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Abstract

Net CO₂ assimilation (A_N) is an important physiological indicator that reflects the photosynthetic capacity. The seasonal and spatial variations of A_N play an important role in carbon uptake simulations, especially for trees. To gain a clearer understanding of the state of the branch carbon balance, it is necessary to more carefully evaluate the dynamic variation of A_N over different gradients in the crown during the growing season. Gas exchange, leaf temperature (T_{leaf}), vapor pressure deficit (VPD), leaf mass per area (LMA) and relative depth into crown (RDINC) were measured throughout the growing season of planted *Larix olgensis* trees. A semiempirical model for predicting multilayered crown A_N was established by incorporating T_{leaf} , VPD, LMA, RDINC and their combinations into a photosynthetic light-response (PLR) curve model using reparameterization. The model was assessed based on goodness of fit (adjusted coefficient of determination, R_a^2 ; root mean square error, RMSE; and Akaike information criterion, AIC) and on the validation results (mean error, ME; mean absolute error, MAE; precision estimation, P) and performed well. The multilayered predicted model of crown A_N lays the foundation for calculating the multilayered photosynthetic production within the crown and determining the range of the functional crown for individual trees.

Keywords: Modified Mitscherlich model; Maximum net CO₂ assimilation; Dark respiration rate; Multilayered predicted model; Vertical variation

Introduction

For trees, some branches in the lower crown usually form the wound and knot after they abscised (Springmann et al. 2011). Artificial pruning (cutting a part of branches present in the lower crown) could reduce the bole damage caused by branch knots in order to improve the economic value of trees (Balandier 1997; Xu 2002; Lam et al. 2005; Kerr and Morgan 2006; Springmann et al. 2011), thus it has been an effective and affordable method in plantation management. The first time of artificial pruning is generally conducted when the forest is closed, and the cost of artificial pruning is usually under 2000 RMB hm⁻² (e.g., 800 - 1200 RMB hm⁻² in Hei longjiang province). However, though some reports have provided the suggestions on pruning intensity or height in different tree species, but it still lacked of theoretical principle. In a single tree crown, not all living branches contribute to the trunk. Some living branches that are present in the lower crown or canopy produce only a small amount of organic matter for maintaining their own growth and respiration, with none allocated to the trunk (Kramer and Kozlowski 1979). Oliver and Larson (1996) first classified crowns into “functional” and “nonfunctional” vertical parts based on whether the branches could produce excess photosynthate to contribute to the growth of the main tree stem. The determination of the height of the functional crown will contribute substantially to artificial pruning. By analyzing the vertical distribution of basal area increments and the branch or leaf biomass of trees, Li et al. (1996) determined the height of functional

crowns but did not present an underlying physiological principle. From a physiological perspective, a functional crown can be defined as a crown that is above the height of the branches that produce sufficient photosynthate to not only maintain self-growth and respiration but also contribute to the tree trunk. Thus, to determine the range of a functional crown, the top priority is to estimate the dynamics of crown photosynthesis.

A dynamic global vegetation model (DGVM) is a biogeographical model to simulate the transient changes in vegetation distribution and function (Sato et al. 2007; Shuman et al. 2014; Fyllas et al. 2014; Fischer et al. 2016; Fisher et al. 2018); these changes involve many physical or physiological processes, including photosynthesis (Sato et al. 2007). To date, many DGVMs have used mechanistically based models for predicting crown or canopy photosynthesis, including the big-leaf model (Amthor 1994), the multistory model (Leuning et al. 1995) and the two-leaf model (Wang and Leuning 1998), which were developed from Farquhar's scheme (Farquhar et al. 1980). These models are usually complex, with a network of submodels to describe biochemical processes (Mayoral et al. 2015), and their behaviors are not easy to predict from their formulations (Sato et al. 2007). However, semiempirical models provide an intermediate option and define photosynthesis according to a mathematical description of a single biochemical process; this group includes the photosynthetic light-response (PLR) curve model, which describes the relationship between the net CO₂ assimilation (A_N) and photosynthetically active radiation (PAR) (Mayoral et al. 2015).

1 PLR curves represent effective tools for identifying series of photophysiological indicators
2 (Henley 1993), such as the apparent quantum yield (AQY), dark respiration rate (R_d), light
3 saturation point (LSP), light compensation point (LCP), and maximum net CO_2 assimilation
4 ($A_{\max}$). All these photophysiological indicators are not only important indexes for evaluating the
5 growth state but also essential elements for calculating plant production. To date, many
6 mathematical models and their derivatives have been applied to describe PLR curves; these
7 models include the rectangular hyperbola (RH) (Baly 1935; Peat 1970; Luo et al. 2000; Rascher
8 et al. 2000), nonrectangular hyperbola (NRH) (Thornley 1976; Bassman and Zwier 1991;
9 Moreno et al. 2002; Dias-Filho 2002; Posada et al. 2009), modified Mitscherlich (MM)
10 (Bassman and Zwier 1991; Lootens et al. 2004; Devacht et al. 2009), and modified rectangular
11 hyperbola (MRH) (Ye et al. 2007) models. In recent years, to expand the application of these
12 models from a single leaf to larger scales, some researchers have incorporated leaf nitrogen
13 content (N), chlorophyll content (CHL), specific leaf area (SLA) or its reciprocal (leaf mass per
14 area, LMA) and the global site factor (GSF) into PLR curve models, thus modifying them
15 (Marino et al. 2010; Lachapelle and Shipley 2012; Xu et al. 2014; Xu et al. 2015; Mayoral et al.
16 2015). N and SLA are strongly related to the vertical position in the living crown of trees
17 (Ellsworth and Reich 1993; Kull 2002; Han et al. 2003; Fellner et al. 2016); thus, we assume that
18 this approach might also be applicable to assessing the photosynthesis of tree crowns according
19 to the relationships between N and SLA and leaf vertical positions within crowns. Relative depth
20 into the crown (ratio of depth into the crown to crown depth; RDINC) is a vertical factor in

crown structure that is widely used as an indicator for simulating crown shape (Ma et al. 2000; Jerez et al. 2004), foliage mass and area distribution (Weiskittel et al. 2006; Yan and Liu 2009; Nelson et al. 2014). Therefore, the objectives of this investigation were (1) to select an optimal PLR curve model for fitting the PLR curves of young planted *Larix olgensis* trees; (2) to explore the relationships between the parameters of the optimal PLR curve model with environmental factors, leaf morphological characteristics, leaf vertical positions and their combinations; (3) to modify the optimal PLR curve model for simultaneous estimation of A_N within the crown of planted *Larix olgensis* trees during the growing season; and (4) to select the best modified model by systematically considering the advantages of model assessment and validation, model structure, and model applicability.

