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A modified nonrectangular hyperbola equation for photosynthetic light-response curves of leaves with different nitrogen status

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Abstract

Chlorophyll index and leaf nitrogen status (SPAD value) was incorporated into the nonrectangular hyperbola (NRH) equation for photosynthetic light-response (PLR) curve to establish a modified NRH equation to overcome the parameter variation. Ten PLR curves measured on rice leaves with different SPAD values were collected from pot experiments with different nitrogen (N) dosages. The coefficients of initial slope of the PLR curve and the maximum net photosynthetic rate in NRH equation increased linearly with the increase of leaf SPAD. The modified NRH equation was established by multiplying a linear SPAD-based adjustment factor with the NRH equation. It was sufficient in describing the PLR curves with unified coefficients for rice leaf with different SPAD values. SPAD value, as the indicator of leaf N status, could be used for modification of NRH equation to overcome the shortcoming of large coefficient variations between individual leaves with different N status. The performance of the SPAD-modified NRH equation should be further validated by data collected from different kinds of plants growing under different environments.

Additional key words: leaf nitrogen; modified nonrectangular hyperbola equation; *Oryza sativa*; photosynthetic light-response curve; SPAD.

Introduction

The PLR curve, which describes the relationship between the leaf net photosynthetic rate (P_N) and the available photosynthetically photon flux density (PPFD), is an analytical tool that helps to identify important features of photosynthetic capability. Several equations have been used by plant physiologists to describe the PLR curve (Thornley 1976, Farquhar *et al*. 1980, Marshall and Biscoe 1980, Hanson *et al.*1987, Xu *et al.* 1995, Ye 2007, Ye *et al.* 2013), among which the NRH equation was one of the most popular (Thornley 1998, Prieto *et al.* 2010, Calama *et al.* 2013), although it performed poorly when photoinhibition occurred under strong light and it always overestimated the parameter of the maximum net photosynthetic rate (P_{Nmax}) (Ye 2007, Ye *et al.* 2013).

Leaf photosynthetic capability is influenced by leaf physiological and morphological features (Wright *et al.* 2004). As a result, the coefficient in PLR curves varies greatly both among species and among individuals of the same species growing in different environments (Lambers *et al.* 1998, Lachapelle and Shipley 2012). For example, the coefficients in the PLR equations for different crops were frequently found to be related to the chlorophyll (Chl) contents, N contents, water status, position, light condition, age, specific leaf mass, and CO_2 concentrations (Leverenz 1987, Evans 1989, Xu *et al.* 1997, Prado and Moraes 1997, Rosati *et al.* 1999, Akhkha *et al.* 2001, Milroy and Bange 2003, Givnish *et al.* 2004, Marshall and Proctor 2004, Quero *et al.* 2008, Akhkha 2010, Marino *et al.* 2010, Lachapelle and Shipley 2012, Chiarawipa *et al.* 2012, Calama *et al.* 2013). When it comes to paddy rice, one of the most important cereal crops in Asian monsoon regions, the photosynthetic characteristics of rice leaves were also related to leaf N content, specific leaf mass, light condition, leaf position, and water stress (Cook and Evans 1983a,b; Peng *et al*. 1995,

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Abbreviations: AE – absolute error; Chl – chlorophyll; N – nitrogen; N1, N2 – the nitrogen fertilization rates, namely 300 (N1) and 200 (N2) kg(N) ha^{-1}; P_N – net photosynthetic rate; P_{Nmax} – maximum net photosynthetic rate; PLR – photosynthetic light response; PPFD – photosynthetically photon flux density; R_D – dark respiration; RMSE – root mean square error; α – initial slope of the PLR curve; β – parameter introduced by incorporating the SPAD-based factor into NRH equation; θ – parameter of the convexity of the PLR curve.
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Murchie *et al.* 2002, Matsuda *et al.* 2004, Marshall and Proctor 2004, Zhang *et al.* 2005, Ohsumi *et al.* 2007, Zhou *et al.* 2007).

