Pak. J. Bot., 47(3): 877-882, 2015.

IMPROVED PERFORMANCE OF PHOTOSYNTHETIC LIGHT RESPONSE EQUATIONS WITH UNIFIED PARAMETERS FOR RICE LEAVES WITH DIFFERENT SPAD VALUES

JUNZENG XU[1,2*], YANHUA WANG [2], SHIHONG YANG[2], SHIZHANG PENG[1] AND WEILI KONG[2,3]

[1]*State Key Laboratory of Hydrology-Water Resources and Hydraulic Engineering, Hohai University, Nanjing 210098, China*
[2]*College of Water Conservancy and Hydropower Engineering, Hohai University, Nanjing 210098, China*
[3]*Quzhou Water Conservancy and Hydropower Investigation and Design Co., Ltd., Quzhou 324002, China*
**Corresponding author e-mail: xjz481@hhu.edu.cn Tel.: +86 25 83786016;*

Abstract

The rectangular hyperbola (RH), Mitscherlich (M) and YE equation were applied to describe the photosynthetic light response (PLR) curves measured from rice leaves with different SPAD values, to reveal the relationship between SPAD values and parameters in different equations, and to establish the modified PLR equations. The parameters in PLR equations are largely varied. SPAD value, as an indicator of leaf N contents, was highly correlated to the parameter of P_{nmax} in RH, M and YE equations. Incorporating the factor SPAD into PLR equations, the modified equations (MRH, MM, and MYE) were established which were feasible to describing the PLR curves for leaves with different SPAD values using the identical parameters for the ten PLR curves as a whole, and perform much better than the general PLR equations (GRH, GM, and GYE). It indicated that incorporating easy available indicators of leaf physiological and morphological traits in the PLR equations, such as SPAD as an indicator of leaf N or Chlorophyll contents, is an easy way to overcome the shortcoming of parameters variation in PLR equations between individuals of the same specie growing in different environments. Further validation should be done for different crops with both SPAD and other possible factors.

Key words: Photosynthetic light response equation, Photosynthesis, Leaf nitrogen content, SPAD, rice.

Introduction

Several photosynthetic light response (PLR) equations have been used by plant physiologists to describe the relationship between leaf net photosynthetic rate (P_n) and the available photosynthetic photon flux density (PPFD), such as rectangular hyperbola (RH), nonrectangular hyperbola (NRH), Mitscherlich (M), and YE equations (Marshall & Biscoe, 1980; Thornley, 1998; Ye, 2007; Lachapelle & Shipley, 2012; Zheng *et al*., 2012). One shared flaw is the PLR parameters in these equations are always leaf specific or environment specific, which varied greatly between both species and individuals of the same specie growing in different environments (Lambers *et al*., 1998; Lachapelle & Shipley, 2012). The reason is that the leaf photosynthetic capability is influenced by its physiological and morphological traits which were changed greatly among the crop species and the growth environments (Wright *et al*., 2004; Kattge *et al*., 2011; Hammad *et al*., 2013). For example, parameters in PLR equations were frequently found to be highly related to the leaf Chlorophyll (Chl) contents, nitrogen (N) contents, water status, light condition, leaf age and specific leaf mass (Leverenz, 1987; Evans, 1989; Stirling *et al*., 1994; Prado & Moraes, 1997; Rosati, *et al*., 1999; Milroy & Bange, 2003; Givnish *et al*., 2004; Marshall & Proctor, 2004; Quero *et al*., 2008; Zhang *et al*., 2008; Akhkha, 2010; Prieto *et al*., 2010; Lachapelle & Shipley, 2012; Chiarawipa *et al*., 2012). Recently, researchers tried to predict leaf PLR parameters using regression to leaf physiological and morphological traits (Marino *et al*., 2010; Lachapelle & Shipley, 2012; Calama *et al*., 2013).

Leaf N content is one of the most important factors linking with leaf photosynthetic capability. It has been used for predicting PLR parameters by Marino *et al*. (2010) and Lachapelle & Shipley (2012). The measurement of leaf N content is always destructive and time-consuming, the SPAD value was adopted as a popular indicator of leaf greenness, leaf Chl and N contents (Peng *et al*., 1996; Loh *et al*., 2002; Uddling *et al*., 2007; Ling *et al*., 2011; Liu *et al*., 2012), which can be measured easily and non-destructively by the commercially available equipment of SPAD-502 meter. Our recent research found that SPAD values were linearly correlated to the coefficients of initial slope of the PLR curve (α) and maximum photosynthetic rate (P_{nmax}) in the NRH equation. The SPAD-modified NRH equation established in our recent studies by incorporating the SPAD into the NRH equation performed acceptable on rice leaves with different SPAD values (Xu *et al*., 2014). But if this idea is applicable to other PLR equations, such as RH, M and YE equations, is still unknown. The objectives of this research are to evaluate the variation of parameters in RH, M and YE equations and its relationship to SPAD values, and to test the performance of the modified PLR equations established by incorporating SPAD values into the PLR equations on rice leaves with different SPAD values.

