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COMPARATIVE PHOTOSYNTHETIC CHARACTERISTICS AND CHLOROPHYLL CONTENT OF FOUR OIL PEONY SPECIES FROM 11 PROVENANCES IN CHINA

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Abstract

Present study showed the photosynthetic characteristics of 4 wild oil peony (Paeonia, Ranunculaceae) species from 11 provenances in different provinces in China and hereby predicted the seed yields of them. By investigating the leaf gas-exchange factors, light-response curves and Chlorophyll contents of the different peonies in April, 2015, several photosynthetic parameters were analyzed and compared. The daily photosynthesis variation curves of eight origins were bimodal while the rest three were unimodal. Results showed that Paeonia rockii from Lintao county and Paeonia delavayi from Wenbishan mountain had significantly higher net photosynthetic rate than the others, suggesting larger photosynthesis capacity. The analysis of net photosynthetic rate reduction showed that Paeonia rockii and Paeonia delavayi had larger photosynthetic abilities than the other two species. Paeonia rockii from Baokang county had the biggest apparent quantum yield and lowest light compensation point of the all, which enabled it to possess the largest radiation use efficiency and shade-endurance. Paeonia delavayi from Wenbishan mountain had the biggest light-saturated net photosynthetic rate coming with the largest photosynthesis potential. Furthermore, the total chlorophyll content comparison showed strong photosynthesis capacity in Paeonia rockii from Baokang county and Paeonia rockii from Lintao county. In summary, Paeonia rockii and Paeonia delavayi especially Paeonia rockii from Lintao county, Paeonia rockii from Baokang county, and Paeonia delavayi from Wenbishan mountain had advantages in photosynthetic capacity to synthesis organic matters and could be screened as superior provenances.

Key words: Oil peony, Photosynthetic characteristics, Chlorophyll content.

Abbreviations: AQY – apparent quantum yield; Ca – air CO2 concentration; Chl a(b) – Chlorophyll a(b); Ci – intercellular CO2 concentration; E – transpiration rate; gs – stomatal conductance; LCP – light compensation point; Ls – ¬¬limiting value of stomata; LSP – light saturation point; LUE – light use efficiency; PAR – photosynthetically active radiation; PD-wbs – Paeonia delavayi native to Wenbishan mountain in Yunnan; PN – net photosynthetic rate; PNmax – light-saturated net photosynthetic rate; PO-dzy – Paeonia ostii native to Dazhuyuan area in Shaanxi; PO-htp – Paeonia ostii native to Hetaoping area in Shaanxi; PO-snj – Paeonia ostii native to Shennongjia mountain in Hubei; PQ-bk – Paeonia qiui native to Baokang county in Hubei; PQ-sn – Paeonia qiui native to Shangnan county in Shaanxi; PQ-xy – Paeonia qiui native to Xunyang county in Shaanxi; PQ-yx – Paeonia qiui native to Yunxi county in Hubei; PR-bk – Paeonia rockii native to Baokang county in Hubei; PR-djg – Paeonia rockii native to Dajiangou area in Shaanxi; PR-lt – Paeonia rockii native to Lintao county in Gansu; RD – dark respiratory rate; RH – relative air humidity; Ta – air temperature; TL – leaf temperature; VPD – vapor-pressure deficit.

Introduction

Edible vegetable oil is indispensable in people's daily life and China is the largest country consuming vegetable oil in the world. Oil peony (*Paeonia, Ranunculaceae*) is a neotype woody oil crop highly researched in China over recent years. Peony seed oil has an oil ratio of up to 27–32% (Han *et al.*, 2015) and more than 90% of the oil is unsaturated fatty acid including oleic acid, linoleic acid and linolenic acid (Sevim *et al.*, 2013; Ning *et al.*, 2015). Whereas soybean oil, which has been widely used as cooking oil, only has 58%–69% unsaturated fatty acid (Rui *et al.*, 2010), showing that Peony seed oil is healthier than soybean oil for human life. And peony seed oil also has anti-diabetic activity certified in mice (Su *et al.*, 2015). The Announcement NO. 9 (2011) of the Ministry of Health of the People's Republic of Chinaapproved peony seed oil as a New Resource Food on March 12, 2011 (Anon., 2011). Therefore, oil peony has been a hot research topic in the field of oil plants lately.

Peony seed oil can be made of selected wild or cultivated peony species. Compare to the well-known ornamental peony, the most prominent difference is that oil peony has fewer petals and has higher seed setting rate. One of the most widely planted oil peonies is *Paeonia ostii* 'Feng Dan White' native to Tongling city in Anhui province (Zhang *et al.*, 2014). Nevertheless, many wild peony species could also be cultivated as oil peony cultivars, which requires us to select and cultivate excellent wild species by a variety of experiments. Peony could be classified into monopetalae with 1–3 whorls petals and multipetalae with numerous whorls petalsin terms of flower type (Liu *et al.*, 1987). Monopetalae peonies have higher seed production because their carpels are patulous and verticillate. In this paper, the four wild oil peony species, having the characteristics of high flowering rate, strong growth potential and high seed-setting rate, are all monopetalae peonies. *Paeonia ostii* and *Paeonia delavayi* (Anon., 2000) have 2–3 whorls of petals. *Paeonia Rockii* has 10 petals (Anon., 1977). *Paeonia qiui* has 5–9 petals (Pei & Hong, 1995).

All crop production primarily depends on photosynthetic capacity and rate (Stoskopf, 1981), and general 90–95% of seeds mass was converted from photosynthetic production. Earlier studies showed that photosynthesis rate is an important yet complicated factor to determine and predict crop biomass accumulation, since photosynthetic capacity is controlled by gene, so crop production can be optimized by improving photosynthetic rate (Gifford, 1974; Gardner *et al.*, 1985). Photosynthetic rate greatly influences the production of oil crops. Photosynthesis is fundamental in both biomass accumulation and productivity and could be best utilized in identifying the efficient groundnut cultivars (Kalariya *et al.*, 2013). Leaves photosynthesis dominated siliques numbers, seeds number per silique and seeds yield (Wang *et al.*, 2016). Because of different original habitats (Pšidová *et al.*, 2015), the photosynthetic characteristics of wild peony species from different origins vary. This paper will study and compare photosynthetic characteristics of 4 wild oil peony species from 11 different provenances for the first time, which were aimed at finding out the advantages and disadvantages in different cultivation conditions and to predicting their relationship to the seed yield from the photosynthesis point.

