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EVALUATIONS OF DIFFERENT LEAF AND CANOPY PHOTOSYNTHESIS MODELS: A CASE STUDY WITH BLACK LOCUST (*ROBINIA PSEUDOACACIA*) PLANTATIONS ON A LOESS PLATEAU

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Abstract

To evaluate the applicability of leaf and canopy photosynthesis models, we compared performance of 6 leaf models and validated 1 canopy model of photosynthesis based on field data of black locust (*Robinia pseudoacacia* L.) plantations on a Loess Plateau in northern China. Leaf photosynthetic light response curves and diurnal canopy photosynthetic rates were observed in the field in August 2009. Leaf photosynthesis was then fitted with Non-rectangular hyperbolic model, Rectangular hyperbolic model, Bassman exponential model, Prado exponential model, Binomial regression model, and Rectangular hyperbolic correction model, and canopy photosynthesis was fitted with an atmosphere-vegetation 2 way interaction model (AVIM). At the leaf scale, the different photosynthesis models demonstrated significant differences in calculating photosynthetic parameters of black locusts, and the Rectangular hyperbolic correction model performed better compared to other models, the limitations and merits of leaf photosynthesis models are also discussed. At the canopy scale, the AVIM model can well simulate the canopy photosynthesis for black locusts on the Loess Plateau. Although this is a case study, our findings may help to better understand the fitting capacity and applicability of these leaf and/or canopy photosynthesis models.

Introduction

Photosynthesis is the only natural conversion mechanism of photon energy into chemical energy, which presents plant biological characteristics and is responsible for 90-95% of the plant biomass accumulation. Photosynthesis is extremely important for the plant material production and global carbon and substance cycle (Tuittila *et al.*, 2004; Qi *et al.*, 2012), and it is the critical basis of the survival, prosperity, and development of all lives on earth (Silva *et al.*, 2004; Akram *et al.*, 2007). However, many key photosynthetic parameters (such as the maximum photosynthetic rate and canopy photosynthetic rate) cannot be measured directly, and they are fitted only by using the empirical models. Accordingly, models of photosynthesis, particularly at leaf and/or canopy scales, have been playing essential roles in predicting plant growths and ecosystem productivities under variable climatic environmental conditions at various scales from spatially homogeneous patches to heterogeneous landscapes, regions, and even the whole globe (Running & Coughlan, 1988; Raich *et al.*, 1991; Running & Gower, 1991; Leuning, 1995; Denning *et al.*, 1996; Kull & Kruijt, 1998).

Leaf photosynthesis models have been extensively developed and applied for various plant species in recent decades, for instance, hyperbolic models (Prioul & Chartier, 1977; Leverenz & Jarvis, 1979; Farquhar *et al.*, 1980; Marshall & Biscoe, 1980; Thornley, 1998), exponential models (Bassman & Zwier, 1991; Prado & DeMoraes, 1997), and binomial regression models (Jassby & Platt, 1976; Farquhar *et al.*, 2001). Nevertheless, previous studies have indicated that variations exist among the photosynthetic parameters fitted by different leaf photosynthesis models, even for the same plant species (Prioul & Chartier, 1977; Ye, 2007). Currently, this phenomenon seriously hampers the comparisons of different studies. Which model could better simulate the leaf photosynthesis? Do these models present significant differences in estimating the photosynthetic parameters? Questions of this kind are still open to investigation.

Canopy photosynthesis models have close relations with stand developments and changing environmental conditions relative to leaf photosynthesis models (Zhang & Xu, 2003). Photosynthesis models at the canopy scale are generally divided into the big leaf model, two-leaf sun/ shade model, and multilayer model. The big-leaf model assumes that the integrated characteristics of the whole canopy can be represented as a single, horizontally extended leaf for the computation of canopy photosynthetic rate (Running & Coughlan, 1988; Running & Gower, 1991; Amthor, 1994). The two-leaf sun/shade model, which stratifies the canopy into sunlit and shaded leaf portions of the canopy (de Pury & Farquhar, 1997; Leuning *et al.*, 1998; Wang & Leuning, 1998) was developed to improve the big-leaf model. In the multilayer model, canopy photosynthetic rate is computed by integrating the properties of various sections in the canopy (Duncan *et al.*, 1967; Caldwell *et al.*, 1986). These canopy photosynthesis models have been accepted and more widely applied, but more simplifications within the canopies focused on deriving numerical integration solutions to ensure efficiency in computation in many studies (Goudriaan, 1986; Liu, 1996; Larocque, 2002). Hence, the simple canopy photosynthesis model which requires only a few direct and non-destructive measurements would be quite appropriate. As it is difficult to obtain representative and accurate measurements of canopy photosynthetic rates to calibrate models, to date, various methods have been used to establish and develop canopy photosynthesis models for specific forest conditions (Norman, 1993; Larocque, 2002), but to our knowledge, little report is available on estimation for canopy photosynthesis of black locust (*Robinia pseudoacacia* L.) trees on the Loess Plateau, which has experienced serious soil erosion and degradation problems (He *et al.*, 2006; Li *et al.*, 2006).

