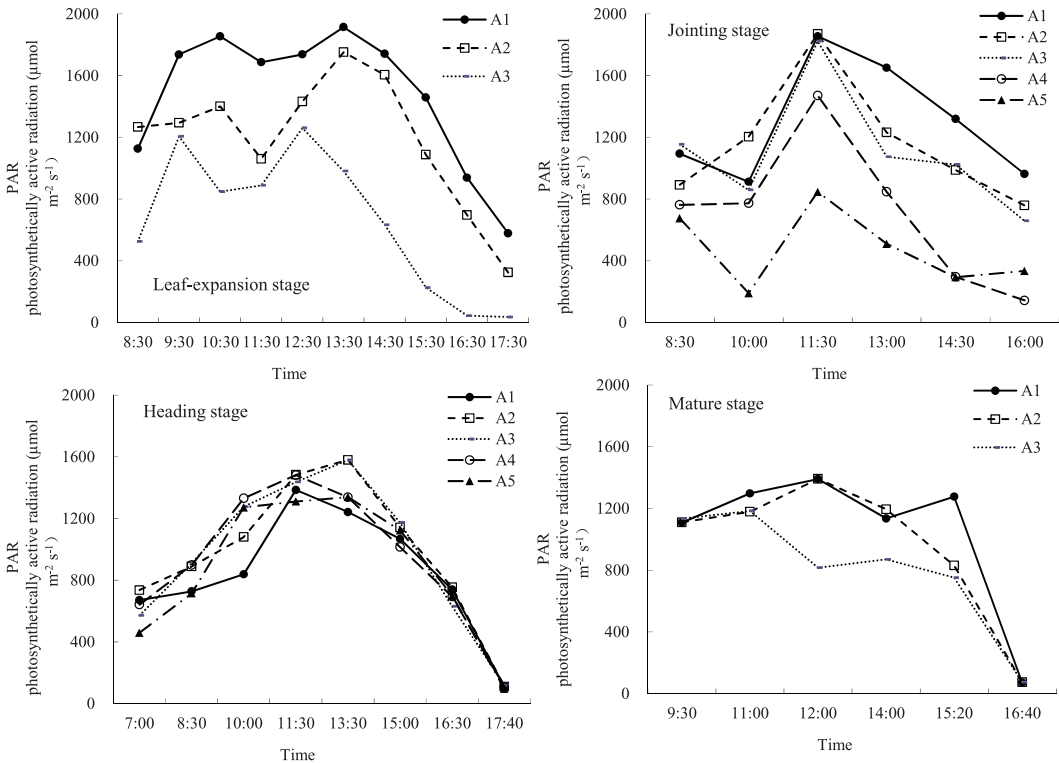


Figure 5. Diurnal variation in photosynthetically active radiation of *Phragmites australis* at four developmental stages and three or five vertical layers.

Diurnal variation in net photosynthesis rate

During the leaf-expansion stage, the diurnal variation in P_n of the A1 layer leaves showed a double-peak curve. The values of P_n were lower in the morning and evening and higher at noon. The peaks were at 11:30 and 13:30 (23.9 and 24.6 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively), and midday depression occurred at about 12:30 (Figure 6). The diurnal variation in P_n of the A2 and A3 layers showed single-peak curves, with the peaks at 12:30 (23.5 and 14.8 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively). The average daily P_n of the A1 layer was 18.5 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, higher than that of the A2 and A3 layers by 1.5 and 8.9 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively (Table 1).

At the jointing stage, the diurnal variation in P_n of the A1 layer leaves showed a double-peak curve. The two peaks were at 11:30 and 14:30 (15.6 and 15.2 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively) and midday depression occurred at around 13:00. Most of the A1 layer leaves were newly developed, and so the P_n was sometimes lower in the A1 layer than in the A2 layer. In the layers below A2 the P_n showed a downward trend with a single-peak curve (Figure 6). The average daily P_n of the A2 layer was 14.9 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, higher than that of the A1, A3, A4, and A5 layers by 1.3, 4.3, 8.1, and 10.7 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ respectively. The P_n decreased with increasing proximity to the plant base (Table 1).

