Abbreviations: ACE – initial carboxylation efficiency; $A_{\text{max}}$ – maximum net photosynthetic rate at CO$_2$-saturation point; AQY – apparent quantum effect; $C_a$ – air CO$_2$ concentration; CCP – CO$_2$-compensation point; Chl – chlorophyll; $C_i$ – intercellular CO$_2$ concentration; CSP – saturated intercellular CO$_2$ concentration; $E$ – transpiration rate; $g_s$ – stomatal conductance; LCP – light-compensation point; LSP – light-saturation point; $P_a$ – net photosynthetic rate; $P_{\text{max}}$ – maximum net photosynthetic rate at light-saturation point; $R_d$ – dark respiration rate; RH – relative humidity; $R_{e}$ – photosynthesis rate; $T_a$ – air temperature; VPD – vapor pressure deficit.

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These authors contributed equally to this work.
In this paper, two different species of ten-year-old peony plants from eight different provenances of China were collected. After transplanting and slowing the seedlings, the photosynthesis and physiology of different oil peony sources were analyzed by observing and measuring the leaf photosynthetic characteristics. The adaptability variances of oil peonies from different provenances to the new environment were compared, and the source of the differences was further explored from the physiological ecology perspectives. This would provide theoretical references for the future oil peony introduction and domestication, breeding of the improved species, and the response approaches as well as adaptation strategies in different environments.

Materials and methods

**Overview of the test area:** The test site is located in Peony Resources Garden of Northwest A&F University, Yangling, Shaanxi, China. The area belongs to continental monsoon climate zone with an annual precipitation of 635.1 mm, an annual average temperature of 12.9°C, an annual average sunshine hours of 2,163.8 h, as well as an annual accumulated temperature of 4,184°C for the temperature over 10°C.

**Plant materials:** The test materials were fine oil peony plants selected from eight provenances, namely Heze, Yuzhong, Lintao, Liuba, Fengxian, Shangzhou, Xunyang, and Ziwuling. Locations and climate factors of each provenance were as follows:

<table>
<thead>
<tr>
<th>Species</th>
<th>Provenance</th>
<th>Abbreviation</th>
<th>Latitude [N]</th>
<th>Longitude [E]</th>
<th>Mean annual temperature [°C]</th>
<th>Mean annual precipitation [mm]</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Paeonia rockii</em></td>
<td>Yuzhong County</td>
<td>PR-yz</td>
<td>35°52'N</td>
<td>104°07'E</td>
<td>6.7</td>
<td>400</td>
</tr>
<tr>
<td></td>
<td>Lintao County</td>
<td>PR-it</td>
<td>35°37'N</td>
<td>103°49'E</td>
<td>7.0</td>
<td>539</td>
</tr>
<tr>
<td></td>
<td>Ziwuling Mountain</td>
<td>PR-zwl</td>
<td>35°20'N</td>
<td>108°02'E</td>
<td>7.4</td>
<td>588</td>
</tr>
<tr>
<td></td>
<td>Liuba County</td>
<td>PR-lb</td>
<td>33°42'N</td>
<td>107°08'E</td>
<td>11.5</td>
<td>886</td>
</tr>
<tr>
<td><em>Paeonia ostii</em></td>
<td>Fengxian County</td>
<td>PO-fx</td>
<td>34°31'N</td>
<td>107°02'E</td>
<td>11.4</td>
<td>625</td>
</tr>
<tr>
<td></td>
<td>Heze City</td>
<td>PO-hz</td>
<td>35°39'N</td>
<td>115°45'E</td>
<td>13.8</td>
<td>663</td>
</tr>
<tr>
<td></td>
<td>Shangzhou Area</td>
<td>PO-sz</td>
<td>33°52'N</td>
<td>109°57'E</td>
<td>13.5</td>
<td>758</td>
</tr>
<tr>
<td></td>
<td>Xunyang County</td>
<td>PO-xy</td>
<td>32°49'N</td>
<td>105°58'E</td>
<td>14.5</td>
<td>1,050</td>
</tr>
</tbody>
</table>

Plants were transplanted to the Peony Resources Garden of Northwest A&F University in September 2015. The growth was stabilized after three years of slow rejuvenation, and the leaf functional traits and photosynthetic characteristics of oil peony plants were measured in the early summer season of 2018.