Moreover, modeling photosynthetic processes for plants in arid and semiarid regions is especially challenging because plants in these regions are often under extreme conditions so that ecosystem nonlinearity is most likely to come into play (Reynolds *et al.*, 1996). The leaf and/or canopy photosynthesis model may perform well when the variation ranges of driving variables (such as temperature, light intensity, and water stresses) are small or moderate, but may fail when these variation ranges are very large (Gao *et al.*, 2004). From the above, the objectives of this paper were: (i) to evaluate the accuracy of six leaf photosynthesis models, and (ii) to validate the applicability for one canopy photosynthesis model in black locusts on the Loess Plateau in northern China. These results may improve our understanding of the predicting capacity of different leaf and/or canopy photosynthesis models and provide useful information on the simulation of ecophysiological process at a larger scale on the Loess Plateau.

Materials and Methods

Site description and sample plots: The study area is located in the Maliantan watershed of Yongshou County (34°48′N, 108°07′E) in the central Loess Plateau, northern China. The area has undergone serious deforestation and then revegetation over the past few decades. The Maliantan watershed has a mean annual precipitation of 601.6 mm and annual mean temperature of 10.8°C, with an annual average potential evaporation of 807.4mm (Luo, 1995), featuring typical geographical and climatic conditions of the Loess Plateau.

Generally, deciduous trees exhibit an obvious seasonality throughout the year, characterized by bud break occurring in April, and leaf-fall in November, with a growth period of about six months (Le Dantec *et al.*, 2000). Estimating the leaf and/or canopy photosynthesis in deciduous forests is not straightforward, as drastic changes in leaf area occur during the growing season, and the associated change in the within-canopy light environment makes estimation a complex process (Kurachi *et al.*, 1993). Therefore, we chose the month of August (2009) when the black locust reaches its maximum annual growth rate (Zou, 1986; Feldhake, 2001). During the peak growth rate period, black locusts' leaves are fully expanded and mature, and the photosynthetic acclimation to micro-climate is more stable compared to other growth stages (Zheng *et al.*, 2011).

Model descriptions

Leaf photosynthesis model descriptions: To evaluate the applicability and capacity of leaf photosynthesis models, we selected six typical and popular models as follows:

Non-rectangular hyperbolic model (Prioul & Chartier, 1977; Herrick & Thomas, 1999).

$$A_n = \frac{(\alpha \times PAR + A_{\max}) - \sqrt{(\alpha \times PAR + A_{\max})^2 - 4 \times \theta \times \alpha \times PAR \times A_{\max}}}{2 \times \theta} - R_d \quad (1)$$

where A_n is the net CO_2 assimilation rate, PAR is the photosynthetic active radiation, α is the initial quantum yield, A_{max} is the maximum photosynthetic rate, θ is the convexity, R_d is the dark respiration rate.

Rectangular hyperbolic model (Thornley, 1998)

$$A_n = \frac{\alpha \times PAR \times A_{\max}}{\alpha \times PAR + A_{\max}} - R_d \quad (2)$$

Bassman exponential model (Bassman & Zwier, 1991)

$$A_n = A_{\max} \times \left(1 - C_0 \times e^{\frac{-\alpha \times PAR}{A_{\max}}}\right) \quad (3)$$

where C_0 is an index that reflects net photosynthetic rate approaching zero at a very weak irradiance.

Prado exponential model (Prado & DeMoraes, 1997)

$$A_n = A_{\max} \times \left(1 - e^{-k \times (PAR - LCP)}\right) \quad (4)$$

where k is a coefficient, LCP is the light compensation point.

Binomial regression model (Thornley, 1976; Farquhar *et al.*, 2001)

$$A_n = a \times PAR^2 + b \times PAR + c \quad (5)$$

where a, b, and c are coefficients.

Rectangular hyperbolic correction model (Ye, 2007)

$$A_n = \alpha \times \frac{1 - \beta \times PAR}{1 + \gamma \times PAR} \times PAR - R_d \quad (6)$$

where β is a correction coefficient, γ is calculated as the ratio of α to A_{max}.

