

## BRIEF COMMUNICATION

# Evaluation of photosynthetic electron flow using simultaneous measurements of gas exchange and chlorophyll fluorescence under photorespiratory conditions

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## Abstract

Simultaneous measurements of leaf gas exchange and chlorophyll fluorescence for *Koeleria paniculata* Laxm. at  $380 \pm 5.6$  and  $600 \pm 8.5 \mu\text{mol mol}^{-1}$  were conducted, and the photosynthetic electron flow via photosystem II (PSII) to photosynthesis, photorespiration, and other electron-consuming processes were calculated. The results showed that the photosynthetic electron flow associated with carboxylation ( $J_c$ ), oxygenation ( $J_o$ ), and other electron-consuming processes ( $J_r$ ) were 72.7, 45.7, and  $29.4 \mu\text{mol(e}^-\text{)} \text{m}^{-2} \text{s}^{-1}$  at  $380 \mu\text{mol mol}^{-1}$ , respectively; and 86.1, 35.3, and  $48.2 \mu\text{mol(e}^-\text{)} \text{m}^{-2} \text{s}^{-1}$  at  $600 \mu\text{mol mol}^{-1}$ , respectively. Our results revealed that other aspects associated with electron-consuming processes, except for photosynthesis and respiration, were neither negligible nor constant under photorespiratory conditions. Using maximum net photosynthetic rate ( $P_{\text{max}}$ ), day respiration ( $R$ ), photorespiration rate ( $R_i$ ), and maximum electron flow via PSII ( $J_{\text{max}}$ ), the use efficiency of electrons via PSII at saturation irradiance to fix  $\text{CO}_2$  was calculated. The calculated results showed that the use efficiency of electrons via PSII to fix  $\text{CO}_2$  at  $600 \mu\text{mol mol}^{-1}$  was almost as effective as that at  $380 \mu\text{mol mol}^{-1}$ , even though more electrons passed through PSII at  $600 \mu\text{mol mol}^{-1}$  than at  $380 \mu\text{mol mol}^{-1}$ .

**Additional key words:** light-response curve of photosynthesis; light-response curve of photosynthetic electron flow via PSII; photosynthesis; photosynthetic electron flow via PSII.

Photosynthetic electron flow through PSII provides reducing power for photosynthetic carbon reduction and photorespiratory carbon oxidation. It may also provide a source for alternative electron sinks (e.g. Badger 1985, Fila *et al.* 2006, Drath *et al.* 2008, Werner *et al.* 2008, Ferrier-Pagès *et al.* 2009, Flexas *et al.* 2009, Li *et al.* 2009, Tissue and Lewis 2010, Eichelmann *et al.* 2011), such as nitrate reduction (e.g. Lee and Titus 1992, Cen *et*

*al.* 2001) and direct reduction of  $\text{O}_2$  in the Mehler reaction (e.g. Badger 1985, Cheng *et al.* 2001, Fila *et al.* 2006, Drath *et al.* 2008, Flexas *et al.* 2009, Li *et al.* 2009). Under photorespiratory conditions, it is considered at present that the electron flows are uniquely devoted to carboxylation and oxygenation cycle driven by Rubisco, and that all other electron-consuming processes are negligible, or at least constant (Cornic and Briantais

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**Abbreviations:** Chl – chlorophyll;  $F_m'$  – maximal fluorescence under light exposure;  $F_s$  – steady-state fluorescence;  $J$  – electron flow via PSII;  $J_c$  – electron flow associated with carboxylation;  $J_o$  – electron flow associated with oxygenation;  $J_{\text{max}}$  – maximum electron flow via PSII;  $J_r$  – electron flow costing attributable to other reactions, with the exception of carboxylative and oxygenative reactions;  $I_{\text{sat}}$  – saturation irradiance corresponding to  $P_{\text{max}}$ ;  $\text{PAR}_{\text{sat}}$  – saturation irradiance corresponding to  $J_{\text{max}}$ ; PSII – photosystem II;  $P_N$  – net photosynthetic rate;  $P_{\text{max}}$  – maximum net photosynthetic rate;  $R$  – day respiration;  $R_i$  – photorespiration rate;  $R_D$  – dark respiration rate;  $\alpha$  – initial slope of light-response curve of photosynthesis;  $\theta$  – initial slope of light-response curve of photosynthetic electron flow via PSII.