Materials and Methods

Provenances and introduction cultivation: All oil peonies were introduced from their provenances in 2013, then they were cultivated in the sunlight greenhouse of peony germplasm resources in NWAFU. Four oil peony species from eleven provenances were measured in this experiment. And different provenance has different natural ecological environment. All oil peonies and the corresponding abbreviations were shown in Table 1:

Table 1. Four oil peony species from eleven provenances were measured in this experiment. The provenances involved four provinces in China.

Species	Provenances	Abbreviations
Paeonia ostii	Shennongjia Mountain in Hubei	PO-snj
	Dazhuyuan Area in Shaanxi	PO-dzy
	Hetaoping Area in Shaanxi	PO-htp
Paeonia rockii	Lintao County in Gansu	PR-lt
	Baokang County in Hubei	PR-bk
	Dajiangou Area in Shaanxi	PR-djg
Paeonia qiui	Yunxi County in Hubei	PQ-yx
	Baokang County in Hubei	PQ-bk
	Xunyang County in Shaanxi	PQ-xy
	Shangnan County in Shaanxi	PQ-sn
Paeonia delavayi	Wenbishan Mountain in Yunnan	PD-wbs

Experimental design: This research was conducted in April, 2015. Photosynthesis parameters and light-response curves were measured in their cultivation fields by *LI-6400XT portable photosynthesis system* (*LI-COR biosciences*, Lincoln, Nebraska, USA). All parameters were measured on fully expanded leaves (the third or fourth leaf from the top) of healthy plants. Chlorophyll content was analyzed in Forestry College in NWAFU.

Leaf gas-exchange measurement: The measured parameters were as following: net photosynthetic rate (P_N), transpiration rate (E), stomatal conductance (g_s), intercellular CO_2 concentration (C_i), air CO_2 concentration (C_a), leaf temperature (T_L), relative air humidity (RH) and photosynthetic active radiation (PAR). Limiting value of stomata (L_s) (Berry & Downton, 1982) and light use efficiency were calculated respectively through the equations:

$$L_s = 1 - C_i/C_a \quad (1)$$

$$LUE = P_N/PAR \quad (2)$$

This measurement spanned from 08:00 h to 17:00 h during clear and cloudless days in April, 2015. For each origin, two leaves per plant were measured from three plants every two hours and two values were logged per leaf. The experiment above repeated twice. The data were averaged by the values measured from 6 peony plants.

P_N-PAR response curve were measured on the another clear and cloudless days in April, 2015. Instrument setup included a standard broad leaf chamber (6cm^2) with a inbuilt red and blue light emitting diode illuminant. The instrument was operated in an Auto-program with PAR gradient of 2000, 1500, 1200, 1000, 800, 600, 400, 200, 100, 50, 20 and 0 μmol(photon) m^{-2} s^{-1}. By analyzing the data with a light response model, parameters including apparent quantum yield (AQY), light-saturated net photosynthetic rate (P_{Nmax}), dark respiratory rate (R_D), light saturation point (LSP) and light compensation point (LCP) were calculated. The equation was:

$$P_N = \alpha\,(1 - \beta \times I)\,(1 + \gamma \times I)^{-1} - R_d \quad (3)$$

where I is light intensity, R_D is dark respiratory rate, and α is the initial slope of light-response curve of photosynthesis when light intensity approaches zero, β and γ are coefficients which are independent of I (Ye, 2007). The experiment above repeated 5 times.

Chlorophyll (Chl) contents: Chl was extracted from 0.05g fresh leaves, which were cut into 1mm wide stripes and each was placed in a 10ml tube filled with organic extract (acetone: 95% alcohol = 2:1). After being kept in dark for 24 hours at room temperature until all leaf stripes became white completely, different organic extracts were analyzed in an *ultraviolet and visible spectrophotometer* (*Model UV-2450/2550,* Shimadzu, Japan) at 645nm and 663nm. The chlorophyll concentrations were calculated by equations of Porra (Porra, 2002). The species from each provenance had 3 replicates and the experiment above repeated twice.

Data analysis: All data were processed statistically with *SPSS Statistics 19.0* (*IBM*, USA.). One-way analysis of variance (*ANOVA*) with the least significant differences (LSD) test was employed to compare photosynthetic parameters among peonies from different provenances. All figures and tables were made by *Sigma Plot* 10.0 (*systat*, USA) and *Excel* (*Microsoft*, USA).

