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Differences in light response characteristics of oil peonies from eight provenances in China

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Abstract

Two tree peony species, *Paeonia ostii* and *Paeonia rockii*, from eight different provenances in China (four provenances for each species) were collected for their photosynthetic characteristics. Their diurnal variations of photosynthesis, the light- and CO_2-response curves and chlorophyll content were determined. Among all eight provenances, Ziwuling *P. rockii* had a significantly higher average daily net photosynthetic rate, showing a superior photosynthetic capacity, followed by Fengxiang *P. ostii* and Xunyang *P. ostii*. In addition, Ziwuling *P. rockii* had the highest maximum net photosynthetic rates, thus, presented a strong photosynthetic potential. Furthermore, Xunyang *P. ostii*, Fengxiang *P. ostii*, and Heze *P. ostii* also exhibited a great photosynthetic capacity and light adaptability, which was consistent with their high chlorophyll *a*/*b* values. Taken together, Ziwuling *P. rockii* had the strongest photosynthetic capacity among all tested sources, followed by Fengxiang *P. ostii*, and Xunyang *P. ostii*, which are recommended to be used as seed sources for oil peony cultivation and cross-breeding.

Additional key words: gas exchange; leaf functional traits; photorespiration; resource acquisition; transpiration rate.

Introduction

The photosynthesis of plants is the main source of terrestrial primary production, which can reflect how well the plants can adapt to the environment. Photosynthetic parameters are an integral part of plant functional traits (Meng *et al*. 2019). Since plant photosynthesis mainly takes place in leaves, the functional traits of the leaves can directly affect photosynthetic rate and duration, which make them essential for the survival and reproduction of plant individuals (Kikuzawa 1991, Reich *et al*. 1997, Li *et al*. 2015). Functional traits mainly include net photosynthetic rate (P_N), respiratory rate, and stomatal conductance (g_s), which reflect the growth and metabolism index of leaves, and have relatively huge variations in terms of time and space (Zhang and Luo 2004, Liu *et al*. 2006, Huang *et al*. 2010). Plants have formed a variety of geographical provenances under the interaction with long-term climatic and geographic environments, and each source adapted to different environments differently. The morphological and physiological manifestations of the plants, which are transplanted to the same place but originated from different provenances, have always been a hot topic of research, as it is significant for exploring adaptation mechanisms of plants, especially for the study of tree response mechanism in the context of climate change.

Tree peony (*Paeonia* section Moutan DC) is a unique woody oil resource in China that has a strong fruit bearing ability and can be used to produce seeds and process peony seed oil (Li 2014, Zhou and Wang 2014). At the moment, *Paeonia ostii* ‘FengDan’ and *Paeonia rockii* are the most widely used tree peony species for oil extraction with good oil performance. The seed oil of oil peony is a new resource of edible oil approved by the Ministry of Health. The unsaturated fatty acid content is around 92.4%, of which α-linolenic acid is as high as 42.8%. It is considered to be the most beneficial and healthy nutrient oil (Zhou *et al*. 2009, Li *et al*. 2012). Vigorously developing and planting oil peony can effectively alleviate the situation that more than 60% of China's edible oil has been imported (Li 2014). However, the problems of unvaried species and low yield have severely restricted the development of oil peony industry. Therefore, the introduction, domestication, and cultivation of oil peonies are extremely urgent.

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Abbreviations: ACE – initial carboxylation efficiency; A_{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_N – net photosynthetic rate; P_{Nmax} – maximum net photosynthetic rate at light-saturation point; R_D – dark respiration rate; RH – relative humidity; R_p – photorespiration rate; t_a – air temperature; VPD – vapor pressure deficit.
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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, Fengxiang, Shangzhou, Xunyang, and Ziwuling. Locations and climate factors of each provenance were as follows:

Species	Provenance	Abbreviation	Latitude	Longitude	Altitude [m]	Mean annual temperature [°C]	Mean annual precipitation [mm]
Paeonia rockii	Yuzhong County	PR-yz	104°07'E	35°52'N	2,495	6.7	400
	Lintao County	PR-lt	103°49'E	35°37'N	2,654	7.0	539
	Ziwuling Mountain	PR-zwl	108°03'E	35°20'N	1,528	7.4	588
	Liuba County	PR-lb	107°08'E	33°42'N	1,547	11.5	886
Paeonia ostii	Fengxiang County	PO-fx	107°02'E	34°31'N	968	11.4	625
	Heze City	PO-hz	115°45'E	35°39'N	52	13.8	663
	Shangzhou Area	PO-sz	109°57'E	33°52'N	1,628	13.5	758
	Xunyang County	PO-xy	105°58'E	32°49'N	846	14.5	1,050

