Front. Agric. China 2010, 4(1): 50–55
DOI 10.1007/s11703-009-0092-0

RESEARCH ARTICLE

Zipiao YE, Zehai ZHAO

A modified rectangular hyperbola to describe the light-response curve of photosynthesis of *Bidens pilosa* L. grown under low and high light conditions

Abstract The light-response curve of leaf net photosynthesis is an important tool for understanding the photochemical efficiency of the photosynthetic process. We measured the light-response of the photosynthetic rate of *Bidens pilosa* L., when grown under high light of 100% full sunlight (HL) and low light of 50% full sunlight (LL) using a gas analyzer Li-6400. The measured data were simulated by a modified rectangular hyperbola. The fitted results showed that the modified rectangular hyperbola described the part of the curve up to the light saturation and the range of levels above the saturation light intensity in *Bidens pilosa* L. well. It was used to directly calculate the main photosynthetic parameters, including the light-saturated net photosynthetic rate (P_{max}), saturation light intensity (I_m), light compensation point (I_c), dark respiration rate, and the initial slope of curve without any additional hypotheses. Good agreement was obtained between the modified rectangular hyperbola estimates and observations of P_{max} and I_m of *B. pilosa* under LH and LL conditions. Furthermore, the modified rectangular hyperbola provided a very easy and simple method for simultaneously simulating the data on the light-response curve of photosynthesis at low irradiances, saturating irradiances, photoacclimation and photoinhibition.

Keywords apparent quantum yield, initial slope, light-saturated net photosynthetic rate, saturation light intensity

Received April 2, 2009; accepted May 16, 2009

Zipiao YE (✉)
Research Center for Jinggangshan Eco-Environmental Sciences, Jinggangshan University; College of Sciences, Jinggangshan University, Ji'an 343009, China
E-mail: yezp@jgsu.edu.cn

Zehai ZHAO
College of Life Sciences, Zhaoqing University, Zhaoqing 526061, China

1 Introduction

Determining the light-response curve of leaf net photosynthesis is important for understanding the photochemical efficiency of the photosynthetic process (Robert et al., 1984). It is also fundamental to understanding the relationship between irradiance and the photosynthetic rate driven by photon energy. When leaves are exposed to the Sun, as the light intensity increases, irradiance passes through the light compensation point of photosynthesis and the net photosynthetic rates ($P(I)$) will increase with increasing irradiance. At higher light intensities, net CO_2 uptake increases until light saturation is reached. There is no further response of net photosynthesis to increasing light. Under certain conditions, further increase in the light intensity causes damage to the photosynthetic apparatus, or photoinhibition (Long et al., 1994; Zhou et al., 2007). Photoinhibition is associated with a partial deactivation of key components of the photosynthetic apparatus. To complicate matters, the various physiological responses to varying intensities of light can occur interactively (Zonneveld, 1998; Marshall et al., 2000).

The photosynthetic response of leaves to incident irradiance has been described by many models and equations (Baly, 1935; Thornley, 1976; Farquhar et al., 1980; Bassman and Zwier, 1991; Prado and Moraes, 1997). These models and equations well describe the process of photosynthetic responses to irradiance at the range of levels below the saturation light intensity. However, there are no available models or equations that can describe the light-response curve of photosynthesis at the range of levels above the saturation light intensity. Furthermore, although these models and equations of the light-response curve of photosynthesis are widely used to simulate data on photosynthesis, they do not resolve certain problems. For example, P_{max} estimated by rectangular hyperbola (Baly, 1935) and non-rectangular hyperbola (Thornley, 1976) are higher than the actual measured values (Evans et al., 1993; Kyei-Boahen et al., 2003; Yu et al., 2004; Leakey et al., 2006), and I_m can not be obtained directly by either of the two models (Ögren and Evans, 1993; Yu et al., 2004; Leakey et al., 2006). Although a good agreement for P_{max} has been obtained from two exponential equations (Bassman and Zwier, 1991; Prado and Moraes, 1997), I_m can hardly be directly estimated by either of the two exponential equations.

In order to resolve the problems mentioned above, we propose a modified rectangular hyperbola of the light-response curve of photosynthesis to describe the light-response curve of photosynthesis of *Bidens pilosa* under low and high light conditions, and estimate the photosynthetic parameters directly without any additional hypotheses.

