Determination of the most effective design for the measurement of photosynthetic light-response curves for planted *Larix olgensis* trees

Qiang Liu1,2, Weiwei Jia1,2* & Fengri Li1,2*

A photosynthetic light-response (PLR) curve is a mathematical description of a single biochemical process and has been widely applied in many eco-physiological models. To date, many PLR measurement designs have been suggested, although their differences have rarely been explored, and the most effective design has not been determined. In this study, we measured three types of PLR curves (High, Middle and Low) from planted *Larix olgensis* trees by setting 31 photosynthetically active radiation (PAR) gradients. More than 530 million designs with different combinations of PAR gradients from 5 to 30 measured points were conducted to fit each of the three types of PLR curves. The influence of different PLR measurement designs on the goodness of fit of the PLR curves and the accuracy of the estimated photosynthetic indicators were analysed, and the optimal design was determined. The results showed that the measurement designs with fewer PAR gradients generally resulted in worse predicted accuracy for the photosynthetic indicators. However, the accuracy increased and remained stable when more than ten measurement points were used for the PAR gradients. The mean percent error (M%e) of the estimated maximum net photosynthetic rate ($P_{\text{max}}$) and dark respiratory rate ($R_d$) for the designs with less than ten measurement points were, on average, 16.4 times and 20.1 times greater than those for the designs with more than ten measurement points. For a single tree, a unique PLR curve design generally reduced the accuracy of the predicted photosynthetic indicators. Thus, three optimal measurement designs were provided for the three PLR curve types, in which the root mean square error (RMSE) values reduced by an average of 8.3% and the coefficient of determination ($R^2$) values increased by 0.3%. The optimal design for the High PLR curve type should shift more towards high-intensity PAR values, which is in contrast to the optimal design for the Low PLR curve type, which should shift more towards low-intensity PAR values.

The photosynthetic light-response (PLR) curve reflects the instantaneous response of the net photosynthetic rate ($P_n$) to different gradients of photosynthetically active radiation (PAR). It can provide measures of many photosynthetic indicators, such as the maximum $P_n$ ($P_{\text{max}}$), dark respiration rate ($R_d$), apparent quantum yield (AQY), light compensation point (LCP) and light saturated point (LSP), for analysing plant photosynthetic activity. In addition, it is also a basic element for modelling the photosynthesis and primary productivity of vegetation and forests. In recent studies, the application of the PLR model has been expanded from a single leaf to larger scales by linking some leaf functional traits and environmental conditions, such as the leaf mass.
Species Number Specific PAR gradients of PLR curves

| Species | Number | Specific PAR gradients of PLR curves |
|---------|--------|-------------------------------------|
| Oryza sativa | 16 | 0, 50, 100, 150, 200, 400, 600, 800, 1,000, 1,200, 1,400, 1,600, 1,800, 1,900, 1950, 2000 |
| Boswellia papyrifera | 15 | 0, 25, 50, 100, 150, 200, 300, 400, 600, 800, 1,000, 1,200, 1,400, 1,600, 2000 |
| Nicotiana tabacum | 14 | 0, 50, 100, 200, 300, 400, 600, 800, 1,000, 1,200, 1,400, 1,600, 1,800, 2000 |
| Populus balsamifera × Populus trichocarpa; Populus maximowiczii × Populus balsamifera | 13 | 0, 50, 100, 300, 400, 500, 600, 700, 800, 900, 1,000, 1,600, 2000 |
| Boswellia papyrifera; Capsicum annuum; Koelreuteria paniculata; Zea mays; Sorghum bicolor | 13 | 0, 50, 100, 200, 400, 600, 800, 1,000, 1,200, 1,400, 1,600, 1,800, 2000 |
| Acer saccharum | 12 | 0, 100, 200, 400, 600, 800, 1,000, 1,200, 1,400, 1,600, 1,800, 2000 |
| Larix olgensis; Larix kaempferi | 13 | 0, 30, 80, 120, 160, 200, 400, 600, 800, 1,000, 1,200, 1,400, 1,600, 2000 |
| Populus trichocarpa × Populus deltoids; Populus trichocarpa; Populus nigra | 12 | 0, 25, 50, 75, 100, 200, 300, 400, 500, 1,000, 1,500, 2000 |
| Pinus cembra | 11 | 0, 50, 100, 200, 300, 400, 500, 750, 1,000, 1,500, 2000 |
| 25 Herbaceous species | 10 | 0, 50, 100, 200, 300, 400, 600, 800, 1,000, 1,310 |
| Zea mays | 10 | 0, 50, 100, 200, 300, 500, 700, 1,000, 1,500, 2000 |
| Larix gmelinii | 10 | 0, 50, 100, 150, 400, 800, 1,200, 1,500, 2000 |
| Ficus insipida; Castilla elastica | 9 | 0, 50, 100, 250, 500, 750, 1,000, 1,500, 2000 |
| Juglans regia | 9 | 0, 25, 50, 100, 250, 500, 1,000, 1,500, 2000 |
| Nothofagus cunninghamii | 9 | 0, 20, 50, 100, 200, 500, 1,000, 1,500, 2000 |
| Kalmia angustifolia | 9 | 0, 10, 50, 100, 200, 300, 400, 600, 800 |
| Pinus ponderosa; Ceanothus cordulatus; Arctostaphylos manzanita | 8 | 10, 50, 100, 200, 500, 800, 1,200, 1,800 |
| Pseudotsuga menziesii; Tsuga heterophylla | 8 | 10, 50, 100, 200, 400, 800, 1,400, 2000 |
| Populus tremuloides; Abies lasiocarpa | 8 | 0, 50, 100, 200, 500, 1,000, 1,500, 2000 |
| Castanea dentata | 8 | 0, 50, 100, 200, 500, 800, 1,200, 1,600 |
| Quercus douglasii | 7 | 50, 100, 200, 400, 600, 1,000, 1,400 |
| Fagus crenata | 7 | 0, 50, 100, 200, 400, 700, 1,000 |
| Helianthus annuus | 7 | 10, 50, 100, 200, 500, 1,500, 2000 |
| Quercus nigra | 6 | 0, 50, 150, 300, 800, 1,800 |
| 25 Herbaceous species | 5 | 75, 150, 175, 500, 700 |