Materials and methods

Site description

The experiments were conducted in 2015 at the Maoershan Forest Farm (127°18'0"E, 127°41'6"E and 45°2'20"N, 45°18'16"N) in northeastern China. The mean annual air temperature, mean air temperature throughout the growing season, mean annual precipitation, and mean elevation in this region are -2.0°C, 21.9°C, 525 mm, and 400 m, respectively. The soil type is a Eutroboralf, and the total forest coverage is approximately 83.3%, 14.7% of which consists of plantations.

Larix olgensis is one of the main reforestation tree species in northeastern China, especially in mountainous regions. The planted area and volume of *Larix olgensis* account for 36% of the total area and 37% of the total volume, respectively, of all the plantations in northeastern China. This

species is apparently light demanding and cold resistant but shade intolerant, and its advantages include rapid growth, strong adaptability and high economic value.

Sample selection

Five sample plots (20 m × 30 m) were established within pure *Larix olgensis* plantations in the same habitat. The diameter at breast height (DBH), tree height (H) and crown width (CW) were measured for each tree whose DBH was greater than 5 cm in each plot, and the quadratic mean diameter (D_g) was calculated for each of five plots. Then, five sample trees whose DBH values were respectively similar to the D_g of the five plots were selected to represent the average state of each plot. The attributes of the sampling plots and corresponding sampled trees are listed in Table 1. Scaffoldings were constructed around each sampled tree to ensure that measurements could be performed at every position in the crown. The crown depth (the distance from the top of the tree to the base of its live crown, CD) of the sampled trees was divided into several segments based on the pseudowhorls (Cluzeau et al. 1994) from top to bottom. Preliminary work was conducted to analyze the horizontal differences between branches of net CO₂ assimilation (A_N) on a leaf-area basis before the photosynthetic needle samples were selected (unpublished data). We divided the tree crown into three vertical layers with equal length, and each layer was divided into two parts (sunny and shaded) based on whether the leaf could receive the direct sunlight. The largest branch was selected in each section, and the PLR curve was measured for a healthy needle cluster in each second-order branch from the base of the branch to the tip of the branch. The results showed that the A_N values of the needles from the middle of a foliated branch adequately

represented the average A_N of the entire branch (Fig. 1a). Thus, three healthy and fully expanded needle clusters located within each segment in the middle of the foliated branches in sunny, semi-sunny and shaded crowns (Fig. 1b, only presents the needle samples from sunny crowns and shaded crowns) were selected for measurements from each sampled tree.

Measurement of PLR curves (fitting data)

PLR curves were generated from measurements performed on fully expanded healthy needles using a portable photosynthesis system (LI-6400, LI-COR, Inc., Lincoln, NE, USA) coupled with a standard light-emitting diode (LED) light source (6400-02B, LI-COR, Inc., Lincoln, NE, USA) at 17 PAR levels (2,200, 2,000, 1,800, 1,600, 1,400, 1,200, 1,000, 800, 600, 400, 200, 150, 100, 60, 40, 15, and 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$). The CO_2 concentration was maintained at 370 ppm, which is similar to the actual CO_2 concentration within the crown, by using a CO_2 mixer (6400-01, LI-COR, Inc., Lincoln, NE, USA) to maintain a stable CO_2 supply in the chamber. The data used in the PLR curves were measured every half-month during the 2017 growing season: May 15th–25th, June 1st–10th, June 15th–25th, July 1st–10th, July 15th–25th, August 1st–10th, August 15th–25th and September 1st–10th.

Measurement of A_N (validation data)

The PLR curves reflect the responses of A_N to the certain PAR gradients that are established artificially. Thus, if we want to estimate the crown A_N based on the crown PLR curve model, it is necessary to collect some A_N values under natural PAR to test the model performance. Thus, for the validation data, we also used the same portable photosynthesis system coupled with a 2 cm ×

3 cm clear chamber bottom (6400-08, LI-COR, Inc., Lincoln, NE, USA) to measure the A_N under natural PAR. The light source was natural light rather than LEDs, and the CO_2 concentration was maintained at the same level (370 ppm) as for the PLR curves measured in the CO_2 mixer. The needle samples for validation of A_N were selected from the same vertical segments as those from which PLR curves were measured. It is necessary to ensure that the validation A_N in each vertical segment is evenly distributed between the inside and outside of the crown in order to obtain the A_N under different gradients of the natural PAR. All the A_N measurements were conducted under natural ambient conditions with no control during the same period as the measurement of the PLR curves. All the validation A_N data were used to test the model as independent samples. The PAR and leaf temperature (T_{leaf}) for each measurement (fitting data and validation data) were respectively measured by a PAR sensor within the 2 cm $\times$ 3 cm clear chamber (6400-08, LI-COR, Inc., Lincoln, NE, USA) and a leaf temperature thermocouple (6400-04, LI-COR, Inc., Lincoln, NE, USA). The corresponding vapor pressure deficit (VPD) for each measurement was automatically calculated by the apparatus and recorded at the same time. The attributes of the PLR curves and A_N throughout the growing seasons are shown in Table 2 and Fig. 2.

Measurements of the RDINC and LMA

The depth into the crown (DINC) of the sampled needles was measured while the data for the PLR curves were being measured, after which the RDINC of each photosynthetic sampled needle was calculated. Once the photosynthetic gas-exchange measurements were completed, needle-cluster samples were scanned immediately and then surveyed with image analysis

software (Image-Pro Plus 6.0, Media Cybernetics, Bethesda, MD, USA) in the laboratory, resulting in a projected leaf area. Then, immediately after their collection in the field, the corresponding needles were dried to a constant weight at 105°C and weighed. LMA was calculated by dividing the projected leaf area by the corresponding needle dry mass.

Statistical analysis

Description of candidate PLR curve models

In this study, we selected the most frequently used models (M, NRH, and MRH) to fit the PLR curves. The equations are described below.

MM equation (Bassman and Zwier 1991):

$$A_N = A_{\max} \times (1 - e^{(-AQY \times PAR / A_{\max})}) - R_d \quad (1)$$

where A_N is the net CO₂ assimilation (μmol m⁻² s⁻¹); $A_{\max}$ is the maximum net CO₂ assimilation (μmol m⁻² s⁻¹); AQY is the apparent quantum yield; PAR is the photosynthetically active radiation (μmol m⁻² s⁻¹); and R_d is the dark respiration rate (μmol m⁻² s⁻¹).

NRH equation (Thornley 1976):

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

where θ is the convexity of the PLR curve; A_N , $A_{\max}$ and AQY are described above.

MRH equation (Ye et al. 2007):

$$A_N = AQY \times \frac{1 - \beta \times PAR}{1 + \gamma \times PAR} \times PAR - R_d \quad (3)$$

where β is a correction factor (dimensionless) and γ is equal to $AQY / A_{\max}$; A_N , PAR, AQY, and R_d are described above.