Our goals for this project were fourfold. The primary objective of our study was to propose the modified model of the light-response curve of leaf net photosynthesis from rectangular hyperbola, followed by using the modified model to fit the light-response curves of photosynthesis of *B. pilosa*, grown under HL and LL. Our third goal was to estimate photosynthetic parameters of *B. pilosa* grown under HL and LL. Finally, we compare the results fitted by rectangular hyperbola (Baly, 1935), non-rectangular hyperbola (Thornley, 1976), exponential equations (Bassman and Zwier, 1991; Prado and Moraes, 1997) and a modified model of the rectangular hyperbola in this paper, to judge their disadvantage and advantage according to the criterion of the ability to describe experimental data.

2 Materials and methods

Experiments were conducted at Zhaoqing University, which is located in Zhaoqing City, Guangdong Province, China. *B. pilosa* is a Chinese herbal medicine with a good curative effect against enteritis, diarrhea and hepatitis. Its seeds were obtained in the field. The reason that we chose *B. pilosa* to measure the light-response curve of photosynthesis was that this species, sensitive to photosynthetic acclimation, could be readily obtained in the field and easily managed.

Plants were grown from seeds germinated under identical soil conditions. Seedlings were planted in pots of 18 cm in height and 20 cm in diameter with a volume of about 4.5 L. Twenty pots each were assigned to both fully sunny and shady conditions. The shading treatment is frequently used against strong solar radiation in South China. Therefore, in our experiment, shade was created using a black plastic net through which a light intensity of 50% sunlight was allowed. All specimens had been planted for about four months and were just in florescence. The leaves used were the seventh to ninth mature leaves. Field experiments were conducted from July 14, 2005 to July 18, 2005.

Gas exchange was measured by a portable photosynthesis measurement system (LI-6400, LI-COR Inc., Lincoln, NE, USA). Leaf gas exchange was determined using 11 levels of photosynthetically active radiation (PAR, in terms of photons) (2000, 1500, 1000, 600, 300, 150, 100, 60, 30, 15 and 0 $\mu mol \cdot m^{-2} \cdot s^{-1}$) at 370 $\mu mol \cdot mol^{-1}$, with leaf temperature at about 32.5°C, and 65.4% relative humidity for the fully sunny conditions. Leaf gas exchange for the shaded leaves was measured at the same PAR at 390 $\mu mol \cdot mol^{-1}$, with about 27.3°C leaf temperature, and 70.6% relative humidity. Measurements were taken on 5 consecutive sunny days. Five minutes were allowed to reach a steady-state condition at each PAR prior to measurement. Three measurements were recorded automatically at 60 s intervals for each PAR. The leaf areas for the individual leaves used for measurements were determined using a leaf area meter (Li-300, LI-COR Inc., Lincoln, NE, USA). The rate of CO_2 emission at zero PAR was assumed to be the R_d of the leaf.

For *B. pilosa* grown under low and high light conditions, plots of net photosynthetic rate against PAR suggested a modified hyperbola rectangular model, which was proposed by Ye (2007) for modeling leaf photosynthesis as a function of PAR. The general form of the modified hyperbola rectangular model is:

$$P(I) = \alpha \frac{1-\beta I}{1+\gamma I} I - R_d,$$

where $P(I)$ is the net photosynthetic rate, I is PAR, R_d is the dark respiration rate, α is the initial slope of the photosynthetic light-response curve when I equals zero, and β and γ are two coefficients.

Fitting of model and method to the measured photosynthetic response to irradiance was completed using the SPSS procedure (SPSS Inc. Chicago, IL, USA) of nonlinear least-squares fitting using the Levenberg-Marquardt algorithm. The program was used to estimate the parameters and determination coefficient (r^2). The latter was used as an indicator of quality of fit of the fitted curve through the measured points.

3 Results

3.1 Light-response curve of photosynthesis

The gas exchange of leaves of *B. pilosa*, grown under HL and LL, was measured at two ambient carbon dioxide (CO_2) concentrations. Leaves growth in HL (Fig. 1a) consistently had higher P_{max} at I_m, compared with the leaves of *B. pilosa* growth in LL (Fig. 1b). $P(I)$ in *B. pilosa* grown under HL increased with irradiances below I_m. When above I_m, the $P(I)$ decreased as irradiances increased. However, $P(I)$ in *B. pilosa* grown under LL decreased as irradiances increased while I was only above 655.40 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