Table 1. Summary of the different PLR designs in part of other researches.
season at the site is 17.0 °C (with a range from −1.3 to 39.4 °C), the average precipitation throughout the growing season is 944 mm. The type of soil is typic Eutroboralfs, and the total forest coverage is approximately 83.3%, including 14.7% plantation.

**PLR measurements.** In this study, three sample plots (20 m × 30 m) were established within 18-year-old pure *L. olgensis* plantations of the same habitat. The diameter at breast height (DBH) and tree height (H) were measured for each tree whose DBH was greater than 5 cm in each plot, and the quadratic mean diameters (Dg) for three plots were calculated independently. Then, three sample trees with DBH values respectively similar to the Dg of the three plots were selected to represent the average state of each plot. According to previous research, the upper limit of the PLR curves was significantly different within different crown whorls in the vertical direction. Thus, we divided the crowns of three sample trees respectively into three equal divisions based on the crown depth (Fig. 1). Three types of PLR curves, which were tagged as High, Middle and Low (Fig. 2), were measured in each division (Upper, Middle and Lower) for a sample tree. The measurements were conducted using a portable photosynthesis system (LI-6400XT, LI-COR, Inc., Lincoln, Nebraska, USA) coupled with a standard light-emitting diode (LED) light source (Li-6400-02B) at 31 PAR levels (2,000, 1,900, 1,800, 1,700, 1,600, 1,500, 1,400, 1,300, 1,200, 1,100, 1,000, 900, 800, 700, 600, 500, 400, 300, 200, 150, 100, 90, 80, 70, 60, 50, 40, 30, 20, 10 and 0 μmol m⁻² s⁻¹). As needle clusters generally overlapped each other, those covered needles could not receive light; therefore, they only have respiration but no photosynthesis. If we do not remove these needles, then they will be calculated into the sample leaf area and consequently reduce the value of the PLR curves. Therefore, the covered needles were removed before measuring to avoid incorrect PLR curve measurements. The reserved sample needles were acclimated for 20 min at a CO₂ concentration of 370 μmol m⁻² s⁻¹ and a PAR value of 1,400 μmol m⁻² s⁻¹. Then, the sample needles were allowed to equilibrate for a minimum of 2 min at each PAR gradient before the data were logged during the measurement of the PLR curves. The PLR curves were measured from 8:00 to 17:00 from the 25th of August to the 27th of August in 2018. The temperature (T) and relative humidity (RH) were approximately 28–30 °C and 30–40% during the measurement, which would not cause stomatal closure. Once the measurements of the PLR curves were performed, the sample needles were scanned and surveyed with Image-Pro Plus 6.0 software (Media Cybernetics, Bethesda, MD, USA) in the laboratory, resulting in a projected leaf area. These methods expand upon those given in previous publications.