1 Model assessment and validation

2 The model assessment was based on the adjusted coefficient of determination (R_a^2), the root
 3 mean square error (RMSE) and the Akaike information criterion (AIC) (Eqs. 4–6), and model
 4 performance was evaluated based on the mean error (ME), mean absolute error (MAE) and the
 5 precision estimation (P) (Eqs. 7–9) as follows:

$$6 \quad R_a^2 = 1 - (1 - R^2) \left(\frac{n-1}{n-p} \right), \text{ where } R^2 = 1 - \frac{\sum_{i=1}^n (y_i - \hat{y}_i)^2}{\sum_{i=1}^n (y_i - \bar{y})^2} \quad (4)$$

$$7 \quad \text{RMSE} = \sqrt{\frac{\sum_{i=1}^n (y_i - \hat{y}_i)^2}{n-p}} \quad (5)$$

$$8 \quad \text{AIC} = n \ln((y_i - \hat{y}_i)^2) - n \ln(n) + 2p \quad (6)$$

$$9 \quad \text{ME} = \sum_{i=1}^n \left(\frac{y_i - \hat{y}_i}{n} \right) \quad (7)$$

$$10 \quad \text{MAE} = \sum_{i=1}^n \left| \frac{y_i - \hat{y}_i}{n} \right| \quad (8)$$

$$11 \quad P = \left(1 - \frac{t_{0.05} \times S_{\hat{y}}}{\hat{y}} \right) \times 100\%, \text{ where } S_{\hat{y}} = \sqrt{\frac{\sum (y_i - \hat{y}_i)}{n \times (n-p)}} \quad (9)$$

12 where y_i is the observed value; $\bar{y}$ is the mean of the observed value; $\hat{y}_i$ is the predicted value;
 13 $t_{0.05}$ is the t value at the 5% probability level; $S_{\hat{y}}$ is the standard error of the mean estimate; n is
 14 the number of observations; and p is the number of parameters.

15 Optimal PLR curve model selection

16 Previous studies have shown that all three candidate models fit the PLR curve well but are most
 17 suitable for different shapes of PLR curves. The curve of the MM model is asymptotic and lacks
 18 an extremum; thus, it is more suitable for fitting the PLR curve under unsaturated conditions (A_N
 19 increases continually as PAR increases) (Ye and Yu 2007). By including an index of curvature,
 20 the NRH model solved the PLR curve with greater convexity (Thornley 1976). The MRH model

is a modified model and is better at fitting the PLR curves of photosaturation (A_N increases first as PAR increases and tends to stabilize, until high PAR occurs) and photoinhibition (A_N increases first as PAR increases but then decreases after PAR becomes greater than the LSP) (Ye 2007; Ye and Yu 2007; Liu et al. 2016). In the present study, the PLR curves included all the above types as a result of vertical variation (Fig. 2). Hence, it was necessary to select an optimal model that was the best suited for fitting all the PLR curves within the crowns of the planted *Larix olgensis* trees. A previous study reported that the vertical variation in shape of PLR curves is obvious in an individual *Larix olgensis* tree (Liu et al. 2016). To determine a unique model that is suitable for fitting all the shapes of PLR curves, the PLR curve data were divided into nine groups according to RDINC at intervals of 0.1. The three candidate models were used for fitting the corresponding groups of PLR curves, and the optimal model that comprehensively considers the goodness of fit (R_a^2 , RMSE and AIC), the model structure and the physiological meaning of the parameters was then selected.

Model modification

The above three models reflect only the response of A_N to PAR at the single-leaf level. However, for trees, the crown A_N also varies with other surrounding environmental conditions, leaf characteristics and spatial position. Thus, the optimal PLR curve models were used to fit all 640 PLR curves, and the correlations between their parameters (AQY , A_{max} and R_d) and T_{leaf} , VPD (representing environmental conditions), LMA (representing leaf characteristics), RDINC (representing spatial position) and the combinations of these were analyzed. Then, the optimal

PLR curve model was modified by incorporating some of the above factors to obtain new models that could estimate the A_N at different vertical positions within the crown during the growing season. The basic form of the modified models is as below:

$$PLR_{OM} \begin{cases} A_{max} = f(x) \\ AQY = g(x) \\ R_d = h(x) \end{cases} \quad (10)$$

where PLR_{OM} is the optimal PLR curve model that will be selected from the equations MM (Eq. 1), NRH (Eq. 2) and MRH (Eq. 3); $f(x)$ is the function of A_{max} and T_{leaf} , VPD, LMA, RDINC or their combinations; $g(x)$ is the function of AQY and T_{leaf} , VPD, LMA, RDINC or their combinations; $h(x)$ is the function of R_d and T_{leaf} , VPD, LMA, RDINC or their combinations; and x represents T_{leaf} , VPD, LMA, RDINC or their combinations.

Numerous modified models can be generated by respectively reparameterizing for A_{max} , AQY and R_d or simultaneously reparameterizing two or three of them. Although more parameterizations based on a greater range of data will produce a better simulation, that approach also increases the complexity and the computation expense (Fisher et al. 2018). The optimal model should comprehensively consider the accuracy and complexity based on natural reality.

In this study, all the coefficients from the different models were determined via nonlinear least-squares fitting (PROC NLIN), which was carried out using SAS 9.3 (SAS Institute Inc., Cary, North Carolina, USA).

Results

Optimal model for fitting PLR curves

Three candidate models (Eqs. 1–3) were separately applied to fit the PLR curves for different RDINC values. The coefficient estimations and goodness of fit were calculated and are listed in Table 3. The R_a^2 values of all three candidate models exhibited decreasing tendencies that were similar to the increase in RDINC; this result indicated that all three candidate models were more suitable for fitting the PLR curves for the upper crown than for the lower crown. The goodness of fit was nearly identical between the NRH and MRH models in each group of RDINC values. Both the NRH and MRH models exhibited a better goodness of fit than did the MM model, but this difference was not significant. The R_a^2 values of the NRH and MRH models were higher than those of the MM model by 0.003 on average, and the RMSE values and AIC values were lower than those of MM model by 0.4% and 0.6% on average, respectively. The fitting results for the three candidate models for three groups with a typical RDINC (0.1, 0.5 or 0.9, representing upper, middle and lower crowns, respectively) are illustrated in Fig. 3, which also shows that the three candidate models all fitted the PLR curves well.

The NRH and MRH models each have four coefficients, some of which have no photophysiological meaning (e.g., θ in NRH and β and γ in MRH). However, the MM model has only three coefficients (AQY , $A_{\max}$ and R_d), all of which are important photosynthetic indicators with true photophysiological meaning. Furthermore, the structure of the MM model is simpler than those of the NRH and MRH models. Considering that the goodness of fit among the three candidate models, the MM model was ultimately selected as the optimal model for fitting the

1 PLR curves of planted *Larix olgensis* trees. The MM model was subsequently further modified
 2 by reparameterization, as follows:

$$3 \quad A_N = A_{\max} \left(1 - e^{(-AQY \cdot PAR / A_{\max})} \right) - R_d, \quad \begin{cases} A_{\max} = f(x) \\ AQY = g(x) \\ R_d = h(x) \end{cases} \quad (11)$$

4 where $f(x)$, $g(x)$ and $h(x)$ are described above.