At the heading stage, the diurnal variation in P_n of the A1, A2 and A3 layers showed single-peak curves, with peaks at 13:30–15:00 (15.6, 14.4 and 14.0 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively). The P_n values were smaller in the A4 and A5 layers, in which the diurnal variation was smooth with no distinct peak. The sunlight intensity was slightly lower than that on the observation days for plants at the leaf-expansion stage and jointing stage, consequently no midday depression was observed in the

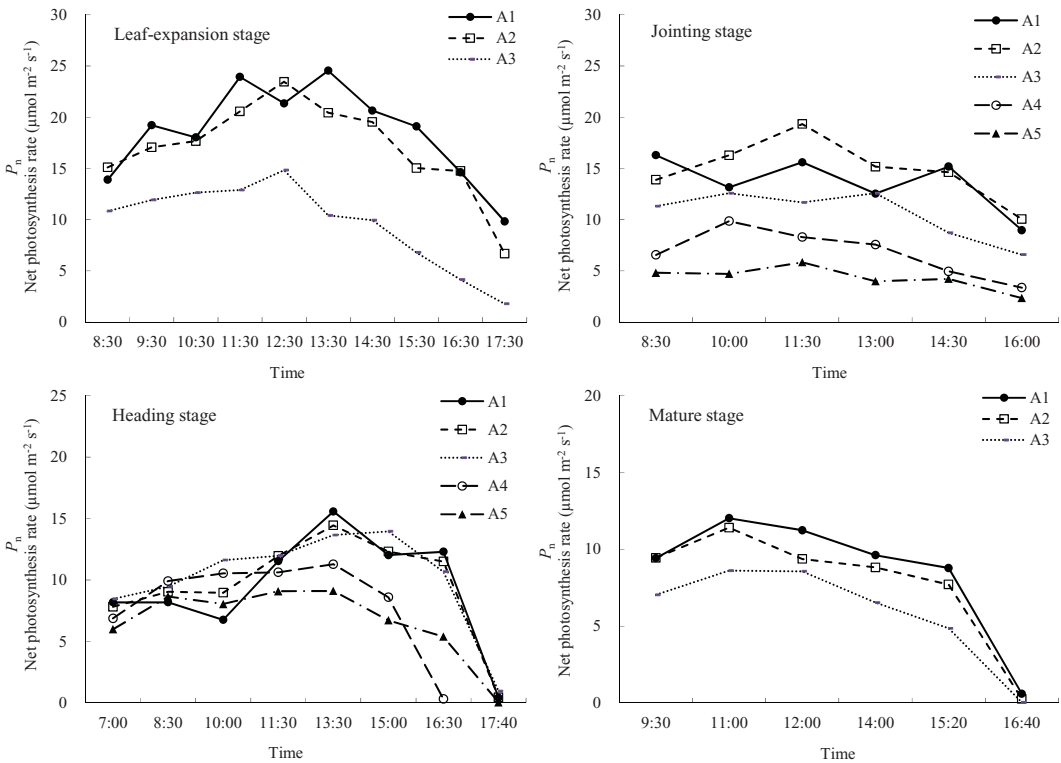


Figure 6. Diurnal variation in net photosynthetic rate of *Phragmites australis* at four developmental stages and three or five vertical layers.

Measurement dates: 2015-5-30 (leaf-expansion stage), 2015-7-3 (jointing stage), 2016-8-3 (heading stage), 2016-9-29 (mature stage). These dates are the same for Figures 7–9.

Table 1. Daily mean values for photosynthetic parameters of *Phragmites australis* leaves at four developmental stages and five vertical layers.

Period	Layer	Photosynthesis parameters			
		$A_n/(\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1})$	$g_s/(\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1})$	$C_i/(\mu\text{mol}\cdot\text{mol}^{-1})$	$T_r/(\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1})$
Leaf-expansion stage	A1	18.5	0.276	227.7	5.5
	A2	17.0	0.263	228.6	5.3
	A3	9.6	0.157	243.5	3.4
Jointing stage	A1	13.6	0.280	237.1	4.8
	A2	14.9	0.322	238.9	5.3
	A3	10.6	0.232	246.1	4.3
	A4	6.8	0.149	253.5	3.1
	A5	4.2	0.106	259.5	2.6
Heading stage	A1	9.4	0.232	290.6	4.7
	A2	9.6	0.249	293.1	5.0
	A3	10.1	0.268	292.4	5.3
	A4	8.5	0.263	301.7	5.2
	A5	6.6	0.214	308.2	4.7
Mature stage	A1	8.6	0.210	301.4	3.7
	A2	7.8	0.232	315.9	4.1
	A3	5.9	0.191	323.5	3.6

upper leaves (Figure 6). The average daily P_n in the A3 layer was $10.1 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, higher than that of the A1, A3, A4 and A5 layers by 0.7, 0.5, 1.6 and $3.5 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively (Table 1).

At the mature stage, the diurnal variation in P_n of the A1, A2 and A3 layers was smooth (Figure 6). The average daily P_n in the A1 layer was $8.6 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, higher than that of the A2 and A3 layers by 0.8 and $2.7 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Table 1).