Plants were transplanted to the Peony Resource 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_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_{Nmax}), dark respiration rate (R_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:

$$P_N = \alpha \times (1 - \beta \times I) \times I/(1 + \gamma \times I) - R_D,$$

where I refers to photosynthetically active radiation, R_D is the dark respiration rate, α refers to the initial slope of the light-response curve, and β and γ 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, 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_{max}), saturated intercellular CO_2 concentration (CSP), CO_2-compensation point (CCP), photorespiration rate (R_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

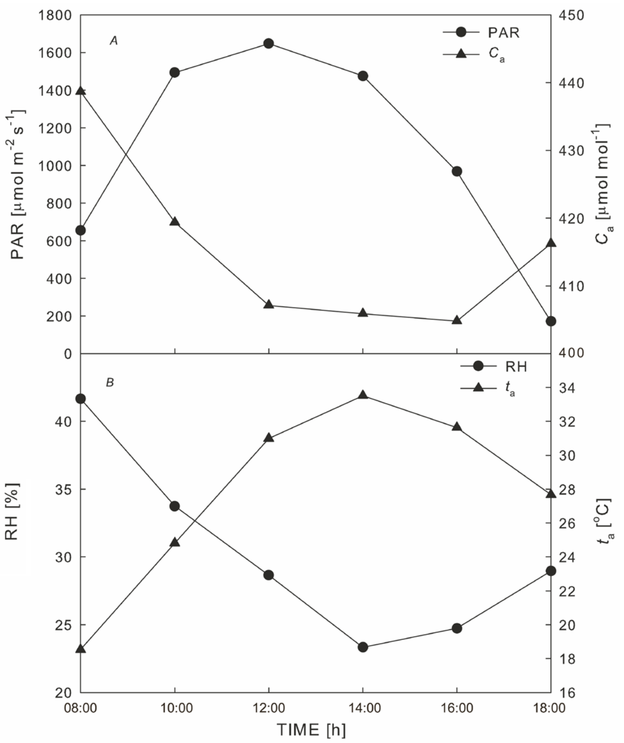

Fig. 1. Diurnal changes of photosynthetically active radiation (PAR), air CO_2 concentration (C_a), air temperature (t_a), and relative humidity (RH) during the experimental period.

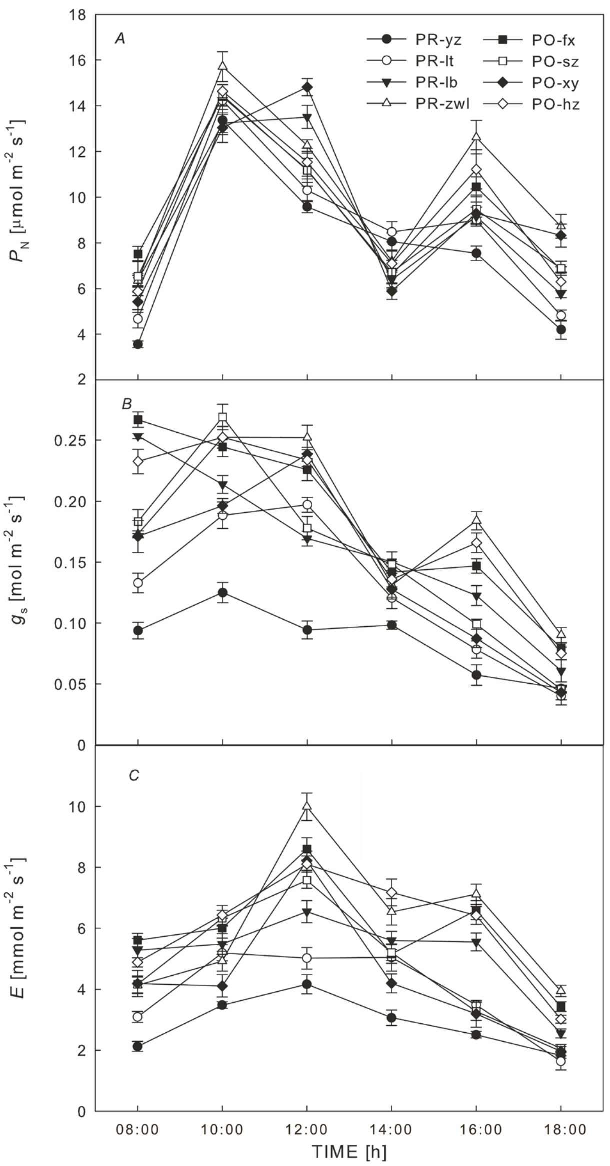

Fig. 2. Diurnal variation of net photosynthetic rate (P_N) (*A*), stomatal conductance (g_s) (*B*), and transpiration rate (*E*) (*C*) of oil peonies in eight provenances.