Materials and Method

Data collection: Ten PLR curves measured by using an LC Pro+ photosynthesis system (ADC BioScientific, England) at 16 PPFD levels (2,000, 1,950, 1,900, 1,800, 1,600, 1,400, 1,200, 1,000, 800, 600, 400, 200, 150, 100, 50 and 0 μmol photon m^{-2} s^{-1}) from full expanded healthy rice leaves under both high and low nitrogen treatments were collected, as well as the corresponding leaf SPAD values measured by using the SPAD-502 (Konica Minolta, Japan). Details about the treatments and measurement can be found in the reference (Xu *et al*., 2014).

PLR equations and modification: The formulae and parameters of the three PLR equations, namely RH, M and YE, are listed in Table 1. For each of the ten PLR curve, parameters in RH, M, and YE equations were determined by non-linear least-square fitting with the Levenberg-Marquardt algorithm. The general PLR equations were also established by non-linear regression over the whole data set of the ten PLR curves. Then, correlations between the parameters of different equations and leaf SPAD values were determined. Based on the correlations between parameters of different equations and leaf SPAD values, a linear correction factor (f(SPAD) = β× SPAD) was incorporated into each PLR equation to establish the modified PLR equations (namely MRH, MM, and MYE equations) (as listed in Table 1).

Statistics: Parameters in each PLR equation for each PLR curve were determined by non-linear least-square fitting, as well as the parameters in the general PLR equations and the modified equations for all the ten PLR curves. For variation analysis of PLR equation parameters, standard error (SDE) and coefficient of variation (CV) were calculated. Correlations between PLR equation parameters and SPAD values were determined. Root mean square error (RMSE) of P_n was calculated for evaluation of different equations. The performance of the modified PLR equations was also compared with the performance of general PLR equations.

Results

Performance of different PLR equations: Parameters and performance of different PLR equations for leaves with different SPAD values are listed in Table 2. It is clear that RH, M and YE equations performed well for each individual leaf. The RMSEs of P_n calculated by RH, M and YE equations fell in the range of 0.291-0.786, 0.168-0.361 and 0.185-0.381 μmol CO_2 m^{-2} s^{-1}, with average of 0.474, 0.283 and 0.285 μmol CO_2 m^{-2} s^{-1}. The M and Ye equations performed a little better than RH equation for different individual leaf. The parameters in RH, M and YE equations were largely varied. The lowest CV was found for parameter of P_{nmax} in M and RH equations, 12.4% and 12.6%. The highest CV (37.8%) was found for parameter of ε in YE equation. Thus, the large variation of parameters for RH, M and YE equations was confirmed between individual rice leaves with different leaf SPAD values. That led to poor performance of the general PLR equations for the ten PLR curves as a whole. The RMSEs were 1.88, 1.87 and 1.85 μmol CO_2 m^{-2} s^{-1}, when the P_n were calculated by general equations of RH, M and YE.

Correlations between equation parameters and leaf SPAD values: Scatter plots and correlation coefficients between the parameters in RH, M and YE equations and leaf SPAD values are plotted in Figures 1 and 2. For RH and M equations, correlation was significant between parameter P_{nmax} and SPAD, but insignificant for parameters of α, R_d, q_{LCP} and LCP. For YE equation, all the four parameters, α, R_d, ε and γ, were insignificantly related to the SPAD values. Since ε and γ in YE equation were characterized as the parameters without physical meaning, saturation irradiance I_m and P_{nmax} were calculated as:

$$I_m = (\sqrt{(\varepsilon+\gamma)/\varepsilon} - 1)/\gamma \quad \text{and} \quad P_{n\max} = P_n(I_m) = \alpha(1-\varepsilon I_m)/(1+\gamma I_m)I_m - R_d$$ (Ye, 2007)

Table 1. Formulas and parameters for rectangular hyperbola (RH), nonrectangular hyperbola (NRH), Mitscherlich (M), and YE equations and the modified equations.

