CO_2 assimilation and chlorophyll fluorescence in green *versus* red *Berberis thunbergii* leaves measured with different quality irradiation

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Abstract

Photosynthesis, photorespiration, and chlorophyll (Chl) fluorescence in green and red *Berberis thunbergii* leaves were studied with two different measuring radiations, red (RR) and "white" (WR). The photosynthetic and photorespiration rates responded differently to the different radiation qualities, which indicate that the carboxylase and oxygenase activities of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO) were affected. Differences in photosynthetic rate between the two color leaves were less under RR than under WR. However, this reduced difference in photosynthetic rate was not correlated with the stomatal response to the measuring radiation qualities. Compared with the WR, the RR reduced the differences in dark-adapted minimum and maximum fluorescence, steady-state fluorescence, light-adapted maximum fluorescence, and actual photochemical efficiency (Φ_{PS2}) of photosystem 2 (PS2), but enlarged the difference in non-photochemical quenching between the two color leaves. Differences in both maximum quantum yield of PS2 and ratio of Φ_{PS2} to quantum yield of CO_2 fixation between the two color leaves were similar under the two measuring radiations. To exclude disturbance of radiation attenuation caused by anthocyanins, it is better to use RR to compare the photosynthesis and Chl fluorescence in green *versus* red leaves.

Additional key words: anthocyanins; intercellular CO_2 concentration; irradiance; leaf absorbance spectra; photorespiration; photosynthesis; quenching; quantum efficiency; respiration rate; ribulose-1,5-bisphosphate carboxylase/oxygenase; stomatal conductance.

Introduction

The responses of photosynthesis to different quality radiation are different, mainly because these radiations have different quantum efficiency of CO_2 fixation and absorption at chloroplasts (Clark and Lister 1975, Evans 1987). Contrasted with green leaves, due to disturbance of anthocyanins to photon absorption (Pietrini and Massacci 1998, Gamon and Surfus 1999, Feild *et al*. 2001, Sims and Gamon 2002, Close and Beadle 2005), the responses of photosynthesis and chlorophyll (Chl) fluorescence to different quality radiation might be more complex in red leaves. For instance, high anthocyanin content in maize leaves could cause a flaw in calculation of the photon absorption by chloroplasts, which could result in a higher ratio of Φ_{PS2}/Φ_{CO2} (Pietrini and Massacci 1998).

Since different quality radiation treatments could induce different responses of photosynthesis and Chl fluorescence (Sun *et al*. 1998, Nishio 2000, Feild *et al*. 2001, Frak *et al*. 2002, Matsuda *et al*. 2004, Nesterenko *et al*. 2006), it is reasonable to speculate that measuring photosynthesis and Chl fluorescence with different quality radiation might cause different results too, which would further puzzle the comparison of these parameters between leaves of different color. However, in comparison of photosynthesis and Chl fluorescence between red and green leaves, little attention has been paid to the influences of different measuring radiations on these characteristics. Two kinds of radiation are mainly used,

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Abbreviations: C_i − intercellular CO_2 concentration; F_M and F_0 − maximum and minimal fluorescence in dark-adapted state; F_V/F_M − maximum quantum yield of PS2; F_M' and F_S − maximum and steady-state fluorescence in radiation-adapted state; g_s − stomatal conductance; NPQ − non-photochemical quenching; PS − photosystem; P_N − net photosynthetic rate; P_r − photorespiration rate; R_D – respiration rate; Φ_{CO2} − quantum efficiency of CO_2 fixation; Φ_{PS2} − actual PS2 efficiency under irradiance.
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"white" (WR) and red-enriched (RR). In contrast with Chls, more yellow-green radiation is absorbed by anthocyanins (Gamon and Surfus 1999, Neill and Gould 1999, Merzlyak and Chivkunova 2000, Gitelson *et al*. 2001). Therefore, under measuring WR compared with RR, the existence of anthocyanins would interfere with comparison of photosynthesis and Chl fluorescence between red and green leaves. Thus a question occurs, is the WR not suitable for the comparing study? If the photosynthesis and Chl fluorescence in red and green leaves are measured with WR, what difference will be caused in contrast to that measured with RR?

We compared photosynthesis and Chl fluorescence in red and green leaves measured with WR and RR in order to have a deeper insight into the effect of different measuring radiation quality on the comparison in photosynthetic characteristics between red and green leaves.