To conformably and insightfully evaluate all the six models, we selected and compared A_{max}, R_d, LCP, and LSP as the parameters involved in these models for their abilities to predict A_n response to PAR. The details of the six models are given in Table 2.

Canopy photosynthesis model descriptions: In a tree canopy, light available to individual leaves decreases according to the Beer's law of light extinction (Kitajima *et al.*, 2005), which in turn leads to a decline in the photosynthetic capacity of the leaves (Hirose & Werger, 1987; Johnson *et al.*, 1989; Anten *et al.*, 1995; Anten, 1997; Kull, 2002). Variations of the leaf photosynthetic capacity within tree crowns are also known to be closely linked to changes in the nitrogen allocation patterns between leaves (Brooks *et al.*, 1996; Hikosaka, 2005; Han & Chiba, 2009). Previous studies found that the leaf nitrogen concentration were highest for upper leaves (which maximized upper leaf response to higher irradiance) and declined progressively toward the bottom of the canopy to affect A_n with LAI depth (Hirose & Werger, 1987; Boote & Pickering, 1994).

The leaf area index (LAI) is considered as the dominant factor at the canopy level, which represents the main surface of exchange for the tree canopy (Le Dantec *et al.*, 2000). Because LAI controls, to a large extent, carbon and water fluxes and light interception, knowledge of LAI is important for quantifying canopy photosynthesis and in turn for evaluating the productivity (Bonan, 1993; Jose & Gillespie, 1997). LAI is a variable of major importance for scaling-up physiological mechanisms occurring at the leaf level (photosynthesis, respiration, transpiration) to the forest canopy level (Running & Coughlan, 1988). A larger LAI would trigger a more sufficient light energy use within the tree crown, which in turn would lead to a higher photosynthetic capacity (and vice versa) (Myneni *et al.*, 2007; Lindroth *et al.*, 2008; Duursma *et al.*, 2009). Thus, as the principal scaling parameter for gross photosynthesis, LAI is necessary to determine the canopy photosynthesis of the black locust trees.

In this study, we chose a model from the plant physiology and ecology module of an atmosphere-vegetation two way interaction model (AVIM) (Rastetter *et al.*, 1991; Ji, 1995; Friend *et al.*, 1997; Li & Ji, 2001; Lu & Ji, 2006), which assumes that the canopy photosynthesis is calculated by integrating the leaf photosynthesis over the whole crown with the assumption that the photosynthetic active radiation and leaf nitrogen concentration decay at the same rate in the canopy. The canopy photosynthetic rate (A_{canopy}) can be expressed as (Lu & Ji, 2006):

$$A_{canopy} = \int_0^{LAI} A(L)dL = \int_0^{LAI} A_o \times e^{-K\times L} dL = \frac{1-e^{-K\times LAI}}{K} \times A_o \quad (7)$$

In the above model, A_o denotes the photosynthetic rate at the top of the canopy; K denotes the extinction coefficient of the canopy, which can be used to estimate light transmittance within the canopy with Beer's law (Goudriaan, 1986; Sakai *et al.*, 2005; Gouasmi *et al.*, 2009):

$$K = -\frac{\ln(I_u / I_o)}{LAI} \quad (8)$$

In which, I_u and I_o is the PAR under and above the canopy, respectively. This assumes horizontally homogeneous foliage characteristics within each layer, and ignores the effects of foliage clustering.

Field measurements: Field measurements were performed under typical and clear weather condition during the period from the third to fourth week of August, 2009. In the study area, three black locust plantations were chosen with the distance to each other ca. 200 meters. In each plantation three sample plots (20 m × 20 m) were randomly selected. The diameter at breast height of each tree in each sample plot was measured using a caliper and the height was determined using a height gauge. The characteristics of these plantations are given in Table 1. In each sample plot, one sample tree was randomly selected to measure leaf photosynthesis, and three sample trees were randomly selected to determine canopy photosynthesis.

Table 1. Characteristics of black locust (*Robinia pseudoacacia*) plantations. The diameter at breast height of each tree in the sample plot of each plantation was measured using a caliper and the height was determined using a height gauge. Data for heights, diameters, canopy heights, and canopy diameters are means ± SE (n = 9).

Plantation	Age (a)	Slope aspect	Slope (°)	Height (m)	Diameter (cm)	Canopy height (m)	Canopy diameter (m)	Stand density (tree numbers ha^{-1})	Altitude (m)
1	19	Sunny slope	7.8	9.1 ± 0.5	8.5 ± 0.4	3.8 ± 0.2	2.7 ± 0.4	2640	1226
2	19	Sunny slope	8.9	8.8 ± 0.4	8.6 ± 0.3	3.5 ± 0.2	3.0 ± 0.5	2715	1237
3	19	Sunny slope	8.2	8.5 ± 0.4	8.3 ± 0.4	3.3 ± 0.2	2.6 ± 0.4	2805	1208

Table 2. Six leaf photosynthesis model descriptions, and parameter computations of the maximum photosynthetic rate (A_{max}), dark respiration rate (R_d), light compensation point (LCP), and light saturation point (LSP).