Equation	Formula	Parameters
RH	$P_n(I) = \frac{\alpha I P_{n\max}}{\alpha I + P_{n\max}} - R_d$	I is PPFD, μmol photon m^{-2} s^{-1}; P_{nmax} is maximum net photosynthesis rate, μmol CO_2 m^{-2} s^{-1}; R_d is the dark respiration, μmol CO_2 m^{-2} s^{-1}; α is the initial slope of the PLR curve, μmol CO_2 μmol^{-1} photons; ε and γ are coefficients. LCP is light compensation point, μmol photon m^{-2} s^{-1}; q_{LCP} is apparent quantum yield at compensation point, μmol CO_2 μmol^{-1} photons; β is the coefficient; SPAD is the leaf SPAD value
MRH	$P_n(I) = \frac{\alpha I P_{n\max}}{\alpha I + P_{n\max}} \beta SPAD - R_d$	
M	$P_n(I) = P_{n\max}(1 - e^{\frac{-q_{LCP}(I-LCP)}{P_{n\max}}})$	
MM	$P_n(I) = P_{n\max}(1 - e^{\frac{-q_{LCP}(I-LCP)}{P_{n\max}}})\beta SPAD$	
YE	$P_n(I) = \alpha \frac{1-\varepsilon I}{1+\gamma I} I - R_d$	
MYE	$P_n(I) = \alpha \frac{1-\varepsilon I}{1+\gamma I} I \beta SPAD - R_d$	

Regressions between SPAD and parameters were I_m = 22.855 SPAD + 1218.5 (R^2 = 0.0337) and P_{nmax} = 0.491 SPAD - 2.0917 (R^2 = 0.6496, $p < 0.05$). When it comes to the NRH equation, correlations were significant between SPAD and parameters of P_{nmax} and α, but insignificant for parameters of θ and R_d (Xu *et al*., 2014). Thus, SPAD is significantly positively related to the parameter P_{nmax} of all the four PLR equations (P_{nmax} calculated from parameters of YE equation), but SPAD is insignificantly related to other parameters in the PLR equations except for the parameter α in NRH equation (Xu *et al*., 2014).

Table 2. Parameters and performance of different photosynthetic light response equation.

SPAD	RH				M				YE				
	Parameters			RMSE	Parameters			RMSE	Parameters				RMSE
	A	P_{nmax}	R_d		P_{nmax}	q_{LCP}	LCP		α	ε	γ	R_d	
49.50	0.0714	30.96	1.94	0.786	23.18	0.0506	26.84	0.361	0.0522	0.000157	0.00101	1.25	0.360
49.11	0.0656	29.38	1.83	0.608	21.93	0.0466	26.94	0.313	0.0522	0.000115	0.00126	1.36	0.381
46.17	0.0383	28.17	1.15	0.410	20.23	0.0298	26.49	0.358	0.0327	0.000096	0.00083	0.89	0.352
49.14	0.0481	27.15	1.12	0.323	20.30	0.0356	17.07	0.326	0.0440	0.000047	0.00142	0.96	0.293
42.35	0.0589	26.02	1.82	0.406	19.29	0.0407	30.55	0.168	0.0477	0.000101	0.00137	1.44	0.201
40.23	0.0419	25.86	1.29	0.484	18.83	0.0315	28.38	0.274	0.0302	0.000179	0.00055	0.71	0.185
43.4	0.0607	27.2	1.32	0.518	20.72	0.0434	17.48	0.240	0.0469	0.000126	0.00116	0.80	0.250
40.14	0.0427	19.49	0.97	0.291	14.82	0.0302	16.95	0.282	0.0383	0.000055	0.00169	0.81	0.256
49.17	0.0512	32.19	1.15	0.407	23.84	0.0392	16.78	0.281	0.0436	0.000091	0.00100	0.82	0.293
41.54	0.0588	28.17	1.54	0.509	21.07	0.0424	23.89	0.223	0.0468	0.000116	0.00116	1.09	0.281
MAX	0.0714	32.19	1.94	-	23.84	0.0506	26.94	-	0.0522	0.000179	0.00169	1.44	-
MIN	0.0383	19.49	0.97	-	14.82	0.0298	16.78	-	0.0302	0.000055	0.00055	0.80	-
SDE	0.0111	3.46	0.35	-	2.52	0.0071	5.47	-	0.00756	0.000041	0.00032	0.26	-
CV	20.6%	12.6%	24.8%	-	12.4%	18.2%	23.6%	-	17.4%	37.8%	28.3%	25.4%	-
General	0.0537	27.29	1.43	1.88	20.34	0.0391	23.52	1.85	0.0434	0.000111	0.00112	1.02	1.85
Modified	0.0568	30.45	1.10	1.51	23.86	0.0459	23.69	1.44	0.0469	0.000118	0.00105	0.863	1.45
	β= 0.0199				β= 0.0189				β= 0.0199				