The diurnal variation in P_n of *P. australis* leaves at four developmental stages and five vertical layers showed single-peak or double-peak curves, with lower values in the morning and evening and higher values at noon. The values of P_n were higher in the upper and middle layers, and lower below the middle layer. The value of P_n below the middle layer decreased gradually with increasing proximity to the plant base, and P_n tended to become more stable as its value decreased. The highest average P_n at the four developmental stages was in the upper or middle layers, and was associated with midday depression. The minimum average P_n was in the lower layers where midday depression did not occur.

Diurnal variation in stomatal conductance

At the leaf-expansion stage, the diurnal variation in G_s of the A1 layer leaves showed a double-peak curve, with lower values in the morning and evening and higher values at noon. The two peaks occurred at 11:30 and 13:30 (0.39 and $0.37 \text{ mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively), and midday depression occurred at 12:30 (Figure 7). The diurnal variation in G_s of leaves in the A2 and A3 layers showed single-peak curves, with peaks at 12:30, (0.39 and $0.29 \text{ mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively). The average daily G_s in the A1 layer was $0.276 \text{ mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, higher than that of the A2 and A3 layers by 0.013 and $0.119 \text{ mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively (Table 1).

At the jointing stage, the diurnal variation in G_s of the A2 layer leaves showed a single-peak curve. The peak was at 11:30 ($0.41 \text{ mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). The G_s tended to decrease below the A2 layer, with the lowest value in the A5 layer (Figure 7). The average daily G_s in the A2 layer was $0.322 \text{ mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, higher than that of the A1, A3, A4 and A5 layers by 0.042, 0.09, 0.173, and $0.216 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively (Table 1).

At the heading stage, the diurnal variation in G_s of the A3 and A4 layer leaves showed double-peak curves, with peaks at 11:30 and 15:00. Leaves of the other layers showed single-peak curves. The values of G_s in the A2, A3 and A4 layers were similar. The highest G_s value was in the A1 layer and the lowest was in the A5 layer (Figure 7). The average daily G_s in the A3 layer was

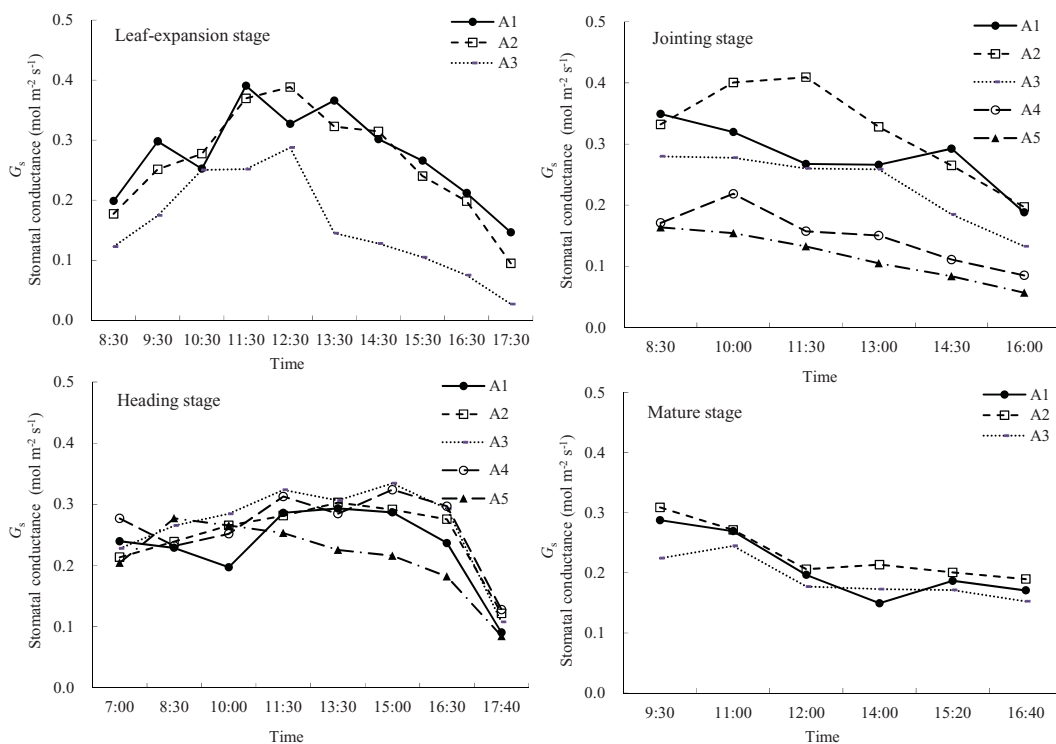


Figure 7. Diurnal variation in stomatal conductance of *Phragmites australis* at four developmental stages and three or five vertical layers.

