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# Photosynthetic and Chlorophyll Fluorescence Characteristics of *Isodon rubescens* (Hemsley) H. Hara

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The ecological and economic cultivation of *Isodon rubescens* is currently being carried out. The demand of *I. rubescens* for light intensity should be made clear to estimate whether the environmental conditions of an area are suitable for cultivating *I. Rubescens* and improve cultivation techniques. The photosynthetic and chlorophyll fluorescence characteristics of *I. rubescens* were determined with a Li-6400 photosynthesis system and PAM-2500 portable chlorophyll fluorescence apparatus. The results showed that there was no obvious midday depression of photosynthesis in *I. rubescens* leaves. The light compensation point and light saturation point of *I. rubescens* leaves were 21.83482 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and 802.262 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively. The $CO_2$ compensation point and $CO_2$ saturation point of *I. rubescens* leaves were 101.7199 $\mu mol \cdot mol^{-1}$ and 1674.514 $\mu mol \cdot mol^{-1}$, respectively. The maximal photochemical efficiency of photosystem II ((Fm-Fo)/Fm) in *I. rubescens* leaves reached 0.7. The electron transport rate of photosystem II in *I. rubescens* leaves reached 20 $\mu mol$ electrons/$(m^2 \cdot s)$. *I. rubescens* can tolerate intense light above the light compensation point and utilize low light. *I. rubescens* leaves have a strong photoprotective capacity. *I. rubescens* can grow in both sunny and shady places. The most important factor affecting photosynthetic efficiency in *I. rubescens* leaves is the concentration of $CO_2$ in air.

*Isodon rubescens* (Hemsley) H. Hara is a perennial subshrub belonging to a genus of the Lamiaceae family[1]. There are several bioactive chemical components in *I. rubescens*, such as oridonin and ponicidin. The dry aerial portions of *I. rubescens* are named rabdosiae rubescentis herba and are used in traditional Chinese medicine for the treatment of sore throats, inflammation and gastrointestinal problems[2,3].

The ecological and economic cultivation of *I. rubescens* is currently being carried out. However, there are different environmental conditions in different places. Wild *I. rubescens* grows on mountains or hills. There are obvious differences between the environmental conditions of mountains and plains. The demand of *I. rubescens* for light intensity should be made clear. The photosynthetic and chlorophyll fluorescence characteristics of *I. rubescens* were studied in this research to define the most suitable environmental conditions for *I. rubescens* cultivation and improve cultivation techniques.

## Results

### Diurnal variation in *I. rubescens* leaf photosynthesis.

The results of the diurnal variation in *I. rubescens* leaf photosynthesis are shown in Table 1. Based on the collected data, the curve of the diurnal variation in *I. rubescens* leaf photosynthesis is shown in Fig. 1.

The diurnal variation in *I. rubescens* leaf photosynthesis indicates that there was no obvious midday depression of photosynthesis. There is still a high net photosynthetic rate in *I. rubescens* leaves at noon with high light intensity. Leaves of *I. rubescens* can utilize very faint light, e.g., with a 20 $\mu mol \cdot m^{-2} \cdot s^{-1}$ intensity. The leaves of *I. rubescens* can photosynthesize even in the faint light of evening.

### Light response curve of *I. rubescens* leaves.

The data from the light response curve of *I. rubescens* leaf photosynthesis are shown in Table 2. Based on the collected data, the curve of the light response of *I. rubescens* leaf photosynthesis is shown in Fig. 2.

The light response curve of *I. rubescens* leaf photosynthesis indicates that the net photosynthetic rate was obviously related to the light intensity when the light intensity was low. The net photosynthetic rate of *I. rubescens* leaves rapidly increased as the light intensity increased from 20–400 $\mu mol \cdot m^{-2} \cdot s^{-1}$. *I. rubescens* leaves were able