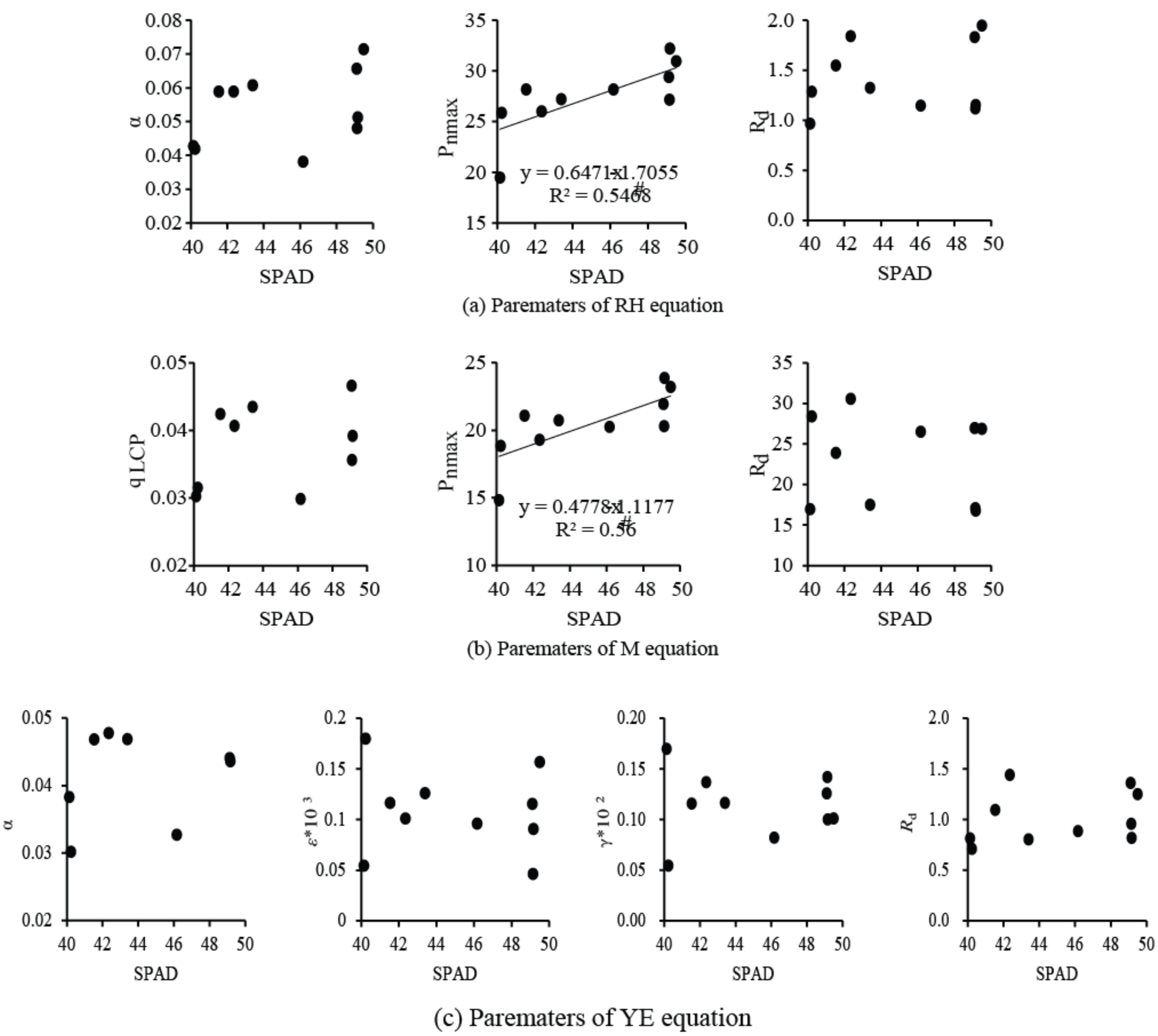

Fig. 1. Scatter plots between parameters in rectangular hyperbola (RH), Mitscherlich (M), and YE equations and leaf SPAD values. (# indicates the linear regression is significant at p<0.05).

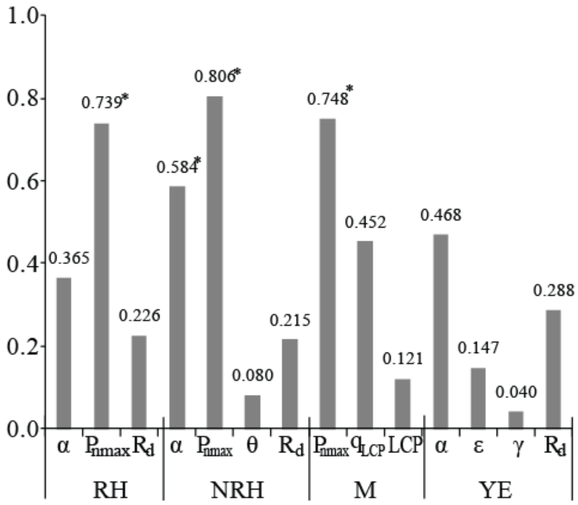

Fig. 2. Correlations between parameters in rectangular hyperbola (RH), nonrectangular hyperbola (NRH), Mitscherlich (M) and YE equations and leaf SPAD values. (* indicate the correlations coefficient R is significant at $p<0.05$; The correlation between SPAD and parameters in NRH equation is cited from reference (Xu *et al*., 2014)).