0.268 mol·m⁻²·s⁻¹, higher than that of the A1, A3, A4 and A5 layers by 0.036, 0.019, 0.005 and 0.054 mol·m⁻²·s⁻¹, respectively (Table 1).

At the mature stage, the diurnal variation in G_s affected by light intensity was higher in the morning and decreased after 12:00. The values of G_s in the A1, A2 and A3 layers were similar (Figure 7). The average daily G_s in the A2 layer was 0.232 mol·m⁻²·s⁻¹, higher than that of the A1 and A3 layers by 0.022 and 0.019 mol·m⁻²·s⁻¹, respectively (Table 1).

The diurnal variation in G_s of *P. australis* leaves at the four developmental stages and five vertical layers showed a similar trend to P_n , in that values were highest in the upper and middle layers, and lowest below the middle layer. The value of G_s below the middle layer decreased gradually with increasing proximity to the plant base, and diurnal variation in G_s tended to decrease as its value decreased. The maximum average G_s values at the four developmental stages were in the upper or middle layers, and the minimum values were in the lower layers.

Diurnal variation in intercellular CO₂ concentration

At the leaf-expansion stage, the diurnal variation in C_i of the A1 layer leaves tended to be higher in the morning and evening and lower at noon, opposite to the patterns shown by P_n and G_s . The daily variation in C_i of the A2 layer leaves was relatively gentle, with multiple peaks and an increasing trend. The daily variation in C_i of the A3 layer leaves showed a double-peak curve, with the peaks at 10:30 and 16:30, and the lowest values at 8:30 and 14:30 (Figure 8). The average daily C_i in the A3 layer was 243.5 mmol·m⁻²·s⁻¹, higher than that of the A1 and A2 layers by 15.8 and 14.9 mmol·m⁻²·s⁻¹, respectively (Table 1).

At the jointing and heading stages, the diurnal variation in C_i of the A1, A2, A3, A4 and A5 layer leaves all showed ‘U’-shaped curves. Values tended to be higher in the morning and evening and

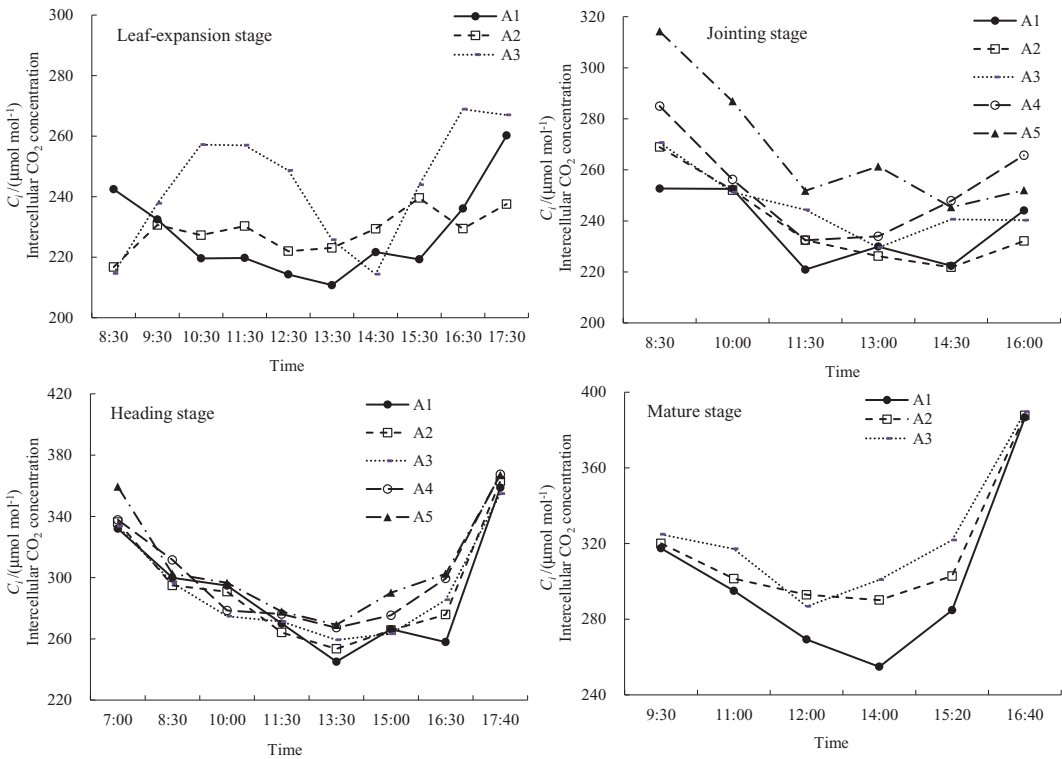


Figure 8. Diurnal variation in intercellular CO_2 concentration of *Phragmites australis* at four developmental stages and three or five vertical layers.