**Diurnal variation in photosynthesis** of plants from various sources was determined with a LI-6400XT portable photosynthesis measurement system (LI-COR, USA). The main measurement indexes were: net photosynthetic rate ($P_\text{N}$), transpiration rate ($E$), stomatal conductance ($g_s$), air CO$_2$ concentration ($C_a$), intercellular CO$_2$ concentration ($C_i$), air temperature ($t_a$), relative humidity (RH), and PAR. The test was performed on a normal sunny day, two weeks after the last leaf fertilization and measurements were taken every two hours between 8:00–18:00 h. Six plants were randomly selected from each plot, and three sunny side branches were selected from each plant, where the third leaf of the plant counting from the top was measured. The leaf chamber was a regular leaf chamber with an area of 6 cm$^2$.

**Light-response curve:** The same LI-6400XT system was used for this test, where 6400-012B red and blue light source was utilized, and the PAR gradient was set to 2,000; 1,800; 1,600; 1,400; 1,200; 1,000; 800, 600, 400, 200, 150, 100, 50, 20, and 0 μmol(photon) m$^{-2}$ s$^{-1}$, respectively, and the CO$_2$ injection system value was set to 400 μmol mol$^{-1}$. The leaf temperature was about 26°C and the vapor pressure deficit (VPD) was about 2 kPa. Three plants were selected per plot, and three leaves from the same location were selected for each plant. All the leaves were subjected to light induction for 20 min before measurements. The apparent quantum effect (AQY), maximum net photosynthetic rate at light-saturation point ($P_{\text{Nmax}}$), dark respiration rate ($R_\text{d}$), light-saturation point (LSP), and light-compensation point (LCP) of each provenance treatment were calculated with the light-response model (Ye 2007, Ye and Yu 2008). The fitting equation was:

$$P_\text{N} = \alpha \times (1 - \beta \times I) \times I/(1 + \gamma \times I) - R_\text{d},$$

where $I$ refers to photosynthetically active radiation, $R_\text{d}$ is the dark respiration rate, $\alpha$ refers to the initial slope of the light-response curve, and $\beta$ and $\gamma$ are coefficients.

**CO$_2$-response curve:** The same LI-6400XT system was used for this test, where the CO$_2$-injection system and LED red and blue light source were used, and the CO$_2$ concentration gradient was set to 400, 300, 200, 150, 100, 50, 400, 400, 600, 800; 1,000; 1,200; 1,500; 1,800; 2,000 μmol mol$^{-1}$, respectively, and the PAR was set to 1,500 μmol(photon) m$^{-2}$ s$^{-1}$. The leaf temperature was about 26°C and VPD was about 2 kPa. The initial carboxylation efficiency (a), maximum net photosynthetic rate at CO$_2$-saturation point ($A_{\text{max}}$), saturated intercellular CO$_2$ concentration (CSP), CO$_2$-compensation point (CCP), photorespiration rate ($R_\text{p}$), and coefficient of determination were calculated according to the CO$_2$-response model (Ye and Yu 2009). The fitting equation was:
$P_N(C_i) = a \times (1 - b \times C_i) \times C_i/(1 + c \times C_i) - R_p,$

where $P_N$ is the net photosynthetic rate, $C_i$ is the intercellular CO$_2$ concentration, $R_p$ is the photorespiration rate, $a$ is the initial carboxylation efficiency of the CO$_2$-response curve, and $b$ and $c$ are the coefficients.

**Chlorophyll (Chl) content:** Chl was extracted by acetone and ethanol mixture. After leaching, the spectral image of each sample was determined by using Shimadzu UV-2450 UV-Vis (Japan) spectrophotometer. The absorbance value at 645 and 663 nm were selected to calculate Chl $a$, Chl $b$, and total Chl content [Chl ($a+b$)]. The results were presented in mg g$^{-1}$ (Porra 2002).