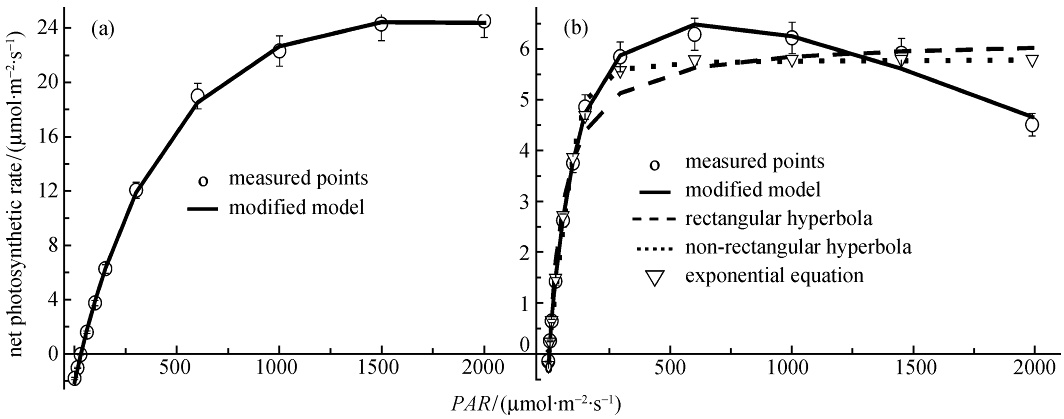

Fig. 1 Photosynthetic light-response of curves of *B. pilosa* grown under high light (a) and low light (b)

The measured data of the photosynthetic light-response of *B. pilosa* growth in HL and LL fit the modified model, and the main photosynthetic parameters were calculated by the model (Table 1). The fitted results showed that the photosynthetic light-response curves of *B. pilosa* growth in LH and LL could be best described by the modified model, with corresponding coefficients of determination (r^2) being 0.9993 and 0.9968, respectively. Calculations of P_{max} by the modified model for *B. pilosa* grown under HL and LL were 24.57 μmol·m^{-2}·s^{-1} and 6.49 μmol·m^{-2}·s^{-1}. The saturation light intensity I_m was 1773.26 μmol·m^{-2}·s^{-1} for HL and 655.40 μmol·m^{-2}·s^{-1} for LL. The measured values of P_{max} and I_m were about 24 μmol·m^{-2}·s^{-1} and 1800 μmol·m^{-2}·s^{-1} (HL), respectively; the measured values of P_{max} and I_m were about 6.5 μmol·m^{-2}·s^{-1} and 650 μmol·m^{-2}·s^{-1} (LL), respectively. Good agreement was obtained between model estimates and observations of P_{max} and I_m for *B. pilosa* growth in LH and LL conditions.

P_{max} estimated by rectangular hyperbola (Baly, 1935) and non-rectangular hyperbola (Thornley, 1976) is 33.62 and 28.61 μmol·m^{-2}·s^{-1} for HL, respectively (Table 2). It is obvious that those fitted values are more than the measured values, about 24 μmol·m^{-2}·s^{-1}. Though P_{max} estimated by exponential equations (Bassman and Zwier, 1991; Prado and Moraes, 1997) is close to the measured values, I_m can not be calculated by exponential equations (Bassman and Zwier, 1991; Prado and Moraes, 1997).

3.2 Light-response curve of photosynthesis at low irradiances

The modified model could best describe the light-response curves of photosynthesis of *B. pilosa*, grown under HL and LL when irradiance was at lower levels (Fig. 2). *P*(*I*) in *B. pilosa* grown under LL was higher than that under HL when *I* was below 100 μmol·m^{-2}·s^{-1}. When at levels above 100 μmol·m^{-2}·s^{-1}, *P*(*I*) growth in LL was less than that in HL (Fig. 2).

In most cases, apparent quantum yield (AQY) can be taken as an indicator to reflect the utilization efficiency of light energy of the plant and also as a powerful tool to assess photosynthetic characteristics of plants (Olsson et al., 1994). The more AQY a plant has, the more utilization efficiency of light energy it has, even at low irradiances. In

Table 1 Results fitted by the modified rectangular hyperbola and measured values of *B. pilosa* grown under low light (LL) and high light (HL) conditions

photosynthetic parameters	HL		LL	
	modified model	measured value	modified model	measured value
light-saturated photosynthetic rate (P_{max})/(μmol·m^{-2}·s^{-1})	24.59**	≈ 24.54	6.49**	≈ 6.5
light saturation point (I_m) /(μmol·m^{-2}·s^{-1})	1773.26**	≈ 1800	646.75**	≈ 650
light compensation point (I_c) /(μmol·m^{-2}·s^{-1})	31.78**	≈ 32	3.17*	≈ 3
dark respiration rate (R_d) /(μmol·m^{-2}·s^{-1})	−2.12**	−2.15	−0.22*	−0.15
initial slope (α)	0.070**	–	0.071**	–
determination coefficient (r^2)	0.9993	–	0.9968	–

Note: ** and * stand for significance at 0.01 and 0.05 probability levels, respectively.