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| Time | Photo (µmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) | Transpiration (mmol $H_2O$ $m^{-2}s^{-1}$) | PARout (µmol$\cdot m^{-2} \cdot s^{-1}$) | Tleaf (°C) | $CO_2$ (µmol$\cdot mol^{-1}$) |
|---|---|---|---|---|---|
| 8:20 | 0.134554 | 0.078752 | 165.3032 | 27.48817 | 374.3593 |
| 10:01 | 0.489859 | 0.100056 | 690.494 | 31.51378 | 364.5589 |
| 11:09 | 0.677691 | 0.16249 | 923.3254 | 33.61967 | 384.1379 |
| 11:46 | 2.431713 | 2.894369 | 1211.345 | 34.83849 | 370.7948 |
| 12:33 | 3.21911 | 2.629756 | 1484.135 | 35.78894 | 361.1602 |
| 13:25 | 2.385099 | 2.6251 | 1697.34 | 36.47706 | 363.1944 |
| 14:53 | 2.390117 | 2.888978 | 1346.388 | 35.82655 | 370.8038 |
| 16:31 | 1.619721 | 2.060572 | 524.8741 | 33.17798 | 359.4734 |
| 17:15 | 1.067346 | 1.362125 | 280.3203 | 32.90131 | 359.0663 |
| 18:09 | 0.166573 | 0.043506 | 163.6786 | 31.8848 | 370.7527 |
| 19:08 | 0.146304 | 0.063026 | 145.7678 | 30.09128 | 366.364 |
| 19:23 | 0.038786 | 0.050609 | 86.26784 | 29.08384 | 366.6463 |

**Table 1.** Diurnal variation in *I. rubescens* leaf photosynthesis (average). Note: PARout is the PAR out of the leaf chamber.
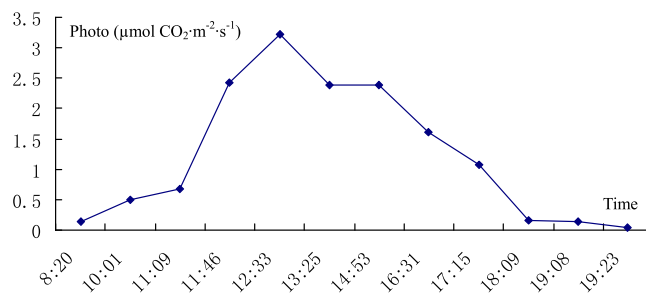


**Figure 1.** Diurnal variation in *I. rubescens* leaf photosynthesis.

to utilize intense light. With light intensities of 400–2200 µmol$\cdot m^{-2} \cdot s^{-1}$, the net photosynthetic rate of *I. rubescens* leaves was high. However, the net photosynthetic rate of *I. rubescens* leaves obviously decreased when the light intensity was above 2200 µmol$\cdot m^{-2} \cdot s^{-1}$.

The results of the light response curve fitted with the modified rectangular hyperbola model are shown in Table 2. The fitted light saturation point and the net photosynthetic rate at this point were very similar to the observed value.

**$CO_2$ response curve of *I. rubescens* leaves.** The $CO_2$ response curve data of *I. rubescens* leaf photosynthesis are shown in Table 3.

Based on the collected data, the curve of the $CO_2$ response of *I. rubescens* leaf photosynthesis is shown in Fig. 3.

The $CO_2$ response curve of *I. rubescens* leaf photosynthesis indicates that the net photosynthetic rate was obviously related to the concentration of $CO_2$ in the air when the $CO_2$ concentration was below 1000 µmol$\cdot mol^{-1}$. However, the effect of the $CO_2$ concentration on the net photosynthetic rate was not obvious when the concentration of $CO_2$ was above 1000 µmol$\cdot mol^{-1}$.

The results of the $CO_2$ response curve fitted with the modified rectangular hyperbola model are shown in Table 3. The fitted $CO_2$ saturation point and the net photosynthetic rate at this point were very similar to the observed value.

**Chlorophyll fluorescence characteristics of *I. rubescens* leaves.** The results of the slow kinetics of chlorophyll fluorescence are shown in Table 4.