Modification of PLR equations: The modified equations, MRH, MM, and MYE, were established by incorporating a linear correcting factor ($\beta\times$ SPAD). The parameters are listed in Table 2. The values of β for MRH, MM, and MYE, were 0.0199, 0.0189, and 0.0199. The reverse values of β in all the three modified equations are higher than the maximum value of SPAD for the ten leaves (49.5). It means the correcting factor of $\beta\times$ SPAD is always lower than 1.0, which implies that leaf without N deficit has high photosynthetic capability, reduced SPAD lead to a lower value of correcting factor $\beta\times$ SPAD. Other parameters in the modified equations were different from the average value of the correspondence parameter of the ten values for specific leaf. The RMSE of the P_n, calculated by the MRH, MM, and MYE equations, were 1.44, 1.39 and 1.34 μmol CO_2 m^{-2} s^{-1}, much lower than the RMSE of P_n calculated by the general equations of GRH, GM, and GYE. Scatter plots (Fig. 3) indicated that the P_n, calculated by the modified equations were more close to the observed than those by the general equations, especially when the P_n was larger than 10 μmol CO_2 m^{-2} s^{-1} (correspondingly PPFD > 400μmol photon m^{-2} s^{-1}).

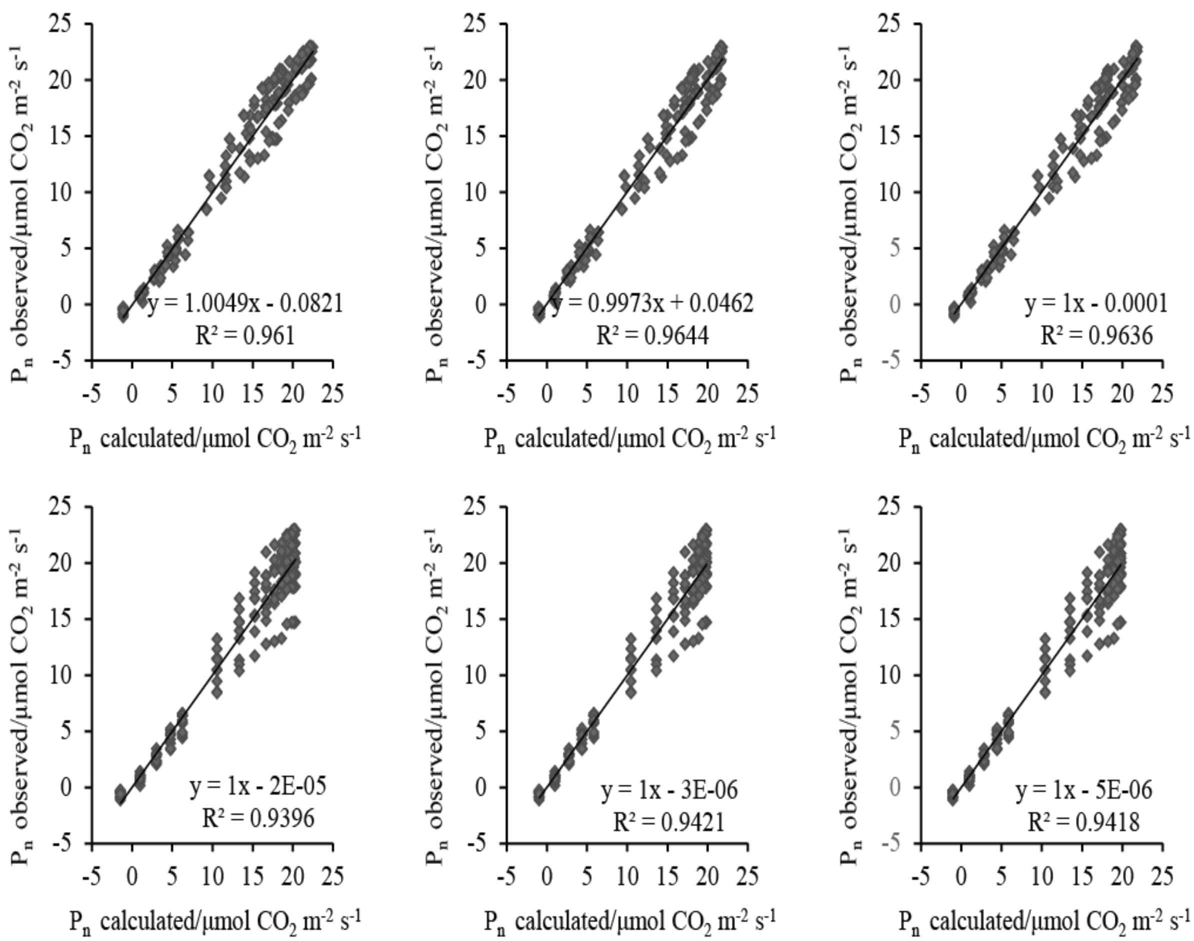

Fig. 3. Observed versus predicted net photosynthetic rates P_n calculated by different photosynthetic light response equation PLR equations. (MRH, MM and MYE denote the modified rectangular hyperbola, modified Mitscherlich, and modified YE equations. GRH, GM and GYE denote the general rectangular hyperbola, general Mitscherlich, and general YE equations).