5 **Relationships between the parameters of the MM model and T_{leaf} , VPD, LMA and RDINC**

6 The coefficient estimates for the MM model (Table 3) showed that $A_{\max}$ and R_d decreased
 7 markedly with increases in the RDINC, but the differences between the PLR curves in each
 8 RDINC group were still clear (Fig. 3). These findings implied that RDINC is an important factor
 9 influencing crown photosynthesis but is not the only such factor. Thus, we fitted all the PLR
 10 curves using the MM model and analyzed the relationships between all three parameters of the
 11 MM model and T_{leaf} , VPD, LMA and RDINC (Fig. 4). $A_{\max}$ exhibited a strong positive
 12 correlation with LMA (Fig. 4c, $r = 0.766$), indicating that a high LMA of needles is usually
 13 accompanied by a high photosynthetic capacity. RDINC exhibited a significant negative
 14 correlation with $A_{\max}$ (Fig. 4d), which was consistent with the above results (Table 3, Fig. 3).
 15 VPD was also negatively correlated with $A_{\max}$ (Fig. 4b), indicating that dry air conditions may
 16 inhibit photosynthesis. $A_{\max}$ also showed a significant correlation with T_{leaf} (Fig. 4a), which
 17 increased with the increase in T_{leaf} but then decreased after T_{leaf} surpassed a certain value
 18 (approximately 28°C). AQY exhibited a strong negative correlation with VPD (Fig. 4f), likely
 19 caused by the negative relationship between $A_{\max}$ and VPD. T_{leaf} and LMA were also slightly

correlated with AQY (Fig. 4e and Fig. 4g), but RDINC was not significantly related to AQY (Fig. 4h). R_d exhibited a strong exponential correlation with T_{leaf} (Fig. 4i, $r = 0.687$), demonstrating T_{leaf} was the most important factor affecting R_d . RDINC also showed a significant negative relationship with R_d (Fig. 4l), likely because the temperature in the upper crown is usually higher than that in the lower crown.

Establishment of the estimated crown A_N model

Based on the relationships between A_{max} and T_{leaf} , VPD, LMA and RDINC, regression analysis was conducted among A_{max} and T_{leaf} , VPD, LMA, RDINC and their combinations. Hence, the combination of LMA, VPD and RDINC was selected as the best variable for estimating A_{max} . Thus, the form of $f(x)$ in Eq. 11 was determined as follows:

$$f(x) = a_0 + a_1 \times \ln\left(\frac{LMA}{VPD \times RDINC}\right) \quad (12)$$

where a_0 and a_1 are estimable parameters.

Similarly, regression analysis among AQY and T_{leaf} , VPD, LMA, RDINC and their combinations was conducted. The results showed that using VPD alone resulted in good estimation of AQY well. Thus, the form of $g(x)$ in Eq. 11 was determined as follows:

$$g(x) = b_0 + b_1 \times VPD \quad (13)$$

where b_0 and b_1 are estimable parameters.

Previous studies showed that R_d could be estimated by the exponential function (Lloyd and Taylor 1994; Rodríguezcalcerrada et al. 2010; Weerasinghe et al. 2014; Meyer et al. 2018) based on the exponential correlation between R_d and T_{leaf} . In this study, because R_d demonstrated a

similar exponential correlation with T_{leaf} , the exponential function was selected as the basic form for $h(x)$ in Eq. 10, which is described as follows:

$$R_d = c_0 \times \exp(c_1 \times T_{leaf}) \tag{14}$$

where c_0 and c_1 are parameters.

As R_d was also significantly related to LMA (Fig. 4j) and RDINC (Fig. 4l), we divided all the R_d values into nine groups according to RDINC at intervals of 0.1 and fitted Eq. 14 to each group to obtain the parameters c_0 and c_1 . Then, the relationships between c_0 and c_1 and the mean values of RDINC were analyzed. Similarly, the R_d was also divided into 10 groups according to LMA at intervals of 10 g m^{-2} , and the relationships between c_0 and c_1 and the mean values of LMA were analyzed (Fig. 5c and Fig. 5d). Then, c_0 and c_1 were further modified by reparameterization using RDINC and LMA respectively and evaluated by R^2 and RMSE. Thus, the final form of $h(x)$ in Eq. 10 was as follows:

$$R_d = (c_0 \times RDINC + c_1) \times \exp((c_2 \times LMA + c_3) \times T_{leaf}) \tag{15}$$

where $c_0 \sim c_3$ are estimable parameters.

Comparison of the assessment and validation of the modified models

After modification of the MM model by incorporating environmental factors (T_{leaf} and VPD), leaf morphological characteristics (LMA) and leaf vertical position (RDINC), the MM model was scaled up from a single leaf to the whorl and even the crown level. However, reparameterization of the original model usually increases the number of parameters, leading to a more complex model structure, making the model inconvenient to use (Mayoral et al. 2015;

1 Fisher et al. 2018). In this study, the MM model was therefore modified by gradually
2 reparameterizing $A_{\max}$, AQY and R_d to nineteen new models (Table 4), to fit all the PLR curve
3 data (Table 2). The nineteen new models were then validated using independent validation data
4 (A_N measured in natural ambient conditions, Table 2). The goodness-of-fit and validation results
5 were calculated and are listed in Table 5. According to the correlations between photosynthetic
6 parameters and the influence factors (Fig. 4), we found that the $A_{\max}$, AQY and R_d values varied
7 significantly with the changes in at least one factor. This indicated that $A_{\max}$, AQY and R_d were
8 not constant values during the growing period. However, among the modified models, only four
9 of them (model 17 – model 20, Table 4) simultaneously considered the dynamic changes in $A_{\max}$,
10 AQY and R_d that conformed to the natural reality. The other modified models, those that ignored
11 the dynamic change in at least one photosynthetic parameter, were not selected even though
12 some of them performed well on goodness of fit and validation results (Table 5). The values of
13 R_a^2 and P for model 17 – model 20 were all greater than 0.88 and 95.60, respectively, which
14 indicated that all four modified models performed well in model fitting and validation. The small
15 differences in RMSE, AIC, ME and MAE among the four models implied that there was no
16 significant difference among them, an idea that also reflected by the comparison of measured and
17 predicted A_N values for the validation data (Fig. 6). Thus, model 17 was finally selected as the
18 best model for predicting the crown A_N of planted *Larix olgensis* trees during the growing season,
19 since it contained fewer parameters than the other three, and it retained good goodness of fit (R_a^2

1 = 0.884, RMSE = 1.51, AIC = 6941) and validation results (ME = 0.097, MAE = 1.458, P =
 2 95.601).