Materials and methods

Plants: *Berberis thunbergii* plants were grown in the field. Nutrients and water were supplied sufficiently throughout to avoid potential nutrient and drought stresses. Leaves of the *B. thunbergii* exposed to sunlight directly produce lots of anthocyanins and become red, whereas leaves shaded by canopy generally produce fewer or no anthocyanins and look green. The two color leaves were used in this study. Five red and five green leaves from five plants were used in all measurements.

Spectrum measurements were performed with a portable *Unispec SC* spectrometer combined with a bifurcated or two straight-fiber optics (*PP Systems*, USA). The instrument employs a solid-state silicon array detector (*MMS-1*, *300-1100 NM*, NIR enhanced with visible blaze; *Hellma Cells*, Forest Hills, NY, USA). The *Unispec* has a nominal spectral range of 300−1 100 nm (average band-to-band spacing 3.3 nm). Thus, for each measurement, the spectrometer program automatically collects 256 data points covering the entire spectral range. Leaf reflectance was measured with a bifurcated fiber optic cable and a leaf clip (*UN1410* and *UN1501*, *PP Systems*, USA). The leaf clip held the fiber at a 60° angle to the adaxial leaf surface (30° from normal). Leaf irradiation was provided through one side of the bifurcated fiber from a halogen lamp in the spectrometer. To calculate reflectance, leaf spectral radiance was divided by the radiance of a 99 % reflective white reference standard (*Spectralon*, *Labsphere*, North Dutton, NH, USA, for more details see Gamon and Surfus 1999). Leaf transmittance was measured with two straight-fiber optics and a custom-made device. One straight-fiber optic was used to irradiate from the leaf adaxial side, and the other was used as a detector from the leaf abaxial side. The custom-made device could make the two straight-fiber tips both hold a 60° angle to each leaf surface respectively front to front. The fiber optic in the leaf clip exposes a much smaller area (1−2 mm diameter) of the leaf to light than does the integrating sphere (14-mm diameter), which will cause some differences in the absolute values of reflectance between the two measurement systems. However, these differences were proportional across the spectrum, and the spectral indices were highly correlated (Sims and Gamon 2002): absorptance = 1 − reflectance − transmittance.

Gas exchange: Net photosynthetic rate (P_N), photorespiration rate (P_r), and respiration rate (R_D) were analyzed with a potable *CIRAS-2* photosynthesis system (*PP Systems*, UK). The CO_2 concentration, air humidity, photon flux density (PFD), and leaf temperature were controlled *via* an automatic control device of the *CIRAS-2*. Two radiation sources were used, one was LED radiation and the other was tungsten halogen lamp. The CO_2 concentration, air humidity, and leaf temperature were maintained at 360 μmol mol^{-1}, 800 Pa, and 25 ºC, respectively. The PFDs were set in the order of 1000, 800, 600, 400, 200, 100, 50, and 30 μmol m^{-2} s^{-1} to obtain P_N-PFD response curve; leaves were adapted to radiation for 3 min under each PFD. P_N measured under two different O_2 concentrations (21 and 2 %) was used to calculate P_r. The quantum efficiency of CO_2 fixation (Φ_{CO2}) was determined by dividing P_N (corrected by R_D) by actual absorbed PFD.

Chl fluorescence was measured using a portable *FMS-2* or *Handy-PEA* fluorometer (*Hansatech*, UK). Firstly, the plant leaves was adapted to the radiation (about 1 000 μmol m^{-2} s^{-1}) for 1 h. Then, the leaves were used to measure the Chl fluorescence parameters under different PFDs.

When using *FMS-2*, the measuring radiation was provided by pulsed amber LED source, whereas the "actinic light" and saturating irradiance were both provided by operating a halogen lamp. At each PFD, the leaves were firstly irradiance-adapted for 200 s under the "actinic light" offered by *FMS-2*, then the steady-state fluorescence (F_S) was measured with the measuring radiation. After that, a pulse of saturating irradiance (about 4 000 μmol m^{-2} s^{-1} PFD) was switched on to obtain the irradiance-adapted maximum fluorescence (F_M'). After finishing the measurement of irradiance-adapted parameters, the leaves were dark adapted with leaf clips (*Hansatech*, UK) for 30 min, then the measuring radiation was switched on to determine the dark-adapted minimum fluorescence (F_0), following a pulse of saturating radiation applied to obtain the dark-adapted maximal fluorescence (F_M).