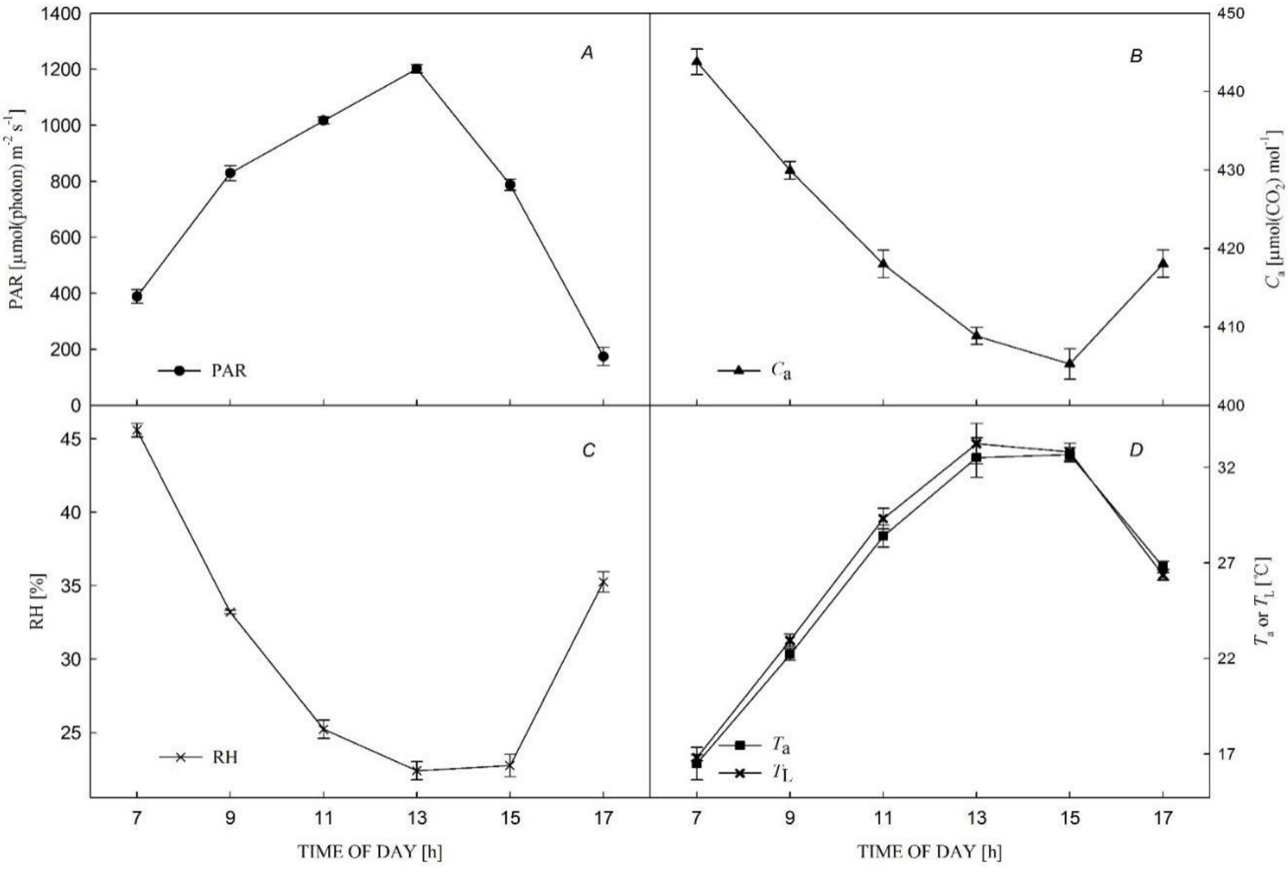

Fig. 1. Diurnal changes of photosynthetically active radiation (PAR) (*A*), air CO_2 concentration (C_a) (*B*), relative air humidity (RH) (*C*) and air temperature (T_a), leaf temperature (T_L) (*D*) during the experimental period in April, 2015. Bars indicate standard errors ($n = 6$).

Results

Diurnal variation of environment factors: From Fig. 1, PAR daily variation can be presented as an unimodal curve (*A*), which has the highest level 1201.29 μmol (photon) m^{-2} s^{-1} at noon and the lowest level both in the early morning and late afternoon. Fig. 1*B* showed that the trend of C_a curve was the opposite of PAR and C_a reached the highest level 443.80 μmol (CO_2) mol^{-1} at 7:00 h due to overnight respiration and slow consumption of CO_2 under low PAR. Then C_a began to decline with the intensifying of photosynthesis to the lowest level 405.27 μmol(CO_2)mol^{-1} at 15:00 h. T_a (*D*) increased slowly at 7:00 h and maintained a stable point 32.51ºC during 13:00 h to 15:00 h following a decreasing to the lowest 26.79ºC. The trend of T_L (*D*) was coincident to T_a, and T_L decreased (*D*) together with the weakening of PAR which lead to C_a recovery after 15:00 h (Shi *et al.*, 2012). RH declined from the highest point 45.60% at 7:00 h to the lowest point 22.41% at 13:00 h and remained at the same level until 15:00 h, after that it began to increase (*C*).

Diurnal changes of gas-exchange parameters: Under natural conditions, diurnal course of plant photosynthesis has two typical forms: unimodal and bimodal (Schulze & Hall, 1982). From Fig. 2, P_N diurnal change of 8 origins (PO-snj, PO-dzy, PO-htp, PR-bk, PR-djg, PQ-bk, PQ-yx and PD-wbs) showed typical bimodal curves, which had two peak values in the morning (Peak I) and afternoon (Peak II) with an obvious "midday depression" (*A*). Peak I of 7 origins occurred at 9:00 h, while that of PO-snj occurred at 11:00 h. Peak II of the 8 origins occurred at 15:00 h and "midday depression point" all occurred at 13:00 h. Diurnal curves of PR-lt, PQ-xy and PQ-sn had only one peak at 9:00 h, which indicated the unimodal type (*B*). According to the daily P_N (μmol(CO_2) m^{-2} s^{-1}) average values of eleven provenances, the descending order is: PR-bk (8.83) > PR-lt (8.78) > PO-htp (8.21) > PD-wbs (7.96) > PO-dzy (7.93) > PR-djg (7.87) > PQ-bk (7.26) > PQ-xy (7.13) > PQ-sn (6.88) > PQ-yx (5.73) > PO-snj (4.97).

As to the Peak value in the morning, the descending order of the eleven oil peony origins was: PR-lt > PD-wbs > PR-bk > PR-djg > PQ-sn > PQ-bk > PO-dzy> PO-htp > PQ-yx > PQ-xy > PO- snj. The maximum Peak value of PR-lt (15.790 μmol (CO_2) m^{-2} s^{-1}), PD-wbs (15.570 μmol (CO_2) m^{-2} s^{-1}) and PR-bk (15.217 μmol (CO_2) m^{-2} s^{-1}) were significantly larger than others. PO-snj, PO-dzy and PO-htp had the same Peak I and II values nearly, whereas the other oil peonies had prominent lower Peak II values. Therefore, *Paeonia ostii* has a larger photosynthetic capacity through the day, because the other oil peonies have smaller photosynthetic capacities in the afternoon. As shown in Fig. 3, g_s values of PO-snj, PO-dzy, PO-htp and PQ-yx began to decrease at 9:00 h while the other 7 oil peonies began to decrease from 7:00 h. For PO-htp, PR-bk and PR-djg, g_s curves reached the lowest point at 13:00 h, after increased to the peak at 15:00 h it started to decrease again.