Discussion

Leaf with different SPAD values has different values of parameters in the typical PLR equations. It confirmed that parameters in the typical PLR equations are largely varied between individual leaves growing in different environments (Lambers *et al*., 1998; Lachapelle & Shipley, 2012). The SPAD value has been tested be a useful indicator of leaf N contents, which was positively linearly correlated to the parameter of P_{nmax} and α in the NRH equation (Xu *et al*., 2014). In current paper, the SPAD value was also positively linearly correlated to the parameter of P_{nmax} in the RH, M and YE equations (Figs. 1 and 2). But Marino *et al*. (2010) and Lachapelle & Shipley (2012) reported a log-linear relationship between coefficients of Mitscherlich or Michaelis-Menten PLR equations and leaf N contents and specific leaf mass. Thus, it is believed that the linear correcting factor of $\beta\times$ SPAD (as listed in Table 1) should be further validated using more PLR curves measured under the conditions of a large varied degree of N deficit, due to the high value of SPAD (from 40.14 to 49.50) in current research and the nonlinear relation between SPAD values and leaf N or Chl contents was sometimes reported by Uddling *et al*. (2007) and Liu *et al*. (2012).

Incorporating the linear correcting factor of $\beta\times$ SPAD into the typical PLR equations, the modified equations (MRH, MM, and MYE) were established, which was feasible to describing the PLR curves for leaves with different SPAD values with unified parameters, and performed better than the general PLR equations (GRH, GM, and GYE) (Fig. 3). The current method is similar to the two-steps method presented by Marino *et al*. (2010), Lachapelle & Shipley (2012), and Calama *et al*. (2013), who predicted the parameters in PLR equations based on the regressions to leaf traits and calculated P_n by different PLR equations with the predicted parameters. The current research just combined the two steps together into a single formula for each equation. Furthermore, this research used the values of SPAD which can be measured easily and non-destructively as the substitute of leaf N contents or leaf Chlorophyll contents.

Based on the current and other relevant researches (Marino *et al*., 2010; Lachapelle & Shipley, 2012; Calama *et al*., 2013; Xu *et al*., 2014), we would like deduced that incorporating the factor of leaf physiological and morphological traits which are highly correlated with the leaf photosynthetic capability, is a reasonable and feasible way to present new method to overcome the shortcoming of parameters variation in PLR equations between individuals of the same specie growing in different environment. According to current research, the easy available substitute of the leaf physiological and morphological traits was preferred being used in the different PLR equations. As an easy available substitute of leaf N contents or leaf Chl contents, SPAD was testified can be used as an indicator of leaf N or Chl contents in the modification of different PLR equations, but the current research were carried out with other factors almost the same. Assuming crop leaf photosynthetic capability are also influenced by factors other than leaf N or Chl contents, such as water status, light condition, leaf age and leaf thickness, the same idea should be validated for many other factors related to leaf photosynthetic capability.

Conclusions

Parameters in the RH, M and YE equations varied greatly between rice leaves with different SPAD values, with parameter P_{nmax} positively linearly correlated to the SPAD values. Incorporating the linear correcting factor of $\beta\times$ SPAD into the PLR equations, the modified equations (MRH, MM, and MYE) were established which was feasible to describing the PLR curves for leaf with different SPAD values with the unified parameters, and perform better than the general PLR equations (GRH, GM, and GYE). It indicated that incorporating easy available indicators of leaf physiological and morphological traits into the PLR equations, such as SPAD as an indicator of leaf N or Chl contents, is an easy way to overcome the shortcoming of parameters variation in PLR equations between individual leaves of the same specie growing in different environments. Further validation should be done for different crops and many other factors related to leaf photosynthetic capability.

Acknowledgments

The research was financially supported by the Fundamental Research Funds for the Central Universities (No. 2012B07514), the National Natural Science Foundation of China (No. 51179051), Jiangsu Overseas Research & Training Program for University Prominent Young & Middle-aged Teachers and Presidents, and Advanced Science and Technology Innovation in Colleges and Universities in Jiangsu Province.

References

Akhkha, A. 2010. Modelling photosynthetic light-response curve in *Calotropis procera* under salinity or water deficit stress using non-linear models. *Journal of Taibah University for Science*, 3: 49-57.