lower at noon, opposite to the pattern observed for P_n (Figure 8). The C_i was highest in the A5 layer, whereas the C_i values in the A1, A2, A3 and A4 layers were similar. At the jointing stage, the average C_i in the A5 layer was $259.5 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, higher than that of the A1, A2, A3 and A4 layers by 22.4, 20.6, 13.4 and 6 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively. At the heading stage, the average C_i in the A5 layer was $308.2 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, higher than that of the A1, A2, A3 and A4 layers by 17.6, 15.1, 15.8, and 6.5 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively (Table 1).

At the mature stage, the C_i of the A1, A2 and A3 layers was higher in the morning and evening and lower at noon with 'U'-shaped curves. The C_i was highest in the A3 layer, and lowest in the A1 layer (Figure 8). The average G_s in the A3 layer was $323.5 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, higher than that of the A1 and A2 layers by 22.1 and 7.6 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively (Table 1).

The diurnal variation in C_i of *P. australis* leaves at the four developmental stages and five vertical layers showed 'U'-shaped curves. The values were higher in the morning and evening and lower at noon, opposite to the pattern observed for A_n . The C_i decreased with increasing proximity to the plant base.

Diurnal variation in transpiration rate

The transpiration rate reflects the ability of a plant to adjust water loss and adapt to a specific environment (Zhang et al. 2011). The diurnal variation in T_r of *P. australis* leaves at the four developmental stages and five vertical layers showed single-peak or double-peak curves, with lower values in the morning and evening and higher values at noon (Figure 9). The maximum average T_r was usually in the upper or middle layers, with values of 5.5, 5.3, 5.3 and 4.1 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in the leaf-

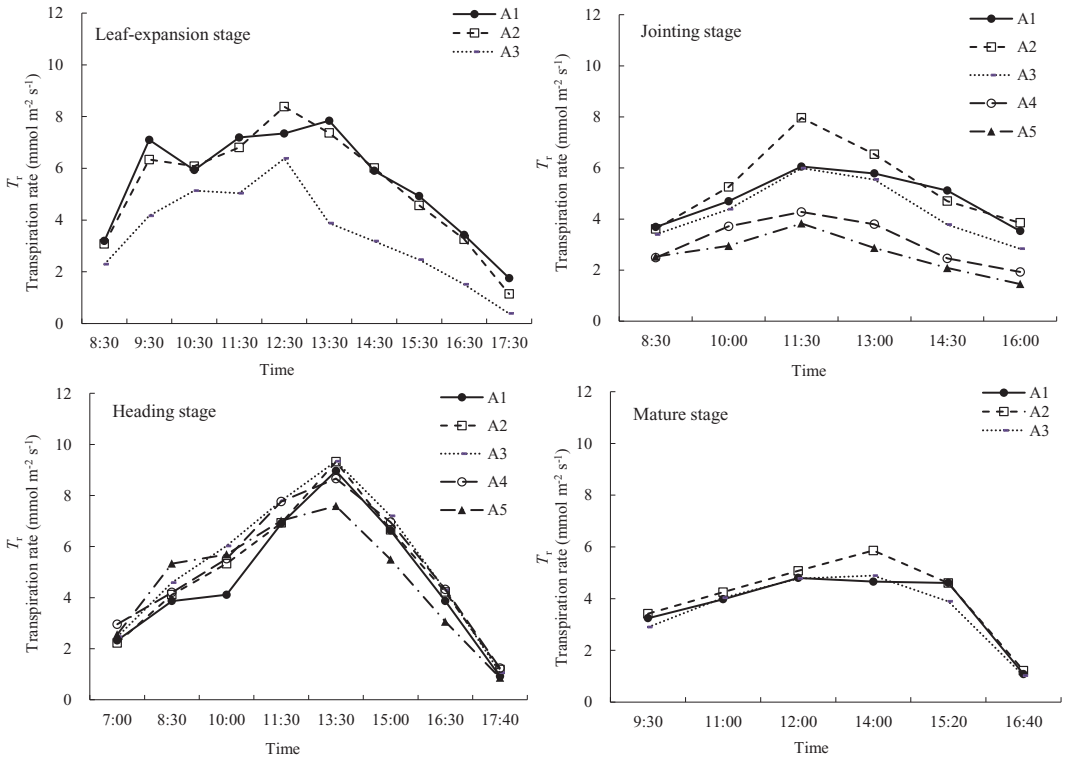


Figure 9. Diurnal variation in transpiration rate of *Phragmites australis* at four developmental stages and three or five vertical layers.

expansion, jointing, heading and mature stages, respectively. The minimum values were in the lower layer, and T_r decreased with increasing proximity to the plant base (Table 1).