The slow kinetics of chlorophyll fluorescence of *I. rubescens* leaves indicates that the maximal photochemical efficiency of photosystem II ((Fm-Fo)/Fm) in *I. rubescens* leaves reached 0.7. The electron transport rate of photosystem II in *I. rubescens* leaves reached 20 µmol electrons/(m²·s). The fraction of energy dissipated as heat via the regulated photoprotective NPQ mechanism (Y(NPQ)) was much more than that passively dissipated in the form of heat and fluorescence (Y(NO)).

The results of the rapid light curves of chlorophyll fluorescence in *I. rubescens* leaves are shown in Table 5. The rapid light curve of chlorophyll fluorescence in *I. rubescens* leaves is shown in Fig. 4.

The rapid light curve of chlorophyll fluorescence in *I. rubescens* leaves was automatically fitted with a PAM-2500 portable chlorophyll fluorescence apparatus according to the model of Eilers and Peeters [5]. The fitted results are shown in Table 5.

| PARin ($\mu$mol·m$^{-2}$·s$^{-1}$) | Photo ($\mu$mol·m$^{-2}$·s$^{-1}$) | Transpiration (mmol m$^{-2}$s$^{-1}$) | Tleaf (°C) | CO$_2$ ($\mu$mol·mol$^{-1}$) |
|---|---|---|---|---|
| 3124.457 | 2.260209 | 4.466418 | 29.3982 | 395.2443 |
| 2198.982 | 4.721694 | 3.573953 | 30.04687 | 392.505 |
| 2000.081 | 4.965527 | 3.807614 | 30.61862 | 391.8968 |
| 1800.327 | 5.001151 | 3.645889 | 29.77489 | 392.8282 |
| 1500.057 | 5.38657 | 3.336598 | 30.33475 | 392.6403 |
| 1200.517 | 5.329608 | 2.987329 | 30.81813 | 391.6764 |
| 1001.321 | 5.443283 | 2.672035 | 30.69158 | 391.8007 |
| 799.9315 | 5.541983 | 2.354444 | 30.53654 | 391.9345 |
| 599.9705 | 5.559295 | 2.089824 | 30.37206 | 391.9419 |
| 499.3938 | 5.348708 | 1.890056 | 30.96318 | 392.7756 |
| 400.1194 | 5.171424 | 1.844144 | 30.15175 | 393.0815 |
| 200.3279 | 3.963617 | 1.612985 | 30.92859 | 394.4694 |
| 149.6206 | 3.822843 | 1.509174 | 30.68748 | 395.1866 |
| 99.69547 | 2.725072 | 1.457733 | 30.33666 | 396.0288 |
| 70.8973 | 1.200702 | 1.417435 | 30.03102 | 398.5548 |
| 30.33922 | 0.248815 | 1.142081 | 29.94907 | 399.1747 |
| 21.26013 | 0.1307 | 1.322936 | 29.69206 | 399.0078 |
| E | 0.050712 | | | |
| M | 0.00021 | | | |
| N | 0.005891 | | | |
| LCP | 21.83482 $\mu$mol·m$^{-2}$·s$^{-1}$ | | | |
| E·LCP | 1.107 | | | |
| LSP | 802.262 $\mu$mol·m$^{-2}$·s$^{-1}$ | | | |
| PLSP | 5.7471 $\mu$mol·m$^{-2}$·s$^{-1}$ | | | |
| R$^2$ | 0.97336 | | | |

**Table 2.** Light response curve of *I. rubescens* leaf photosynthesis (average). Note: PARin is the PAR in the leaf chamber. PLSP is the net photosynthetic rate at the light saturation point.
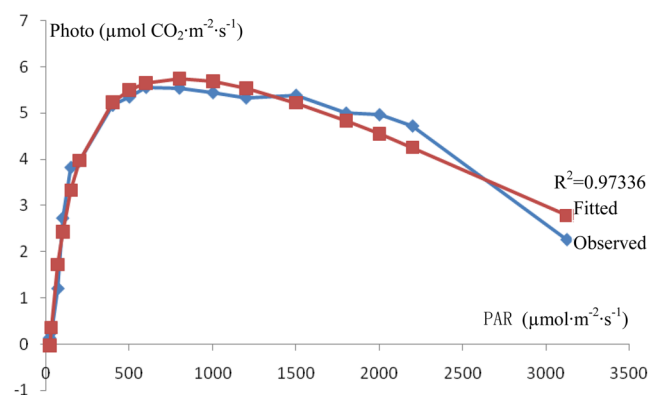