**Model descriptions.** In this study, the PLR curves were fitted with the modified Mitscherlich equation:

\[
P_n = P_{\text{max}} \times \left(1 - e^{(-AQY \times \frac{\text{PAR}}{P_{\text{max}}})}\right) - R_d
\]

where \(P_{\text{max}}\) is the maximum net photosynthetic rate (μmol m⁻² s⁻¹), AQY is the apparent quantum yield, and \(R_d\) is the dark respiration rate (μmol m⁻² s⁻¹).
Model assessment and validation. The assessment of the PLR curve model was based on the root mean square error (RMSE, Eq. 2) and the coefficient of determination ($R^2$, Eq. 3). The predicted accuracies of the photosynthetic indicators were evaluated by the mean error (ME, Eq. 4) and the mean percent error (M%E, Eq. 5) as follows:

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

$$R^2 = 1 - \frac{\sum_{i=1}^{n} (\hat{y}_i - \bar{y})^2}{\sum_{i=1}^{n} (y_i - \bar{y})^2}$$  \hspace{1cm} (3)

$$\text{ME} = \frac{1}{n} \sum_{i=1}^{n} \left( \frac{y_i - \hat{y}_i}{y_i} \right)$$  \hspace{1cm} (4)

$$\text{M%E} = \frac{1}{n} \sum_{i=1}^{n} \left( \frac{y_i - \hat{y}_i}{y_i} \right) \times 100\%$$  \hspace{1cm} (5)

where $y_i$ is the observed value; $\bar{y}$ is the mean of the observed values; $\hat{y}_i$ is the predicted value; $n$ is the number of observations; and $p$ is the number of parameters.

Determination of the optimal design for measuring the PLR curve. The 31 observed $P_n$ values corresponding to 31 PAR gradients in each PLR curve were classified into 26 groups based on the number of PAR gradients from 5 to 30, in which 0 and 2000 were fixed points. In each group, the method of non-repetitive random sampling was used to ensure that all the combinations were considered and all the sampling designs were listed in Table 2. In total, there were more than 530 million combinations of PAR gradients to be fitted by using the “dplyr” package in R software\(^6\), and the whole fitting process took more than 200 h. Then, the best combination with the smallest RMSE value and largest $R^2$ value in each group was selected. Thereafter, the predicted accuracies of the estimated parameters, such as $P_{max}$, AQY and $R_d$, which represent the important photosynthetic indicators, were evaluated by the ME and M%E. Finally, the most effective design for PLR measurement was determined by considering the minimum measured PAR gradients based on the premise of ensuring acceptable accuracy of the estimated photosynthetic indicators.

Results
Performance of different PLR measurement designs. The goodness of fit (RMSE and $R^2$) of all the designs with different combinations of PAR gradients in each group were calculated, and the corresponding values for the best combination are shown in Fig. 3. The results showed that the RMSE values in the Low and
Middle PLR curve types were, on average, 75.4% and 70.7% smaller than those in the High PLR curve type; the $R^2$ values in the Middle PLR curve type were greater than those in the High and Low PLR curve types, although they were, on average, 0.012 and 0.028 greater. The performance of the fitting results became stable when the number of PAR gradients was more than 5.

Table 2. Summary of the sampling designs.

| Number of method points of PAR | Number of combinations | Number of method points of PAR | Number of combinations |
|-------------------------------|------------------------|-------------------------------|------------------------|
| 5                             | $C_{5}^1 = 3654$       | 18                            | $C_{18}^5 = 67863915$  |
| 6                             | $C_{6}^2 = 23751$      | 19                            | $C_{19}^6 = 51895935$  |
| 7                             | $C_{7}^3 = 118755$     | 20                            | $C_{20}^7 = 34597290$  |
| 8                             | $C_{8}^4 = 475020$     | 21                            | $C_{21}^8 = 20030010$  |
| 9                             | $C_{9}^5 = 1560780$    | 22                            | $C_{22}^9 = 10015005$  |
| 10                            | $C_{10}^6 = 4292145$   | 23                            | $C_{23}^{10} = 4292145$|
| 11                            | $C_{11}^7 = 10015005$  | 24                            | $C_{24}^{11} = 1560780$|
| 12                            | $C_{12}^8 = 20030010$  | 25                            | $C_{25}^{12} = 475020$ |
| 13                            | $C_{13}^9 = 34597290$  | 26                            | $C_{26}^{13} = 118755$ |
| 14                            | $C_{14}^{10} = 51895935$ | 27                           | $C_{27}^{14} = 23751$  |
| 15                            | $C_{15}^{11} = 67863915$ | 28                          | $C_{28}^{15} = 3654$   |
| 16                            | $C_{16}^{12} = 77558760$ | 29                          | $C_{29}^{16} = 406$    |
| 17                            | $C_{17}^{13} = 77558760$ | 30                          | $C_{30}^{17} = 29$     |
| –                             | –                      | Total                         | 536,870,475            |