Vertical characteristics of light-response parameters

Based on the non-rectangular hyperbola model, the light-response curve of *P. australis* leaves was determined and used to calculate P_{max} , α , R_d , and I_c (Table 2).

Table 2. Photosynthesis light-response parameters of *Phragmites australis* at four developmental stages and five vertical layers.

Period	Layer	Light-response parameters						R ²
		$A/(\text{mol}\cdot\text{mol}^{-1})$	$P_{max}/(\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1})$	$R_d/(\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1})$	k	$I_c/(\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1})$		
Leaf-expansion stage	A1	0.063	32.73	2.240	0.000	38.17	0.999	
	A2	0.068	37.72	1.932	0.118	29.76	0.999	
	A3	0.052	25.44	1.333	0.001	27.05	0.991	
Jointing stage	A1	0.048	20.55	1.296	0.002	28.81	0.986	
	A2	0.059	26.13	1.475	0.001	26.49	0.999	
	A3	0.053	23.38	1.302	0.000	26.01	0.995	
	A4	0.058	18.01	1.582	0.167	29.46	0.999	
	A5	0.076	14.83	1.660	0.002	24.59	0.999	
Heading stage	A1	0.065	29.84	1.695	0.000	27.65	0.994	
	A2	0.052	27.65	1.597	0.002	32.59	0.998	
	A3	0.057	24.94	2.769	0.001	54.64	0.994	
	A4	0.045	18.77	2.783	0.000	72.61	0.997	
	A5	0.045	15.75	2.403	0.000	63.01	0.992	
Mature stage	A1	0.033	6.20	0.736	0.020	25.25	0.948	
	A2	0.049	10.89	1.333	0.000	31.00	0.967	
	A3	0.044	7.09	0.620	0.001	15.44	0.973	

Under certain conditions, P_{\max} reflects the maximum photosynthetic capacity of plant leaves (Tartachnyk and Blanke 2004). The growth rate of *P. australis* in the leaf-expansion stage was rapid and its photosynthetic ability was high. The highest P_{\max} value was in the A2 layer ($37.7 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), and the lowest P_{\max} value was in the A3 layer ($25.4 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). The jointing and heading stages were stable growth periods, with higher photosynthetic ability than that at the leaf-expansion stage. At the jointing stage, the maximum P_{\max} value was in the A2 layer ($26 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and the minimum P_{\max} value was in the A5 layer ($14.8 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). At the heading stage, the maximum P_{\max} value was in the A1 layer ($29.8 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and the minimum P_{\max} value was in the A5 layer ($15.8 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). At the mature stage, the leaves of *P. australis* were yellow and senescent in the lower layers and their photosynthetic ability was weak. The maximum P_{\max} value was in the A2 layer ($10.9 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). The highest P_{\max} was at the leaf-expansion stage and lowest P_{\max} was at the mature stage. At each developmental stage, P_{\max} was higher in the upper or middle layers, and lower in the lower or bottom layers, and values decreased with increasing proximity to the plant base.

Quantum efficiency reflects the ability of plant leaves to use light energy, especially their ability to use weak light. The higher the value of α , the stronger the ability to use weak light. Values of α are generally in the range of 0.03 to 0.06 under natural conditions (Xie and Yang 2009a; Lv et al. 2016). The value of α for leaves of *P. australis* in the Liaohe Delta ranged from 0.033 and 0.076, slightly higher than the range commonly observed for other plant species. There was no obvious relationship between α values and the different vertical layers. The mean α in the leaf-expansion, jointing, heading and mature stages was 0.060, 0.059, 0.053 and 0.042, respectively. The ability of *P. australis* to use weak light was stronger at the leaf-expansion and jointing stages than at the heading and mature stages.