Leaf photosynthesis model	A_{max} (μmol CO_2 m^{-2} s^{-1})	R_d (μmol CO_2 m^{-2} s^{-1})	LCP (μmol m^{-2} s^{-1})	LSP (μmol m^{-2} s^{-1})
Non-rectangular hyperbolic model	Calculation	Calculation	$\frac{A_{max} \times R_d - \theta \times R_d^{\;2}}{\alpha \times (A_{max} - R_d)}$	Integration of hyperbolic model and linear regression under PAR values between 0 and 200 μmol m^{-2} s^{-1}
Rectangular hyperbolic model	Calculation	Calculation	$\frac{A_{max} \times R_d}{\alpha \times (A_{max} - R_d)}$	Integration of hyperbolic model and linear regression under PAR values between 0 and 200 μmol m^{-2} s^{-1}
Bassman exponential model	Calculation	$A_{max} \times (C_0 - 1)$	$\frac{A_{max} \times \ln(C_0)}{\alpha}$	$\frac{A_{max} \times \ln(100 \times C_0)}{\alpha}$
Prado exponential model	Calculation	$A_{max} \times (e^{k\times LCP} - 1)$	Calculation	$\frac{\ln(100)}{k} + LCP$
Binomial regression model	$\frac{4 \times a \times c - b^2}{4 \times a}$	C	$\frac{-b \pm \sqrt{b^2 - 4 \times a \times c}}{2 \times a}$	$-\frac{b}{2 \times a}$
Rectangular hyperbolic correction model	$\alpha \times \left(\frac{\sqrt{\beta+\gamma} - \sqrt{\beta}}{\gamma}\right)^2 - R_d$	Calculation	$\frac{\alpha - \gamma \times R_d - \sqrt{(\gamma \times R_d - \alpha)^2 - 4 \times \alpha \times \beta \times R_d}}{2 \times \alpha \times \beta}$	$\frac{\sqrt{\frac{(\beta + \gamma)}{\beta}} - 1}{\gamma}$

Leaf photosynthesis measurements: A scaffold was used to access the canopy for intact measurements of leaf photosynthesis. Three mature and healthy leaves on the south branches at the middle layer of each sample tree canopy were selected to evaluate the response of net CO_2 assimilation rate (A_n) to photosynthetic active radiation (PAR) by using the light source (Li-Cor 6400-02B LED; Li-Cor Inc., Lincoln, NE, USA). Black locusts' biological clock can significantly influence the stomatal movements and photosynthetic enzyme activities, thus the photosynthetic light response (A/PAR) curves were measured during 9:00-11:00 (local time). Photosynthetic responses to PAR were constructed by taking measurements at 14 PAR values, ranging from 0 to 2000 μmol m^{-2} s^{-1}, and leaves acclimated to each light level with 3 minutes before switching. At the same time, the ambient CO_2 concentration was stabilized under local condition (360 ± 2 μmol mol^{-1}) through the CO_2 buffer bottle, and the atmospheric relative humidity was 41± 1%.

Measured values of photosynthesis (A_{max}, R_d, LCP, and LSP) are estimated according to A/PAR curve data. Specifically, measured A_{max} is considered as the maximum value of net CO_2 assimilation rate obtained from A/PAR curve data, measured R_d is taken as the opposite value of A_n under 0 μmol m^{-2} s^{-1} PAR, measured LCP is estimated to the PAR value when A_n approaches to zero, and measured LSP is approximately equal to the PAR value when A_n reaches the observed maximum among A/PAR curve data (Ye, 2007; Ye & Yu, 2008b, 2009).

Canopy photosynthesis measurements: The canopy was divided into three layers, each representing approximately one-third of the height of the canopy. Three leaves from each of the four orientations (East, South, West, and North) were randomly selected for gas exchange measurements from the middle of each canopy layer. Gas exchange measurements were carried out in-situ on the selected leaves under local irradiance by using the portable gas exchange system (Li-Cor 6400; Li-Cor Inc., Lincoln, NE, USA) from 6:00 to 18:00 (local time).