However, those factors were always overlooked in PLR equations. Only few researchers predicted the PLR equation coefficients using regression to leaf physiological and morphological features. Calama *et al.* (2013) calculated the parameters in the NRH equation by regression models with leaf temperature, soil moisture, global site factor, and needle type as inputs, and then predicted the P_N of pine needles by using the NRH equation. Marino *et al.* (2010) and Lachapelle and Shipley (2012) established allometric equations for estimating parameters of Mitscherlich and Michaelis-Menten PLR equations with the leaf N content and specific leaf mass as inputs, and then applied the estimated parameters for P_N estimation. Those modifications of PLR equations mentioned above were all established for upland crops. When it comes to rice, Ohsumi *et al.* (2007) took leaf N contents into the model to calculate the leaf photosynthetic rate based on the difference between CO_2 concentrations at leaf surface and in intercellular airspaces, the internal conductance, and stomatal conductance. But according to our best knowledge, no research was done on rice to incorporate those factors into the PLR equations.

The leaf N content was one of the most important factors linking to leaf photosynthetic capability, and it was used for predicting parameters of the PLR curves by Marino *et al.* (2010) and Lachapelle and Shipley (2012). The chemical determination of leaf N or Chl contents is always destructive and time-consuming. Nondestructive, portable Chl meters (such as *Konica Minolta SPAD-502* and *Opti-Sciences CCM-200*) are adopted as convenient substitutes. The *SPAD-502* Chl meter measures SPAD (Soil Plant Analysis Development) value based on the transmission of red light at 650 nm, at which Chl absorbs light, and transmission of infrared light at 940 nm, at which no absorption occurs (Wood *et al.* 1993, Markwell *et al.* 1995). Compared to the traditional, destructive methods, this equipment might provide a substantial saving in time, space, and resources. The SPAD value is a popular indicator to reflect the 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). It is still unknown, if the easy available SPAD value can be incorporated into the PLR equation as the indicator of the leaf N contents to present the universal PLR equation with identical parameters for certain plant species growing under different N status.

Thus, in current research with rice, the SPAD value was incorporated into the NRH equation, to establish the modified NRH equation which can be used to describe the PLR curves of rice leaves with different N status using the unified parameters.

Materials and methods

Experiment and measurement: Pot experiments were conducted in 2008 at Kunshan irrigation and drainage experimental station (31º15′15″N, 120°57′43″E) in the subtropical monsoon climate region of China. The study area has the average annual air temperature of 15.5°C and the mean annual precipitation of 1,097 mm. The soil was of a yellow mud type, a waterloggogenic paddy soil formed from lacustrine deposit. The top 20 cm of soil was collected in a zig-zag pattern from the field with long-term (> 50 years) rice cultivation. The soil samples were air-dried and ground before they were passed through a 5-mm sieve to remove sand and coarse root fragments, and then mixed thoroughly. The contents of soil organic matter and total N were 30.3 g kg^{-1} and 1.8 g kg^{-1}. The soil was filled into the bottom-sealed pots (16 cm in diameter, 45 cm high) with a bulk density of 1.35 g cm^{-3} for 10–40 cm deep soil, and 1.30 g cm^{-3} for 0–10 cm top soil. The pots were buried (with 10 cm of the pots above ground) in a rice field to avoid warming of the pots and soil inside. The pots were flooded and puddled, and a basal fertilizer was mixed into the soil before rice (*Oryza sativa* Linn. subsp. *japonica* Kato, variety Jia 33) was transplanted with 3 tillers in each pot on June 25, 2008.