The light compensation point reflects the ability of plant leaves to use weak light (Qi et al. 2013). The smaller the value of I_c , the stronger the ability to use weak light. In the leaf-expansion stage, the I_c of *P. australis* leaves was in the range of 27.1 to 38.2 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (average, 31.7 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). The maximum value was in the A1 layer, and the minimum value was in the A3 layer; *P. australis* leaves in the lower layer were better able to use weak light. At the jointing stage, the I_c of *P. australis* leaves ranged from 24.6 to 29.5 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (average, 27.1 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). The I_c values were similar in each layer, but the ability of *P. australis* leaves to use weak light was slightly higher at the jointing stage than at the leaf-expansion stage. At the heading stage, the I_c of *P. australis* leaves was in the range of 27.7 to 72.6 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (average, 50.1 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). The maximum value was in the A4 layer, and the minimum value was in the A1 layer. Thus, the ability to use weak light was higher in the upper layer than in the middle and lower layers, and was lower at the heading stage than at the leaf-expansion and jointing stages. At the mature stage, I_c was in the range of 15.4 to 31.0 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (average, 23.9 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). The minimum value was in the A3 layer, and the ability to use weak light was higher at the mature stage than at the other stages. Thus, the leaf stages could be ranked, from highest ability to use weak light to lowest, as follows: mature stage > jointing stage > leaf-expansion stage > heading stage.

Discussion

In most previous studies on leaf photosynthesis in *P. australis*, leaves were selected from a single layer at a certain developmental stage, typically the third fully expanded leaf from the top of the plant (equivalent to upper-layer leaves in the present study). The results of this study showed that the highest net photosynthetic rate, stomatal conductance and transpiration rate were sometimes in the top layer, and sometimes in the upper or middle layer. The lowest values were always recorded in the bottom layer. Photosynthetic ability depends on the genetic characteristics of the plant, but a suitable external environment can enhance photosynthetic potential (Han et al. 2009). Leaves in the upper layer received higher intensity solar radiation; thus, their net photosynthetic rate was higher. However, the upper layer leaves were usually young, and their structure and physiological functions

were not fully mature, so they did not always show the highest net photosynthetic rate. It is well established that leaves in the middle layer show optimal photosynthetic function and have fully developed cell and tissue structures (Han et al. 2012). However, shading by upper layers weakened photosynthesis of leaves in the middle layer, and leaves in the lower layer tended to show lower net photosynthetic rates associated with decreased solar radiation (Figure 5, 6). Therefore, detailed observations of upper- and middle-layer leaves of *P. australis* better reflected the maximum photosynthetic efficiency.

The upper or middle layer leaves exhibited midday depression under high light intensity, but not under low light intensity. Given the low incident light, leaves in the lower and bottom layers did not exhibit midday depression because of natural shading. Leaves of *P. australis* exhibited midday depression at light intensities in the range of 1700–2000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. However, in some cases, there was no photoinhibition at light intensities $\geq 2000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Therefore, high light intensity is not essential for midday depression. Previous studies have shown that midday depression is affected by environmental factors such as temperature and humidity and physiological factors such as stomatal conductance and intercellular CO_2 concentration (Farquhar and Sharkey 1982; Xu 1997). A decrease in the net photosynthetic rate results from two factors: a decrease in stomatal conductance that prevents CO_2 from entering the leaf (stomatal limitation), and inhibition of photosynthesis in mesophyll cells that decreases the use of CO_2 (non-stomatal limitation). The former causes a decrease in intercellular CO_2 concentration, whereas the latter increases the intercellular CO_2 concentration (Xu 1997; Qi et al. 2016). With increasing proximity to the base of *P. australis* plants, the net photosynthetic rate and stomatal conductance gradually decreased and the intercellular CO_2 concentration increased. These results indicated that non-stomatal limitation caused the decrease in net photosynthetic rate nearer to the plant base, because of the lower photosynthetic activity of the mesophyll cells. In upper- or middle-layer leaves of *P. australis* in the Liaohe Delta wetland that exhibited midday depression, the CO_2 concentration declined with decreasing stomatal conductance, indicating that stomatal limitation was the main reason for the midday depression in these layers. However, previous studies have demonstrated that midday depression in *P. australis* can be caused by non-stomatal factors including salinization, drought, and high water levels (Zhong et al. 2014, Ding et al. 2015). Other studies showed that the growth rate and photosynthetic rate of *P. australis* slowed at salt concentrations $> 5.84 \text{ g/kg}$ (Hanganu et al. 1999, Lissner et al. 1999) and when water level was above -50 cm (Qi et al. 2016).

The P_{max} of leaves of *P. australis* in the Liaohe Delta wetland was in the range of 6.2 to 37.7 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Inter-seasonal differences were notable, with P_{max} values of 37.7, 26.1, 29.8, and 10.9 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at the leaf-expansion, jointing, heading and maturity stages, respectively. The highest P_{max} value was in the upper or middle layer. Wu et al. (2009) reported that the highest P_{max} of *P. australis* in the Hangzhou Bay wetland, China, was 27.4 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in July (the hottest month). They concluded that an increase in temperature promoted photosynthetic enzyme activity in leaves, and so temperature was positively correlated with photosynthesis. The highest P_{max} of *P. australis* leaves in the Liaohe Delta wetland in July (the hottest month) was 26.1 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (in upper leaves), slightly less than that recorded in the Hangzhou Bay wetland (beach wetland). However, the highest P_{max} values for leaves of *P. australis* in Liaohe Delta wetland were recorded in cooler months, June and August (37.7 and 29.8 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively). At our study site, an increase in temperature may have decreased photosynthetic activity, leading to a decrease in the net photosynthetic rate. This would be consistent with the conclusions about the factors causing midday depression mentioned above.