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1991, Epron *et al.* 1995, Valentini *et al.* 1995).

Until recently, research focused on the photosynthetic electron flows *via* PSII consumed by carboxylation and oxygenation cycle (e.g. White and Critchley 1999, Cheng *et al.* 2001, Long and Bernacchi 2003, Fila *et al.* 2006, Moradi and Ismail 2007, Drath *et al.* 2008, Rodolfo-Metalpa *et al.* 2008, Werner *et al.* 2008, Ferrier-Pagès *et al.* 2009, Flexas *et al.* 2009, Li *et al.* 2009, Tissue and Lewis 2010, Eichmann *et al.* 2011), and Valentini *et al.* (1995) and Epron *et al.* (1995) gave the expression of the partitioning of electrons to photosynthesis and photorespiration, and the equation of the expression (Valentini *et al.* 1995, Epron *et al.* 1995) was widely used to investigate in plant physiology (e.g. Cheng *et al.* 2001, Long and Bernacchi 2003, Fila *et al.* 2006, Li *et al.* 2009, Tissue and Lewis 2010, Eichmann *et al.* 2011). However, whether the other electron-consuming processes, except for the partitioning of electrons to photosynthesis and photorespiration, are negligible or constant, have not been closely examined. We used seedlings of *Koeleria bipinnata* Laxm. at normal CO<sub>2</sub> concentration (380 µmol mol<sup>-1</sup>) and at high CO<sub>2</sub> concentration (600 µmol mol<sup>-1</sup>) under photorespiratory conditions to check whether the other electron-consuming processes, except for the electron requirements of photosynthesis and photorespiration, are negligible or constant, as well as estimate the use efficiency of photosynthetic electron flow *via* PSII.

In 2008, one-year-old seedlings of *K. bipinnata* were transplanted from Baiyuan germchit factory in Taishun, Wenzhou. Then they were grown and cultivated outdoors at the Botanical Garden of Wenzhou Vocational & Technical College. Water and nutrients were managed normally during the whole growth period. Experiments were conducted in August 2010. Maximum photosynthetically active radiation (PAR) during growth exceeded 2,000 µmol m<sup>-2</sup> s<sup>-1</sup> on sunny days. Plants were selected for uniformity. In all experiments, the most recent, the youngest fully expanded leaves were used. The leaf gas exchange [including net photosynthetic rate ( $P_N$ ), stomatal conductance ( $g_s$ ), intercellular CO<sub>2</sub> concentration ( $C_i$ )] and chlorophyll (Chl) fluorescence [e.g. photosynthetic electron flows ( $J$ )] were performed simultaneously from 9:00 to 11:30 h and from 14:30 to 17:00 h, respectively, using a Li-6400-40 Leaf Chamber Fluorometer (Li-Cor, Lincoln, NE, USA) on four leaves per seedling (5 seedlings per locality) in each sampling occasion. Leaf temperature during measurements was maintained at 30 ± 0.1°C at a relative humidity of about 60%. Prior to measurements, the leaves were placed in the cuvette for 60 min after reaching a steady state of CO<sub>2</sub> exchange at a PAR of 1,600 µmol m<sup>-2</sup> s<sup>-1</sup>. The ambient CO<sub>2</sub> concentration in the cuvette was maintained at 380 and 600 µmol mol<sup>-1</sup> with a CO<sub>2</sub> mixer, respectively.

Measurements of CO<sub>2</sub> gas exchange and Chl fluorescence parameters in response to PAR were made at