3 **Simulation of the responses of crown A_N to influencing factors**

4 To better understand the responses of A_N within the crown to the varied environment,
 5 environmental conditions of three quality levels (extremely harsh, normal and excellent) were
 6 established for comparing the different performance of A_N (Fig. 7). As T_{leaf} and VPD were highly
 7 correlated with each other and as they both had upper and lower limits under natural conditions,
 8 the environmental conditions should be set in a reasonable range according to the actual
 9 measurements. Finally, the extreme environment was represented by 40°C T_{leaf} and 4 kPa VPD;
 10 the normal environment was represented by 30°C T_{leaf} and 2 kPa VPD; and the excellent
 11 environment was represented by 20°C T_{leaf} and 1 kPa VPD. All the above combinations of T_{leaf}
 12 and VPD are dependent on the measured values. The dynamic variation in LMA usually
 13 represented the different development phases of needles; thus, it was set to 40 g m⁻², 80 g m⁻² or
 14 120 g m⁻², respectively, to represent the preliminary expansion, expanding and fully expanded
 15 stages of needles. RDINC was set to 0.1, 0.5 or 0.9 to represent the upper, middle and lower
 16 crowns, respectively. The results showed that the environmental conditions, leaf morphological
 17 characteristics and vertical position synchronously influenced A_N (Fig. 7). The upper crown
 18 generally exhibited a greater photosynthetic capacity than did the lower crown, but the difference
 19 was weaker with decreasing PAR, and this phenomenon was more obvious when the
 20 environment became better (Fig. 7a, 7b and 7c). The PLR curves for the upper crown exhibited

obvious fluctuation with the three gradients of environmental conditions (Fig. 7), presumably because the needles in the upper crown are exposed to environmental stresses more frequently, and the variations in the environment of the upper crown are more sensitive and larger (Han et al. 2003). The photosynthetic capacities of the upper, middle and lower crown generally exhibited a rapid increment during leaf expansion (LMA increased from 40 g m^{-2} to 80 g m^{-2}), and this increase then slowed after the leaves were fully expanded (Fig. 7c, 7f and 7i). Environmental conditions exerted an obvious influence on A_N . When the environment was extremely bad (high temperature and low humidity), the A_N values of the upper, middle and lower crowns were very low (Fig. 7a, 7b and 7c). Taking A_{N-2000} (the A_N value when PAR was $2000 \mu\text{mol m}^{-2} \text{ s}^{-1}$) as an example, the A_{N-2000} values of the upper, middle and lower crowns under an extreme environment (Fig. 7a, 7b and 7c) were $7.36 \mu\text{mol m}^{-2} \text{ s}^{-1}$, $5.12 \mu\text{mol m}^{-2} \text{ s}^{-1}$ and $4.73 \mu\text{mol m}^{-2} \text{ s}^{-1}$ lower on average than those under an excellent environment (Fig. 7g, 7h and 7i) during leaf expansion.

Discussion

The simulation of photosynthesis plays an important role in many dynamic global vegetation models (DGVMs) (Sitch et al., 2003; Thornton et al. 2007; Shuman et al. 2014; Fyllas et al. 2014; Weng et al. 2015; Fischer et al. 2016; Fisher et al. 2018). In the above DGVMs, photosynthesis is always simulated on the basis of the Farquhar scheme (Farquhar et al. 1980), but its behavior is not easy to predict from its formulation (Sato et al. 2007). Mechanistically based models are very complex and use a network of submodels to describe biochemical processes that define

1 photosynthesis. Semiempirical models provide an intermediate option and define photosynthesis
2 according to a mathematical description of a single biochemical process (Mayoral et al. 2015).
3 PLR curve models, which describe the relationship between the A_N and PAR, belong to this
4 group. In recent years, a series of studies successfully incorporated leaf morphological
5 characteristics (N, LMA and SPAD) into PLR curve models to extend their scope of application
6 (Marino et al. 2010; Lachapelle and Shipley 2012; Xu et al. 2014; Xu et al. 2015), which
7 inspired us to test whether this approach could also be applied in trees.

8 Vertical variation in leaf photosynthesis is a common phenomenon and has been described in
9 many reports (e.g., Woodman 1971; Han et al. 2003; Niinemets et al. 2004; Hamada et al. 2016).

10 This variation is mainly attributed to the variation in both leaf physiological features (Reich et al.
11 1990; Kull 2002; Chiarawipa et al. 2012) and the microenvironment (Rook and Corson 1978).

12 Our results (Fig. 3 and Fig. 4) are also in agreement with the above reports, as we found that the
13 A_N values within the lower crown were clearly smaller than those within the upper crown, which
14 was in accordance with the theory of low light acclimation (Kull 2002; Niinemets 2004).

15 However, the PLR curves presented significant differences, even for the same RDINC (Fig. 3),
16 further indicating that RDINC is not the only factor affecting crown photosynthesis. In this study,

17 T_{leaf} exhibited a significant parabolic correlation with A_{max} (Fig. 4a); this phenomenon has also
18 been reported in many other studies (Hikosaka et al. 2007; Way and Sage 2008; Wieser et al.
19 2010; Lin et al. 2012; Calama et al. 2013; Mayoral et al. 2015). We observed that a high VPD
20 usually inhibited photosynthesis (Fig. 4b), consistent with other studies (Vygodskaya et al. 1997;

Day 2000; Shirke and Pathre 2004; Pinto et al. 2012; Rashid et al. 2018). This phenomenon was more obvious in the upper crown (Fig. 8), presumably because the leaves in the upper crown are exposed to environmental stresses more frequently and because the variations in VPD in the upper crown are more sensitive and larger (Han et al. 2003). Xu et al. (2017) further confirmed that a low VPD could increase the ecosystem photosynthetic potential. LMA plays an important role in predicting leaf physiological function (Cavaleri et al. 2010) and serves as a parameter in ecosystem modeling as well as an indicator of the potential growth rate (Fellner et al. 2016). LMA has been positively related to $A_{\max}$ (Bond et al. 1999, Kenzo et al. 2006, Meinzer et al. 2008, Sperlich et al. 2015), which was also observed in the present study (Fig. 4c). In contrast, some researchers found a negative relationship between $A_{\max}$ and LMA (Marshall and Monserud 2003; Koch et al. 2004; Xiao et al. 2006; Han 2011), which was probably associated with the higher LMA (greater than 300 g m⁻²) than that observed in our study (less than 130 g m⁻²). Previous investigations have suggested that a high LMA hinders mesophyll conductivity to CO₂ and consequently reduces $A_{\max}$ (Han 2011; Mullin et al. 2009).