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:

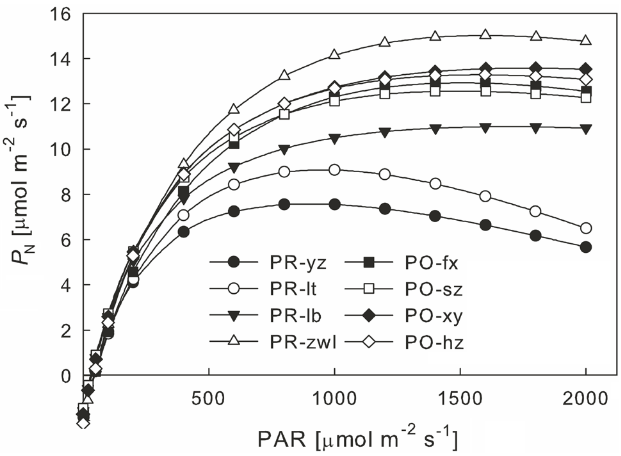

Fig. 3. Light-response curve of oil peonies in eight provenances. PAR – photosynthetically active radiation; P_N – net photosynthetic rate.

unimodal and bimodal. As shown in Fig. 2*A*, 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. 2*A*, 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 μmol(CO_2) m^{-2} 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. 2*B*. 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. 2*C*, 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 μmol(photon) m^{-2} s^{-1}, P_N values increased linearly with the increase of light intensity, whereas when PAR was greater than 200 μmol(photon) m^{-2} s^{-1}, the growth rate of P_N became slower, and with the light intensity increased, P_N 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,

Table 1. Comparison of light-response parameters of oil peonies from eight provenances. AQY – apparent quantum efficiency; P_{Nmax} – maximum net photosynthetic rate at light-saturation point; LSP – light-saturation point; LCP – light-compensation point; R_D – 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*.

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

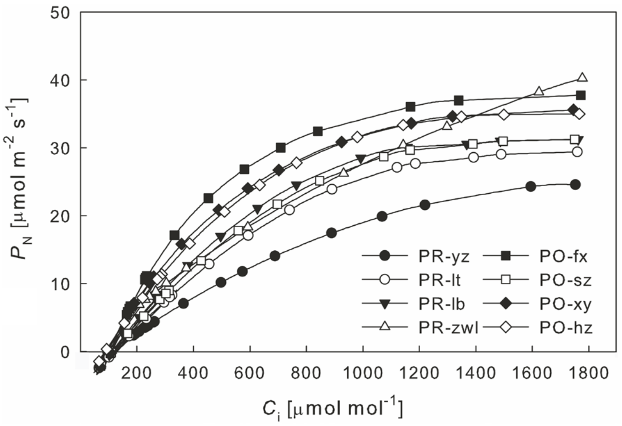

Fig. 4. CO_2-response curve of oil peonies in eight provenances. P_N – net photosynthetic rate; C_i – intercellular CO_2 concentration.

P_N 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_N 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_{Nmax} value is a parameter characterizing the photosynthetic potential. The larger the leaf P_{Nmax} value, the greater is the photosynthetic potential of the plant. The P_{Nmax} 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_{Nmax} values between provenances of PO-xy, PO-hz, PO-sz, and PO-fx. The R_D is an indicator of the respiration intensity of plant cells. High R_D 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_D of PO-hz (2.19 µmol m^{-2} s^{-1}) was significantly higher than in other provenances, whereas the R_D 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_N 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_N 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_N gradually increased and then became stable, where P_N 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_N value compared to the other six sources at the same intercellular CO_2 concentration. However, in PR-zwl, P_N 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_{max} – maximum net photosynthetic rate at CO_2-saturation point; CSP – saturated intercellular CO_2 concentration; CCP – CO_2-compensation point; R_p – photorespiration 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*.