**Figure 2.** Light response curve of *I. rubescens* leaf photosynthesis.

The rapid light curve of chlorophyll fluorescence in *I. rubescens* leaves indicates that the maximum quantum yield of PSII with a saturated pulse after dark adaptation (Fv'/Fm' x ETR factor/2) was higher than the effective quantum yield of PSII (Y(II)). The initial slope (alpha) signifying the maximum photosynthetic efficiency was higher than the apparent quantum yield fitted in the light response curve of *I. rubescens* leaves.

## Discussion and Conclusion

The modified rectangular hyperbola model is suitable for fitting light response curves and CO$_2$ response curves. We compared the fit of the light response curve and CO$_2$ response curve of *Paeonia lactiflora* created with different models. It was found that the fit results based on the modified rectangular hyperbola model were more similar than the results from other models to the observed values[6].

*I. rubescens* is a heliophyte plant, which can tolerate intense light. There are very few reports about photosynthesis of *I. Rubescens*. There was no obvious midday depression of photosynthesis in *I. rubescens* leaves in terms of this study. The midday photosynthetic depression occurred in most of plants. The factors such as intense light,

| $CO_2$ ($\mu mol \cdot mol^{-1}$) | Photo ($\mu molCO_2 \cdot m^{-2} \cdot s^{-1}$) | Transpiration ($mmolH_2Om^{-2} \cdot s^{-1}$) | Tleaf (°C) | PARin ($\mu mol \cdot m^{-2} \cdot s^{-1}$) |
|---|---|---|---|---|
| 1981.063 | 13.28118 | 1.711614 | 30.67786 | 1200.049 |
| 1779.07 | 13.74822 | 2.076798 | 30.12322 | 1200.109 |
| 1477.98 | 13.9082 | 2.422849 | 30.99781 | 1199.903 |
| 1381.585 | 12.22414 | 2.429738 | 30.03088 | 1199.725 |
| 1181.821 | 11.9153 | 2.542288 | 30.79212 | 1198.881 |
| 983.2891 | 11.6798 | 2.593174 | 30.62088 | 1199.717 |
| 785.1578 | 10.43091 | 2.605263 | 30.6294 | 1199.769 |
| 588.2518 | 8.370093 | 2.598826 | 29.70778 | 1199.477 |
| 392.7176 | 5.688908 | 2.572764 | 29.82269 | 1199.592 |
| 361.7573 | 3.743928 | 2.235932 | 30.30235 | 1200.262 |
| 286.5714 | 2.378747 | 2.31753 | 30.69262 | 1200.178 |
| 256.2721 | 2.153212 | 2.340206 | 30.60159 | 1199.589 |
| 197.9524 | 1.113644 | 1.946278 | 30.54132 | 1201.117 |
| 148.4747 | 0.958305 | 2.032948 | 30.34006 | 1201.138 |
| 99.09576 | 0.396179 | 2.113611 | 30.11915 | 1201.403 |
| 69.56865 | 0.095351 | 2.193027 | 29.91523 | 1201.294 |
| E | 0.050712 | | | |
| M | 0.00021 | | | |
| N | 0.005891 | | | |
| CCP | 101.7199 $\mu mol \cdot mol^{-1}$ | | | |
| E·CCP | 1.107 | | | |
| CSP | 1674.514 $\mu mol \cdot mol^{-1}$ | | | |
| PCSP | 13.62882 $\mu mol \cdot m^{-2} \cdot s^{-1}$ | | | |
| $R^2$ | 0.98526 | | | |

**Table 3.** $CO_2$ response curve of *I. rubescens* leaf photosynthesis (average). Note: CCP is the $CO_2$ compensation point. CSP is the $CO_2$ saturation point. PCSP is the net photosynthetic rate at the $CO_2$ saturation point. PARin is the PAR in the leaf chamber.