**Data processing:** Microsoft Excel 2010 was used to sort data and SPSS 20.0 was used for variance analysis (ANOVA), regression analysis, and Duncan's multiple comparison. Charts were drawn with Sigmaplot 10.0. Pearson's method was utilized to analyze the correlation between various indexes of peony leaf functional traits.

**Results**

**Photosynthetic diurnal variation:** Fig. 1 reflects the diurnal trend of the main environmental indexes that affected the leaf photosynthetic rate. During the test, the amount of PAR was lower in the morning and evening but higher during the day, reaching the maximum at noon. The $C_a$ in the air first decreased and then increased. The plants accumulated quite a lot of CO$_2$ after overnight respiration, and photosynthetic rate was low in the morning CO$_2$ due to low light level so that $C_a$ was at the highest state in the morning, with a maximum value of 438.67 μmol mol$^{-1}$. Then, as the light intensity increased, the rate of photosynthesis also increased. Therefore $C_a$ gradually decreased until 16:00 h and increased slightly after that. Due to direct sunlight, $t_a$ went higher with the increasing PAR, reaching a maximum of 33.8°C at 14:00 h, and then slowly decreased. However, the daily trend of RH was opposite to that of PAR and $t_a$, i.e., dropped first and then rose. The highest level was reached at 8:00 h in the morning, and the lowest level occurred at 14:00 h.

Under natural conditions, the diurnal variation process of plant photosynthesis can be categorized into two types:
Differences in Light Responses of Oil Peonies

Table 1. Comparison of light-response parameters of oil peonies from eight provenances. AQY – apparent quantum efficiency; \( P_{\text{max}} \) – maximum net photosynthetic rate at light-saturation point; LSP – light-saturation point; LCP – light-compensation point; \( R_0 \) – dark respiration rate. Data represent means ± SD of six independent experiments. Different letters in the same column indicate significant differences at the 5% which are Duncan’s multiple comparison test groups for one-dimensional ANOVA.

<table>
<thead>
<tr>
<th>Species</th>
<th>AQY</th>
<th>( P_{\text{max}} ) [( \mu \text{mol m}^{-2} \text{s}^{-1} )]</th>
<th>LSP [( \mu \text{mol m}^{-2} \text{s}^{-1} )]</th>
<th>LCP [( \mu \text{mol m}^{-2} \text{s}^{-1} )]</th>
<th>( R_0 ) [( \mu \text{mol m}^{-2} \text{s}^{-1} )]</th>
<th>Decisive factor</th>
</tr>
</thead>
<tbody>
<tr>
<td>PR-yz</td>
<td>0.0530 ± 0.0026a</td>
<td>7.59 ± 0.50c</td>
<td>894.13 ± 51.00c</td>
<td>42.89 ± 2.59a</td>
<td>1.97 ± 0.05a</td>
<td>0.9984</td>
</tr>
<tr>
<td>PR-lt</td>
<td>0.0458 ± 0.0027c</td>
<td>9.09 ± 0.43b</td>
<td>951.38 ± 40.79a</td>
<td>45.30 ± 2.06b</td>
<td>1.87 ± 0.08bc</td>
<td>0.9982</td>
</tr>
<tr>
<td>PR-lb</td>
<td>0.0562 ± 0.0017a</td>
<td>10.99 ± 0.50c</td>
<td>1,682.95 ± 47.69b</td>
<td>31.88 ± 2.51bc</td>
<td>1.62 ± 0.07bc</td>
<td>0.9988</td>
</tr>
<tr>
<td>PR-zwl</td>
<td>0.0498 ± 0.0020c</td>
<td>15.02 ± 1.06d</td>
<td>1,592.17 ± 37.32a</td>
<td>43.01 ± 2.00c</td>
<td>1.99 ± 0.14c</td>
<td>0.9998</td>
</tr>
<tr>
<td>PO-fx</td>
<td>0.0436 ± 0.0026c</td>
<td>12.93 ± 0.57b</td>
<td>1,503.89 ± 46.66a</td>
<td>44.69 ± 2.33a</td>
<td>1.81 ± 0.08bc</td>
<td>0.9983</td>
</tr>
<tr>
<td>PO-sz</td>
<td>0.0526 ± 0.0021a</td>
<td>12.56 ± 0.58a</td>
<td>1,487.76 ± 40.84c</td>
<td>29.93 ± 1.68c</td>
<td>1.46 ± 0.08c</td>
<td>0.9996</td>
</tr>
<tr>
<td>PO-xy</td>
<td>0.0540 ± 0.0017a</td>
<td>13.58 ± 0.71a</td>
<td>1,764.85 ± 38.05d</td>
<td>34.46 ± 1.50d</td>
<td>1.71 ± 0.14ad</td>
<td>0.9998</td>
</tr>
<tr>
<td>PO-hz</td>
<td>0.0566 ± 0.0022a</td>
<td>13.28 ± 0.69c</td>
<td>1,569.08 ± 61.20d</td>
<td>42.87 ± 2.51a</td>
<td>2.19 ± 0.14a</td>
<td>0.9997</td>
</tr>
</tbody>
</table>