To determine LAI (m^2 of leaves per m^2 of ground), images of each sample tree at the four orientations (East, South, West and North) were acquired using a digital camera equipped with a hemispheric lens (Minolta DiMAGE X, Konica Minolta Inc., Tokyo, Japan) at sunset according to the protocol (Regent Instruments Inc., Québec, Canada). Subsequently, the images were analyzed using WinScanopy software (WinScanopy-2005a, Regent Instruments Inc., Québec, Canada) to obtain LAI (Frazer *et al.*, 2001).

To estimate the canopy photosynthetic rate of the sample tree, the net CO_2 assimilation rates measured at the three layers and four orientations were averaged. The multiplication of mean net CO_2 assimilation rate and LAI was taken as the net CO_2 assimilation rate of the whole tree (Barron-Gafford *et al.*, 2007; Zheng *et al.*, 2011).

Statistical analysis: Calculations for photosynthetic parameters of different leaf photosynthesis models were performed using the nonlinear regression methods in the SPSS software program (version 13, SPSS Inc., Chicago, USA). Analysis of variance (ANOVA), related coefficient (R^2), Akaike Information Criterion (*AIC*) and Bayesian Information Criterion (*BIC*) were conducted, using SPSS, to test the applicability and capacity of leaf and/or canopy photosynthesis models on the photosynthetic parameters of black locusts. The difference between parameter means was considered significant when the *P*-value of the ANOVA *F*-test was less than 0.05.

Results

Comparison and evaluation of leaf photosynthesis models: To better understand the applicability and capacity of the leaf photosynthesis models, data from gas exchange measurements of black locust trees on the Loess Plateau were fitted and analyzed (Fig. 1). The photosynthetic light response (A/PAR) curves of black locusts, as illustrated in Fig. 1 shows that in the beginning, the net CO_2 assimilation rate (A_n) increases rapidly under the photosynthetic active radiation (PAR) values between 0 and 200 μmol m^{-2} s^{-1}. In this stage, PAR may be the main limiting factor to photosynthesis. Subsequently, the A_n increases slowly with the increasing PAR and even decreases slightly, which is likely because A_n presents the light supersaturation phenomenon, and leaves cannot adequately absorb and utilize the high-intensity lights due to the limit of the enzymatic reaction. In our study, although most leaf photosynthesis models can predict the response of A_n to PAR, different models demonstrate different fitting capacities and effects (Fig. 1). Among these six models, the Rectangular hyperbolic correction model shows a greater simulation effect compared to other five leaf photosynthesis models (Fig. 1f), while the fitting capacity of the Binomial regression model is relatively weak (Fig. 1e).

To further compare and evaluate these models, the main photosynthetic parameters involved in the six models were calculated (Table 3). For the maximum photosynthetic rate (A_{max}), the Rectangular hyperbolic correction model has a greater fitting capacity, the simulated A_{max} is proximal with the measured value. However, the Non-rectangular hyperbolic model, Rectangular hyperbolic model, and Binomial regression model overestimate the A_{max}. In contrast, the Bassman exponential model and Prado exponential model underestimate the A_{max}.

For the dark respiration rate (R_d), the Rectangular hyperbolic correction model also has a better predicting effect among all these models, while the R_d simulated by the Bassman and/or Prado exponential model and Binomial regression model is significantly lower and higher than the measured value, respectively.

For the light compensation point (LCP), all models do not fit quite well, but no statistically marked differences exist in the simulated and measured LCP for the Non-rectangular hyperbolic model, Rectangular hyperbolic model, and Rectangular hyperbolic correction model. However, the Bassman and Prado exponential models have significantly lower LCPs relative to the observed LCPs, and the Binomial regression model cannot even fit the LCP value.