Two N fertilization rates were used in the pot experiments, 300 (N1) and 200 (N2) kg(N) ha^{-1}. Urea was used as the N fertilizer, and it was applied in three split doses (the basal fertilizer/ tiller fertilizer/ panicle fertilizer ratio was = 5:3:2). All pots also received the basal application of 105 kg(P_2O_5) ha^{-1} and 105 kg(K_2O) ha^{-1}. The leaf PLR curve were measured by using an *LC-Pro+* photosynthesis system (*ADC BioScientific Ltd*., Hoddesdon, UK) at clear sky. The second youngest, fully expanded, healthy rice leaves from different N treatments were selected and illuminated at a PPFD of 2,000 μmol m^{-2} s^{-1} until a steady state was reached. Then P_N was measured at 16 levels of PPFD (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 m^{-2} s^{-1}), with the temperature and relative humidity of 30 ± 1°C and 75 ± 1%, respectively. Triplicate readings of SPAD were taken near the midrib of the same leaf by using the Chl meter (*SPAD-502*, *Konica Minolta*, Osaka, Japan) (Loh *et al.* 2002). Ten PLR curves and the corresponding leaf SPAD values measured during August 10–21 (in the jointing-booting stage) were selected for the calibration and modification of the NRH equation.

Nonrectangular hyperbola and modified nonrectangular hyperbola equations: For each PLR curve, coefficients of the NRH equation (Eq. 1) were determined by nonlinear least-square fitting. Based on the correlation between the coefficients of the NRH equations and the leaf SPAD values, the modified NRH equation (Eq. 2) was established by incorporating the SPAD into the NRH equation. Thus, we assumed that initial slope of the PLR curve (α) and P_{Nmax} in the modified NRH equation was equal to the maximum value for the NRH equations for the ten PLR curves, and then the parameter of the convexity of the PLR curve (θ), dark respiration (R_D), and the parameter introduced by incorporating the SPAD-based factor into NRH equation (β) in the Eq. 2 were also determined by nonlinear least-square fitting, based on all ten PLR curve data.

The NRH equation was as follows (Marshall and Biscoe 1980, Thornley 1998):

$$P_N(I) = \frac{\alpha I + P_{Nmax} - \sqrt{(\alpha I + P_{Nmax})^2 - 4\theta \alpha I P_{Nmax}}}{2\theta} - R_D \quad (1)$$

where I is PPFD and θ is the convexity of the PLR curve.

The modified NRH equation was as follows:

$$P_N(I) = \beta \frac{\alpha I + P_{Nmax} - \sqrt{(\alpha I + P_{Nmax})^2 - 4\theta \alpha I P_{Nmax}}}{2\theta} \mathrm{SPAD} - R_D \quad (2)$$

Statistical analysis: The coefficients in the NRH equation (Eq. 1) and in the modified NRH equation (Eq. 2) were determined by nonlinear least-square fitting, which were realized by the *1stOPT* (*7D-Soft High Technology Inc.*, China) with Levenberg-Marquardt (LM) algorithm. For the performance evaluation of the NRH and modified NRH equations, the errors of P_N were calculated by Eqs. 3 and 4 from the values calculated by different equations compared with the observed values, including the average absolute error (AE) and the root mean square error (RMSE). The performance of the modified NRH equation was also compared with the general NRH equation, which was established by nonlinear least square regression over the whole data set of ten PLR curves. Scatter plots between P_N values calculated by different equations and observed values were used to evaluate the performance of both modified NRH and the general NRH equation, as well as the linear regressions of P_{Nobs} = a + b P_{Ncal} (Piñeiro *et al.* 2008).

$$\mathrm{AE} = \frac{1}{n}\sum_{i=1}^{n} \left| P_{Ncal,i} - P_{Nobs,i} \right| \quad (3)$$

$$\mathrm{RMSE} = \sqrt{\frac{1}{n}\sum_{i=1}^{n} (P_{Ncal,i} - P_{Nobs,i})^2} \quad (4)$$

where $P_{Ncal,i}$ and $P_{Nobs,i}$ are the P_N calculated by the different equations and the corresponding observed value. n = 160 is the total number of P_N data.