When using *Handy-PEA*, an array of three LEDs was used as radiation source. Fluorescence was detected using a *PIN*-photodiode after passing through a long-pass filter.

All the fluorescence transients were recorded in a time span from 10 μs to 1 s with a data acquisition rate of 10 μs for the first 300 μs. At each PFD, the leaves were also firstly irradiance-adapted for 200 s under the radiation offered by *Handy-PEA*. Then, the leaf was exposed to a saturating irradiance (about 3 000 μmol m^{-2} s^{-1} PFD) for 1 s to obtain the irradiance-adapted Chl *a* fluorescence transient. After that, the leaves were also dark adapted with the leaf clips for 30 min, then the dark-adapted Chl *a* fluorescence transients were measured. The peak fluorescence of the light- and dark-adapted fluorescence transient is used as F_M' and F_M. An algorithm is used to determine the line of best fit through the initial data points (4−16) recorded at the onset of irradiation. This line of best fit is extrapolated to time zero (the start of irradiation) to determine F_0. The radiation-adapted F_0 is approximated as F_S (Susplugas *et al*. 2000).

Maximum quantum yield of photosystem 2 (F_V/F_M) and the actual PS2 efficiency under irradiance (Φ_{PS2}) were calculated according to Genty *et al*. (1989): $F_V/F_M = (F_M - F_0)/F_M$, $\Phi_{PS2} = (F_M' - F_S)/F_M'$. Non-photochemical quenching (NPQ) was calculated according to Demmig-Adams and Adams (1996): $NPQ = F_M/F_M' - 1$.

Results

Spectra: The emission wavelengths of the *CIRAS-2* WR and the *FMS-2* WR were almost identical in the range of visible radiation (400−700 nm), and both maximum emission wavelengths were within the range of 590−700 nm (Fig. 1). However, the emission wavelengths of the *CIRAS-2* LEDs and the *Handy-PEA* LEDs were different. The emission wavelength peak of *CIRAS-2* LED light was 640 nm with a small peak in the blue radiation at 446 nm, whereas the emission wavelength peak of *Handy-PEA* RR was at 660 nm. Yorio *et al*. (2001) reported that photosynthesis was not enhanced by supplement of blue radiation in leaves of lettuce under red-LED radiation. Furthermore, due to carotenoid and flavonoid absorption, blue radiation has a lower quantum efficiency of carbon fixation in the visible region (Clark and Lister 1975, Evans 1987, Sun *et al*. 1998). Therefore, in studying photosynthesis the LED radiation of *CIRAS-2* could be regarded as a RR source.

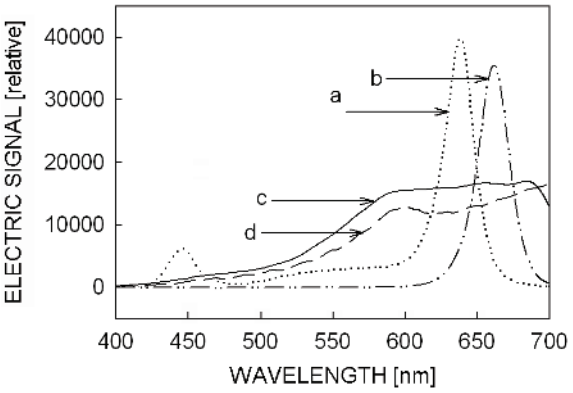

Fig. 1. Spectra of different radiation sources (*a*: *CIRAS-2* red radiation; *b*: *Handy-PEA* red radiation; *c*: *CIRAS-2* "white light"; *d*: *FMS-2* "white light"). Means (n = 5).

The absorptance spectra of red and green leaves were obviously different in the range of visible radiation: the green leaves had an absorbance trough in the green radiation range (Fig. 2).