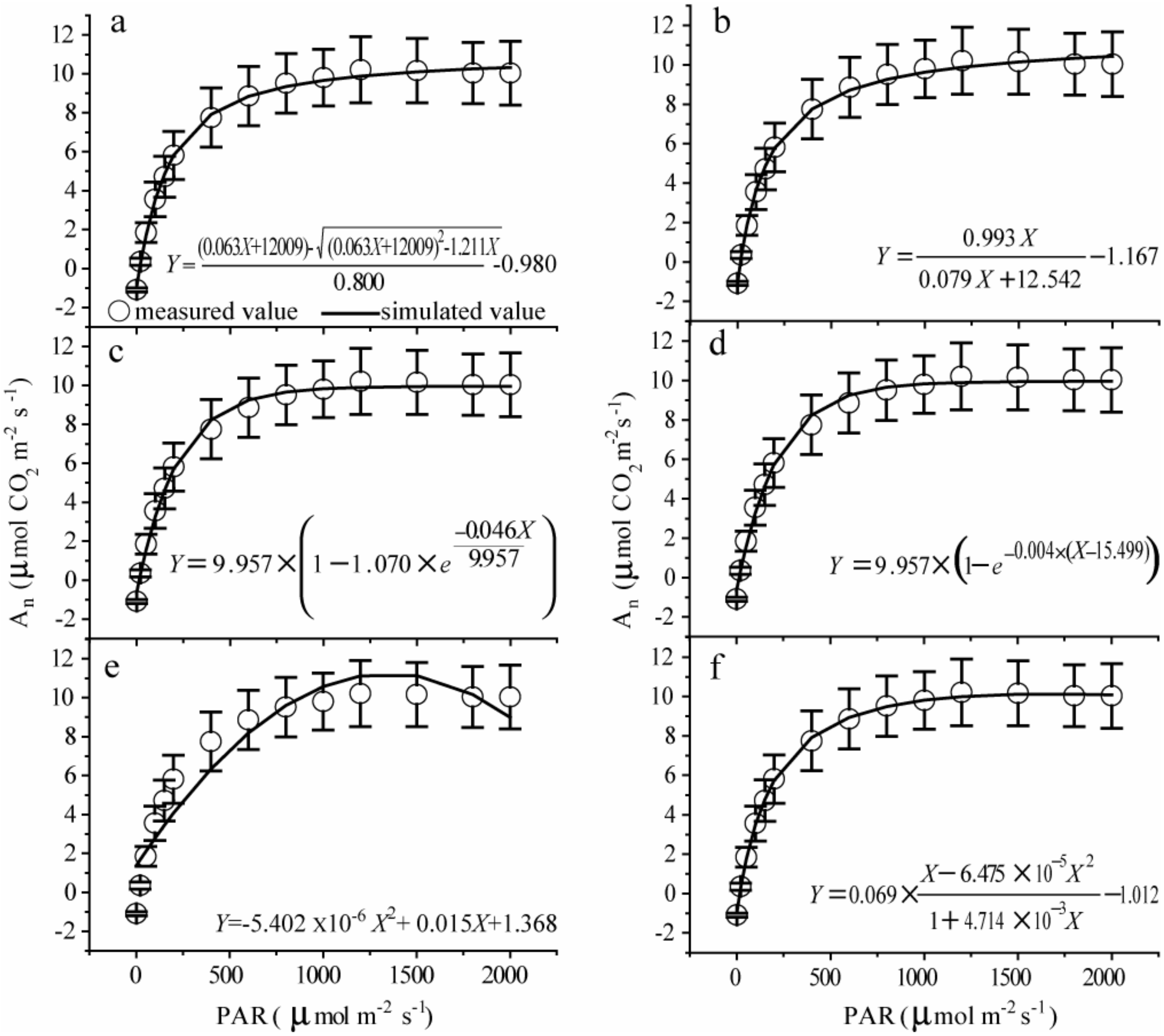

Fig. 1. Simulations of (a) Non-rectangular hyperbolic model, (b) Rectangular hyperbolic model, (c) Bassman exponential model, (d) Prado exponential model, (e) Binomial regression model, and (f) Rectangular hyperbolic correction model on measured net CO_2 assimilation rate (A_n) response to photosynthetic active radiation (PAR) of black locust trees. The mean values ± SE (n=9).

Table 3. Calculations of the maximum photosynthetic rate (A_{max}), dark respiration rate (R_d), light compensation point (LCP), and light saturation point (LSP) using different leaf photosynthesis models with measured values of black locust trees. Akaike Information Criterion (*AIC*) and Bayesian Information Criterion (*BIC*) are used to compare model performance. The lower the value of *AIC* and/or *BIC*, the greater the fitting effect of the model. The mean values ± SE (n=9).

Model	A_{max} (μmol CO_2 m^{-2} s^{-1})	R_d (μmol CO_2 m^{-2} s^{-1})	LCP (μmol m^{-2} s^{-1})	LSP (μmol m^{-2} s^{-1})	R^2	*AIC*	*BIC*
Non-rectangular hyperbolic model	12.01 ± 1.84	0.98 ± 0.14	17.96 ± 2.79	376.99 ± 23.23***	0.997	-22.02	-21.62
Rectangular hyperbolic model	12.54 ± 1.82	1.17 ± 0.15	17.55 ± 2.68	390.95 ± 24.14***	0.996	-19.83	-19.44
Bassman exponential model	9.96 ± 1.55	0.67 ± 0.06***	15.50 ± 2.94*	1060.89 ± 107.67*	0.995	-15.58	-15.19
Prado exponential model	9.96 ± 1.55	0.67 ± 0.06***	15.50 ± 2.94*	1060.89 ± 107.67*	0.995	-15.58	-15.19
Binomial regression model	11.25 ± 1.80	1.37 ± 0.46*	No solution	1354.16 ± 10.95	0.911	9.60	9.99
Rectangular hyperbolic correction model	10.14 ± 1.61	1.01 ± 0.15	17.32 ± 2.64	1708.36 ± 161.73**	0.999	-28.54	-28.14
Measured value	≈10.27 ± 1.71	≈1.09 ± 0.10	≈19.67 ± 0.33	≈1300.00 ± 50.00	/	/	/

For each parameter, asterisks indicate significant difference between the simulated and measured value at *: $p \le 0.05$; **: $p \le 0.01$; ***: $p \le 0.001$.