Results

PLR curves with different SPAD values: The SPAD values were significantly higher in N1 treatment than in N2 treatment and resulted in the higher P_N rate at high PPFD level in N1 treatment (Fig. 1). The difference in P_N between leaves with different SPAD was small when the PPFD was lower than 500 μmol(photon) m^{-2} s^{-1}, and the difference in P_N increased when the PPFD was high. The maximum P_N increased from 14.70 (in the leaf with SPAD of 40.14) to 22.88 μmol(CO_2) m^{-2} s^{-1} (in the leaf with SPAD of 49.17). Generally, the leaves with higher SPAD values had the higher P_N rates at high PPFD. However, curves from leaves with SPAD of 41.54 and 43.4 of the N2 treatment showed slightly higher P_{Nmax} value than the curves with SPAD of 49.14 and 46.17 from the N1 treatment. That might be ascribed to the difference in leaf age, which was another important trait related to leaf photosynthesis (Chiarawipa *et al.* 2012).

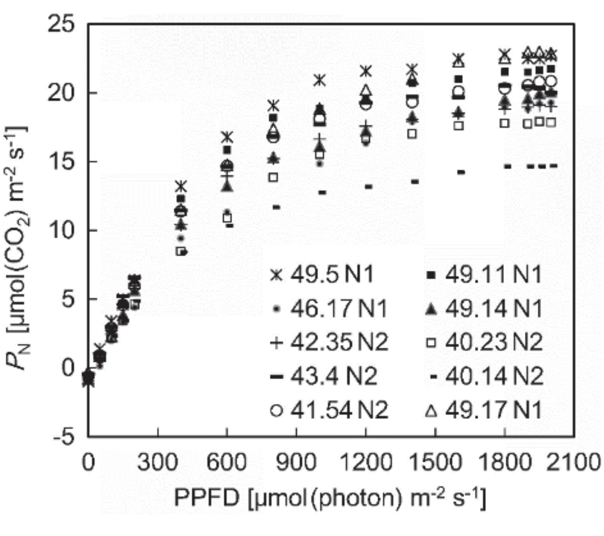

Fig. 1. Net photosynthetic rate (P_N) response to available photosynthetically photon flux density (PPFD) for rice leaves with different SPAD values. N1 and N2 – 300 kg(N) ha^{-1} and 200 kg(N) ha^{-1} treatments, respectively.

Coefficients of NRH equation *vs.* SPAD: For each PLR curve, the NRH equation fitted very well, with RMSE ranging from 0.140 to 0.341 μmol(CO_2) m^{-2} s^{-1} (mean = 0.221). Some researchers found that the NRH equation performed poorly when photoinhibition occurred under strong light (Ye 2007, Ye *et al.* 2013). In the current research, it performed well because there was no photoinhibition found in the PLR curves (Fig. 1). But the problem was that the parameters largely varied among the different PLR curves. The coefficients varied in the NRH equation for each PLR curve with the change of leaf SPAD. α, P_{Nmax}, θ, and R_D varied in the ranges of 0.0252–0.0412, 17.51–27.89, 0.486–0.856, and 0.456–1.205, respectively, with the average values of 0.0365, 23.44, 0.671, and 0.772, respectively. The coefficients of α and P_{Nmax} increased linearly with the increase of leaf SPAD,