CO_2 assimilation: The red *B. thunbergii* leaves were exposed to sunlight directly, whereas the green leaves were shaded by the canopy. P_N was lower under PFD below 200 μmol m^{-2} s^{-1} but higher under PFD above 200 μmol m^{-2} s^{-1} in the red leaves than in the green leaves (Fig. 3*A,E*). This demonstrates that the red leaves had characteristics of sun-growing plants, whereas the green leaves had characteristics of shade-growing plants. However, the differences in P_N between the two color leaves were smaller under RR than under WR (Fig. 4*A*). P_r was higher in the red leaves than in the green leaves in both the RR and WR (Fig. 3*B,F*). However, the differences in P_r between the two color leaves were similar under the two measuring radiations (Fig. 4*B*). In addition, the stomatal conductance (g_s) was higher in the red leaves than that in the green leaves under the both RR and WR (Fig. 3*C,G*). But the difference in g_s between the red and green leaves was more obvious under RR than under WR (Fig. 4*C*). The intercellular CO_2 concentration (C_i) was also different between the green and red leaves under the two measuring radiations (Fig. 3*D,H*). The distinctions in C_i were more pronounced under RR than under WR (Fig. 4*D*). The R_D was identical in the two color leaves under the two measuring radiations (Fig. 5).

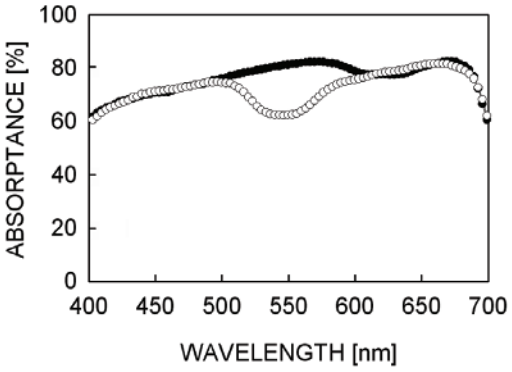

Fig. 2. Absorptance spectra of red (●) and green (○) *Berberis thunbergii* leaves under 1 000 μmol m^{-2} s^{-1} PFD. Means (n = 5).

Chl fluorescence: After 30 min dark adaptation, when measured with RR, there were no differences in F_0 and F_M between the two color leaves, whereas when measured with WR, both F_0 and F_M were lower in the red leaves than in the green leaves (Fig. 6*A,B,D,E*). Therefore, the differences in F_0 and F_M between the green and red leaves were more obvious under WR than under RR (Fig. 6*D,E*). Nevertheless, there were no differences in F_V/F_M between the green and red leaves under the two measuring radiations (Fig. 6*C,F*).

F_S and F_M' were lower, whereas Φ_{PS2} and NPQ were higher in the red leaves than in the green leaves under both RR and WR (Fig. 7). However, the differences in F_S, F_M', Φ_{PS2}, and NPQ between the green and red leaves were significantly different under the two measuring radiations (Fig. 8). The differences in F_S, F_M', and Φ_{PS2} were more pronounced under WR than RR (Fig. 8*A,B,D*), whereas the difference in NPQ was more obvious under RR (Fig. 8*C*).

Ratio of Φ_{PS2}/Φ_{CO2}: Though it was higher under WR than RR, the ratio of Φ_{PS2}/Φ_{CO2} was similar in the two color leaves under the two measuring radiations (Fig. 9).

Discussion

Photosynthesis: In the red *B. thunbergii* leaves, the photon-saturated P_r was higher under RR whereas the R_D and photon-saturated P_N were identical under the two measuring radiations (Figs. 3 and 5), namely the total CO_2 assimilation rate was lower under WR. In contrast with RR, under WR anthocyanins absorbed yellow-green radiation (Fig. 2) and reduced the total absorbed radiation at chloroplast as a radiation filter, but in no way could this change the rate of total CO_2 assimilation once the irradiance was saturating. Therefore, PFD at chloroplast did not limit the lower photon-saturated P_N under WR. Several studies showed that the RuBPCO activities changed when plants were grown under different radiation qualities (Eskins *et al*. 1991, Matsuda *et al*. 2004). Poskuta (1968) exhibited similar P_N and R_D with different P_r under different measuring radiation qualities. We also observed that the responses of P_N and P_r to the two measuring radiation qualities were different (Figs. 3 and 4), suggesting that the carboxylase and oxygenase of RuBPCO were affected by the measuring radiation quality. Therefore, the changed RuBPCO activities might account for the higher total CO_2 assimilation under RR in the red leaves.

Unlike in red leaves, in the green leaves the P_N and P_r were both lower under the WR than RR (Fig. 3), which demonstrated that the different measuring radiation qualities had different effects on the RuBPCO in the different color leaves. In addition, though RR enlarged the difference in g_s between the two color leaves, it decreased the difference in P_N with an enlarged difference in C_i between the two color leaves (Fig. 4), which implied that the difference in P_N between the two color leaves under the two measuring radiations was not correlated with the stomatal factor but with non-stomatal factors.