The peak I values of the rest four were close to each other. In addition, the peak II values of all these six provenances were significantly lower than the peak I values.

Stomatal conductance (\( g_s \)) refers to the ability of plant pores to conduct CO\(_2\) and water. The trend of \( g_s \) daily variation curve in different provenances is shown in Fig. 2B. The \( g_s \) of PO-sz, PO-hz, and PO-yz started to decrease at 10:00 h, and the \( g_s \) of PO-fx and PR-lb began to decline at 8:00 h, while in PO-zwl, PO-xy, and PR-lt \( g_s \) began to drop from 12:00 h. Only PO-hz, PR-zwl, and PO-fx showed the \( g_s \) values increased starting from 16:00 h, the other five provenances showed a continuous decreasing trend until the end of the test.

According to Fig. 2C, starting from 8:00 h, the \( E \) of oil peonies in all eight provenances increased with the increase of \( g_s \). However, the magnitude of the increase varied greatly. Except for PR-lt, the \( E \) of the other seven sources reached their maximum at noon and then started to drop (PR-lt was not resistant to strong light, therefore when the light reached its maximum at noon; it restrained the rate of photosynthesis and promoted stomatal closure to result in the decreasing \( E \)). The maximum transpiration rate of PR-zwl was significantly higher than that of the other provenances, indicating a higher capacity of water transport and regulation as well as a higher demand of water at this stage. The \( E \) of PR-zwl and PO-fx started to increase again at 16:00 h, whereas other provenances continued to decrease.

Light-response curves: The light-response curve illustrates the ability of plants to adapt to changes in external light intensity. The hypervisor model was used to fit the light-response values and obtain the ideal results for the oil peonies from different provenances \((R^2 = 0.9982–0.9998;\) Fig. 3, Table 1). In Fig. 3, we can see that when \( PAR \) was less than 200 \( \mu \text{mol} \text{(photons)} \text{m}^{-2} \text{s}^{-1} \), the growth rate of \( P_s \) became slower, and with the light intensity increased, \( P_s \) curve gradually flattened and light was saturated at one point. The light-response curves of PR-zwl, PO-xy, PO-hz, PO-fx, PO-sz, and PR-lb were relevantly close to each other; for all of them, the light-response curve of oil peonies in eight provenances.

Fig. 3. Light-response curve of oil peonies in eight provenances. PAR – photosynthetically active radiation; \( P_N \) – net photosynthetic rate.

unimodal and bimodal. As shown in Fig. 2A, out of eight provenances, six of them, PO-hz, PO-fx, PO-sz, PO-xy, PR-lb, and PR-zwl, had bimodal curves for \( P_N \) daily variation. Whereas the other two, PR-yz and PR-lt, were unimodal. The bimodal curve had two distinct peaks, peak I and II, and also showed the photosynthetic an phenomenon of midday respose in leaf photosynthesis. Among the six bimodal sources, PO-hz, PO-fx, PO-sz, and PR-zwl had the peak I appeared at 10:00 h while PO-xy and PR-lb had the peak I appeared at 12:00 h. For all the six provenances, peak II occurred at 16:00 h, and the photosynthetic midday depression occurred at 14:00 h. Furthermore, as shown in Fig. 2A, the photosynthetic diurnal variation curves of PR-yz and PR-lt were unimodal, and both had peaks occurred at 10:00 h. The \( P_N \) daily average of eight provenances ranging from large to small was in following order: PR-zwl > PO-fx > PO-xy > PO-hz > PO-sz > PR-lb > PR-lt > PR-yz.

