

BRIEF COMMUNICATION

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

Z.P. YE^{*,#,+}, Q. YU^{**}, and H.J. KANG^{***}

Research Center for Jinggangshan Eco-Environmental Sciences, Jinggangshan University, Ji'an 343009, P.R. China^{*}
 Plant Functional Biology and Climate Change Cluster, University of Technology Sydney, NSW 2007, Australia^{**}
 Department of Landscape Architecture, Wenzhou Vocational and Technical College, Wenzhou 325026, P.R. China^{***}
 College of Maths and Physics, Jinggangshan University, Ji'an 343009, P.R. China[#]

Abstract

Simultaneous measurements of leaf gas exchange and chlorophyll fluorescence for *Koeleria paniculata* Laxm. at 380 ± 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 $29.4 \mu\text{mol}(e^-) \text{m}^{-2} \text{s}^{-1}$ at $380 \mu\text{mol mol}^{-1}$, respectively; and 86.1 , 35.3 , and $48.2 \mu\text{mol}(e^-) \text{m}^{-2} \text{s}^{-1}$ 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_{max}), day respiration (R), photorespiration rate (R_1), and maximum electron flow via PSII (J_{max}), the use efficiency of electrons via PSII at saturation irradiance to fix CO_2 was calculated. The calculated results showed that the use efficiency of electrons via PSII to fix 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 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

Received 14 October 2011, accepted 30 May 2012.

⁺Corresponding author; fax: +86-796-8100455, e-mail: yezp@jgsu.edu.cn; yezp2004@sina.com

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_{max} – maximum electron flow via PSII; J_r – electron flow costing attributable to other reactions, with the exception of carboxylative and oxygenative reactions; I_{sat} – saturation irradiance corresponding to P_{max} ; PAR_{sat} – saturation irradiance corresponding to J_{max} ; PSII – photosystem II; P_N – net photosynthetic rate; P_{max} – maximum net photosynthetic rate; R – day respiration; R_1 – photorespiration rate; R_D – dark respiration rate; α – initial slope of light-response curve of photosynthesis; θ – initial slope of light-response curve of photosynthetic electron flow via PSII.

Acknowledgements: The authors are grateful to anonymous referees for valuable comments and helpful suggestions. The authors would like to thank editors for editing the paper and correcting the language. This research was supported by the Natural Science Foundation of China (Grant No. 30960031), the Natural Science Foundation of Jiangxi Province (Grant No. 2009GZN0076) and the Key Discipline of Atomic and Molecular Physics in Jiangxi Province (2011-1015).

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, Eichelmann *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, Eichelmann *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 CO₂ concentration (380 μmol mol⁻¹) and at high CO₂ concentration (600 μmol mol⁻¹) 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⁻² s⁻¹ 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 CO₂ 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 CO₂ exchange at a PAR of 1,600 μmol m⁻² s⁻¹. The ambient CO₂ concentration in the cuvette was maintained at 380 and 600 μmol mol⁻¹ with a CO₂ mixer, respectively.

Measurements of CO₂ 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⁻² s⁻¹]. At each PAR, CO₂ 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⁻² s⁻¹) 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⁻¹. Measurements of photorespiration rate (R_1) at corresponding saturation irradiance were performed at 0.21 mol(O₂) mol⁻¹ (*i.e.*, 21% O₂) and 0.02 mol(O₂) mol⁻¹ (*i.e.*, 2% O₂), when CO₂ concentration was 380 and 600 μmol mol⁻¹, 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 CO₂ reduction and J_o is the flow funneled into collective O₂-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).

$$J_c = 4(P_N + R + R_1) \quad (2)$$

$$J_o = 8R_1 \quad (3)$$

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).

$$J_c = \frac{1}{3} [J_T + 8(P_N + R_1)] \quad (4)$$

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

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, α is the initial slope of light response curve of photosynthesis, and λ and γ are two coefficients.

A statistical program based on the Marquard algorithm was used to find the least-squares solution to obtain α , λ , γ , 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 θ is the initial slope of the light-response curve of photosynthetic electron flow via PSII, ε and ϕ 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 θ , ε , and ϕ . 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 ± 0.7 and 15.62 ± 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 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 CO_2 concentration of 380 $\mu\text{mol mol}^{-1}$, respectively.