Table 2 Results fitted by three models of light-response curve of photosynthesis and measured values of *B. pilosa* grown under high light (HL) conditions

photosynthetic parameters	α	P_{max}/(μmol·m^{-2}·s^{-1})	I_m/(μmol·m^{-2}·s^{-1})	I_c/(μmol·m^{-2}·s^{-1})	R_d/(μmol·m^{-2}·s^{-1})	determination coefficient (r^2)
rectangular hyperbola	0.086	33.62**	–	24.54**	−2.53**	0.9962
non-rectangular hyperbola	0.058	28.61**	–	31.71**	−1.84**	0.9998
Prado-Moraes model	0.066	24.81**	–	32.08**	−2.05**	0.9998
exponential equation	0.061	24.81**	–	32.79**	−2.08**	0.9998
modified model	0.070	24.59**	1773.26**	31.78**	−2.12**	0.9995
measured data	–	≈24.54	≈ 1 800	≈32	−2.15	–

Note: ** means significance at 0.01 probability level.

order to calculate the apparent quantum yield, the general method is to fit the measured data by line equation at low irradiances (⩽200 μmol·m^{-2}·s^{-1}) (Walker, 1989). In actual conditions, however, AQY differed significantly when irradiances were under different fitted irradiance scopes (Table 3).

In Table 3, it is obvious that AQY of *B. pilosa* grown in LL was less than that of *B. pilosa* grown in HL. However, the initial slope (α) of *B. pilosa* grown in LL was higher than that of *B. pilosa* grown in HL (Table 1). When using AQY as an indicator to assess the utilization efficiency of the light energy of plants, we would draw a conclusion that the efficiency of *B. pilosa* grown in LL was lower than that under the HL condition. This conclusion conflicts with other experimental results (Murchie et al., 2002; Walters et al., 2003; Amiard et al., 2005). Additionally, no matter what the response of *B. pilosa* grown in LL and HL was, the light-response of photosynthesis was non-linear at low level irradiances (Fig. 2).

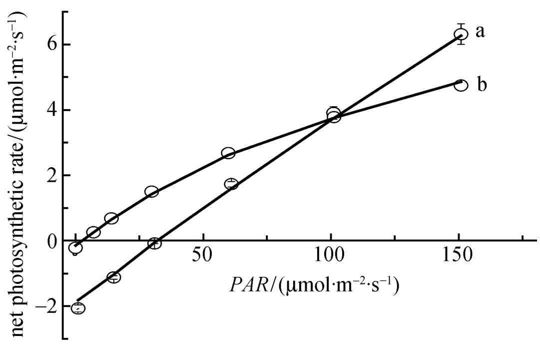

Fig. 2 Photosynthetic light-response curves of *B. pilosa* grown under high light (HL) (a) and low light (LL) (b) at low irradiances

4 Discussion

The differences in the investigated P_{max} for *B. pilosa* between growth in HL and LL observed in this study were very similar to those reported earlier for different plants (Murchie et al., 2002; Walters et al., 2003; Amiard et al., 2005; Boonman et al., 2008). Leaves exposed to HL had greater photosynthetic capacity than shaded leaves (Lambers et al., 1998). This is true in comparison with whole plants exposed to different irradiances (Evans and Poorter, 2001).

The modified rectangular hyperbola could best describe the light-response curves of photosynthesis of *B. pilosa* grown in HL and LL, including at low level irradiances and above the saturation light intensities (Figs. 1 and 2). The rectangular hyperbola (Baly, 1935), non-rectangular hyperbola (Thornley, 1976) and exponential equations (Bassman and Zwier, 1991; Prado and Moraes, 1997) did not describe the light-response curve of photosynthesis of *B. pilosa* grown in LL (Fig. 1(b)) because they were four asymptotes without extreme values.