Figure 3. Root mean square error (RMSE) and the coefficient of determination ($R^2$) of different designs for measuring the three types of photosynthetic light response (PLR) curves. High, Middle and Low represent three typical PLR curves that were measured in the Upper, Middle and Lower positions within the crown, respectively. PAR represents photosynthetically active radiation.

Middle PLR curve types were, on average, 75.4% and 70.7% smaller than those in the High PLR curve type; the $R^2$ values in the Middle PLR curve type were greater than those in the High and Low PLR curve types, although they were, on average, 0.012 and 0.028 greater. The performance of the fitting results became stable when the number of PAR gradients was more than 5.

Influence of the different PLR measurement designs on the estimated photosynthetic indicators. Figure 4 shows the influence of the different PLR measurement designs on the estimated photosynthetic
indicators (AQY, \( R_d \) and \( P_{\text{max}} \)). The M%E values for estimating AQY in all three types of PLR curves were small and fluctuated between 4 and \(-4\%\) (Fig. 4a–c). The estimated AQY of the High PLR curve type was overestimated on average (Fig. 4a), but the estimated AQY of the Low PLR curve type was underestimated on average (Fig. 4c). The absolute M%E values of the estimated AQY for the designs with less than ten measured points were, on average, 9.5 times greater than the values for those with more than ten measured points. The M%E values for estimating \( R_d \) were lowest when the number of PAR gradients was set to five regardless of the High, Middle or Low PLR curve types (\(-18\%, -26\% \) and \(-25\%, \) Fig. 4d–f); then, the M%E values remained between 10 and \(-10\%\) in all types of PLR curves when the number of measured points for the PAR gradients was more than 10. The estimated \( R_d \) values were overestimated in all three types of PLR curves (Fig. 4d–f) when the number of measured points for the PAR gradients was less than 10. However, the estimated \( R_d \) exhibited a similar regulation as the AQY, which was overestimated for the High PLR curve type (Fig. 4d) and underestimated for the Low PLR curve type (Fig. 4f) when the number of measured points of the PAR gradients was more than 10. The absolute M%E values of the estimated \( R_d \) for the designs with less than ten measured points were, on average, 6.7 times greater than the values for the designs with more than ten measured points. The M%E values for estimating \( P_{\text{max}} \) were lower when less than ten measured points were used for the PAR gradients, indicating that the \( P_{\text{max}} \) values were overestimated on average. Then, these values remained between 1 and \(-1\%\) for all types of PLR curves until more than ten measured points for the PAR gradients were used. The absolute M%E values of the estimated \( P_{\text{max}} \) values for the designs with fewer than ten measured points were, on average, 4.8 times greater than the values for the designs with more than ten measured points.

**Determination of the optimal measuring design of the PLR curve.** 10 PAR gradients achieved good performance for the PLR fitting and parameter estimations (Fig. 4) according to the above results. Thus, we determined the optimal measurement design by contrasting the performance of all combinations of the 10 PAR gradients in the three types of PLR curves (Table 3). In addition, we also evaluate the performance between our new measurement design and the other designs for the same Larch species\(^{24,28}\) based on the goodness of fit (Table 3). The results showed that the optimal designs for measuring the three types of PLR curves were differ-
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Table 3. Comparison between the new optimal measurement designs and other measurement designs of three types of PLR curves. New is our optimal measurement design for the PLR curve; and TI and TII are another two designs in different papers for the same larch species (Table 1).

Discussion

The PLR curve is an important semiempirical model for describing the response of the photosynthetic characteristics among different trees.