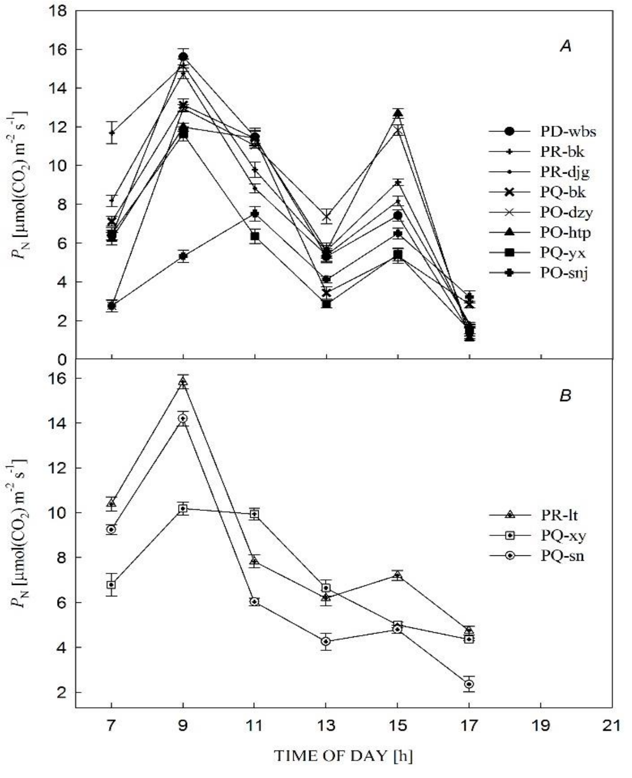

Fig. 2. Diurnal change curves of net photosynthetic rate (P_N) of peonies from 8 provenances in bimodal type (*A*) and of peonies from 3 provenances in unimodal type (*B*) during the experimental period in April, 2015. Bars indicate standard errors (*n* = 6). PD-wbs, PO-dzy, PO-htp, PO-snj, PQ-bk , PQ-sn, PQ-xy, PQ-yx , PR-bk, PR-djg, and PR-lt denoted the eleven Chinese oil peony materials in this research, which indicate *Paeonia delavayi* from Wenbishan mountain in Yunnan, *Paeonia ostii* from Dazhuyuan area in Shaanxi,*Paeonia ostii* from Hetaoping area in Shaanxi, *Paeonia ostii* from Shennongjia mountain in Hubei, *Paeonia qiui* from Baokang county in Hubei, *Paeonia qiui* from Shangnan county in Shaanxi, *Paeonia qiui* from Xunyang county in Shaanxi, *Paeonia qiui* from Yunxi county in Hubei, *Paeonia rockii* from Baokang county in Hubei, *Paeonia rockii* from Dajiangou area in Shaanxi and *Paeonia rockii* from Lintao county in Gansu, respectively.

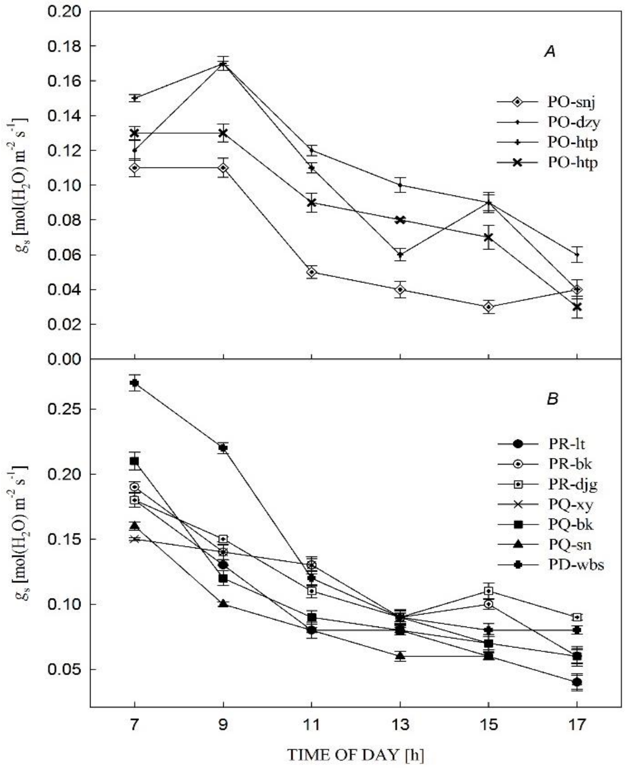

Fig. 3. Diurnal change curves of stomatal conductance (g_s) of oil peonies from 11 provenances during the experimental period in April, 2015. Bars indicate standard errors (*n* = 6). PD-wbs, PO-dzy, PO-htp, PO-snj, PQ-bk , PQ-sn, PQ-xy, PQ-yx , PR-bk, PR-djg, and PR-lt denoted the eleven Chinese oil peony materials in this research, which indicate *Paeonia delavayi* from Wenbishan mountain in Yunnan, *Paeonia ostii* from Dazhuyuan area in Shaanxi, *Paeonia ostii* from Hetaoping area in Shaanxi, *Paeonia ostii* from Shennongjia mountain in Hubei, *Paeonia qiui* from Baokang county in Hubei, *Paeonia qiui* from Shangnan county in Shaanxi, *Paeonia qiui* from Xunyang county in Shaanxi, *Paeonia qiui* from Yunxi county in Hubei, *Paeonia rockii* from Baokang county in Hubei, *Paeonia rockii* from Dajiangou area in Shaanxi and *Paeonia rockii* from Lintao county in Gansu, respectively.

Response characteristics to light: According to Fig. 4*A*, it was found that P_N of PO-snj and PO-dzy continued to increase when PAR was in the range of 0–1500 μmol (photon) m^{-2} s^{-1} and it declined slightly when PAR exceeded 1500 μmol (photon) m^{-2} s^{-1}. Similarly, the peak P_N of PQ-xy, PO-htp, PQ-yx, PQ-bk and PQ-sn occurred when PAR was 1200 μmol (photon) m^{-2} s^{-1}. As for PR-bk, PR-djg, PR-lt and PD-wbs, the PAR values are 1000, 800, 600 and 600 μmol (photon) m^{-2} s^{-1} respectively. Therefore, we concluded that 7 oil peony origins have higher light adaptive capacity expect PR-bk, PR-djg, PR-lt and PD-wbs. The curves of PD-wbs declined sharply when PAR exceeded 600 μmol (photon) m^{-2} s^{-1}, suggesting the strong sunlight would weaken the photosynthetic capacity of PD-wbs.