Chl fluorescence signal is positively correlated with the exciting irradiance. The similar F_0 and F_M in the red and green leaves under RR but lower F_0 and F_M in the red leaves under WR (Fig. 6) demonstrated that the absorption was relatively lower in chloroplasts of the red leaves under WR. This might be attributed to the attenuation of radiation by anthocyanins. Interestingly, no difference in F_V/F_M was observed between the red and the green leaves both under RR and WR indicating that the F_0 and F_M were affected proportionally by the attenuation of radiation.

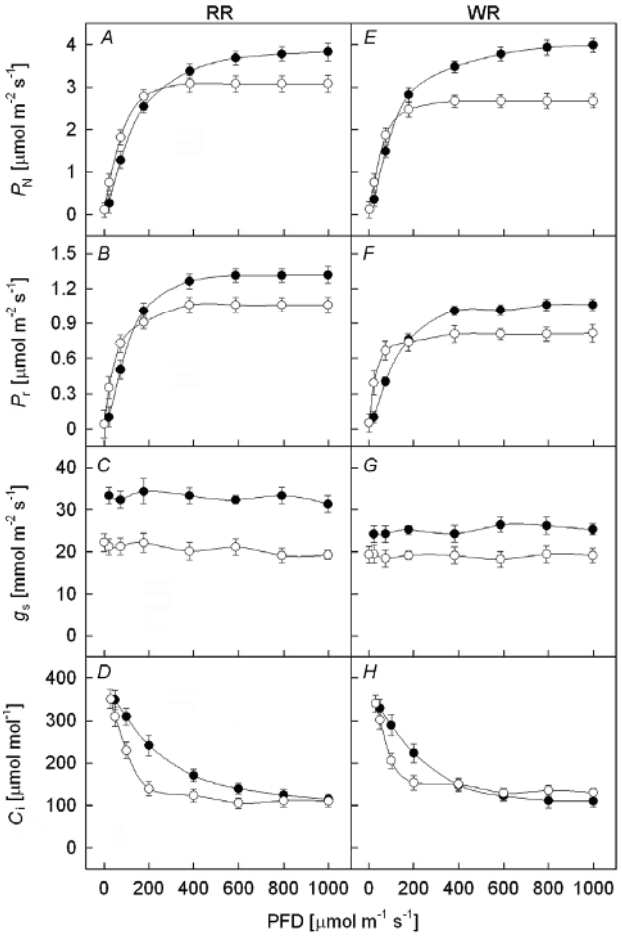

Fig. 3. Responses of net photosynthetic rate (P_N), photorespiration rate (P_r), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) to different red, RR (*A*−*D*) or "white", WR (*E*−*H*) measuring radiation photon flux density (PFD) in red (●) and green (○) *Berberis thunbergii* leaves. Means ± SD (n = 5).