For the light saturation point (LSP), most photosynthesis models show pronounced differences of LSP between the estimated and measured values except the Binomial regression model. Moreover, our findings illustrate that the values of A_{max}, R_d, LCP, and LSP simulated by the Bassman exponential model and Prado exponential model are the same (Table 3). Although all models have very similar R^2 values from 0.911 to 0.999, the statistical results of *AIC* and *BIC* clearly demonstrate that there are considerable differences in these model performances. The model fitting effects follow the pattern: Rectangular hyperbolic correction model > Non-rectangular hyperbolic model > Rectangular hyperbolic model > Bassman exponential model = Prado exponential model > Binomial regression model (Table 3).

Validation of the canopy photosynthesis model: To gain information regarding the accuracy of the canopy photosynthesis model, the simulated and measured values were compared and analyzed (Fig. 2). In the diurnal dynamics of gas exchange in black locusts, from 6:00 to 18:00, the simulated A_{canopy} by the AVIM model presents a good consistency with the measured value at each measuring time point. Between the measured and calculated $A_{canopy,}$ there is no statistically significant difference, and a close agreement (Fig. 2).

Moreover, the applicability of the canopy photosynthesis model and the correlation equation were also examined with the data measured in this experiment (Fig. 3). Our results show that the simulated A_{canopy} values, by using the AVIM model, have strong correlations with the measured ones for black locust trees (Fig. 3). These validation results indicate that the AVIM model can well predict the diurnal dynamics of canopy photosynthesis for black locusts on the Loess Plateau.

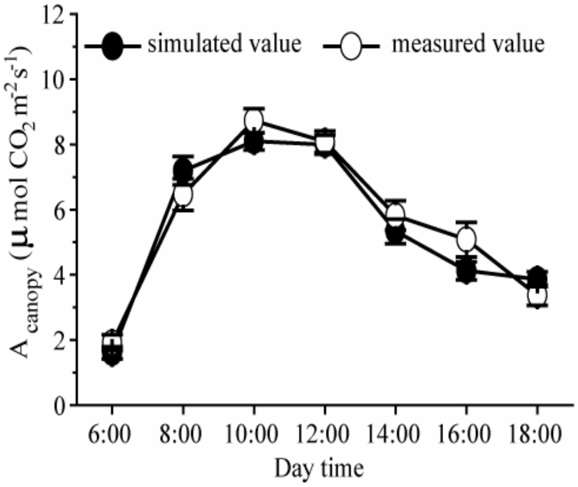

Fig. 2. Diurnal dynamics of simulated and measured canopy photosynthetic rate (A_{canopy}) in black locust trees on the Loess Plateau. The mean values ± SE (n=27).

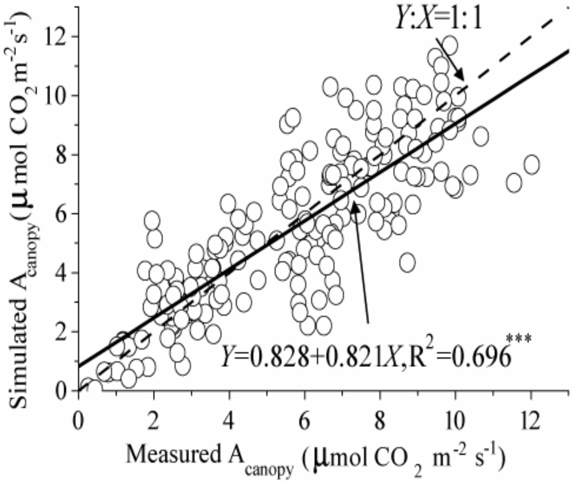

Fig. 3. Correlations of simulated and measured canopy photosynthetic rate (A_{canopy}) in black locust trees on the Loess Plateau. *** indicates significant correlations between the simulated and measured values at $p \leq 0.001$ (n=189).