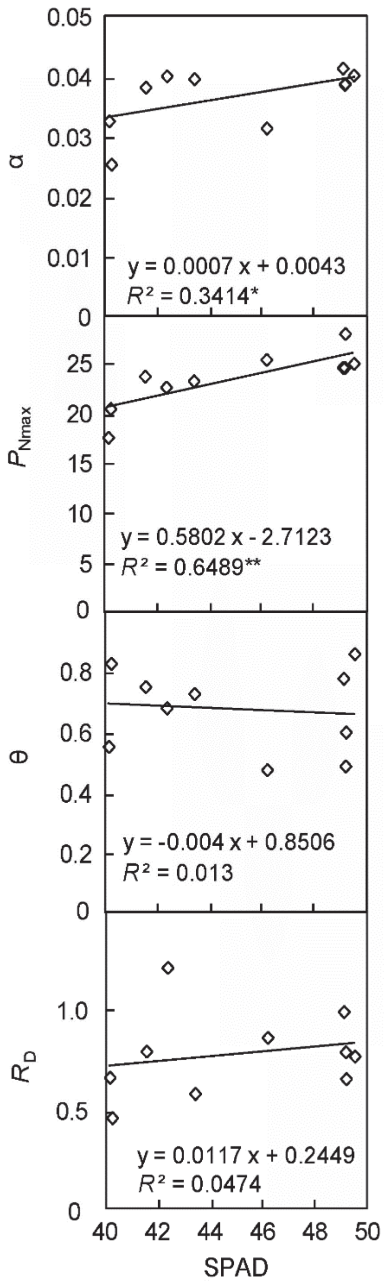

Fig. 2. Relations between leaf SPAD and the coefficients of the maximum net photosynthesis rate (P_{Nmax}), initial slope of the curve (α), convexity of the curve (θ), and dark respiration rate (R_D) in nonrectangular hyperbola (NRH) photosynthetic light response (PLR) equation. * and ** – significant at 0.90 and 0.95 confidence levels, respectively.

but the coefficients of θ and R_D were likely controlled by factors other than SPAD (Fig. 2). The linear relationships between SPAD and the coefficients of α and P_{Nmax} were significant at 0.90 and 0.95 confidence levels, respectively.

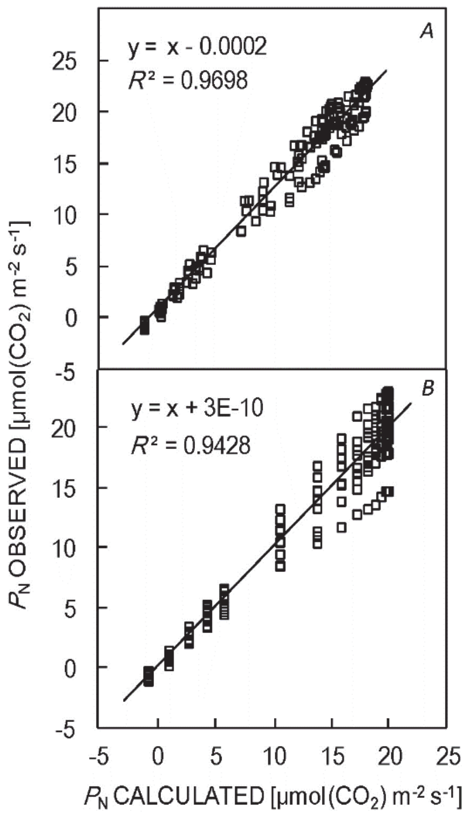

Fig. 3. The photosynthetic rate (P_N) calculated by the modified nonrectangular hyperbola equation (NRH) (*A*) and by the general NRH (*B*).

Performance of the modified NRH equation: By incorporating an SPAD-based adjustment factor into the NRH equation, the modified NRH equation was established as Eq. 2. For the modified NRH equation, the coefficients of α and P_{Nmax} were set as the maximum values for ten PLR curves (α = 0.04127 and P_{Nmax} = 27.89). θ, R_D, and β in Eq. 2 were determined as 0.757, 0.568, and 0.018, respectively. The coefficients of R_D and θ were quite different from the average values (0.671 and 0.772) for ten NRH equations of each PLR curve. For the general NRH equation, the parameters of α and P_{Nmax} (0.0365 and 23.20) were almost the same as the average value of the ten NRH equations of each PLR curve (0.0365 and 23.44). The parameters of θ and R_D (0.702 and 0.788) were different from the average value of the ten NRH equations of each PLR curve (0.671 and 0.772). The scatter plots indicated the P_N calculated by the modified NRH equation (Fig. 3*A*) performed better than the NRH equation with the average coefficients of the ten PLR curves (Fig. 3*B*). The errors of RMSE and AE were 1.34 and 1.01 μmol(CO_2) m^{-2} s^{-1} in P_N calculation by the modified NRH, *i.e.*, much lower than the error by the general NRH equation [1.85 and 1.34 μmol(CO_2) m^{-2} s^{-1}].