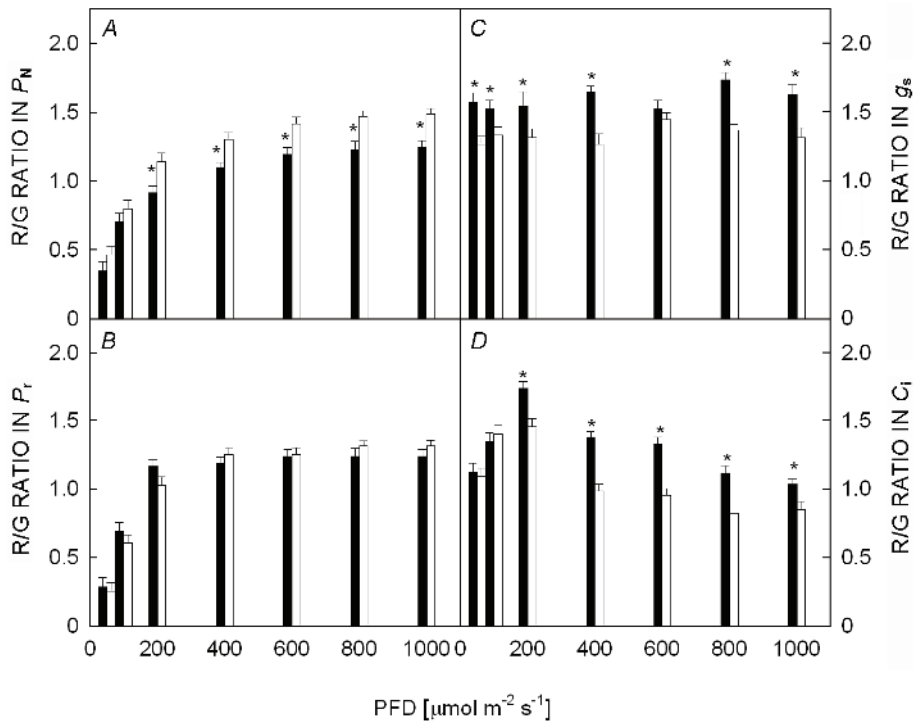

Fig. 4. Ratio of *Berberis thunbergii* red to green leaves (R/G) in (*A*) net photosynthetic rate (P_N), (*B*) photorespiration rate (P_r), (*C*) stomatal conductance (g_s), and (*D*) intercellular CO_2 concentration (C_i) under different red, RR (■) and "white", WR (□) measuring radiation PFD. Means ± SD (n = 5). $^*p$<0.05, F-test.

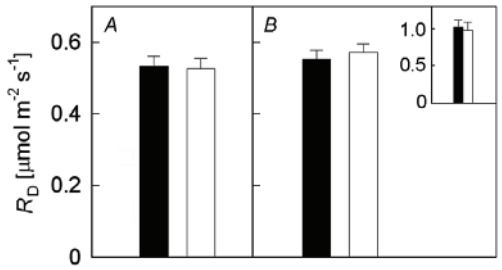

Fig. 5. The respiratory rate in the dark (R_D) in *Berberis thunbergii* red (■) and green (□) leaves under red, RR (*A*) or "white", WR (*B*) measuring radiation, and the ratio of red to green leaves (R/G) in R_D under red, RR (■) or "white", WR (□) measuring radiations (*insert figures* in Fig. 5*B*). Means ± SD (n = 5).

F_0 and F_M should be measured in fully dark-adapted leaves, namely no photochemical reaction is activated at this time, whereas F_S and F_M' are measured in the irradiation-adapted leaves in which the photochemical reactions have been fully activated. In leaves, the absorbed photons are consumed by three ways: photochemical reactions, heat dissipation, and fluorescence (Krause and Weis 1991). These three processes compete with each other. We found that the photochemical reactions such as P_N and P_r were higher in the red than in the green leaves (Fig. 3), therefore, perhaps the greater partition of photon energy to photochemical reaction resulted in the lower F_S and F_M' of the red leaves (Fig. 7).

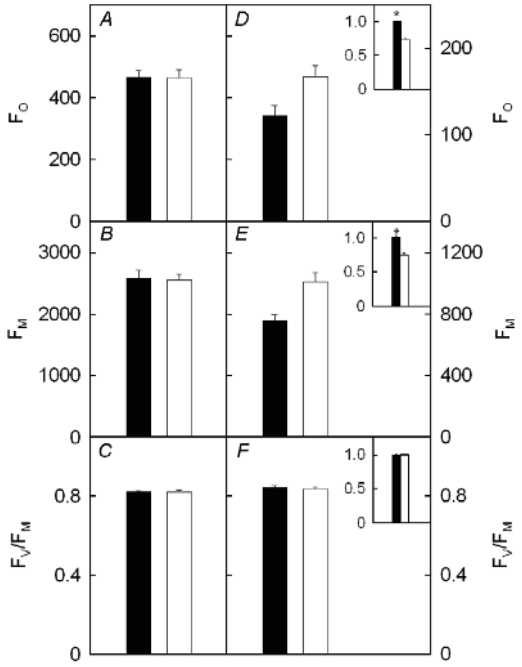

Fig. 6. The dark-adapted minimum fluorescence (F_0), maximum fluorescence (F_M), and the maximum quantum yield of photosystem 2 (F_V/F_M) in *Berberis thunbergii* red (■) and green (□) leaves under red, RR (*A*−*C*) or "white", WR (*D*−*F*) measuring radiation, and the ratio of red to green leaves (R/G) in F_0, F_M, and F_V/F_M under RR (■) or WR (□) (*insert figures* in Fig. 6*D*−*F*). Means ± SD (n = 5). $^*p$<0.05, F-test.

