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Sensitivity of wild and domesticated *Rhododendron chrysanthum* to different light regime (UVA, UVB, and PAR)

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Abstract

Effects of UV radiation on photosynthetic capacity of wild and domesticated *Rhododendron chrysanthum* were compared by applying PAR (P), P + UVA (PA), and P + UVA + UVB (PAB) radiation for 3 d, respectively. Results showed that photosynthetic activity of two *R. chrysanthum* types was not affected by UVA but inhibited by UVB, and the inhibitory effects of UVB were dose-dependent. Changes in nonphotochemical quenching suggest that the range of photosynthetic capacity is ranked as follows: 24–48 h of UVB dose < wild type < 72 h of UVB dose < domesticated type, indicating that the wild type initiated photoprotective function in response to UVB stress due to its lower photosynthetic capacity, while domesticated type did not due to its higher photosynthetic capacity. Taken all the given data together, the wild type was more sensitive to UV stress, but it showed more effective mechanisms of counteracting it.

Additional key words: alpine plant; photoinhibition; photoprotection; photosynthesis.

Introduction

Though accounting for only a small fraction of the total UV radiation, UVB (280–315 nm) has been traditionally considered as stress as it can potentially induce a number of deleterious effects in plants, including growth reduction, partial inhibition of photosynthesis, changes in plant biochemistry, oxidative damage, and disruption of the integrity and function of important macromolecules (DNA, proteins, and lipids) (Rastogi *et al.* 2010, Albert *et al.* 2011, Hideg *et al.* 2013, Widel *et al.* 2014).

Some studies found no effect of UVB on the net photosynthesis (Klem *et al*. 2012, Alonso *et al*. 2015) due to a short-term treatment. Some studies found low levels of UVB increased net photosynthesis (Yang and Yao 2008, Klem *et al*. 2015, Vidović *et al*. 2015, Guidi *et al*. 2016). However, the deleterious effects of UVB on photosynthesis have been observed mostly under high, unnatural doses of UVB (Dehariya *et al*. 2012).

Photon energy captured by a Chl *a* molecule can either drive photosynthesis (photochemical quenching, q_P), be emitted as fluorescence, or be converted to heat (non-photochemical quenching, q_N and NPQ) (Schreiber 2004). Over the past 30 years, the measurement of the Chl *a* fluorescence has proven to be a powerful method of assessing the properties of the photosynthetic apparatus (Schreiber 2004, Ralph and Gademann 2005). Light curves provide detailed information on the saturation characteristics of electron transport, as well as the overall photosynthetic performance of a plant. Derived cardinal points of a rapid light curve (α, E_k, and $rETR_{max}$) describe the photosynthetic capacity of a leaf. The relative ETR, rETR, is an approximation of the rate of electrons pumped through the photosynthetic chain (Beer *et al*. 2001). α reflects photosynthetic rate in light-limited region of light curve. The rise of the curve in the light-limiting region (α) is proportional to efficiency of light capture (effective quantum yield, Schreiber 2004). Minimum saturating irradiance, E_k, is related to quenching, where photochemical quenching dominates below E_k, while nonphotochemical quenching dominates the fluorescence quenching above E_k (Henley 1993). $rETR_{max}$ is maximum relative electron transport rate. Under moderate irradiance, the capacity of the electron transport chain limits photosynthesis and the curve reaches a plateau, where maximum photosynthetic capacity occurs ($rETR_{max}$) (Schreiber 2004). Photochemical quenching, q_P, namely the fluorescence quenching caused by photosynthesis, reflects the level of photosynthetic

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Abbreviations: D – domesticated type of *Rhododendron chrysanthum*; E_k – minimum saturating irradiance; F_v/F_m – maximum quantum yield of PSII; NPQ – nonphotochemical quenching; P – PAR; PA – PAR + UVA; PAB – PAR + UVA + UVB; rETR – relative electron transport rate; $rETR_{max}$ – maximum relative electron transport rate; q_P – photochemical quenching; W – wild type of *R. chrysanthum*; α – photosynthetic rate in light-limited region of light curve; Φ_{PSII} – effective quantum yield of PSII.
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activity. Nonphotochemical quenching, NPQ, reflects the ability of plants to dissipate excess light energy as heat, reflecting the photoprotective ability of plant. Maximum quantum yield of PSII, F_v/F_m, reflects the potential maximum photosynthetic capacity of plants (photosynthetic efficiency). Effective quantum yield of PSII, Φ_{PSII}, is actual photosynthetic capacity or actual photosynthetic efficiency at any light state.

In previous laboratory investigations, inhibition of F_v/F_m was observed in oat (*Avena sativa* L.) due to UVB radiation, suggesting the photoinhibition changes in the PSII of the leaves (Skórska 1999). During a 10-d study of winter wheat (*Triticum aestivum* L.) treated by enhanced UVB radiation, decreased photosynthetic rate (P_N) and F_v/F_m were observed (Yang *et al*. 2007). The ratio of F_v/F_m was significantly reduced by UVB in two grapevine (*Vitis vinifera* L.) cultivars (Schoedl *et al*. 2013). Similar results can be seen from the experiments outdoors under ambient UV. For example, Reddy *et al*. (2004) found that UVB exposure of cotton (*Gossypium hirsutum L.*) led to reduced F_v/F_m, in addition to reductions in net photosynthesis. Fluorescence measurements indicated enhanced F_v/F_m ratio and reduction capacity after exclusion of solar UV (Dehariya *et al*. 2012).