Discussion

To assess the reliability of leaf photosynthesis models, we quantitatively compared several aspects of the simulated and observed data. The merits and limitations of the comparative approach for model data evaluation are discussed. The maximum photosynthetic rate (A_{max}) fitted by the Non-rectangular and/or Rectangular hyperbolic model is markedly higher than the measured value (Table 3), and this result is in accordance with the conclusion of Yu *et al.* (2004).

In addition, these two hyperbolic models belong to the asymptotes which do not have the extremum (Fig. 1), and thus can not compute the light saturation point (LSP). They can only calculate the LSP by integrating the fitted A_{max} and linear regression under the low light radiation (Richardson & Berlyn, 2002), but the obtained LSP is significantly lower compared to the measured value (Table 3). Previous studies reported that the LSP simulated, via the integration of the hyperbolic model and linear regression, was pronouncedly lower relative to the observed one (Richardson & Berlyn, 2002), and their conclusions support our results.

In our study, the Bassman and Prado exponential models underestimate all the photosynthetic parameters of black locusts (Table 3), and they also can not obtain the LSP directly, but only have to suppose that the LSP corresponds to the photosynthetic active radiation (PAR) related 99 % value of A_{max} (Bassman & Zwier,1991; Prado & DeMoraes, 1997). In addition, we found that these two models have consistent photosynthetic parameters and fully coincident fitting curves (Fig. 1; Table 3). Hence, the Bassman and Prado exponential models are considered as two equation forms which respond to the same photosynthesis curve.

For the Binomial regression model, the calculated parameters do not have biological significance, for instance, the net CO_2 assimilation rate (A_n) is still the positive value when the PAR is equal to zero (Fig. 1), and the model can not fit the light compensation point (LCP).

As a result, this model is not appropriate for black locusts on the Loess Plateau.

The Rectangular hyperbolic correction model improves the Rectangular hyperbolic model (Ye, 2007), and it accurately fits the photosynthesis response process under the low and/or hard light conditions. The Rectangular hyperbolic correction model can compute the LSP directly, but in our study it overestimates the LSP value of black locusts on the Loess Plateau (Table 3). This is probably because, although the model was developed based on the mathematical approach and successfully applied in the winter wheat (Ye & Yu, 2008a), from the biological perspective, the A/PAR curves of black locusts have visible inflexions (Fig. 1), and there are no marked differences of A_{ns} when the PAR exceed the LSP value. Nevertheless, the Rectangular hyperbolic correction model can very well fit main photosynthetic parameters of black locusts on the Loess Plateau (Table 3), particularly for the A_{max} and R_d.

The canopy photosynthesis model and its applicability were examined with the data measured in this experiment. In general, canopy photosynthesis is a complicated process, as the leaves in the upper part of the plant canopy are usually well insolated, while the leaves lower in the canopy are usually shaded (Kikuzawa, 2003; Hikosaka, 2005; Barron-Gafford *et al.*, 2007). Recent studies have shown that the upper canopy leaves have greater rates of photosynthesis and stomatal conductance than the middle or lower canopy leaves in many tree species (Gunderson *et al.*, 2002; Sellin & Kupper, 2005). Although the theory of gas exchange processes in forest canopies is well understood, modeling of gas exchange in forest canopies is still a scientific challenge (Jarvis, 1995; Ibrom *et al.*, 2006) because of the complexity of a real forest crown forces compromise between rigorous process parameterization and simplifying schemes. Given that there are numerous reasons for a forest stand model to fail, the output quality has to be interpreted carefully. To gain confidence in a canopy photosynthesis model, model projections are often compared with observations (Ibrom *et al.*, 2006). Accordingly, this paper tried to use a simple canopy photosynthesis model from AVIM to simulate the canopy photosynthetic rate of black locusts on the Loess Plateau. Since it is difficult to calibrate the model, the results reported in this study can be considered a validation of the model's performance in predicting canopy photosynthesis. Our results indicated that, despite some slight disagreements between the measured and simulated diurnal dynamics of canopy photosynthetic rates (Fig. 2) may be related to light environments and leaf structure within the crown, the fitting capacity and applicability of the AVIM model is good for canopy photosynthesis of black locusts on the Loess Plateau.

Overall, at the leaf scale, different photosynthesis models have various limitations and merits and thus show significant differences in calculating photosynthetic parameters of black locusts. The Rectangular hyperbolic correction model performs better than other leaf photosynthesis models. In addition, at the canopy scale, the AVIM model can simulate the canopy photosynthesis in black locust plantations on the Loess Plateau well. Although this is a case study, our results highlight fitting capacity discrepancies in leaf photosynthesis models and emphasize the applicability for the canopy photosynthesis model. Nevertheless, these results need to be applied and tested in more communities and/or larger spatial and temporal scales in the future.

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