To date, many equations have been applied to fit PLR curves for many different plants (e.g., Baly 1935; Thornley 1976; Bassman and Zwier 1991; Luo et al. 2000; Dias-Filho 2002; Lootens et al. 2004; Ye 2007; Posada et al. 2009). In most PLR curve models, there is a mathematical definition for each parameter, but they often do not have the desired ecophysiological meaning (Lobo et al. 2013). Liu et al. (2016) compared the applicability of the main PLR curve models of four typical shapes of PLR curves and confirmed that the MRH model expressed the best

1 stability for the various types of PLR curves. In this study, three frequently applied models (MM,
 2 NRH and MRH) were used to fit PLR curves for different RDINC values. The model assessment
 3 (based on R_a^2 , RMSE and AIC) did not differ significantly among the three models (Table 3),
 4 mainly because the shapes of the PLR curves fitted for each RDINC were not significantly
 5 different. Finally, because it had a simpler structure with fewer parameters and because those
 6 parameters have ecophysiological meaning, the MM model was selected as the optimal model
 7 for fitting the PLR curves of the planted *Larix olgensis* trees.

8 Marino et al. (2010), Lachapelle and Shipley (2012), and Xu et al. (2014; 2015) have
 9 successfully incorporated N, LMA, and the chlorophyll index (SPAD) into PLR curve models to
 10 solve the problem of parameters variation among different crop species or among different
 11 growth environments. Similarly, the MM model was modified by reparameterization in this
 12 study, according to the relationships between the parameters of the MM model ($A_{\max}$, AQY and
 13 R_d) and T_{leaf} , VPD, LMA, RDINC and their combinations. VPD is a comprehensive indicator
 14 reflecting temperature and humidity and has been demonstrated to be more important than
 15 temperature and PAR in causing the midday depression of A_N (Pathre et al. 1998). Thus, we used
 16 VPD instead of T_{leaf} in combination with LMA and RDINC to reparameterize the parameter
 17 ($A_{\max}$) of the MM model. Because $A_{\max}$ was positively related to LMA (Fig. 4c) and negatively
 18 related to VPD (Fig. 4b) and RDINC (Fig. 4d), the parameter of the MM model was
 19 reparameterized based on this combination as $\frac{LMA}{VPD \times RDINC}$. Our results showed that AQY was
 20 strongly and negatively related to VPD (Fig. 4f), likely due to the restraint imposed by a high

VPD on stomatal conductance (Day 2000; Awada et al. 2003; Voelker et al. 2017). As confirmed by many reports, R_d exponentially increased with increasing temperature (Fig. 4i) and could be estimated well by the exponential function (Lloyd and Taylor 1994; Way and Sage 2008; Rodríguez-calcerrada et al. 2010; Lin et al. 2012; Calama et al. 2013; Weerasinghe et al. 2014 Meyer et al. 2018). In addition, we found that R_d exhibited a significant relationship with RDINC (Fig. 4l). Thus, further reparameterization was conducted by incorporating RDINC into the exponential function in order to scale up the R_d estimation model from the leaf level to the crown level.

In this study, the MM model was modified to obtain 19 new models (Table 4) by gradually reparameterizing its three parameters. Compared with the other modified models, model 17 considered the main factors affecting photosynthesis, retained relatively few parameters and presented better model assessment and validation results (Table 5). Thus, model 17 was selected as the best model for predicting the crown A_N of planted *Larix olgensis* trees during the growing season. In contrast to previous mechanistic models (Amthor 1994; Leuning et al. 1995; Wang and Leuning 1998), our model was developed from a semiempirical model (PLR curve model) that focused on only a single biochemical process between A_N and PAR. The model still showed a sound physiological basis, although some other physiological biochemical processes of photosynthesis were weakened, and it could be easily fitted to gas-exchange measurements (Mayoral et al. 2015). Some studies have used the same approach to establish the A_N of herbaceous species (Marino et al. 2010; Lachapelle and Shipley 2012), rice (Xu et al. 2014; Xu

et al. 2015) and saplings (Calama et al. 2013; Mayoral et al. 2015). However, only a single factor, such as N , CHL , LMA or GSF , was considered in these previous studies. For trees, environmental conditions, leaf morphological characteristics and leaf spatial positions all affect photosynthesis, and neglecting these factors will therefore result in incorrect carbon uptake simulations (Wilson et al. 2001; Tanaka et al. 2002; Kosugi et al. 2003; Grassi et al. 2005; Coble et al. 2016), which is one of the reasons that model 17 was ultimately selected as the best model. The estimation of dynamic crown A_N is an important part of calculating the accumulated photosynthate. Based on the accumulated photosynthate and the growth of the tree organs, we can test the accuracy of the previous method for determining the functional crown (Li et al. 1996) and further correct it. In this study, we established a model for estimating the dynamic and multilayered crown A_N during the growing season, and this model was not as complex as the mechanistically based physiological models. This model is a basic and important step in determining the height of the functional crown, which contributes significantly to effective artificial pruning. However, the model still presents some shortfalls: (1) although we measured abundant PLR curve data from five sampled trees, the data were insufficient for extrapolating the method from an individual tree to a whole stand; (2) all five sampled trees represented an average tree of the whole stand; therefore, they do not reflect the differences among trees of different sizes; and (3) age, competition from neighboring trees and soil conditions also influence the photosynthetic capacity of the crown but were not considered in our study. These issues need be addressed in future studies based on more detailed data.

Conclusions

Environmental conditions are the main factors affecting instantaneous A_N within the crown. The development of leaf morphological characteristics during the growing season can fully represent the seasonal variations in the photosynthetic capacity. In this study, a semiempirical model for predicting the crown A_N of planted *Larix olgensis* trees was established by modifying the PLR curve model. This model consisted of five important factors, PAR, T_{leaf} , VPD, LMA and RDINC, which can represent the instantaneous, seasonal and spatial variations in A_N within the crown. Some complex physiological and biochemical processes were weakened in our study, but the new semiempirical model still exhibited a good prediction accuracy. In addition, the new model was more convenient to apply than were mechanistic models. According to our model, the dynamic A_N in each vertical gradient of the crown throughout the growing season could be estimated, laying the foundation for calculating multilayered photosynthetic production within the crown and determining the range of the functional crown for individual trees.

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Table 1. Attributes of sample plots and corresponding sample trees for *Larix olgensis* plantation

Sample trees [*]			Sample plots [†]					
Tree NO.	DBH(cm)	H(m)	Plot NO.	Range of DBH(cm)	Range of H(m)	Mean DBH(cm)	Mean H(m)	Stand density(trees ha ⁻¹)
I	10.75	10.33	P1	5.0-16.0	6.0-12.8	9.92	9.23	2200
II	11.15	10.52	P2	5.3-15.9	5.3-13.2	10.59	10.19	2400
III	10.90	10.81	P3	5.2-14.1	7.1-10.5	9.73	9.62	3200
IV	10.80	10.35	P4	5.0-16.7	5.8-13.0	10.13	9.63	2920
V	11.69	10.80	P5	5.2-16.5	6.3-12.7	10.92	10.3	2430

^{*}Tree NO. = tree number, DBH = diameter at breast height, H = tree height; [†] Plot NO. = plot number, Mean DBH = mean value of diameter at breast height, Mean H = mean value of tree height.