| PAR ($\mu mol \cdot m^{-2} \cdot s^{-1}$) | (Fm-Fo)/ Fm | Y(II) | Y(NPQ) | Y(NO) | qN | qP | ETR ($\mu mol$ electrons$\cdot m^{-2} \cdot s^{-1}$) |
|---|---|---|---|---|---|---|---|
| 198 | 0.725319 | 0.25 | 0.468 | 0.282 | 0.755 | 0.528 | 20.8 |
| 198 | 0.75982 | 0.239 | 0.534 | 0.227 | 0.835 | 0.57 | 19.9 |
| 198 | 0.727212 | 0.274 | 0.453 | 0.273 | 0.731 | 0.527 | 22.8 |
| Average | 0.7374 | 0.2543 | 0.485 | 0.261 | 0.7737 | 0.5417 | 21.167 |

**Table 4.** Slow kinetics of chlorophyll fluorescence.
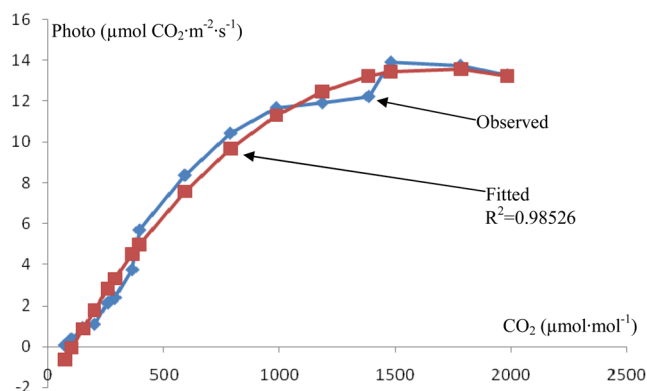


**Figure 3.** $CO_2$ response curve of *I. rubescens* leaf photosynthesis.

| PAR | Y(II) | Y(NPQ) | Y(NO) | NPQ | qN | qP | qL | ETR |
|---|---|---|---|---|---|---|---|---|
| 0 | 0.7900 | 0.000 | 0.210 | 0.000 | 0.000 | 1.0000 | 1.0000 | 0.00 |
| 6 | 0.6763 | 0.018 | 0.306 | 0.059 | 0.067 | 0.8670 | 0.5890 | 1.70 |
| 31 | 0.4633 | 0.206 | 0.330 | 0.644 | 0.458 | 0.6663 | 0.3803 | 6.03 |
| 101 | 0.2837 | 0.421 | 0.295 | 1.456 | 0.683 | 0.4687 | 0.2593 | 12.03 |
| 198 | 0.2007 | 0.531 | 0.268 | 1.997 | 0.763 | 0.3597 | 0.2000 | 16.70 |
| 363 | 0.1363 | 0.601 | 0.263 | 2.299 | 0.795 | 0.2550 | 0.1377 | 20.77 |
| 619 | 0.0920 | 0.646 | 0.262 | 2.465 | 0.822 | 0.1877 | 0.1047 | 23.93 |
| 981 | 0.0677 | 0.669 | 0.263 | 2.546 | 0.828 | 0.1393 | 0.0767 | 27.87 |
| 1386 | 0.0540 | 0.684 | 0.262 | 2.617 | 0.833 | 0.1120 | 0.0613 | 31.43 |
| 2015 | 0.0397 | 0.699 | 0.261 | 2.682 | 0.837 | 0.0837 | 0.0457 | 33.60 |
| 2970 | 0.0320 | 0.708 | 0.260 | 2.734 | 0.842 | 0.0690 | 0.0380 | 40.17 |
| 3588 | 0.033 | 0.716 | 0.251 | 2.849 | 0.834 | 0.065 | 0.033 | 49.9 |
| 4292 | 0.027 | 0.725 | 0.248 | 2.922 | 0.838 | 0.054 | 0.027 | 49.4 |
| a | −0.00000359906 | | | | | | | |
| b | 0.033474211 | | | | | | | |
| c | 5.362466019 | | | | | | | |
| Fv'/Fm' x ETR factor/2 | 0.33167 electrons/photons | | | | | | | |
| Alpha | 0.08 electrons/photons | | | | | | | |
| ETRmax | 52.333μmol electrons/(m²·s) | | | | | | | |
| Ik | 705.3μmol electrons/(m²·s) | | | | | | | |
| Fv'/Fm' | 0.78988 | | | | | | | |
| R² | 0.99038 | | | | | | | |