Fig. 4*B* exhibited a tendency of a sharp increase followed by a slow decrease overall for LUE. The peak values of LUE in PR-lt, PO-snj, PD-wbs, PR-bk and PR-djg occurred at 200 μmol (photon) m^{-2} s^{-1}. It reached 100 μmol(photon) m^{-2} s^{-1}, where as for PQ-xy, PO-dzy, PO-htp, PQ-yx, PQ-bk and PQ-sn the indicated that P_N of these five origins were unable to maintain a liner growth after PAR critical PAR was 100 μmol (photon) m^{-2} s^{-1} (Fig. 4*A*).

Light-responded P_N values of 11 oil peonies were fitted based on the new mathematical model, and satisfactory results were obtained (R^2=0.946–0.999, Table 2). From Table 2, AQY ranged from 0.0487 to 0.0959, and the descending order was PQ-bk > PR-lt > PQ-yx > PQ-sn > PD-wbs > PO-htp > PQ-xy > PO-snj > PR-djg > PR-bk > PO-dzy. The maximum AQY obtained from PQ-bk was significantly higher than that of others, so PQ-bk had the largest LUE in low PAR stage. PO-dzy had the minimum value and the others did not have significant differences.

P_{Nmax} of 11 oil peonies ranged from 5.950 to 13.954 μmol (CO_2) m^{-2} s^{-1}. A higher P_{Nmax} value indicates a greater photosynthetic potential of the corresponding oil peony. The descending order of P_{Nmax}, therefore of the photosynthetic potential, was PD-wbs > PO-dzy > PQ-yx > PQ-xy > PO-htp > PR-bk > PQ-bk > PR-djg > PR-lt > PQ-sn > PO-snj. PD-wbs had the biggest P_{Nmax}, and the P_{Nmax} of PO-dzy, PQ-yx, PQ-xy and PO-htp was significantly bigger than the others after them. while that of PQ-sn and PO-snj was significant smaller among 11 values. And the P_{Nmax} of the rest four oil peonies were converged.

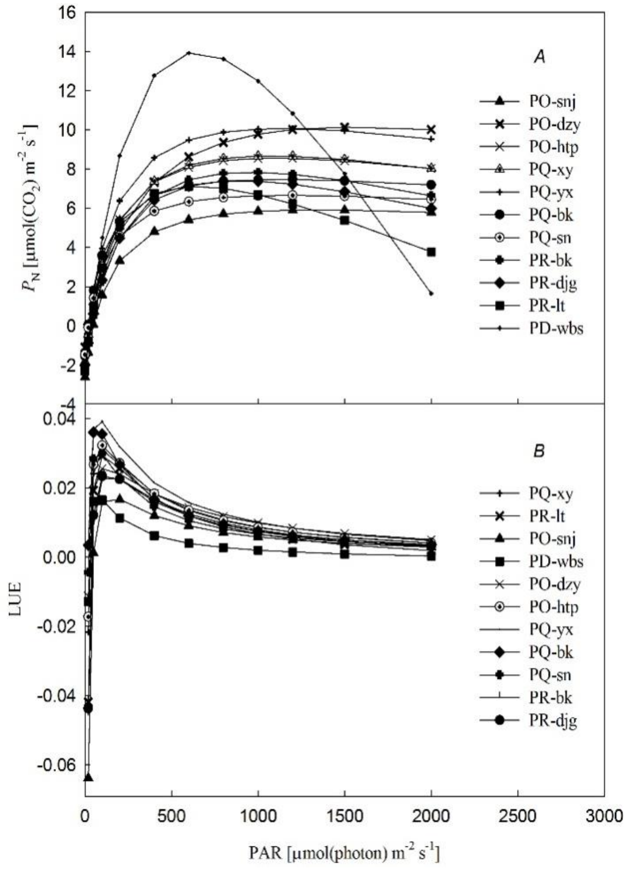

Fig. 4. Net photosynthetic rate (P_N)-PAR response curves (*A*) and LUE-PAR curves (*B*) for oil peonies from 11 provenances. Bars indicate standard errors (*n* = 5). PD-wbs, PO-dzy, PO-htp, PO-snj, PQ-bk , PQ-sn, PQ-xy, PQ-yx , PR-bk, PR-djg, and PR-lt denoted the eleven Chinese oil peony materials in this research, which indicate *Paeonia delavayi* from Wenbishan mountain in Yunnan, *Paeonia ostii* from Dazhuyuan area in Shaanxi, *Paeonia ostii* from Hetaoping area in Shaanxi, *Paeonia ostii* from Shennongjia mountain in Hubei, *Paeonia qiui* from Baokang county in Hubei, *Paeonia qiui* from Shangnan county in Shaanxi, *Paeonia qiui* from Xunyang county in Shaanxi, *Paeonia qiui* from Yunxi county in Hubei, *Paeonia rockii* from Baokang county in Hubei, *Paeonia rockii* from Dajiangou area in Shaanxi and *Paeonia rockii* from Lintao county in Gansu, respectively.