Table 2. Statistics of physiological factors, morphological factors, environmental factors and vertical positions of samples for planted *Larix olgensis* trees

Variables*	Fitting data†				Validation data			
	Mean	Std.	Min.	Max.	Mean	Std.	Min.	Max.
Sample size	n=8434 (640 PLR curves)				n=395			
$A_n / \mu\text{mol m}^{-2} \text{ s}^{-1}$	5.31	4.44	-3.90	27.49	4.45	4.51	-1.47	19.58
$T_{\text{leaf}} / ^\circ\text{C}$	28.2	3.58	15.45	39.37	29.60	4.97	18.91	38.52
VPD / kPa	1.75	0.68	0.64	4.32	1.80	0.93	0.22	3.88
PAR / $\mu\text{mol m}^{-2} \text{ s}^{-1}$	767	724	0.00	2200	470	507	0.00	2073
LMA / g m^{-2}	59.9	20.3	24.0	127.5	61.0	17.7	28.4	127.5
RDINC	0.52	0.27	0.08	0.99	0.54	0.25	0.09	0.99

* A_n = net CO_2 assimilation, T_{leaf} = leaf temperature, VPD = vapor pressure deficit, PAR = photosynthetically active radiation, LMA = leaf mass per area, RDINC = relative depth into crown. †mean = mean value, std. = standard deviation, min. = minimum value, max. = maximum value, n = sample numbers, PLR = photosynthetic light response.

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Table 3. Coefficient estimations and goodness-of-fit of candidate models

Model*	RDINC	Coefficient estimation [†]			Goodness-of-fit [‡]		
	AQY	$A_{\max}$ ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	R_d ($\mu\text{mol m}^{-2} \text{s}^{-1}$)		R_a^2	RMSE ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	AIC
M	0.1–0.2	0.0394	14.69	1.41	0.750	3.188	2351
	0.2–0.3	0.0385	12.07	1.41	0.781	1.721	1190
	0.3–0.4	0.0384	10.80	1.04	0.710	2.508	1233
	0.4–0.5	0.0397	10.02	0.91	0.757	2.075	874
	0.5–0.6	0.0398	8.93	0.94	0.767	1.774	594
	0.6–0.7	0.0373	7.38	0.78	0.751	1.502	427
	0.7–0.8	0.0365	7.19	0.71	0.687	1.720	633
	0.8–0.9	0.0363	6.98	0.83	0.672	1.715	612
	0.9–1.0	0.0350	5.96	0.61	0.590	1.722	648
	AQY	$A_{\max}$ ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	R_d ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	θ	R_a^2	RMSE ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	AIC
NRH	0.1–0.2	0.0507	17.48	1.83	0.250	0.752	2341
	0.2–0.3	0.0495	14.13	1.76	0.277	0.784	1181
	0.3–0.4	0.0496	12.51	1.37	0.290	0.715	1227
	0.4–0.5	0.0495	11.40	1.18	0.361	0.759	868
	0.5–0.6	0.0465	9.94	1.14	0.463	0.768	590
	0.6–0.7	0.0446	8.17	0.95	0.446	0.754	422
	0.7–0.8	0.0431	7.95	0.87	0.456	0.689	630
	0.8–0.9	0.0427	7.70	0.98	0.457	0.674	609
	0.9–1.0	0.0476	6.67	0.80	0.593	1.717	644
	AQY	β	R_d ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	γ	R_a^2	RMSE ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	AIC
MRH	0.1–0.2	0.0538	0.000027	1.86	0.0028	0.752	2341
	0.2–0.3	0.0538	0.000024	1.81	0.0035	0.784	1181
	0.3–0.4	0.0543	0.000025	1.42	0.0040	0.715	1227
	0.4–0.5	0.0555	0.000035	1.24	0.0044	0.759	867
	0.5–0.6	0.0546	0.000050	1.21	0.0048	0.769	589
	0.6–0.7	0.0524	0.000043	1.00	0.0057	0.754	421
	0.7–0.8	0.0518	0.000040	0.93	0.0058	0.689	629
	0.8–0.9	0.0522	0.000033	1.05	0.0061	0.674	609
	0.9–1.0	0.0531	0.000024	0.83	0.0075	0.593	644

*M = Mitscherlich model, NRH = nonrectangular hyperbola, MRH = modified rectangular hyperbola. [†]AQY = apparent quantum yield, $A_{\max}$ = maximum net CO₂ assimilation, R_d = dark respiration rate, β , γ and θ are estimated parameters. [‡] R_a^2 = adjusted coefficient of determination, RMSE = root mean square error, AIC = akaike's information criterion.