thirteen PAR levels [2,000; 1,800; 1,600; 1,400; 1,200; 1,000; 800; 600; 400; 200; 100; 50, and 0 µmol m<sup>-2</sup> s<sup>-1</sup>]. At each PAR, CO<sub>2</sub> assimilation and steady-state fluorescence ( $F_s$ ) were monitored to ensure that they reached a steady state (3~5 min) before a reading was taken. Maximal fluorescence under light exposure ( $F_m'$ ) was obtained using a 0.8-s saturating pulse of light (~8,000 µmol m<sup>-2</sup> s<sup>-1</sup>) to the leaf to reduce all the PSII centers. After measuring the leaf gas exchange and Chl fluorescence, the light-response curves of photosynthesis were fitted using a model of light-response curve of photosynthesis (Ye and Yu, 2008) to calculate saturation irradiance (corresponding to the maximum net photosynthetic rate,  $P_{max}$ ) at 380 and 600 µmol mol<sup>-1</sup>. Measurements of photorespiration rate ( $R_i$ ) at corresponding saturation irradiance were performed at 0.21 mol(O<sub>2</sub>) mol<sup>-1</sup> (i.e., 21% O<sub>2</sub>) and 0.02 mol(O<sub>2</sub>) mol<sup>-1</sup> (i.e., 2% O<sub>2</sub>), when CO<sub>2</sub> concentration was 380 and 600 µmol mol<sup>-1</sup>, respectively.  $R$  is the day respiration rate under light from processes other than photorespiration, which is usually estimated by the respiration rate measured in the dark.

Data were analyzed by one-way analysis of variance (ANOVA) to test for differences in parameters, using the SPSS statistical package (SPSS, Chicago, USA). Data are presented as means with standard errors.

Using the equations of Valentini *et al.* (1995) and Epron *et al.* (1995), and assuming that the linear electron flows are uniquely devoted to the carboxylation and oxygenation cycle driven by Rubisco, and that all other electron-consuming processes are negligible, or at least constant (Cornic and Briantais 1991, Epron *et al.* 1995, Valentini *et al.* 1995), the total electron flow ( $J$ ) under photorespiratory conditions was calculated as:

$$J = J_c + J_o \quad (1)$$

where  $J_c$  is the electron flow associated with CO<sub>2</sub> reduction and  $J_o$  is the flow funneled into collective O<sub>2</sub>-dependent dissipative processes, such as photorespiration and the Mehler reaction. This calculation requires knowledge of  $R$  which was assumed to be equal to respiration measured in the dark.  $J_c$  and  $J_o$  were calculated using Eqs. 2 and 3 according to Epron *et al.* (1995) and Valentini *et al.* (1995).

$$J_c = 4 (P_N + R + R_i) \quad (2)$$

$$J_o = 8 R_i \quad (3)$$

While all other electron-consuming processes, except for the electron flows to photosynthesis and photorespiration are negligible, or at least constant (Cornic and Briantais 1991, Epron *et al.* 1995, Valentini *et al.* 1995), combining Eqs. 1–3,  $J_c$  and  $J_o$  might be simplified and were calculated from Eqs. 4–5 according to Epron *et al.* (1995) and Valentini *et al.* (1995).

$$J_c = \frac{1}{3} [J_T + 8(P_N + R_i)] \quad (4)$$

$$J_o = \frac{2}{3} [J_T - 4(P_N + R_l)] \quad (5)$$

If we consider that all other electron-consuming processes, except for the electron flows to photosynthesis and photorespiration, are not negligible, or constant, Eq. 1 will be modified as

$$J = J_c + J_o + J_r \quad (6)$$

where  $J_r$  is defined as the electron flow costing attributable to other reactions, with the exception of carboxylative and oxygenative reactions.

The data for photosynthesis *vs.* irradiance were fitted to the following equation (Ye and Yu 2008):

$$P_N = \alpha \frac{1 - \lambda I}{1 + \gamma I} I - R_D \quad (7)$$

where  $I$  is the PAR,  $R_D$  is the dark respiration rate,  $\alpha$  is the initial slope of light response curve of photosynthesis, and  $\lambda$  and  $\gamma$  are two coefficients.

A statistical program based on the Marquard algorithm was used to find the least-squares solution to obtain  $\alpha$ ,  $\lambda$ ,  $\gamma$ , and  $R_D$ . Subsequently, the saturation irradiance ( $I_{sat}$ ) and  $P_{max}$  can be obtained using Eqs. 8 and 9, respectively.

$$I_{sat} = \frac{\sqrt{(\lambda + \gamma)/\lambda} - 1}{\gamma} \quad (8)$$

$$P_{max} = \alpha \left( \frac{\sqrt{\lambda + \gamma} - \sqrt{\lambda}}{\gamma} \right)^2 - R_D \quad (9)$$

The data for photosynthetic electron *vs.* irradiance were fitted using Eq. 10.

$$J = \theta \frac{1 - \varepsilon I}{1 + \phi I} I \quad (10)$$

where  $\theta$  is the initial slope of the light-response curve of photosynthetic electron flow *via* PSII,  $\varepsilon$  and  $\phi$  are two coefficients. Eq. 10 is similar to Eq. 7 formally, except for  $R_D$ .