Discussion

Leaf SPAD value was considered as the indicator of leaf greenness, *i.e.*, leaf Chl and N content (Loh *et al.* 2002, Uddling *et al.* 2007, Ling *et al.* 2011, Liu *et al.* 2012); leaf Chl and N contents were highly related to leaf photosynthetic capability (Leverenz 1987, Evans 1989, Milroy and Bange 2003, Givnish *et al.* 2004, Akhkha 2010, Marino *et al.* 2010, Lachapelle and Shipley 2012). In the current research, rice leaf with high SPAD values had generally high P_N values at high PPFD (Fig. 1), the coefficients of α and P_{Nmax} in the NRH equation increased linearly with the increase of leaf SPAD (Fig. 2). Thus, SPAD is a useful indicator reflecting leaf Chl or N content, and hence leaf photosynthetic capability. The modified NRH equation with SPAD as the indicator of leaf Chl and N contents performed acceptably with the unified coefficients for leaves with different SPAD values. It performed better than the general NRH equation.

The performance was also better than the results obtained by using the Mitscherlich and Michaelis-Menten PLR equations (R^2 = 0.88 and 0.89), with the coefficients calculated by using allometric equations with leaf N content and specific leaf mass as independent variables (Lachapelle and Shipley 2012). Because Lachapelle and Shipley (2012) applied their allometric equation on leaves from multispecies plant which were different in their leaf N contents, specific leaf mass, and light conditions. In current research, it was applied on single crop species with different SPAD values, while other factors (such as water- and light conditions) did not change. Thus, the SPAD-modified NRH equation overcame the shortcoming of the traditional PLR equations which coefficients largely varied among individual leaves. Furthermore, this method was easy to apply, because SPAD values could be measured easily and nondestructively compared with leaf N or Chl content. Further validation of this idea would be valuable for different PLR equations based on data collected from different plant species (both monocots and dicots, both C_3 and C_4 plants). Using other factors related to leaf photosynthetic traits, such as leaf age and specific leaf mass, would be also worth trying.

The SPAD range was relatively narrow (40.14–49.5), because both the N fertilization rates [200 and 300 kg(N) ha^{-1}] were high. The SPAD values were higher than most of the critical values (32– 40) for the diagnose of N-deficiency (Peng *et al.* 1995, Balasubramanian *et al.* 2000, Singh *et al.* 2001, Huang *et al.* 2008, Swain and Sandip 2010, Ghosh *et al.* 2013). Thus, the linear relationships between SPAD and the values of α and P_{Nmax} might be restricted to the prerequisite of high leaf SPAD range, as well as the linearly adjustment factor ($\beta \times$SPAD) in the modified NRH equation. It was different from the results of Marino *et al.* (2010) and Lachapelle and Shipley (2012) who found a log-linear relationship between the coefficients of Mitscherlich or Michaelis-Menten PLR equations and leaf N content and specific leaf mass. SPAD values were reported also sometimes as nonlinearly related to leaf N or Chl content (Uddling *et al.* 2007, Ling *et al.* 2011, Liu *et al.* 2012). Thus, the performance of the linear adjustment factor (β×SPAD) in the modified NRH equation should be further evaluated using more PLR curves measured under the larger N-deficiency scale.

Conclusion: The PLR curves of rice and the coefficients in the NRH equation changed with the different SPAD values. In the NRH equation, the coefficients of α and P_{Nmax} increased linearly with the increase of leaf SPAD. The modified NRH equation was established by multiplying the linear adjustment factor (β×SPAD) in the NRH equation. This performed acceptably in describing the PLR curves with the unified coefficients in rice leaves with the different SPAD values. Thus, SPAD, which can be measured easily and nondestructively with portable commercial equipment, is a useful indicator to reflect the leaf N status and the leaf photosynthetic capability. The modified NRH equation with SPAD as the indicator of the leaf N status overcame the shortcoming of the traditional PLR equations where the coefficients largely varied among individual leaves with the different leaf N status. The performance of the linear SPAD-based adjustment factor in the modified NRH equation should be further validated with more PLR curves measured under the conditions of largely varying N deficit. It would also valuable to verify the SPAD-modified model with data collected from other kinds of plants growing under different environments.

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