Calama, R., J. Puértolas, G. Madrigal and M. Pardos. 2013. Modeling the environmental response of leaf net photosynthesis in *Pinus pinea L*. natural regeneration. *Ecological Modelling*, 251: 9-21.

Chiarawipa, R., Y. Wang, X.Z. Zhang, Z.H. Han and M. Rueangkhanab. 2012. Modeling light acclimation of photosynthetic response in different ages of vine leaves. *ISHS Acta Horticulturae*, 956: 255-260.

Evans, J.R. 1989. Photosynthesis and nitrogen relationships in leaves of C_3 plants. *Oecologia*, 78: 9-19.

Givnish, T.J., R.A. Montgomery and G. Goldstein. 2004. Adaptive radiation of photosynthetic physiology in the *Hawaiian lobeliads*: light regimes, static light responses, and whole-plant compensation points. *Am. J. Bot.*, 91: 228-24.

Hammad, H.M., A. Ahmad, W. Farhad, F. Abbas, K. Qasim and S. Saeed. 2013. Nitrogen stimulates phenological traits, growth and growing degree days of maize. *Pak. J. Agri. Sci*., 50:337-343.

Kattge, J., S. Diaz, S. Lavorel, I.C. Prentice, P. Leadley, G. Bonish, E. Garnier, M. Westoby, P.B. Reich, I.J. Wright, J.H.C. Cornetlissen, C. Violle, S. Pharrison, P.M.V. Bodegom, M. Reichstein, B.J. Enquist, N.A. Soudzilovskaia, D.D. Ackerly, M. Anand, O. Atkin, M. Bahn, T.R. Baker, D. Baldocchi, R. Bekker, C.C. Blanco, B. Blonder, W.J. Bond, R. Bradstock, D.E. Bunker, F. Casanoves, J.C. Bares, J.Q. Chambers, F.S. Chapin, J. Chave, D. Coomes, W.K. Cornwell, J.M. Craine, B.H. Dobrin, L. Duarte, W. Durka, J.

Elser, G. Esser, M. Estiarte, W.F. Fagan, J. Fang, F.F. Mendez, A. Fiedlis, B. Finegan, O. Flores, H. Ford, D. Frank, G.T. Freshet, N.M. Fyllas, R.V. Gallagher, W.A. Green, A.G. Gutierrez, T. Hickler, S.I. Higgins, J.G. Hodgson, A. Jalili, S. Jansen, C.A. Joly, A.J. Kerkhoff, D. Kirkup, K. Kitajima, M. Kleyer, S. Klotz, J.M.H. Knops, K. Kramer, I. Kuhn, H. Kurokawa, D. Laughlin, T.D. Lee, M. Leishman, F. Lens, T. Lenz, S.L. Lewis, J. Lloyd, J. Llusia, F. Louault, S. Ma, M.D. Mahecha, P. Manning, T. Massad, B.E. Medlyn, J. Messier, A.T. Molesa, S.C. Muller, K. Nadrowski, S. Naeem, U. Niinemets, S. Nollert, A. Nuske, R. Ogaya, J. Oleksyn, V.G. Onipchenko, Y. Onoda, J. Ordonez, G. Overbeck, W.A. Ozinga, S. Patino, S. Paula, J.G. Pausas, J. Penuelas, O.L. Phillips, V. Pillar, H. Poorter, L. Poorter, P. Poschlod, A. Prinzing, R. Proulx, A. Rammig, S. Reinsch, B. Reu, L. Sack, B.S. Negret, J. Sardans, S. Shiodera, B. Shipley, A. Seefert, E. Sosinski, J.F. Soussana, E. Swaine, N. Swenson, K. Thompson, P. Thornton, B. Yguel, S. Zaehle, A.E Zanne and C. Wirth. 2011. TRY – A global database of plant traits. *Global Change Biology*, 17: 2905-2935.

Lachapelle, P.P. and B. Shipley. 2012. Interspecific prediction of photosynthetic light response curves using specific leaf mass and leaf nitrogen content: effects of differences in soil fertility and growth irradiance. *Ann. Bot.*, 109: 1149-1157.

Lambers, H., F.S. Chapin and T.L. Pons. 1998. *Plant physiological ecology*. New York: Springer.

Leverenz, J.W. 1987. Chlorophyll content and the light response curve of shade-adapted conifer needles. *Physiologia Plantarum*, 71: 20-29.

Ling, Q., W. Huang and P. Jarvis. 2011. Use of a SPAD-502 meter to measure leaf chlorophyll concentration in Arabidopsis thaliana. *Photosynthesis Res.*, 107: 209-214.

Liu, Z.A., J.P. Yang and Z.C. Yang. 2012. Using a chlorophyll meter to estimate tea leaf chlorophyll and nitrogen contents. *J. Soil Sci. Plant Nut.*, 12: 339-348.