The peak I values of the six peony sources with bimodal curve was ranked in descending order as: PR-zwl > PO-xy > PO-hz > PO-sz > PO-fx > PR-lb. The peak I value of PR-zwl was 15.78 \( \mu \text{mol} \text{(CO}_2\text{)} \text{m}^{-2} \text{s}^{-1} \), which was significantly higher than that of other five provenances. The peak I values of the rest four were close to each other. In addition, the peak II values of all these six provenances were significantly lower than the peak I values.

Stomatal conductance (\( g_s \)) refers to the ability of plant pores to conduct CO\(_2\) and water. The trend of \( g_s \) daily variation curve in different provenances is shown in Fig. 2B. The \( g_s \) of PO-sz, PO-hz, and PO-yz started to decrease at 10:00 h, and the \( g_s \) of PO-fx and PR-lb began to decline at 8:00 h, while in PO-zwl, PO-xy, and PR-lt \( g_s \) began to drop from 12:00 h. Only PO-hz, PR-zwl, and PO-fx showed the \( g_s \) values increased starting from 16:00 h, the other five provenances showed a continuous decreasing trend until the end of the test.

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$P_{\text{S}}$ value continued to increase when PAR ranged from 0 to 1,600 μmol(photon) m$^{-2}$ s$^{-1}$, and it decreased slightly after PAR exceeded this value. The $P_{\text{S}}$ value for both PR-lt and PR-yz sources reached the maximum at PAR of 800 μmol(photon) m$^{-2}$ s$^{-1}$, and it decreased rapidly after the PAR exceeded 1,000 μmol(photon) m$^{-2}$ s$^{-1}$ and when photoinhibition appeared. Overall, the trend of maximum net photosynthetic rate of the eight provenances was: PR-zwl > PO-xy > PO-hz > PO-fx > PO-sz > PR-lb > PR-lt > PR-yz, indicating that PR-zwl had the greatest demand for light. Therefore, we can conclude that the oil peonies from six provenances, except for the PR-lt and PR-yz, all had a strong light adaptability. In addition, when PAR exceeded 1,000 μmol(photon) m$^{-2}$ s$^{-1}$, the photo-response curves of PR-lt and PR-yz decreased sharply, indicating that strong light could weaken their photosynthetic capacity.

The AQY reflects conversion and utilization efficiency of light energy at the weak-light stage. Among the eight provenances, the AQY values of PO-hz, PR-lb, PO-xy, PR-yz, and PO-sz were relatively high and similar to each other, but they were significantly higher than that of PO-fx and PR-lt. It indicated that PO-hz, PR-lb, PO-xy, PR-yz, and PO-sz had higher light-utilization efficiency at the low-light stage. The $P_{\text{Smax}}$ value is a parameter characterizing the photosynthetic potential. The larger the leaf $P_{\text{Smax}}$ value, the greater is the photosynthetic potential of the plant. The $P_{\text{Smax}}$ of PR-zwl was 15.02 μmol(CO$_2$) m$^{-2}$ s$^{-1}$, which was significantly higher than all other provenances and no significant differences were observed in $P_{\text{Smax}}$ values between provenances of PO-xy, PO-hz, PO-sz, and PO-fx. The $R_0$ is an indicator of the respiration intensity of plant cells. High $R_0$ indicates strong respiration expenditure in the process of photosynthetic organic synthesis, which is neither beneficial to the organic accumulation in plants nor plant growth. The $R_0$ of PO-hz (2.19 μmol m$^{-2}$ s$^{-1}$) was significantly higher than in other provenances, whereas the $R_0$ of PO-sz (1.46 μmol m$^{-2}$ s$^{-1}$) was by far the lowest among all the provenances. A larger LSP shows the plant preferring the sun more, while a smaller LCP indicates a higher ability to utilize the weak light as well as a stronger ability to adapt to the weak light. Among all eight provenances, the LSP of PO-xy was by far the largest, whereas the LCP of PO-sz was by far the smallest, indicating that PO-xy was a heliophilous plant and could adapt to a wider range of light intensities.