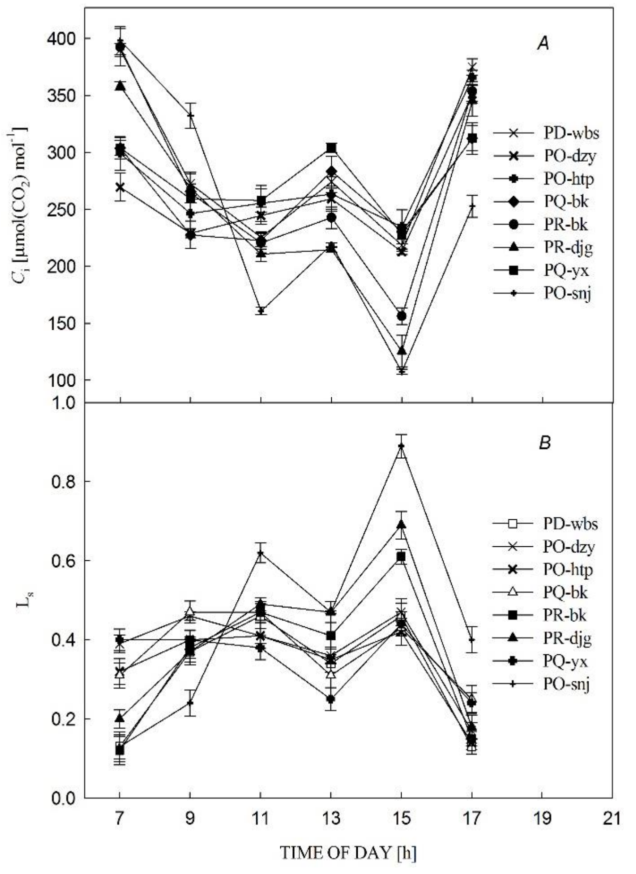

Fig. 6. Diurnal change curves of C_i (*A*) and L_s (*B*) of oil peonies from 8 provenances whose P_N daily change curves were bimodal type. Bars indicate standard errors (*n* = 6). PD-wbs, PO-dzy, PO-htp, PO-snj, PQ-bk , PQ-yx , PR-bk, and PR-djg denoted eight Chinese oil peony materials in this research, which indicate *Paeonia delavayi* from Wenbishan mountain in Yunnan, *Paeonia ostii* from Dazhuyuan area in Shaanxi, *Paeonia ostii* from Hetaoping area in Shaanxi, *Paeonia ostii* from Shennongjia mountain in Hubei, *Paeonia qiui* from Baokang county in Hubei, *Paeonia qiui* from Yunxi county in Hubei, *Paeonia rockii* from Baokang county in Hubei and *Paeonia rockii* from Dajiangou area in Shaanxi, respectively.

R_D is the general living cells respiration of the plants. Higher R_D reveals a larger self consumption. The R_D values of PO-snj and PD-wbs were 2.67 and 2.66 µmol m^{-2} s^{-1}respectively, which were larger than the others, illustrating larger self consumptions. In comparison, PO-dzy had the smallest R_D (1.13 µmol m^{-2} s^{-1}), thus the weakest respiration consumption.

Table 2 also indicated that LSP and LCP values of 11 oil peonies differed significantly in the experiment. A bigger LSP means a stronger sun-endurance. And a bigger LCP implies a stronger shade-endurance and a greater ability to adapt weak light. The range of LSP was 634.3–1557.0µmol(photon) m^{-2} s^{-1}. The ascending order of LSPwas PR-lt < PD-wbs < PR-djg < PR-bk < PQ-xy < PO-htp < PQ-yx < PQ-sn < PQ-bk < PO-snj < PO-dzy. It showed that PO-dzy, PO-snj and PQ-bk had higher LSP. LCP ranged from 18.3 to 49.4 µmol (photon) m^{-2} s^{-1}. The ascending order of LCPwas PQ-bk < PQ-yx < PQ-sn < PO-htp < PO-dzy <PQ-xy < PD-wbs < PR-lt < PR-djg < PR-bk < PO-snj. It showed that PQ-bk , PO-htp and PO-dzy had lower LCP. Therefore, PQ-bk, PQ-snj and PO-dzy could adapt wider irradiation range than the peonies from rest 8 provenances, which suggested larger photosynthetic capacity and intercepting radiation capacity (Andrade *et al.*, 2002; Li *et al.*, 2013). Small interception is an important limiting factor of the growth rate in spring as to winter oilseed rape (Diepenbrock, 2000). So it can be inferred that PQ-bk, PQ-snj and PO-dzy had higher growth rate and grew better than others.

Chl content: Chl is a main pigment absorbing light energy during photosynthesis (Maxwell & Johnson, 2000). Leaf chl content is a well known reference system when quantifying physiological reactions (Wittmann *et al.*, 2001). And chl content is also one of the most important factors in determining photosynthesis rate (Garty *et al.*, 2001) and dry matter production (Ghosh *et al.*, 2004). In addition, Chl *a* is a more direct factor involved in determining photosynthetic activity (Sesták, 1966). The contents of Chl *a*, Chl *b* and Chl *a+b* of PO-snj, PR-bk, PR-lt, PR-djg and PD-wbs and PQ-yx were significantly higher than the others (Fig. 5*A*). Chl *a+b* content decreased in this order: PO-snj > PR-bk > PR-lt > PR-djg > PD-wbs > PQ-sn > PQ-bk = PO-htp > PQ-xy > PQ-yx > PO-dzy. Shaded plants have a relatively higher content of Chl *b* than Chl *a* (Singh, 1994; Baig *et al.*, 2005), the Chl *a/b* ratio was higher in direct sun than in shade for Juglans reiga (Atanasova *et al.*, 2003). Fig. 5*B* showed that the Chl *a/b* ratio of PD-wbs was significantly higher and that of PQ-yx was significantly lower than the others, which were contrary to Chl *b/a* ratio. Therefore, the lowest and highest Chl *b/a* ratio in PD-wbs and PQ-yx respectively can preliminarily imply the minimum and the maximum shade-endurance of them among the oil peonies from 11 provenances.