Though $P(I)$ in *B. pilosa* grown under LL was higher than that under HL when I was below 100 μmol·m^{-2}·s^{-1} (Fig. 2), at levels above 100 μmol·m^{-2}·s^{-1}, the $P(I)$ grown in LL was less than that in HL. Additionally, I_c and R_d in *B. pilosa* grown in LL were much lower than those in HL, indicating that it is beneficial to *B. pilosa* growth and matter accumulation in LL when irradiances are at low levels. However, at the saturation light intensity, P_{max} in *B. pilosa* grown in HL condition was about 3.78 times higher than that in LL; and the I_m of *B. pilosa* grown in HL was about 2.71 times higher than that in LL, with 655.40 μmol·m^{-2}·s^{-1}I_m of *B. pilosa* grown under LL. This showed that *B. pilosa* grown in LL was easily affected by irradiance.

Table 3 AQY in *B. pilosa* grown under low light (LL) and high light (HL) conditions when irradiances were under different fitted irradiance scopes

PAR	⩽150 μmol·m^{-2}·s^{-1}	⩽100 μmol·m^{-2}·s^{-1}	⩽60 μmol·m^{-2}·s^{-1}
AQY (LL)	0.033**	0.039**	0.048**
AQY (HL)	0.056**	0.060**	0.063**

Note: ** means significance at 0.01 probability level.

Therefore, growth under LL was not beneficial to *B. pilosa* compared to growth under HL.

At present, rectangular hyperbola (Baly, 1935), non-rectangular hyperbola (Thronley, 1976) and exponential equations (Bassman and Zwier, 1991; Prado and Moraes, 1997) have been most frequently used in studies like ours, and these models and exponential equations can well describe the light-response curve of photosynthesis when the light intensity is below the saturation light intensity. However, the process of photosynthetic response to irradiance over saturation light intensity can not be described accurately by these models and exponential equations. Additionally, these P_{max} values fitted by rectangular hyperbola and non-rectangular hyperbola models were higher than the measured values (Evans et al., 1993; Kyei-Boahen et al., 2003; Yu et al., 2004; Leakey et al., 2006), and I_m could not be obtained directly by the two models (Kyei-Boahen et al., 2003; Yu et al., 2004; Leakey et al., 2006). To estimate I_m, the two models must be coupled with other methods (Walker, 1989; Richardson and Berlyn, 2002). However, I_m estimated by this method is much less than any of the measured values. Also, exponential equations (Bassman and Zwier, 1991; Prado and Moraes, 1997) can not estimate I_m directly because they are also asymptotes without the extreme value. I_m can be estimated only if $P(I)$ equals 99% P_{max}, and the corresponding light intensity is I_m. It is obvious that I_m estimated by this method does not have the real values of saturation light intensities of plants.

AQY is a powerful tool for assessing the utilization efficiency of light energy of plants (Olsson et al., 1994). It should be noted that the values fitted by linear equations are not unique (Table 2). The initial slope (α) in *B. pilosa* grown under LL was higher than that of the plants grown under HL, whereas AQY of plants grown under LL was less than that of the plants grown under HL when irradiance was below 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$. These results contradict themselves.

In conclusion, the modified rectangular hyperbola which can accurately describe the photosynthetic light-response of *B. pilosa*, grown under HL and LL, contains three parameters. It is known that *B. pilosa* grown in LL and HL has similar light-response curves of photosynthesis (Fig. 1), with their main photosynthetic parameters, e.g. P_{max}, I_m, R_d, I_c and α differing significantly. The P_{max} in *B. pilosa* grown in LL is much lower than that in HL despite $P(I)$ in LL being higher than that in HL at low irradiances (100 $\mu mol \cdot m^{-2} \cdot s^{-1}$). Furthermore, in Fig. 1b the modified model has more advantages than any one of the non-rectangular hyperbola, rectangular hyperbolas, Prado-Moraes model and exponential equation because the modified model can accurately describe *B. pilosa* grown under HL and LL in a wide range of irradiances, including low irradiances, and over saturation light intensities under different environmental conditions. The rectangular hyperbola, non-rectangular hyperbola and exponential equations do not describe the light-response curve of photosynthesis when irradiance is over the saturation light intensities. The fitted results of *B. pilosa*, grown under HL and LL showed that the modified model can, in a more simple and accurate way, describe the photosynthetic light-response curve of a leaf containing three parameters in a wide range of light intensities, which is a general model of great value for application to photosynthesis and plant physiology.