**CO$_2$-response curves:** The response curve of $P_{\text{S}}$ to CO$_2$ reflects the adaptability of plants to CO$_2$. In this experiment, the hyperbolic correction model was used to fit the CO$_2$ response values, and the ideal result was obtained ($R^2$=0.9966 ~ 0.9995; Fig. 4, Table 2). Fig. 4 shows that the response tendency of $P_{\text{S}}$ to the change of intercellular CO$_2$ concentration ($C_i$) was similar in all provenances except for PR-zwl. With the increase of CO$_2$ concentration, $P_{\text{S}}$ gradually increased and then became stable, where $P_{\text{S}}$ increased more rapidly before the $C_i$ reached 1,000 μmol mol$^{-1}$, then increased slower until reached and remained at the maximum level. PO-fx had the highest $P_{\text{S}}$ value compared to the other six sources at the same intercellular CO$_2$ concentration. However, in PR-zwl, $P_{\text{S}}$ continued increasing even at the maximum set value of CO$_2$, showing a prominent adaptability and photosynthetic potential to a higher CO$_2$ concentration.

Table 2 shows that the ACE of different provenances oil peonies differed greatly. The ACE of PO-fx was the highest and significantly higher than that of other provenances, indicating a higher utilization efficiency of CO$_2$ at low

Table 2. Comparison of CO$_2$-response parameters of oil peonies from eight provenances. ACE – initial carboxylation efficiency; $A_{\text{max}}$ – maximum net photosynthetic rate at CO$_2$-saturation point; CSP – saturated intercellular CO$_2$ concentration; CCP – CO$_2$-compensation point; $R_0$ – photospiration rate. Data represent means ± SD of six independent experiments. Different letters in the same column indicate significant differences at the 5% which are Duncan’s multiple comparison test groups for one-dimensional ANOVA.

<table>
<thead>
<tr>
<th>Species</th>
<th>ACE</th>
<th>$A_{\text{max}}$ [μmol m$^{-2}$ s$^{-1}$]</th>
<th>CSP [μmol mol$^{-1}$]</th>
<th>CCP [μmol mol$^{-1}$]</th>
<th>$R_0$ [μmol m$^{-2}$ s$^{-1}$]</th>
<th>Decisive factor</th>
</tr>
</thead>
<tbody>
<tr>
<td>PR-yz</td>
<td>0.0319 ± 0.0030$^d$</td>
<td>25.01 ± 1.63$^c$</td>
<td>1,928.37 ± 51.06$^b$</td>
<td>103.84 ± 6.79$^b$</td>
<td>3.20 ± 0.28$^c$</td>
<td>0.9968</td>
</tr>
<tr>
<td>PR-lt</td>
<td>0.0481 ± 0.0031$^{de}$</td>
<td>28.58 ± 1.09$^b$</td>
<td>1,416.20 ± 62.36$^d$</td>
<td>118.81 ± 4.53$^b$</td>
<td>5.47±0.45$^d$</td>
<td>0.9978</td>
</tr>
<tr>
<td>PR-lb</td>
<td>0.0605 ± 0.0026$^d$</td>
<td>30.57 ± 1.79$^d$</td>
<td>1,323.56 ± 35.68$^g$</td>
<td>110.87 ± 7.56$^b$</td>
<td>6.36 ± 0.38$^d$</td>
<td>0.9992</td>
</tr>
<tr>
<td>PR-zwl</td>
<td>0.0401 ± 0.0031$^{ef}$</td>
<td>56.31 ± 4.13$^e$</td>
<td>2,893.73 ± 94.93$^a$</td>
<td>73.29 ± 3.04$^d$</td>
<td>2.76 ± 0.11$^f$</td>
<td>0.9989</td>
</tr>
<tr>
<td>PO-fx</td>
<td>0.1051 ± 0.0072$^a$</td>
<td>37.75 ± 1.56$^a$</td>
<td>1,740.54 ± 47.25$^f$</td>
<td>105.73 ± 5.83$^b$</td>
<td>8.53 ± 0.66$^a$</td>
<td>0.9966</td>
</tr>
<tr>
<td>PO-sz</td>
<td>0.0534 ± 0.0031$^{de}$</td>
<td>30.54 ± 2.21$^d$</td>
<td>1,392.69 ± 46.74$^b$</td>
<td>111.74 ± 5.90$^b$</td>
<td>5.73 ± 0.23$^{de}$</td>
<td>0.9974</td>
</tr>
<tr>
<td>PO-xy</td>
<td>0.0905 ± 0.0126$^a$</td>
<td>35.58 ± 0.52$^e$</td>
<td>1,703.07 ± 56.83$^e$</td>
<td>84.81 ± 3.54$^c$</td>
<td>7.00 ± 0.29$^b$</td>
<td>0.9995</td>
</tr>
<tr>
<td>PO-hz</td>
<td>0.0734 ± 0.0054$^c$</td>
<td>34.45 ± 2.15$^c$</td>
<td>1,428.38 ± 63.35$^d$</td>
<td>87.35 ± 2.09$^c$</td>
<td>6.04 ± 0.34$^{ad}$</td>
<td>0.9982</td>
</tr>
</tbody>
</table>