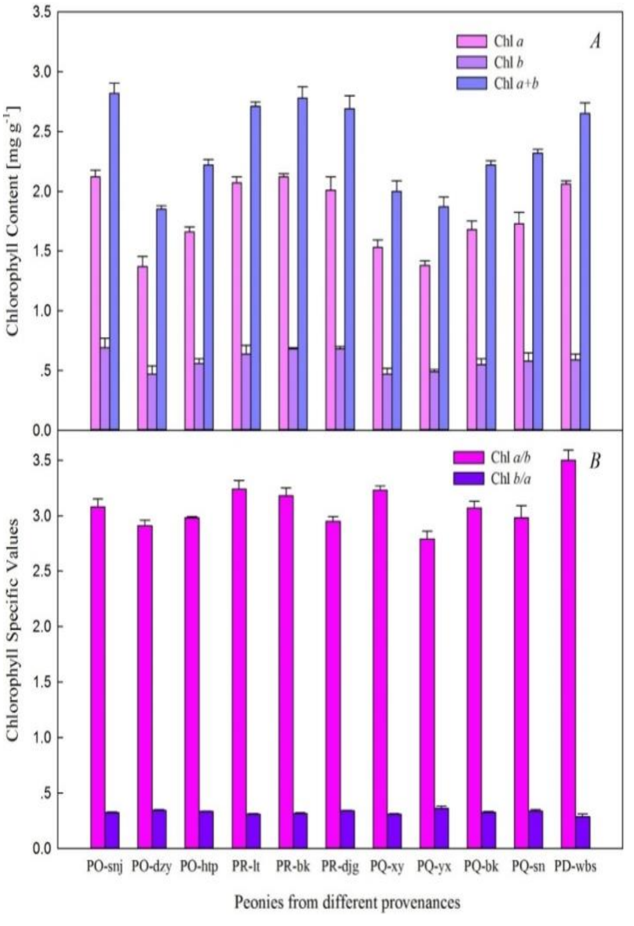

Fig. 5. Chlorophyll content (Chl *a*, Chl *b* and Chl *a+b*) (*A*) and specific values (Chl *a/b* and Chl *b/a*) (*B*) of oil peonies from 11 provenances. Bars indicate standard errors ($n = 6$). PD-wbs, PO-dzy, PO-htp, PO-snj, PQ-bk , PQ-sn, PQ-xy, PQ-yx , PR-bk, PR-djg, and PR-lt denoted the eleven Chinese oil peony materials in this research, which indicate *Paeonia delavayi* from Wenbishan mountain in Yunnan, *Paeonia ostii* from Dazhuyuan area in Shaanxi, *Paeonia ostii* from Hetaoping area in Shaanxi, *Paeonia ostii* from Shennongjia mountain in Hubei, *Paeonia qiui* from Baokang county in Hubei, *Paeonia qiui* from Shangnan county in Shaanxi, *Paeonia qiui* from Xunyang county in Shaanxi, *Paeonia qiui* from Yunxi county in Hubei, *Paeonia rockii* from Baokang county in Hubei, *Paeonia rockii* from Dajiangou area in Shaanxi and *Paeonia rockii* from Lintao county in Gansu, respectively.

Discussion

This study investigated the photosynthetic characteristics of four different oil peony species from eleven provenances and predicted the yield size through their photosynthetic characteristics. According to the order of diurnal average P_N values, the higher values in PR-bk, PR-lt, PR-htp and PD-wbs indicated that they had larger photosynthetic abilities. Meanwhile, *Paeonia rockii* and *Paeonia delavayi* had higher P_N values according to morning peak value order. Particularly theP_N Peak value of PR-lt and PR-bk were significantly higher than the other peonies. Since photosynthetic rate is a heritable characteristic (Branch & Jejr, 1984), the photosynthesis capacity of *Paeonia rockii* and P*aeonia delavayi* especially PR-lt, PR-bk and PD-wbs was stronger.

The g_s is an crucial factor representing stomatal aperture. Data showed that leafg_s correlated positively with P_N (Wang *et al.*, 2017). And there is a feedback loop between the substomatic cavities gap CO_2 concentration and g_s: when CO_2 concentration decreases, g_s increases. With more CO_2 absorbed through the boosting of leaf photosynthesis, C_i starts to increase. Then the increase of C_i regulates g_s to decrease in a feedback way (Xu, 2002). According to the experiment results, g_s values of the oil peonies from 7 origins (except for PO-snj, PO-dzy, PO-htp and PQ-yx) began to decrease at 7:00 h because RH decreased and VPD increased simultaneously, which finally resulted into a stronger water loss through the decrease of *E* and g_s. There is moisture on the surface of mesophyll cell walls becasuse water is continuously turning into vapor and becoming the moisture, which affects the air humidity of the surrounding environment. The opening degree of stomatal aperture is directly controlled by the air humidity (PAN, 2012???), and this phenomenon has adaptive significance on the cultivation of oil peonies. The oil peonies from these 7 origins have direct sensitive response to RH, hence they have a wider range of cultivation-geography. Since the g_s values of the oil peonies from the rest 4 origins were mainly regulated by C_i and were not sensitive to RH, they could only be cultivated in humid environment.

Data dependence analysis found that C_i has a negative correlation with the L_s for all oil peonies under the study. According to Farquhar (And & Sharkey, 1982), there are mainly two precipitating factors that lead to the decrease of photosynthetic rate: If P_N reduces with the decrease of C_i and the increase of L_s, then the main cause of P_N reduction is the decrease of g_s. However, if P_N reduces with the increase of C_i, then the main limiting factor of photosynthesis can't be stomata factor, which is the weaker photosynthetic ability of mesophyll. In other words, the decrease of P_N was either due to the stomata limitation or the weakened photosynthetic ability of mesophyll, both of which can be affected by environmental conditions (Cai *et al.*, 2012). This study demonstrated that the relationship between the reduction of P_N and the changing trend of C_i and L_s differs among species. Among the 8 peonies whose P_N diurnal curves were bimodal type, *Paeonia rockii* (PR-bk, PR-djg) and *Paeonia delavayi* (PD-wbs) had a C_i decrease and a L_s increase (Fig. 6*A*,*B*) with the decline of P_N from 9:00 h to 11:00 h (Fig. 3), which indicates that the P_N reduction was caused by the decrease of g_s during this time period; *Paeonia rockii* (PR-bk, PR-djg) and *Paeonia delavayi* (PD-wbs) had a C_i increase with P_N declining from 11:00 h to 13:00 h (Fig. 3), which indicates the P_N reduction was caused by weakened photosynthetic ability of mesophyll during this time period. Similarly it proves that the decline of P_N in *Paeonia ostii* (PO-dzy, PO-htp) and *Paeonia qiui* (PQ-bk, PQ-yx) was caused by weakened photosynthetic ability of mesophyll between 9:00 h to 13:00 h. Thus the mesophyll photosynthetic ability of *Paeonia rockii* and *Paeonia delavayi* began to reduce at 11:00 h while that of *Paeonia ostii* and *Paeonia qiui* began to reduce at 9:00 h. It showed that the mesophyll of *Paeonia rockii* and *Paeonia delavayi* have larger photosynthetic ability.

Table 2. Paremeters of PN-PAR response curves for oil peonies from 11 provenances measured in April, 2015.