A statistical program based on the Marquard algorithm was used to find the least-squares solution to obtain  $\theta$ ,  $\varepsilon$ , and  $\phi$ . Subsequently,  $J_{max}$  and the saturation irradiance ( $PAR_{sat}$ ) corresponding to  $J_{max}$  were calculated from Eqs. 11 and 12, respectively.

$$PAR_{sat} = \frac{\sqrt{(\varepsilon + \phi)/\varepsilon} - 1}{\phi} \quad (11)$$

$$J_{max} = \theta \left( \frac{\sqrt{\varepsilon + \phi} - \sqrt{\varepsilon}}{\phi} \right)^2 \quad (12)$$

$P_{max}$  estimated by Eq. 9 is  $10.4 \pm 0.7$  and  $15.62 \pm 0.41$   $\mu\text{mol}(\text{CO}_2) \text{ m}^{-2} \text{ s}^{-1}$ , respectively;  $I_{sat}$  estimated by Eq. 8 is  $1,235.5 \pm 57.1$  and  $1,588.1 \pm 68.5$   $\mu\text{mol m}^{-2} \text{ s}^{-1}$ , respec-

tively.  $P_{max}$ ,  $I_{sat}$  and other photosynthetic parameters (*e.g.*  $I_c$  and  $R_D$ ) estimated by Eq. 7, derived from light-response curve of photosynthesis (Fig. 1A), are in very close agreement with the measured data ( $R^2=0.999$ ). At saturation irradiance the stomatal conductance ( $g_s$ ) is about 0.177 and 0.204  $\text{mol}(\text{H}_2\text{O}) \text{ m}^{-2} \text{ s}^{-1}$  at  $\text{CO}_2$  concentration of 380 and 600  $\mu\text{mol mol}^{-1}$ , respectively; and at saturation irradiance corresponding to  $C_i$  is about 251.03 and 243.71  $\mu\text{mol mol}^{-1}$  at  $\text{CO}_2$  concentration of 380  $\mu\text{mol mol}^{-1}$ , respectively.

$J_{max}$  estimated by Eq. 12 is  $147.76 \pm 3.1$  and  $169.55 \pm 4.3$   $\mu\text{mol}(\text{e}^-) \text{ m}^{-2} \text{ s}^{-1}$ , respectively;  $PAR_{sat}$  estimated by Eq. 11 is  $1,350.6 \pm 42.32$  and  $1,480.50 \pm 47.9$   $\mu\text{mol m}^{-2} \text{ s}^{-1}$ , respectively.  $PAR_{sat}$  and  $J_{max}$  estimated by Eqs. 11 and 12, derived from light-response curves of photosynthetic electron flow *via* PSII (Fig. 1B), are in very close agreement with the measured data ( $R^2=0.999$ ).

Moreover, using values of  $P_{max}$ ,  $J_{max}$ ,  $R_l$  and  $R_l$ , at saturation irradiance  $J_c$  and  $J_o$  can be calculated using Eqs. 2 and 3, respectively. It shows that  $J_c/J_{max}$  is 49.2% at 380  $\mu\text{mol mol}^{-1}$ , and 50.8% at 600  $\mu\text{mol mol}^{-1}$  indicating that the use efficiency of electrons from PSII at 380  $\mu\text{mol mol}^{-1}$  is almost equal to that at 600  $\mu\text{mol mol}^{-1}$  at saturation irradiance. Some parameters (*e.g.*  $J_{max}$ ,  $J_c$ ,  $J_o$ , and  $J_r$ ) estimated by Eqs. 2, 3 and 6, derived from photosynthetic light response and light-response curves of photosynthetic electron flow *via* PSII in Fig. 1A and 1B respectively, are summarized in Table 1.