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

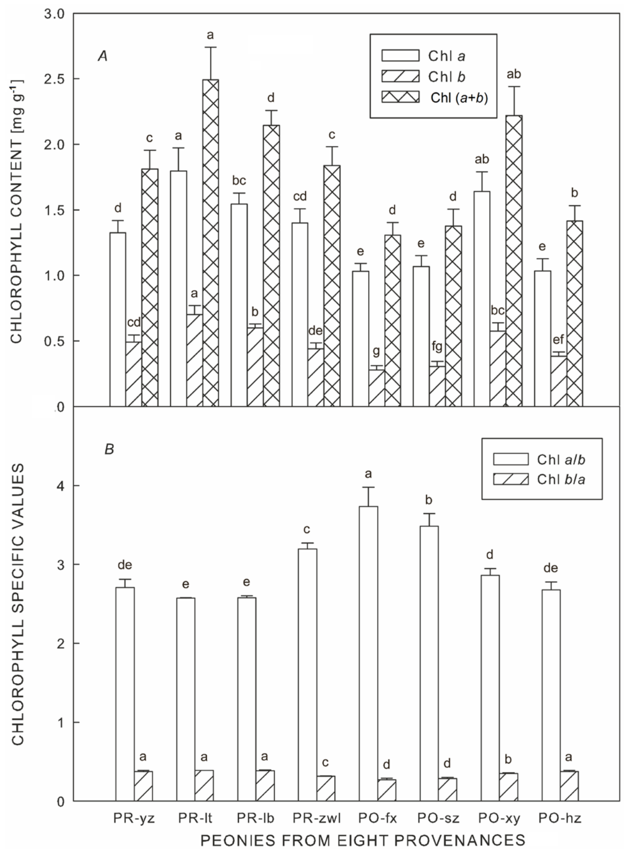

Fig. 5. The contents of chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl *b*), sum of chlorophyll *a* and chlorophyll *b* (Chl *a*+*b*) (*A*), ratio of chlorophyll *a* to chlorophyll *b* (Chl *a*/*b*) and ratio of chlorophyll *b* to chlorophyll *a* (Chl *b*/*a*) (*B*) in oil peonies from eight provenances. Data are means of three replications and bars indicate the standard deviation of the means (n = 3). *Different letters* on the bars indicate significant differences at the 5% which are *Duncan*'s multiple comparison test groups for one-dimensional *ANOVA*.

CO_2 concentration, while PR-yz was the opposite. The A_{max} represents photosynthetic capacity. Among all tested sources, PR-zwl had the highest A_{max} value, highest saturated intercellular CO_2 concentration, as well as the lowest R_p, indicating the strongest photosynthetic capacity, adaptability to a wider range of CO_2 concentrations as well as a prominent organic accumulation due to less R_p consumption.

Chl content: PR-lt had the highest contents of Chl *a*, Chl *b*, and Chl (*a*+*b*), which were 1.80, 0.70, 2.49 mg g^{-1}, respectively (Fig. 5*A*). The Chl *b* content was significantly higher than that of other provenances. PR-lt had similar Chl *a* and Chl *a*+*b* contents with PO-xy, but significantly higher than that of the rest sources. PO-fx had the lowest Chl *a*, Chl *b* and Chl *a*+*b*, which were 1.03, 0.28, 1.31 mg g^{-1}, respectively. The descending order of Chl *a*+*b* was: PR-lt > PO-xy > PR-lb > PR-zwl > PR-yz > PO-hz > PO-sz > PO-fx. No significant differences were observed between PO-hz, PO-sz, and PO-fx. PO-fx had the highest Chl *a*/*b* value of 3.73, which was by far the highest among all sources (Fig. 5*B*). However, it had the lowest Chl *b*/*a* value, whereas PR-lt had the highest Chl *b*/*a* value of 0.39. Therefore, PR-lt had the strongest shade tolerance and PO-fx had the weakest shade tolerance among the eight tested provenances.

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 CO_2 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_N 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 CO_2, O_2, and H_2O. 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 CO_2 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_N value occurred between the peak I and 14:00 h, which was caused by the decrease of stomatal conductance, whereas the second P_N 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-lb, PO-xy, PR-yz, and PO-sz had higher light-utilization efficiency at the low-light stage. P_{Nmax} and A_{max} values are parameters for characterizing photosynthetic potential (Farquhar and Sharkey 1982, Cai *et al*. 2012). The larger the leaf P_{Nmax} and A_{max} values, the greater the photosynthetic potential of the plant. PR-zwl had the largest P_{Nmax} and A_{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-fx, 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-lt 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.

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