**Table 5.** Rapid light curve of chlorophyll fluorescence in *I. rubescens* leaves (average). Note: Fv'/Fm' x ETR factor/2 is the maximum quantum yield of PSII with a saturated pulse after dark adaptation. Alpha is the initial slope. ETRmax is the maximum electron transport rate. Ik is the minimum saturation of the light intensity.
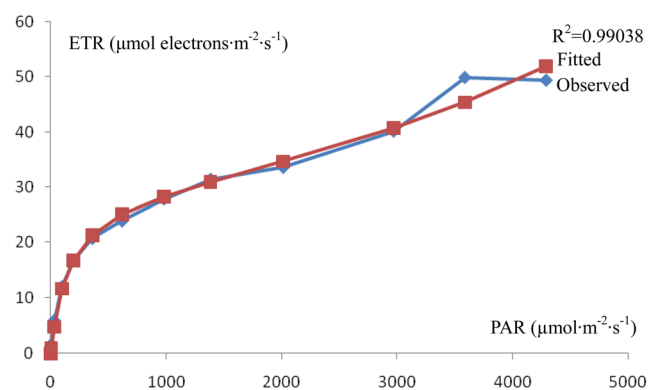


**Figure 4.** Rapid light curve of chlorophyll fluorescence in *I. rubescens* leaves.

high air temperature, low soil moisture, low air humidity and so on can cause midday photosynthetic depression[7–10]. There is no midday photosynthetic depression in some other plants, such as C$_4$ plants (Characterized by the Hatch-Slack photosynthetic pathway), CAM plants (plants with crassulacean acid metabolism) and aquatic plant[11,12]. Some plants perform midday photosynthetic depression in a certain environment but express no midday photosynthetic depression in another environment. Their performances are affected by environment or some chemicals[13–16]. The environment of *I. rubescens* studied in this paper was consistent with that of yield *I. rubescens*. It was sunny day and the light intensity was highest in a year in the locality when the data were determined. *I. rubescens* performed no midday photosynthetic depression in the severe environment, which indicated that it would similarly perform in suitable environment. Therefore, *I. rubescens* can tolerate intense light.

There was no obvious difference between the net photosynthetic rate of light saturation point and that of light intensities of 2000 μmol·m$^{-2}$·s$^{-1}$ although the light saturation point of *I. rubescens* leaves was 802.262 μmol·m$^{-2}$·s$^{-1}$. Therefore, there was no obvious effect of intense light above the light saturation point on the photosynthesis of *I. rubescens* leaves. The net photosynthetic rate of the light intensities of 1484.135 μmol·m$^{-2}$·s$^{-1}$ was the highest in diurnal variation of photosynthesis because the temperature was suitable for it at that time. *I. rubescens* can also tolerate low light. Leaves of *I. rubescens* can utilize low light (i.e., at an intensity of 20 μmol·m$^{-2}$·s$^{-1}$). Therefore, *I. rubescens* can grow on shady slopes. The most important factor affecting the photosynthetic

efficiency in *I. rubescens* leaves is the concentration of $CO_2$ in the air. Photosynthesis in *I. rubescens* leaves was not obviously affected by high concentrations of $CO_2$ alone.

The maximum electron transport rate (ETRmax) in *I. rubescens* leaves was far higher than the observed electron transport rate (ETR). The chlorophyll fluorescence characteristics of *I. rubescens* leaves showed that there was very large potential for photosynthesis in *I. rubescens* leaves. The fraction of energy dissipated as heat via the regulated photoprotective NPQ mechanism (Y(NPQ)) was much more than that passively dissipated in the form of heat and fluorescence (Y(NO)). The minimum saturation light intensity (Ik) was far less than the light saturation point (LSP). Therefore, *I. rubescens* leaves can tolerate intense light.