Peonies	AQY [mol mol^{-1}]	P_{Nmax} [μmol(CO_2) m^{-2} s^{-1}]	R_D [μmol m^{-2} s^{-1}]	LCP [μmol m^{-2} s^{-1}]	LSP [μmol m^{-2} s^{-1}]
PO-snj	0.0736 ± 0.00928^{bc}	5.950 ± 0.332^{g}	2.67 ± 0.21^{a}	49.4 ± 0.8^{a}	1349.5 ± 6.1^{b}
PO-dzy	0.0487 ± 0.00891^{d}	10.160 ± 0.369^{b}	1.13 ± 0.12^{g}	25.8 ± 0.5^{g}	1557.0 ± 6.4^{a}
PO-htp	0.0813 ± 0.00913^{abc}	8.565 ± 0.311^{c}	1.78 ± 0.10^{de}	25.3 ± 0.3^{g}	1099.0 ± 6.2^{e}
PR-lt	0.0885 ± 0.01130^{ab}	7.055 ± 0.297^{ef}	2.42 ± 0.18^{ab}	33.0 ± 0.1^{d}	634.3 ± 2.9^{i}
PR-bk	0.0656 ± 0.01137^{cd}	7.837±0.402^{d}	2.22 ± 0.22^{bc}	39.7 ±1.0^{b}	957.7 ± 4.7g
PR-djg	0.0657 ± 0.00951^{cd}	7.409 ± 0.385^{de}	2.05 ± 0.18^{cd}	37.2 ± 0.3^{c}	888.0 ± 4.7^{h}
PQ-xy	0.0776 ± 0.01094^{abc}	8.642 ± 0.484^{c}	1.89 ± 0.18^{Ed}	27.0 ± 0.3^{f}	1077.6 ± 5.6^{f}
PQ-yx	0.0854 ± 0.01098^{ab}	10.021 ± 0.501^{b}	1.45 ± 0.06^{f}	19.2 ± 0.3^{i}	1138.8 ± 5.9^{d}
PQ-bk	0.0959 ± 0.00749^{a}	7.577 ± 0.318^{de}	1.55 ± 0.14^{ef}	18.3 ± 0.2^{j}	1346.0 ± 6.0^{b}
PQ-sn	0.0853 ± 0.00956^{ab}	6.631 ± 0.302^{f}	1.53 ± 0.12^{ef}	21.4 ± 0.7^{h}	1189.6 ± 7.3^{c}
PD-wbs	0.0833 ± 0.00956^{abc}	13.954 ± 0.582^{a}	2.66 ± 0.20^{a}	31.4 ± 0.6^{e}	642.4 ± 3.8^{i}

Values for apparent quantum yield (AQY), light-saturated net photosynthetic rate (P_{Nmax}), dark respiratory rate (R_D), light saturation point (LSP) and light compensation point (LCP) are mean ± SD (n = 5). Different *samll letters* following values indicate significant difference according to LSD test (p<0.05).
PD-wbs, PO-dzy, PO-htp, PO-snj, PQ-bk, PQ-sn, PQ-xy, PQ-yx , PR-bk, PR-djg, and PR-lt denoted the eleven Chinese oil peony materials in this research, which indicate *Paeonia delavayi* from Wenbishan mountain in Yunnan, *Paeonia ostii* from Dazhuyuan area in Shaanxi, *Paeonia ostii* from Hetaoping area in Shaanxi, *Paeonia ostii* from Shennongjia mountain in Hubei, *Paeonia qiui* from Baokang county in Hubei, *Paeonia qiui* from Shangnan county in Shaanxi, *Paeonia qiui* from Xunyang county in Shaanxi, *Paeonia qiui* from Yunxi county in Hubei, *Paeonia rockii* from Baokang county in Hubei, *Paeonia rockii* from Dajiangou area in Shaanxi and *Paeonia rockii* from Lintao county in Gansu, respectively.

Due to solar radiation intensity rising, T_a rose and RH decreased at noon, which then lead to the enhance of leaf VPD. The enhanced VPD strengthened transpiration, which resulted in the quick decrease of soil water potential and a temporary water deficit of leaf. Then the opening of stomata aperture weakened and stomatal resistance increased, which hindered the diffusion of CO_2 into mesophyll tissue. Hence, CO_2 supply was reduced and photosynthetic rate decreased rapidly. It explained the “midday depression” appeared in oil peonies photosynthesis with bimodal daily P_N progress.

Photosynthetic quantum efficiency can be described as the number of CO_2 molecular assimilated and fixed or the number of O_2 molecular released by one photon absorbed by photosynthetic apparatus. AQY can be therefore evaluated if the reflection and transmission losses are not taken into account (Xu, 2002). It is a good indicator of light usage efficiency of photosynthetic apparatus (Farquhar & Sharkey, 1982), where a higher AQY value indicates a higher efficiency of transforming light energy of leaves. The order of average AQY of four wild oil peony species was: *Paeonia qiui* (0.0861) ＞*Paeonia dalavayi* (0.0833) ＞*Paeonia rockii* (0.0733) ＞*Paeonia ostii* (0.0679), which showed that the radiation utility capacity of *Paeonia qiui* was the strongest while that of *Paeonia ostii* was the weakest. Furthermore, the experiment results showed that the PQ-bk has the maximum AQY and the values of PQ-bk, PR-lt, PQ-yx and PQ-sn were significantly higher (p<0.05) than the others, which indicated that these four origins have larger radiation use capacity. According to Fig. 5*A*, PO-snj had the maximum chlorophyll content. It demonstrated that PO-snj had more advantages in maintaining light energy than the other peonies (Mao *et al.*, 2007). However, PR-bk, PR-lt and PD-wbs have higher Chl *a*+*b* content in fact, which verified that they have higher photosynthetic rates (Garty *et al.*, 2001).

Photosynthetic parameters and chlorophyll content were positively correlated with seed yield of soybean (Betzelberger *et al.*, 2010), so it would be parallel to oil peony. Since PR-bk, PR-lt and PD-wbs have both higher photosynthesis rate and chlorophyll content, hereby we conclude they could have larger seed outputs if artificial cultivated widely. In conclusion, by taking daily maximum P_N, Peak P_N, AQY and Chlorophyll content into consideration, we confirmed *Paeonia rockii* and *Paeonia delavayi* especially PR-lt, PR-bk, and PD-wbs have larger capacity of photosynthesis as well as photosynthesizing organic matters. Therefore, we can predict these two oil peony species from three provenances would have a larger seed production and they could be introduced and cultivated widely in China as superior provenances.

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