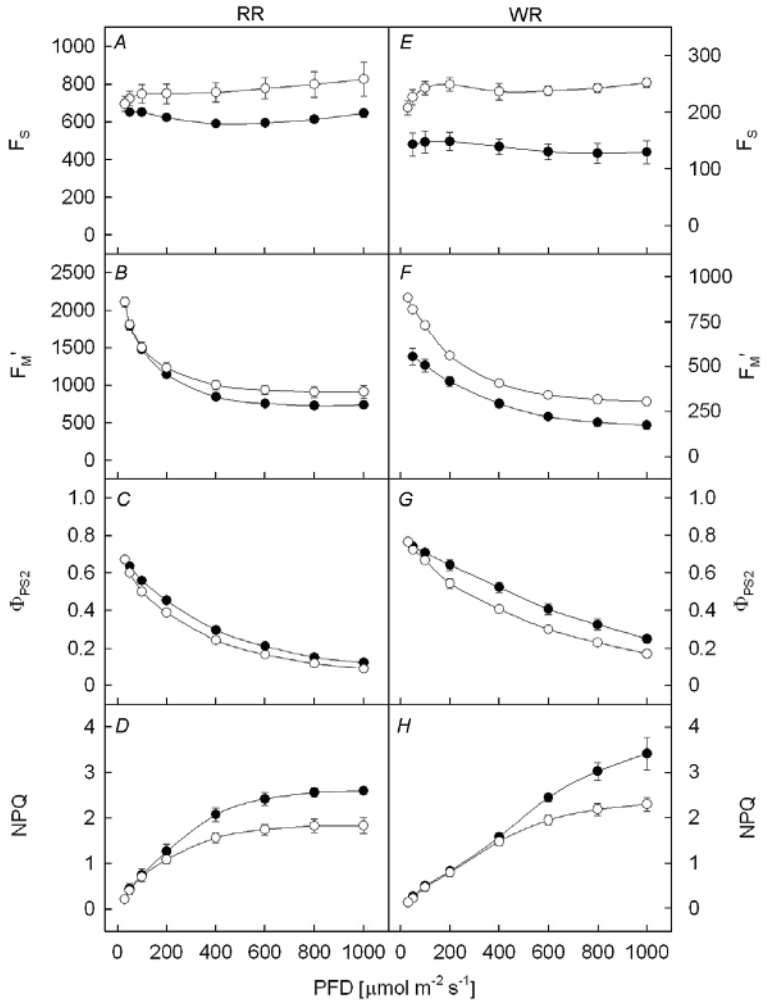

Fig. 7. Responses of steady-state fluorescence (F_S), irradiation-adapted maximum fluorescence (F_M'), the actual photochemical efficiency of photosystem 2 (Φ_{PS2}), and non-photochemical quenching (NPQ) to different PFD supplied with red, RR (*A*−*D*) and "white", WR (*E*−*H*) measuring radiations in red (●) and green (○) *Berberis thunbergii* leaves. Means ± SD (n = 5).