For the High PLR curve type, the PAR gradients shifted more towards high PAR values, but for the Low PLR curve type, the PAR gradients shifted more towards low PAR values. Our new designs performed better than the other designs in all three types of PLR curves, with increased $R^2$ values and decreased RMSE values. The performances of the estimated photosynthetic indicators were compared between our new design and the two other designs for the three types of PLR curves (Fig. 5). Significant difference of the accuracy for parameter estimations between our new design and the two other designs was appeared (Table 4). The results showed that the AQY and $P_{\text{max}}$ values were generally overestimated in all three types of PLR curves by our new design (Fig. 5a,c,d,f). The $R_q$ values were also overestimated in the Low PLR curve type but underestimated in the High and Middle PLR curve types (Fig. 5b,e). The AQY and $R_q$ values from the TI design were obviously underestimated (Fig. 5a,b,d,e), and the $P_{\text{max}}$ values were obviously underestimated in the High and Middle PLR curve types but overestimated in the Low PLR curve type (Fig. 5c,f). In addition, the estimated AQY, $R_q$ and $P_{\text{max}}$ values also exhibited greater differences when using the TII design than those exhibited when using our new design. In summary, our new design provided better estimations for AQY, $R_q$ and $P_{\text{max}}$ values in all three types of PLR curves.

The special PAR gradients that are frequently chosen in most designs are 0 μmol m$^{-2}$ s$^{-1}$ and 2000 μmol m$^{-2}$ s$^{-1}$ (Table 1) because the $R_q$ is a specific $P_e$ value when PAR is 0 μmol m$^{-2}$ s$^{-1}$ and the peak of PAR on a sunny day is approximately 2000 μmol m$^{-2}$ s$^{-1}$. In previous studies, the number of PAR gradients for PLR curve measurement was at least 5, although most of these gradients included more than seven points and the greatest number of PAR gradients was 17.13,18 (Table 1). However, few studies have explored the difference between different PLR measurement designs. In this study, we analysed the performance of all PLR curve measurement designs with the number of PAR gradients ranging from 5 to 31. The results showed that the fitting results remained relatively stable when more than 5 PAR gradients were used (Fig. 3). The accuracies of the estimated photosynthetic indicators (AQY, $R_q$ and $P_{\text{max}}$) were worse when there were fewer PAR gradients. However, the accuracy increased when the number of PAR gradients was set to more than 10 (Fig. 4), indicating that 10 PAR gradients may be the most effective design as the measurement of 10 PAR gradients requires relatively little time while ensuring acceptable accuracy for the estimation photosynthetic indicators. The accuracies of the estimated AQY, $R_q$ and $P_{\text{max}}$ values were more stable for the Middle PLR curve type than those for the High and Low PLR curve types, and the accuracies were more stable for the Middle PLR curve type than for the High and Low PLR curve types when more than 10 PAR gradients were measured (Fig. 4). This finding suggests that different designs for PLR curve measurement will have a weak influence on the photosynthetic indicators for the Middle PLR curve type, which indicates that measuring the Middle PLR curve type is more stable if the aim is to compare the photosynthetic characteristics among different trees.

Three optimal measurement designs were suggested for the three types of PLR curves (Table 3) because these designs performed better than the other designs, especially in terms of the accuracy of the estimated
photosynthetic indicators (AQY, \(R_d\), and \(P_{\text{max}}\), Fig. 5). In addition, we found that the optimal design for the High PLR curve type shifted more towards the high-intensity PAR, which was in contrast to the optimal design for the Low PLR curve type, which shifted more towards the low-intensity PAR.

**Conclusions**

PLR curves for a single tree crown generally exhibit obviously vertical variations; thus, the use of a unique measurement design to fit all the PLR curves in a whorl crown does not provide accurate results. The measurement design for the High PLR curve type should shift more towards the high intensity of PAR; however, that for the
Low PLR curve type should shift more towards the low intensity of PAR. The accuracies of the estimated AQY, \( R_\text{a} \) and \( F_\text{max} \) values for the Middle PLR curve type were more stable than those for the High and Low PLR curve types.

**Data availability**

All data generated or analysed during this study can be found at: https://datadryad.org/stash/share/TZhg9SyYY

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**Author contributions**

Q.L., W.J. and F.L. conceived of the study and designed the methodology; Q.L. collected and analysed the data; Q.L., W.J. and F.L. led the writing of the manuscript. All authors contributed substantially to the drafts and provided final approval for publication.

**Competing interests**

The authors declare no competing interests.

**Additional information**

**Correspondence** and requests for materials should be addressed to W.J. or F.L.

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