*I. rubescens* performs no midday photosynthetic depression and can tolerate intense light. It can utilize low light and possesses high value of Fv/ Fm (the maximal photochemical efficiency of photosystem II). This indicated that *I. rubescens* leaves have a strong photoprotective capacity. However, the growth and cultivation of *I. rubescens* are affected by many factors such as light, air temperature, rainfall, soil, and so on[17,18]. This study is aimed at the photosynthetic and chlorophyll fluorescence characteristics of *I. rubescens*. The suitable environment for the growth and cultivation of *I. rubescens* still needs to study.

## Materials and Methods

**Instruments.** Li-6400 Photosynthesis system (LI-6400 Inc., Lincoln, NE, USA). PAM-2500 portable chlorophyll fluorescence apparatus (PAM-2500, Walz, Germany).

**Materials.** Approximately 60 *I. rubescens* plants were dug up from Taihang Mountain and evenly planted in 12 flowerpots (30 cm in diameter and 35 cm in depth) in March 2018. Then, the plants were irrigated to ensure that they grew well.

**Determination of photosynthetic characteristics.** The photosynthetic characteristics of mature leaves on the *I. rubescens* plants were determined on June 5–7 (sunny day, the light intensity is highest in a year), 2019. The concentration of $CO_2$ in the air was approximately 370 μmol·mol$^{-1}$ when the diurnal variation of photosynthesis was determined. The temperature of the leaf chamber was set at 30 °C, and the concentration of $CO_2$ in the leaf chamber was set at 400 μmol·mol$^{-1}$ when the light response curve was determined. The light intensity in the leaf chamber was set at 1200 μmol·m$^{-2}$·s$^{-1}$, and the temperature of the leaf chamber was set at 30 °C when the $CO_2$ response curve was determined. These photosynthetic characteristics were determined with the Li-6400 Photosynthesis system. Each determination was repeated three times.

**Determination of chlorophyll fluorescence characteristics.** The fluorescence characteristics of mature leaves on the *I. rubescens* plants were determined on June 7–8, 2019. The leaves were under dark adaptation for 30 min before the determination of the chlorophyll fluorescence characteristics. The slow kinetics of chlorophyll fluorescence were determined before determining the light curve of chlorophyll fluorescence. The tests were repeated three times.

**Data analysis.** The light response curve and $CO_2$ response curves were analysed with SPSS (Statistical Product and Service Solutions, International Business Machines Corporation, USA). The light response curve and $CO_2$ response curve were all fitted with a modified rectangular hyperbola model[4].

Modified rectangular hyperbola model:

$$\text{Photo} = E \cdot (1 - M \cdot PAR) \cdot (PAR - LCP)/(1 + N \cdot PAR)$$

PAR is the value of light intensity in the light response curve (or the value of concentration of $CO_2$ in $CO_2$ response curve). Photo is the net photosynthetic rate. LCP is the light compensation point (or $CO_2$ compensation point). E, M and N are parameters. E is also the apparent quantum yield. The dark respiration rate under the light compensation point = E·LCP. The light saturation point is calculated as follows:

$$(\text{LSP}) = (((M + N) \cdot (1 + N \cdot LCP)/M)^{1/2})/-1)/N.$$

The net photosynthetic rate under the light saturation point (LSP) or $CO_2$ saturation point (CSP) can be calculated according to the model.

The data related to the determination of the light curve of chlorophyll fluorescence were automatically fitted according to the model of Eilers and Peeters[5].

The model of Eilers and Peeters is as follows:

$$\text{ETR} = PAR/(a \cdot PAR^2 + b \cdot PAR + c)$$

ETR is the electron transport rate of photosynthetic system II. PAR is the fluorescence intensity. The letters a, b and c are parameters.

## Data availability

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## Author contributions

JIAN Zaiyou. Designed the study, implemented the experiment and wrote the manuscript. ZHOU Xiuren. Participate in the experiment. TIAN Jing. Participate in the data analysis.

## Competing interests

The authors declare no competing interests.

## Additional information