J_{max} estimated by Eq. 12 is 147.76 ± 3.1 and 169.55 ± 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_i 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_i) 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 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), 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.*

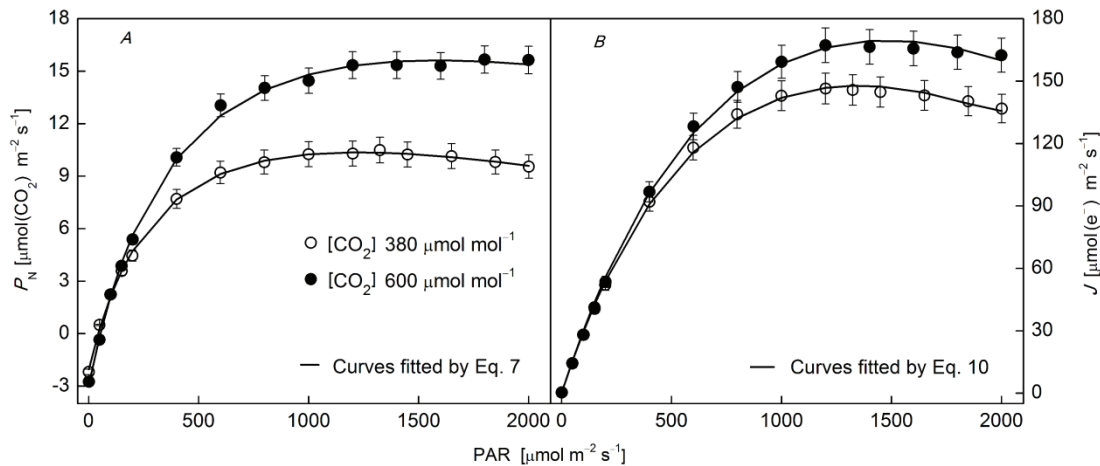


Fig. 1 Irradiance-response curves of P_N (A) and J (B). Measurements were made at leaf temperature of $30 \pm 0.1^\circ\text{C}$. CO_2 concentrations are $380 \mu\text{mol mol}^{-1}$ and $600 \mu\text{mol mol}^{-1}$, respectively. Each measured data point represents the average of five replications with 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 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	[CO_2] $380 \mu\text{mol} \cdot \text{mol}^{-1}$		[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_{max} [%]	49.2	46.1	50.8	39.7
J_o/J_{max} [%]	30.9	53.9	20.8	60.3
J_r/J_{max} [%]	19.9	-	28.4	-

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

J_c/J_{max} was found to be 49.2% and 50.8% at saturation irradiance, with 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 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, 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.* $J_o = 8R_1$) 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_1 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 $J_c = 4(A + R + R_1)$ and $J_o = 8R_1$, respectively. In the present study, it was demonstrated that other electron-consuming processes, apart from those involved in photosynthesis and photorespiration, coexist.