The light compensation point is the light intensity at which the rate of photosynthesis is equal to the rate of respiration. Generally, when the light compensation point and light saturation point are lower, the plant is a shade-demanding plant; if they are higher, the plant is a light-demanding plant (Ke et al. 2004). The light compensation point of leaves of *P. australis* in the Liaohe Delta wetland was in the range of 15.4 to 72.6 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, and the average I_c value in each layer was 23.9–50.1 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. These values are between those of a shade-demanding plant ($< 20 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)

and a light-demanding plant ($50\text{--}100\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). Xie and Yang (2009a) showed that the I_c of *P. australis* in a freshwater wetland of Yellow River Delta was $21\text{--}28\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ from the end of May to early June, and the P_{max} was $4.6\text{--}17.8\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Those values are lower than the values obtained during the same period in the present study (values of I_c $27.1\text{--}38.2\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; values of P_{max} $25.4\text{--}37.7\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). Xie and Yang (2009b) concluded that stomatal limitation was the main factor leading to the decrease in photosynthetic capacity under water deficit in the Yellow River Delta, which has similar environmental conditions to those of our study site. However, in their experiments, *P. australis* grown in pots also showed a limited photosynthetic capacity. Zhong et al. (2014) reported that the I_c of *P. australis* in the reclaimed tidal wetland at Dongtan of Chongming Island, China, was $37.4\text{--}44.8\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in August, which is within the range of values recorded during the same period in the current study (values in upper and middle layers, $27.7\text{--}54.6\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). The soil type at Dongtan, Chongming Island, was coastal salt soil, and there was a short flooding time during the growing season. Therefore, water or salt stress may explain why the maximum value of I_c was not higher there than in the Liaohe Delta wetland.

The photosynthetic parameters of *P. australis* leaves are influenced by the selected leaf size, developmental stage, plant vigor, and position of the observed leaf, and may be associated with geographical location, wetland type, plant genotype, and environmental factors, among other factors. In addition, the difference between the selected model and the method to estimate parameters might lead to greater differences in the fitting parameters.

Canopy resistance has been often used to simulate evapotranspiration using the Penman–Monteith model (Whitley et al. 2009), but there are no methods to measure canopy resistance directly. How to scale-up leaf stomatal resistance to canopy resistance is a key problem in evapotranspiration simulations for reed wetlands (Yu et al. 2014). Therefore, measurements of leaf gas exchange and photosynthetic parameters in each canopy layer of *P. australis*, combined with the leaf area index for each canopy layer and canopy flux data, will be useful for scale-up to the canopy or ecosystem level. This multi-layer model of canopy resistance could be extended to estimate eco-system-scale evapotranspiration.

Conclusion

We measured the diurnal variation in P_{max} , G_s , and T_r for leaves of *P. australis* in the Liaohe Delta wetland at four developmental stages and five vertical layers. These parameters showed single-peak or double-peak curves with lower values in the morning and evening and higher values at noon. The recorded values were higher in the upper and middle layers, and gradually decreased below the middle layer with increasing proximity to the plant base. The leaves in the upper or middle layers showed midday depression under strong light intensity, but not under weak light intensity. Similarly, midday depression was not observed in the lower and bottom layers, which were shaded by the leaves above. The diurnal variation in C_i of *P. australis* leaves exhibited a ‘U’-shaped curve, with higher values in the morning and evening and lower values at noon, opposite to the pattern observed for P_n . The value of C_i decreased with increasing proximity to the plant base. *Phragmites australis* leaves in the leaf-expansion stage showed a strong photosynthetic ability and the highest P_{max} values, whereas leaves in the mature stage showed weaker photosynthetic ability the lowest P_{max} values. The development stages of leaves were ranked, from highest average ability to weak light to lowest, as follows: mature stage > jointing stage > leaf stage > heading stage. Environmental factors and the physiological and biochemical characteristics of the plant affect photosynthetic characteristics. Therefore, understanding the photosynthetic characteristics of the *P. australis* wetland requires detailed observations of photosynthesis at different growth stages, under different climatic conditions, and at different vertical leaf positions on the plant.

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