For *K. bipinnata*, the measured photorespiration rate ( $R_l$ ) was about 5.7 and 4.4  $\mu\text{mol}(\text{CO}_2) \text{ m}^{-2} \text{ s}^{-1}$  at 380 and 600  $\mu\text{mol mol}^{-1}$ , respectively, and that  $J_o = 68.1$  and 67.4  $\mu\text{mol}(\text{e}^-) \text{ m}^{-2} \text{ s}^{-1}$  when calculated using Eq. 5, respectively, while  $J_o = 45.7$  and 35.3  $\mu\text{mol}(\text{e}^-) \text{ m}^{-2} \text{ s}^{-1}$  when calculated using Eq. 4, respectively. Some parameters (*e.g.*,  $J_{max}$ ,  $J_c$ , and  $J_o$ ) estimated by Eqs. 4 and 5, derived from photosynthetic light response and light-response curves of photosynthetic electron flow *via* PSII in Fig. 1A and 1B, respectively, are summarized in Table 1.

Photosynthetic electron transport drives both Rubisco-associated  $\text{CO}_2$  fixation and photorespiration, and also supplies electrons to other alternative electron sinks (*e.g.* Badger 1985, Fila *et al.* 2006, Drath *et al.* 2008, Werner *et al.* 2008, Ferrier-Pagès *et al.* 2009, Flexas *et al.* 2009, Li *et al.* 2009, Miyake 2010, Tissue and Lewis 2010, Eichelmann *et al.* 2011). Our results reveal that electron-consuming processes other than those involved in photosynthesis and photorespiration exist, because  $J_r$  is 29.4 and 48.2  $\mu\text{mol}(\text{e}^-) \text{ m}^{-2} \text{ s}^{-1}$  at 380 and 600  $\mu\text{mol mol}^{-1}$ , respectively. This demonstrates that the other electron-consuming processes are neither negligible nor constant under photorespiratory conditions at 380 and 600  $\mu\text{mol mol}^{-1}$ . Among all the other electron-consuming processes, nitrate reduction (*e.g.* Lee and Titus 1992, Cen *et al.* 2001),  $\text{O}_2$  function as an electron acceptor in Mehler reaction (*e.g.* Badger 1985, Cheng *et al.* 2001, Fila *et al.* 2006, Drath *et al.* 2008, Flexas *et al.* 2009, Li *et al.*

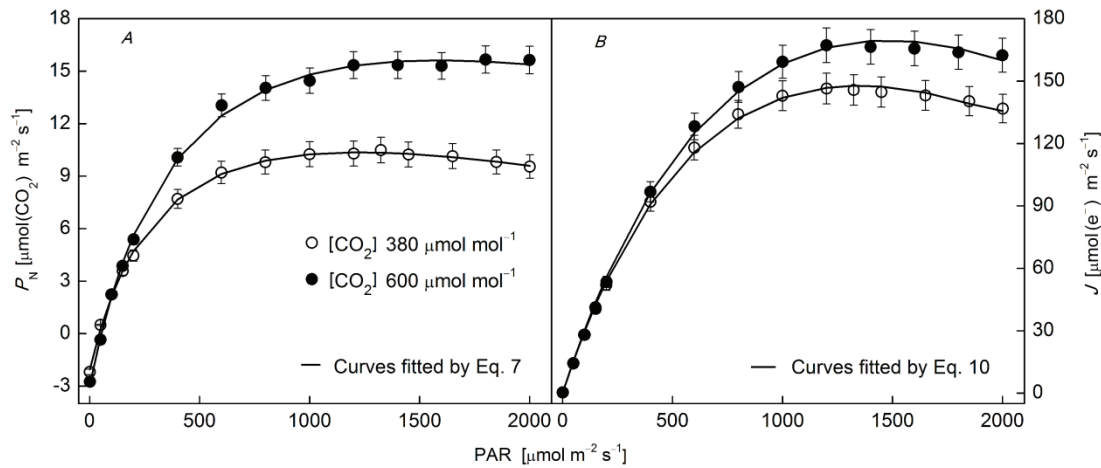


Fig. 1 Irradiance-response curves of  $P_N$  (A) and  $J$  (B). Measurements were made at leaf temperature of  $30 \pm 0.1^\circ\text{C}$ .  $\text{CO}_2$  concentrations are  $380 \mu\text{mol mol}^{-1}$  and  $600 \mu\text{mol mol}^{-1}$ , respectively. Each measured data point represents the average of five replications with standard error. PAR – photosynthetically active radiation,  $P_N$  – net photosynthetic rate.