Acknowledgements We would like to thank Professor Govindjee at Illinois University (USA) for his great help and encouragement. We also thank Dr. Xinguang Zhu at Illinois University (USA) for discussions and valuable advice. This research was supported by the National Natural Science Foundation of China (Grant No. 30960031).

References

Amiard V, Mueh K E, Demmig-Adams B, Ebbert V, Turgeon R, Adams W W (2005). Anatomical and photosynthetic acclimation to the light environment in species with differing mechanisms of phloem loading. Proc Natl Acad Sci USA, 102: 12968–12973

Baly E C (1935). The kinetics of photosynthesis. Proc Roy Soc, B117: 218–239

Bassman J, Zwier J C (1991). Gas exchange characteristics of *Populus trichocarpa, Populus deltroids* and *Populus trichocarpa*×*P. deltroids* clone. Tree Physiol, 8: 145–149

Boonman A, Prinsen E, Gilmer F, Schurr U, Petters A J M, Voesenek L, Pons T L (2007). Cytokinin import rate as a signal for photosynthetic acclimation to canopy light gradients. Plant Physiol, 143: 1841–1852

Evans J G, Jakonbsen I, Ögren E (1993). Photosynthetic light-response curves. 2: Gradients of light absorption and photosynthetic capacity. Planta, 189: 191–200

Evans J R, Poorter H (2001). Photosynthetic acclimation of plants to growth irradiance: the relative importance of specific leaf area and nitrogen partitioning in maximizing carbon gain. Plant, Cell Environ, 24: 755–767

Farquhar G D, Caemmerer S, Berry J A (1980). A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. Planta, 149: 78–90

Kyei-Boahen S, Lada R, Astatkie T, Gordon R, Caldwell C (2003). Photosynthetic response of carrots to varying irradiances. Photosynthetica, 41: 1–5

Lambers H, Chapin F S, Pons T L (1998). Plant Physiological Ecology. New York: Springer

Leakey A D B, Uribelarrea M, Ainsworth E A, Naidu S L, Pogers A, Ort D R, Long S P (2006). Photosynthesis, productivity, and yield of maize are not affected by Open-Air elevation of CO_2 concentration in the absence of drought. Plant Physiol, 140: 779–790

Long S P, Humpheris S, Falkowski P G (1994). Photoinhibition of photosynthesis in nature. Annu Rev Plant Biol, 45: 633–662

Marshall H L, Geider R J, Flynn K J (2000). A mechanistic model of photoinhibition. New Phytol, 145: 347–359

Murchie E H, Hubbert S, Chen Y Z, Peng S B, Horton P (2002). Acclimation of rice photosynthesis to irradiance under field conditions. Plant Physiol, 130: 1999–2010

Ögren E, Evans J R (1993). Photosynthetic light-response curves I. the influence of CO_2 partial pressure and leaf inversion. Planta, 189: 182–190

Olsson T, Leverenz J W (1994). Non-uniform stomata closure and the apparent convexity of the photosynthetic photon flux density response curve. Plant, Cell Environ, 17: 701–710

Richardson A, Berlyn G (2002). Changes in foliar spectral reflectance and chlorophyll fluorescence of four temperate species following branch cutting. Tree Physiol, 22: 499–506

Robert E S, Mark A, John S B (1984). Kok effect and the quantum yield of photosynthesis. Plant Physiol, 75: 95–101

Thornley J H M (1976). Mathematical Models in Plant Physiology. London: Academic Press

Walker D A (1989). Automated measurement of leaf photosynthetic O_2 evolution as a function of photon flux density. Philos T R Soc, B323: 313–326

Walters R G, Shephard F, Rogers J J M, Rolfe S A, Horton P (2003). Identification of mutants of *Arabidopsis* defective in acclimation of photosynthesis to the light environment. Plant Physiol, 131: 472–481

Ye Z P (2007). A new model for relationship between light intensity and the rate of photosynthesis in *Oryza sativa*. Photosynthetica, 45: 637–640

Yu Q, Zhang Y Q, Liu Y F, Shi P L (2004). Simulation of the stomatal conductance of winter wheat in response to light, temperature and CO_2 changes. Ann Bot, 93: 435–441

Zhou Y H, Lan H M, Zhang J H (2007). Inhibition of photosynthesis and energy dissipation induced by water and high light stresses in rice. J Exp Bot, 58: 1207–1217

Zonneveld C (1998). Photoinhibition as affected by photoacclimation in phytoplankton: a model approach. J Theor Biol, 193: 115–123