Fig. 4. CO$_2$-response curve of oil peonies in eight provenances. $P_{\text{S}}$ – net photosynthetic rate; $C_i$ – intercellular CO$_2$ concentration.
The concentration, as well as the yield, is also significantly higher than that of other sources. Since PR-zwl has the strongest photosynthetic capacity among the eight oil peony provenances, followed by PO-fx, PO-xy, PO-hz, and PO-sz.

Discussion

During the long process of evolution and development, plants have interacted with the environment and gradually formed morphological and physiological structures that can adapt to the external environment changes, mainly reflecting in the differences of leaves, roots, seeds, and other plant characteristics (Violle et al. 2007). Leaf photosynthesis is one of the most important physiological traits within plant leaf functional traits, which is related to crop growth and yield (Song et al. 2012, Rao et al. 2018). The net photosynthetic rate reflects the abilities of CO₂ fixation and organic matter accumulation (Song et al. 2013), and the relationship between net photosynthetic rate and yield has been controversial. Some researchers think that there is a positive correlation between the two (Medrano et al. 2003, Velička et al. 2007, Liu et al. 2017), and it is possible to breed high-yield varieties by increasing the net photosynthetic rate of single leaves. Others believe the two are negatively correlated, and the relationship between net photosynthetic rate and yield in different periods may also be inconsistent (Zhang et al. 2011). In fact, the yield is essentially determined by the photosynthetic capacity and photosynthetic rate of the leaves. The results of this study showed that the daily average \( P_a \) value of PR-zwl was significantly higher than that of other provenances under natural conditions, indicating a stronger photosynthetic capacity. At the same time, according to the morning peak of the net photosynthetic rate, the peak I of PR-zwl was also significantly higher than that of other sources. Since the photosynthetic rate is a heritable plant trait, we can conclude that PR-zwl has the strongest photosynthetic capacity among the eight oil peony provenances, followed by PO-fx, PO-xy, PO-hz, and PO-sz.