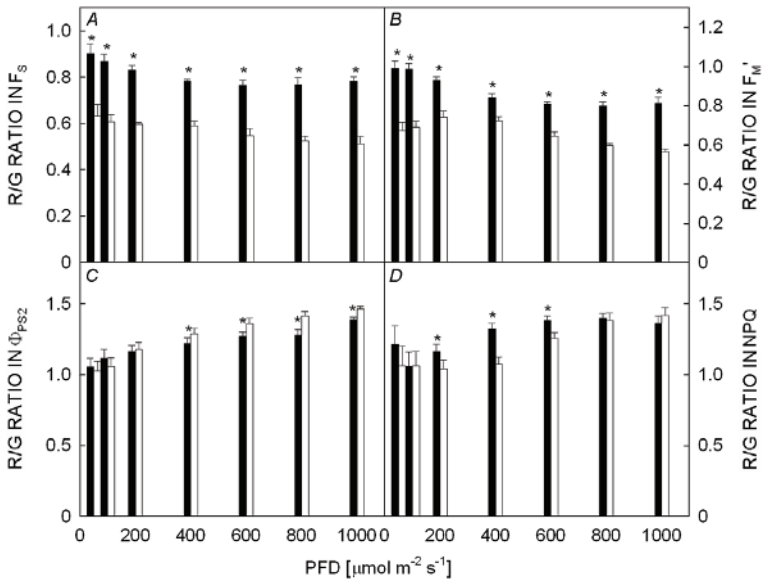

Fig. 8. Ratio of *Berberis thunbergii* red leaves to green leaves (R/G) in (*A*) steady-state fluorescence (F_S), (*B*) irradiance-adapted maximum fluorescence (F_M'), (*C*) actual photochemical efficiency of photosystem 2 (Φ_{PS2}), and (*D*) non-photochemical quenching (NPQ) under different red, RR (■) and "white", WR (□) measuring radiation PFD. Means ± SD (n = 5). $^*p$<0.05, F-test.

In the red leaves, since radiation attenuation by anthocyanins affected the F_0 and F_M proportionally and did not affect the F_V/F_M under WR (Fig. 6), it is reasonable to suppose that the F_S and F_M' should be affected proportionally by the anthocyanins. Then differences in Φ_{PS2} and NPQ between the two color leaves should be also

similar under the two measuring radiations. However, under WR the differences in F_S, F_M', and Φ_{PS2} were enlarged but difference in NPQ was reduced between the two color leaves (Figs. 7 and 8) demonstrating that the anthocyanins did not affect the F_S and F_M' proportionally. Is this correlated with the different photochemical state of leaves? Is the activation of photochemical reaction or other mechanisms involved? Further studies are needed to illuminate this.

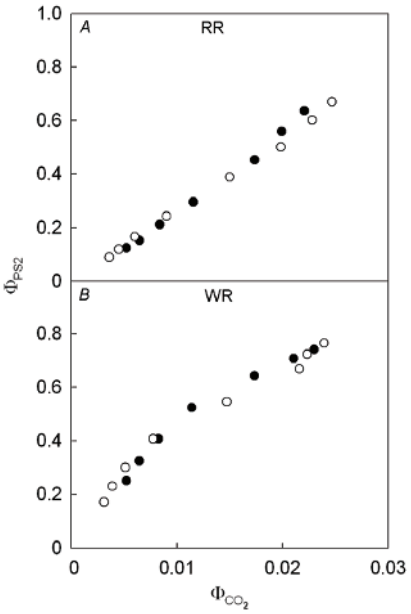

Fig. 9. The relationship between actual photochemical efficiency of photosystem 2 (Φ_{PS2}) and quantum efficiency of CO_2 fixation (Φ_{CO2}) in *Berberis thunbergii* red (●) and green (○) leaves under different red, RR (*A*) or "white", WR (*B*) measuring radiation PFDs at 360 μmol mol^{-1} CO_2.

Ratio of Φ_{PS2}/Φ_{CO2}: Pietrini and Massacci (1998) argued that high anthocyanin content could cause a flaw in calculation of photon absorbance by the chloroplasts, resulting in higher Φ_{PS2}/Φ_{CO2}. But they did not show the measuring radiation quality they used. If WR was used, no doubt, the photon absorbance by chloroplast pigments would be overestimated in high anthocyanin content leaves due to the absorption of yellow-green radiation. However, under RR the ratio Φ_{PS2}/Φ_{CO2} will not be influenced by the photon absorption characteristics of anthocyanins. Our results showed that Φ_{PS2}/Φ_{CO2} of the green and red leaves was almost identical under RR and WR (Fig. 9), which demonstrated that under WR the absorption of photons by anthocyanins not only affected the calculation of the absorption at the chloroplast, but also affected the calculation of the Φ_{PS2}. The absorption of yellow-green radiation by anthocyanins could result in an overestimation of absorbance by chloroplast pigments, why could not it result in an overestimation of Φ_{PS2}? Our results showed that the anthocyanins did enlarge the difference in Φ_{PS2} between the two color leaves under WR in contrast to RR (Fig. 8). Certainly, the different Φ_{PS2}/Φ_{CO2} in the two measuring radiations was also partly attributed to the different instruments in addition to the different radiation quality, but the difference in the instruments did not affect the comparison between the two color leaves.

In conclusion, the measuring radiation qualities affected photosynthesis, photorespiration, and Chl fluorescence in the green leaves differently, and the radiation attenuation by anthocyanins complicated these differences. It is better to use RR to compare photosynthetic characteristics in green *versus* red leaves to exclude the disturbance of anthocyanins.

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