Loh, F.C.W., J.C. Grabosky and N.L. Bassuk. 2002. Using the SPAD-502 meter to assess chlorophyll and nitrogen content of Benjamin fig and Cottonwood leaves. *Hort. Tech.*, 12: 682-686.

Marino, G., M. Aqil and B. Shipley. 2010. The leaf economics spectrum and the prediction of photosynthetic light response curves. *Functional Ecology*, 24: 263-272.

Marshall, B. and P.V. Biscoe. 1980. A model for C_3 leaves describing the dependence of net photosynthesis on irradiance. I. Derivation. *J. Exp. Bot.*, 120: 29-39.

Marschall, M. and C.F. Proctor. 2004. Are bryophytes shade plants? Photosynthetic light responses and proportions of chlorophyll a, chlorophyll b and total carotenoids. *Ann. Bot.*, 94: 593-603.

Milroy, S.P. and M.P. Bange. 2003. Nitrogen and light responses of cotton photosynthesis and implications for crop growth. *Crop Sci.*, 43: 904-913.

Peng, S., F.V. Garcia, R.C. Laza, A.L. Sanico, R.M. Visperas and K.G. Cassman. 1996. Increased N-use efficiency using a chlorophyll meter on high yielding irrigation rice. *Field Crops Res.*, 47: 243-252.

Prieto, J,A,, E,G, Giorgi and J.P. Pena. 2010. Modelling photosynthetic-light response on Syrah leaves with different exposure. *Vitis*, 49: 145-146.

Prado, C.H.B.A. and J.A.P.V. Moraes. 1997. Photosynthetic capacity and specific leaf mass in twenty woody species of Cerrado vegetation under field condition. *Photosynthetica*, 33: 103-112.

Quero, J.L., R. Villar and T. Marañón. 2008. Leaf traits and photosynthesis light response of *Quercus suber* seedlings grown in a combination of light and water regimes. In: *Suberwood, new challenges for the integration of cork oak forests and products.* (Eds.): J. Vázquez-Piqué, H. Pereira and A. González-Pérez. Universidad de Huelva, Huelva, pp. 75-84.

Rosati, A., G. Esparza, T.M. Dejong and R.W. Pearcy. 1999. Influence of canopy light environment and nitrogen availability on leaf photosynthetic characteristics and photosynthetic nitrogen-use efficiency of field-grown nectarine trees. *Tree Physiology*, 19: 173-180.

Stirling, C.M., C. Aguilera, N.R. Baker and S.P. Long. 1994. Changes in the photosynthetic light response curve during leaf development of field grown maize with implications for modelling canopy photosynthesis. *Photosynthesis Res.*, 42: 217-225.

Thornley, J.H.M. 1998. Dynamic model of leaf photosynthesis with acclimation to light and nitrogen. *Ann. Bot.*, 81: 421-430.

Uddling, J., J.G. Alfredsson, K. Piikki and H. Pleijel. 2007. Evaluating the relationship between leaf chlorophyll concentration and SPAD-502 chlorophyll meter readings. *Photosynthesis Res.,* 91: 37-46.

Wright, I.J., P.B. Reich, M. Westoby, D.D. Ackerl, Z. Baruch, F. Bongers, J.C. Bares, T. Chapin, J.H.C. Cornelissen, M. Diemer, J. Flexas, E. Garnier, P.K. Groom, J. Gulias, K. Hikosaka, B.B. Lamont, T. Lee, W. Lee, C. Lusk, J.J. Midgley, M.L. Navas, U. Niinemets, J. Oleksyn, N. Osada, H. Poorter, P. Poot, L. Prior, V.I. Pyankov, C. Roumet, S.C. Thomas, M.G. Tjoelker, E.J. Veneklaas and R. Villar. 2004. The worldwide leaf economics spectrum. *Nature,* 428: 821-827.

Xu, J.Z., Y.M. Yu, S.Z. Peng, S.H. Yang and L.X. Liao. 2014. A modified nonrectangular hyperbola equation to describe photosynthetic light response curves with different leaf nitrogen status. *Photosynthetica,* 52: 117-123

Ye, Z.P. 2007. A new model for relationship between irradiance and the rate of photosynthesis in *Oryza sativa*. *Photosynthetica*, 45: 637-640.

Zhang, S.B., H. Hu and Z.R. Li. 2008. Variation of photosynthetic capacity with leaf age in an alpine orchid, *Cypripedium flavum. Acta Physiologiae Plantarum,* 30: 381-388.

Zheng, Y., Z. Zhao, J.J. Zhou and H. Zhou. 2012. Evaluations of different leaf and canopy photosynthesis models: a case study with black Locust (*Robinia Pseudoacacia*) plantations on a loess plateau. *Pak. J. Bot.,* 44: 531-539.

(Received for publication 10 March 2014)