References

- Badger, M.R.: Photosynthetic oxygen exchange. – *Annu. Rev. Plant Physiol.* **36**: 27-53, 1985.
- Cen, Y.P., Turpin, D.H., Layzell, D.B.: Whole-plant gas exchange and reductive biosynthesis in white lupin. – *Plant Physiol.* **126**: 1555-1565, 2001.
- Cheng, L.L., Fuchigami, L.H., Breen, P.J.: The relationship between photosystem II efficiency and quantum yield for CO₂ assimilation is not affected by nitrogen content in apple leaves. – *J. Exp. Bot.* **52**: 1865-1872, 2001.
- Cornic, G., Briantais, J.M.: Partitioning of photosynthetic electron flow between CO₂ and O₂ reduction in a C₃ leaf (*Phaseolus vulgaris* L.) at different CO₂ concentrations and during drought stress. – *Planta* **183**: 178-184, 1991.
- Drath, M., Kloft, N., Batschauer, A., Marin, K., Novak, J., Forchhammer, K.: Ammonia triggers photodamage of photosystem II in the cyanobacterium *Synechocystis* sp. strain PCC 6803. – *Plant Physiol.* **147**: 206-215, 2008.
- Eichelmann, H., Oja, V., Peterson, R.B., Laisk, A.: The rate of nitrite reduction in leaves as indicated by O₂ and CO₂ exchange during photosynthesis. – *J. Exp. Bot.* **62**: 2205-2215, 2011.
- Epron, D., Godard, D., Cornic, G., Genty, B.: Limitation of net CO₂ assimilation rate by internal resistances to CO₂ transfer in the leaves of two tree species (*Fagus sylvatica* L. and *Castanea sativa* Mill.). – *Plant Cell Environ.* **18**: 43-51, 1995.
- Ferrier-Pagès, C.E., Tambutté, E., Zamoum, T., Segonds, Merle, P.-L., Bensoussan, N., Allemand, D., Garrabou, J., Tambutté, S.: Physiological response of the symbiotic gorgonian *Eunicella singularis* to a longterm temperature increase. – *J. Exp. Biol.* **212**: 3007-3015, 2009.
- Fila, G., Badeck, Franz-W., Meyer, S., Corovic, Z., Ghashghaie, J.: Relationships between leaf conductance to CO₂ diffusion and photosynthesis in micropropagated grapevine plants, before and after *ex vitro* acclimatization. – *J. Exp. Bot.* **57**: 2687-2695, 2006.
- Flexas, J., Barón, M., Bota, J. *et al.*: Photosynthesis limitations during water stress acclimation and recovery in the drought-adapted *Vitis* hybrid Richter-110 (*V. berlandieri* × *V. rupestris*). – *J. Exp. Bot.* **60**: 2361-2377, 2009.
- Lee, H.J., Titus, J.S.: Nitrogen accumulation and nitrate reductase activity in MM. 106 apple trees as affected by nitrate supply. – *J. Hort. Sci.* **67**: 273-281, 1992.
- Li, Y., Gao, Y.X., Xu, X.M., Shen, Q.R., Guo, S.W.: Light-saturation photosynthesis rate in high-nitrogen rice (*Oryza sativa* L.) leaves in related to chloroplastic CO₂ concentration. – *J. Exp. Bot.* **60**: 2351-2360, 2009.
- Long, S.P., Bernacchi, C.J.: Gas exchange measurements, what can they tell us about the underlying limitations to photosynthesis? Procedures and sources of error? – *J. Exp. Bot.* **54**: 2393-2401, 2003.
- Miyake, C.: Alternative electron flows (water-water cycle and cyclic electron flow around PSI) in photosynthesis: Molecular mechanisms and physiological functions. – *Plant Cell Physiol.* **51**: 1951-1963, 2010.
- Moradi, F., Ismail, A.M.: Responses of photosynthesis, chlorophyll fluorescence and ROS-scavenging systems to salt stress during seedling and reproductive stages in rice. – *Ann. Bot.* **99**: 1161-1173, 2007.
- Rodolfo-Metalpa, R., Huot, Y., Ferrier-Pagès, C.: Photosynthetic response of the Mediterranean zooxanthellate coral *Cladocora caespitosa* to the natural range of light and temperature. – *J. Exp. Biol.* **211**: 1579-1586, 2008.
- Tissue, D.T., Lewis, J.D.: Photosynthetic responses of cottonwood seedlings grown in glacial through future atmospheric [CO₂] vary with phosphorus supply. – *Tree Physiol.* **30**: 1361-1372, 2010.
- Valentini, R., Epron, D., Angelis P.D.E., Matteucci, G., Dreyer, E.: *In situ* estimation of net CO₂ assimilation, photosynthetic electron flow and photorespiration in Tukey oak (*Q. cerris* L.) leaves: diurnal cycles under different levels of water supply. – *Plant Cell Environ.* **18**: 631-640, 1995.
- Werner, T., Holst, K., Pörs, Y., Guivarc'h, A., Mustroph, A., Chriqui, D., Grimm, B., Schmölling, T.: Cytokinin deficiency causes distinct changes of sink and source parameters in tobacco shoots and roots. – *J. Exp. Bot.* **59**: 2659-2672, 2008.
- White, A.J., Critchley, C.: Rapid light curves: a new fluorescence method to assess the state of the photosynthetic apparatus. – *Photosynth. Res.* **59**: 63-72, 1999.
- Ye, Z.P., Yu, Q.: A coupled model of stomatal conductance and photosynthesis for winter wheat. – *Photosynthetica* **46**: 637-640, 2008.