Table 4. Model structures and forms of modified models

Model No.	Model form*	Re-parameterized factors†
Model 1	$A_n = a_0 \times (1 - \exp(-b_0 \times PAR/a_0)) - c_0$	None
Model 2	$A_n = (a_0 \times \ln(LMA/VPD \times RDINC) + b_0) \times (1 - \exp(-c_0 \times PAR/(a_0 \times \ln(LMA/VPD \times RDINC) + b_0))) - d_0$	A_{max}
Model 3	$A_n = a_0 \times (1 - \exp(-(b_0 \times VPD + c_0) \times PAR/a_0)) - d_0$	AQY
Model 4	$A_n = a_0 \times (1 - \exp(-b_0 \times PAR/a_0)) - c_0 \times e^{(d_0 \times T_{leaf})}$	R_d
Model 5	$A_n = a_0 \times (1 - \exp(-b_0 \times PAR/a_0)) - c_0 \times e^{((d_0 \times LMA + e_0) \times T_{leaf})}$	R_d
Model 6	$A_n = a_0 \times (1 - \exp(-b_0 \times PAR/a_0)) - (c_0 \times RDINC + d_0) \times e^{(e_0 \times T_{leaf})}$	R_d
Model 7	$A_n = a_0 \times (1 - \exp(-b_0 \times PAR/a_0)) - (c_0 \times RDINC + d_0) \times e^{((e_0 \times LMA + f_0) \times T_{leaf})}$	R_d
Model 8	$A_n = (a_0 \times \ln(LMA/VPD \times RDINC) + b_0) \times (1 - \exp(-c_0 \times PAR/(a_0 \times \ln(LMA/VPD \times RDINC) + b_0))) - d_0 \times e^{(e_0 \times T_{leaf})}$	A_{max}, R_d
Model 9	$A_n = (a_0 \times \ln(LMA/VPD \times RDINC) + b_0) \times (1 - \exp(-c_0 \times PAR/(a_0 \times \ln(LMA/VPD \times RDINC) + b_0))) - d_0 \times e^{((e_0 \times LMA + f_0) \times T_{leaf})}$	A_{max}, R_d
Model 10	$A_n = (a_0 \times \ln(LMA/VPD \times RDINC) + b_0) \times (1 - \exp(-c_0 \times PAR/(a_0 \times \ln(LMA/VPD \times RDINC) + b_0))) - (d_0 \times RDINC + e_0) \times e^{(f_0 \times T_{leaf})}$	A_{max}, R_d
Model 11	$A_n = (a_0 \times \ln(LMA/VPD \times RDINC) + b_0) \times (1 - \exp(-c_0 \times PAR/(a_0 \times \ln(LMA/VPD \times RDINC) + b_0))) - (d_0 \times RDINC + e_0) \times e^{((f_0 \times LMA + g_0) \times T_{leaf})}$	A_{max}, R_d
Model 12	$A_n = (a_0 \times \ln(LMA/VPD \times RDINC) + b_0) \times (1 - \exp(-(c_0 \times VPD + d_0) \times PAR/(a_0 \times \ln(LMA/VPD \times RDINC) + b_0))) - e_0$	A_{max}, AQY
Model 13	$A_n = a_0 \times (1 - \exp(-(b_0 \times VPD + c_0) \times PAR/a_0)) - d_0 \times e^{(e_0 \times T_{leaf})}$	AQY, R_d
Model 14	$A_n = a_0 \times (1 - \exp(-(b_0 \times VPD + c_0) \times PAR/a_0)) - d_0 \times e^{((e_0 \times LMA + f_0) \times T_{leaf})}$	AQY, R_d
Model 15	$A_n = a_0 \times (1 - \exp(-(b_0 \times VPD + c_0) \times PAR/a_0)) - (d_0 \times RDINC + e_0) \times e^{(f_0 \times T_{leaf})}$	AQY, R_d
Model 16	$A_n = a_0 \times (1 - \exp(-(b_0 \times VPD + c_0) \times PAR/a_0)) - (d_0 \times RDINC + e_0) \times e^{((f_0 \times LMA + g_0) \times T_{leaf})}$	AQY, R_d
Model 17	$A_n = (a_0 \times \ln(LMA/VPD \times RDINC) + b_0) \times (1 - \exp(-(c_0 \times VPD + d_0) \times PAR/(a_0 \times \ln(LMA/VPD \times RDINC) + b_0))) - e_0 \times e^{(f_0 \times T_{leaf})}$	A_{max}, AQY, R_d
Model 18	$A_n = (a_0 \times \ln(LMA/VPD \times RDINC) + b_0) \times (1 - \exp(-(c_0 \times VPD + d_0) \times PAR/(a_0 \times \ln(LMA/VPD \times RDINC) + b_0))) - e_0 \times e^{((f_0 \times LMA + g_0) \times T_{leaf})}$	A_{max}, AQY, R_d
Model 19	$A_n = (a_0 \times \ln(LMA/VPD \times RDINC) + b_0) \times (1 - \exp(-(c_0 \times VPD + d_0) \times PAR/(a_0 \times \ln(LMA/VPD \times RDINC) + b_0))) - (e_0 \times RDINC + f_0) \times e^{(g_0 \times T_{leaf})}$	A_{max}, AQY, R_d
Model 20	$A_n = (a_0 \times \ln(LMA/VPD \times RDINC) + b_0) \times (1 - \exp(-(c_0 \times VPD + d_0) \times PAR/(a_0 \times \ln(LMA/VPD \times RDINC) + b_0))) - (e_0 \times RDINC + f_0) \times e^{((g_0 \times LMA + h_0) \times T_{leaf})}$	A_{max}, AQY, R_d

* A_n = net CO₂ assimilation, LMA = leaf mass per area, VPD = vapor pressure deficit, RDINC = relative depth into crown, PAR = photosynthetic active radiation, T_{leaf} = leaf temperature, ln() is logarithmic function. † A_{max} = maximum net CO₂ assimilation, R_d = dark respiration rate, AQY = apparent quantum yield.

Table 5. Results of goodness-of-fit and validations of all modified models

Model NO.	Parameter estimations								Goodness-of-fit*			Validation†		
	a_0	b_0	c_0	d_0	e_0	f_0	g_0	h_0	R_a^2	RMSE ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	AIC	ME ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	MAE ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	P (%)
Model 1	9.38	0.036	0.922						0.612	2.77	17162	0.086	1.865	93.899
Model 2	3.30	-4.847	0.041	1.104					0.864	1.64	8318	0.082	1.526	95.337
Model 3	9.48	-0.012	0.052	0.682					0.644	2.65	16425	0.321	1.654	94.050
Model 4	9.37	0.036	0.525	0.020					0.612	2.77	17167	0.121	1.848	93.874
Model 5	7.85	0.019	-28.14	0.002	-0.245				0.679	2.51	15557	0.357	2.028	93.540
Model 6	9.70	0.040	0.832	-0.186	0.060				0.695	2.45	15128	0.412	2.041	93.491
Model 7	8.13	0.022	40.58	-24.39	0.001	-0.141			0.697	2.44	15071	0.423	2.026	93.500
Model 8	3.36	-5.240	0.039	0.042	0.109				0.868	1.61	8085	0.324	1.579	94.957
Model 9	3.42	-5.507	0.040	0.048	0.0001	0.097			0.873	1.58	7748	-0.729	1.775	95.751
Model 10	3.76	-6.872	0.043	-0.276	0.334	-0.061			0.803	1.97	11455	-1.030	1.881	95.779
Model 11	3.83	-7.225	0.043	0.688	0.026	-0.147	0.109		0.874	1.57	7647	0.068	1.503	95.474
Model 12	3.31	-4.895	-0.013	0.061	0.941				0.884	1.51	6944	0.095	1.463	95.592
Model 13	9.52	-0.012	0.052	10.939	-0.100				0.649	2.63	16312	0.273	1.629	94.177
Model 14	10.32	-0.017	0.075	1.991	-0.001	0.066			0.709	2.39	14737	0.228	1.782	94.315
Model 15	9.58	-0.012	0.053	2.362	-0.882	0.027			0.777	2.09	12476	0.381	1.898	94.080
Model 16	9.10	-0.010	0.042	6.646	-3.015	0.0005	-0.042		0.837	1.79	9844	0.393	1.874	94.101
Model 17	3.31	-4.887	-0.013	0.061	1.065	-0.004			0.884	1.51	6941	0.097	1.458	95.601
Model 18	3.28	-4.740	-0.013	0.061	1.011	-0.0001	-0.001		0.887	1.49	6740	0.045	1.418	95.728
Model 19	3.57	-6.003	-0.014	0.064	-1.844	2.755	-0.020		0.887	1.49	6761	0.079	1.435	95.651
Model 20	3.470	-5.584	-0.014	0.062	-2.095	2.602	-0.0004	0.008	0.887	1.49	6746	0.058	1.416	95.714

* R_a^2 = adjusted coefficient of determination, RMSE = root mean square error, AIC = akaike's information criterion. †ME = mean error, MAE = mean absolute error, P = precision estimation.