Table 1. Results calculated from Eqs. 2–6 derived from light-response curves of photosynthesis and RLCs for *K. bipinnata* at two  $\text{CO}_2$  concentrations with gas exchange and chlorophyll fluorescence measured simultaneously at saturation irradiance, respectively. Mean  $\pm$  SE ( $n = 5$ ). Units:  $J_c$ ,  $J_o$  and  $J_r$  [ $\mu\text{mol}(\text{e}^-) \text{m}^{-2} \text{s}^{-1}$ ]. Statistical significance is denoted as: \*\*\* $P < 0.0001$ .

Parameters	[ $\text{CO}_2$ ] $380 \mu\text{mol} \cdot \text{mol}^{-1}$		[ $\text{CO}_2$ ] $600 \mu\text{mol} \cdot \text{mol}^{-1}$	
	Eqs. 2, 3 and 6	Eqs. 4 and 5	Eqs. 2, 3 and 6	Eqs. 4 and 5
$J_c$	$72.7 \pm 6.6^{***}$	$79.7 \pm 3.3^{***}$	$86.1 \pm 5.3^{***}$	$102.2 \pm 5.9^{***}$
$J_o$	$45.7 \pm 4.9^{***}$	$68.1 \pm 1.8^{***}$	$35.3 \pm 3.4^{***}$	$67.4 \pm 3.9^{***}$
$J_r$	$29.4 \pm 2.9^{***}$	-	$48.2 \pm 3.7^{***}$	-
$J_c/J_{\text{max}}$ [%]	49.2	46.1	50.8	39.7
$J_o/J_{\text{max}}$ [%]	30.9	53.9	20.8	60.3
$J_r/J_{\text{max}}$ [%]	19.9	-	28.4	-

2009), and water-water cycle (Miyake 2010) may be considered as the alternative electron sinks.

$J_c/J_{\text{max}}$  was found to be 49.2% and 50.8% at saturation irradiance, with  $\text{CO}_2$  concentration at 380 and  $600 \mu\text{mol mol}^{-1}$ , respectively. This shows that *K. bipinnata* at  $600 \mu\text{mol mol}^{-1}$  utilized electron from PSII almost as effectively as at  $380 \mu\text{mol mol}^{-1}$  in  $\text{CO}_2$  reduction, even though more electrons passed through PSII at  $600 \mu\text{mol mol}^{-1}$  than at  $380 \mu\text{mol mol}^{-1}$ . This is an interesting phenomenon, and the exact cause for this phenomenon is still unclear. Furthermore, the present results do not support the finding of Epron *et al.* (1995) that ribulose-1,5-bisphosphate (RuBP) regeneration remains the major sink for photosynthetic electron consumption under photorespiratory conditions. Our results show that RuBP regeneration and other electron-consuming processes (*e.g.*, N reduction,  $\text{O}_2$  acceptor, and photorespiration) are almost the same electron sinks (Table 1). By comparison

the data in Table 1, it showed that the total electron flows via PSII ( $J$ ) should be calculated using Eq. 6 under photorespiratory conditions, while  $J_c$  and  $J_o$  should be calculated using Eqs. 2 and 3 respectively. By assuming that mitochondrial respiration (*i.e.*  $J_o = 8R_i$ ) is measured,  $J_r$  can be easily calculated as  $J_r = J - J_c - J_o$ , because  $J$  can be obtained by chlorophyll fluorescence, and  $P_N$ ,  $R$ , and  $R_i$  can be measured by leaf gas exchange.

In conclusion, under photorespiration conditions, as all other electron-consuming processes except for the electron flows to photosynthesis and photorespiration are neither negligible nor constant, the partitioning of electron flows to photosynthesis and photorespiration should be calculated as  $J_c = 4(A + R + R_i)$  and  $J_o = 8R_i$ , respectively. In the present study, it was demonstrated that other electron-consuming processes, apart from those involved in photosynthesis and photorespiration, coexist.

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