Stomata are the channels for gas exchange between plants and the external environment for CO₂, O₂, and H₂O. The size of the pore diameter directly determines the strength of plant leaf transpiration and the rate of photosynthesis, which in turn affects material accumulation rates. Studies showed that there is a feedback regulation between the CO₂ concentration and the stomatal conductance in the inferior stomatal space (Betzelberger et al. 2010). A decrease in photosynthetic rate may be due to stomatal limitation or a decrease in photosynthetic capacity of mesophyll tissue (Hetherington and Woodward 2003), where both induced factors can be affected by environmental conditions (Chen et al. 2002). In this study, six of the eight oil peony's diurnal variations of photosynthesis curves were bimodal. The first decrease of \( P_a \) value occurred between the peak I and 14:00 h, which was caused by the decrease of stomatal conductance, whereas the second \( P_a \) value decrease after the peak II was caused by the decrease in photosynthetic capacity of the leaf mesophyll tissue. Temperature and transpiration rate might be the causes that peak I occurred
at different times for different oil peony sources. The light-response curve and CO$_2$-response curve can reflect the plant adaptability to changes in light intensity and CO$_2$ concentration, they can also reflect the potential photosynthetic capacity of the plants. They can be affected by various factors, such as Chl quantity and respiration rate. In this study, the fitting correlation coefficient of light-response value and CO$_2$-response value of oil peony was relatively high, which well reflected the differences of the net photosynthetic rate change between different oil peony sources under various light conditions and CO$_2$ concentrations. Both LCP and LSP can be used as indicators to evaluate plant’s light energy utilization ability. A smaller LCP value shows higher plant utilization ability for weak light, whereas a larger LSP value means higher utilization ability of strong light. Among eight tested sources, PO-xy had significantly the highest LSP value, indicating a heliophilous plant with a stronger ecological adaptability to light than that of other provenances. The LCP of PO-sz was significantly lower than of other provenances, indicating a higher ability to utilize weak lights. A small LSP value and a large LCP value means a narrower utilization range of light. AQY is a way to measure the maximum efficiency of light energy conversion in photosynthesis. It can correctly reflect the changes of the organization and function of the photosynthetic apparatus, as well as the ability for leaves to use weak light. AQY value is positively correlated with the amount of the pigment-protein complexes for absorbing and converting light energy and the ability to utilize weak light. The study showed that PO-hz, PR-1b, PO-xy, PR-yz, and PO-sz had higher light-utilization efficiency at the low-light stage. $P_{\text{max}}$ and $A_{\text{max}}$ values are parameters for characterizing photosynthetic potential (Farquhar and Sharkey 1982, Cai et al. 2012). The larger the leaf $P_{\text{max}}$ and $A_{\text{max}}$ values, the greater the photosynthetic potential of the plant. PR-zwl had the largest $P_{\text{max}}$ and $A_{\text{max}}$ values among all eight tested sources, therefore the greatest photosynthetic capacity.

Chl is the main pigment that absorbs light energy during plant photosynthesis (Xiong et al. 2012). Chl content is a critical reference parameter for the quantitative calculation of plant physiological responses (Watling et al. 2000). It is also an important factor in determining photosynthetic rate and the total dry matter accumulation (Maxwell and Johnson 2000). Its content directly affects the plant photosynthetic ability. In general, the shade-tolerant plants usually have a relatively high Chl b content (Wittmann et al. 2001). The ratio of Chl a/b reflects the percentage of light-harvesting pigment complex II in all Chl-containing structures, where higher ratio indicates a stronger light-harvesting ability. In this study, PO-It, PO-sz, and PR-zwl had relatively higher Chl a/b value, indicating higher utilization rates of light energy. Studies showed that walnuts had higher Chl b/a values under shading than under light conditions (Garty et al. 2001). Chl b/a values of PR-It and PR-yz were relatively high but they had lower net photosynthetic rate as well as a lower tolerance of strong light, showing a strong shade tolerance.

In this study, the leaf structure characteristics and yield results were not incorporated in the photosynthetic characteristics of oil tree peony experiment. They will be investigated in the future studies.

**Conclusion:** According to the positive correlation between photosynthesis and yield, combined with the response strategies of oil peonies from different provenances to environmental changes, we were able to predict the bearing capacity and adaptability of different provenances, and to filter out the optimal oil peony provenance. The results showed that PR-zwl, PO-fx, and PO-xy had relatively strong advantages in photosynthesis and outstanding adaptability to the environment. Therefore, they can be used as excellent provenances for oil peony cultivation and the parents for hybrid breeding of oil peony.

**References**


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