Response of plants to UVB radiation is turned out to be the result of a comprehensive balance of injury, remediation, and acclimation (Quesada *et al.* 1995, Jansen *et al*. 1998). While there is still little information regarding the mechanistic changes driving UVB-mediated increases in photosynthesis, recent work on the woody shrub *Pimelea ligustrina* demonstrated that UVA radiation increased *in situ* photosynthetic rates in *P. ligustrina* by 12%, a response which was attributed to the excitation of Chl *a* by UVA directly (Turnbull *et al.* 2013). Some studies found UVA enhanced net photosynthesis (Yang and Yao 2008, Bernal *et al*. 2015, Štroch *et al*. 2015) and increased the quantum yield efficiency of plants (Kolb *et al*. 2001). Some studies found that UVA did not affect the quantum yield efficiency of most vegetables and monocots (Guruprasad *et al*. 2007, Yang and Yao 2008, Bernal *et al*. 2015, Štroch *et al*. 2015). However, other studies found that UVA radiation had a detrimental effect on photosynthesis (Turcsányi and Vass 2000) and reduced the quantum yield efficiency of plants (Tohidi-Moghadam *et al*. 2012, Joshi *et al*. 2013).

Responses of photosynthesis to UVB radiation can be regulated by other environmental factors, such as climatic factors, PAR, nutrient status, drought, CO_2, and particularly growth temperature (Murali and Teramura 1987, Sullivan and Teramura 1990, Visser *et al*. 1997, Yang *et al*. 2007). Vidović *et al*. (2015) reported that the effects on white-edged Swedish ivy might be influenced by the UVB/PAR ratio during the experiment at low PAR levels, the quantum yield efficiency increased but was not affected at higher PAR. The net photosynthetic rate of cotton (*Gossypium hirsutum* L.) plants treated by 0.16 W m^{-2} UVB radiation did not change at 24/16°C (day/night temperature) but decreased at 30/22 and 36/28°C (Reddy *et al*. 2004). However, UVB-induced photoinhibition of cucumber (*Cucumis sativus* L.) cotyledons was relieved by increasing temperature from 20 to 25°C (Takeuchi *et al*. 1993). In a 10-d study of winter wheat (*Triticum aestivum* L.) treated by enhanced UVB radiation, low temperature intensified UVB-induced photoinhibition, which was indicated by decreased P_N and F_v/F_m and by weakened antioxidant system (Yang *et al*. 2007). Future studies will also need to consider the potential interactive effects between UVB and UVA and other environmental factors with particular interest in growth temperature (Yang *et al*. 2007).

Rhododendron chrysanthum only grows at altitudes between 1,300 and 2,650 m at the Changbai Mountain in the southeastern part of Jilin Province in China. At the top of the mountain, the annual average temperature is –7.3°C. The harsh climate and poor soil at the top of the Changbai Mountain are serious challenge for plants. The long adaptive evolution process of *R. chrysanthum* allows it to resist cold temperatures, drought, strong UV radiation, and other abiotic stresses (Zhou *et al*. 2017). *R. chrysanthum* plants grown on top of the mountain (wild type) and in plain (domesticated for 10 years) were chosen for testing the adaptability of plants to UV radiation.

Physiological characteristics of two *R. chrysanthum* types were reported in our previous study (Zhou *et al*. 2017). A total of 1,395 proteins were identified, among which 137 proteins were upregulated in the wild *R. chrysanthum*. The activities of superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidases (APXs), and glutathione peroxidase (GPX) were significantly higher and the expression of APXs and GPX also increased in the wild *R. chrysanthum*. Moreover, the interaction network analysis of these enzymes also revealed that the antioxidant enzymes play important roles in the stress resistance in plants (Zhou *et al.* 2017). Understanding the effect of UV on alpine plants are limited, although pioneering work of Albert *et al*. (2005) demonstrated that leaves of *Salix arctica*, an alpine plant living in 2,000–2,800 m a.s.l., were less stressed under UVB exclusion as compared to leaves exposed to high PAR and high UVB. These reports suggest the necessity for further study on possible defense mechanisms of alpine plants irradiated with UV.

In the present study, we used the *R. chrysanthum* as a material to study the adaptability of photosynthesis capacity of alpine plants to UVB and UVA radiation. We also tried to investigate whether the strong solar UV radiation on the top of Changbai Mountain affects the photosynthesis of plants and if so, what is the adaptability of typical alpine plants to cope up with the strong UV radiation for long-term living in harsh environments on the plateau.

Materials and methods

Plant material: *Rhododendron chrysanthum* was collected at altitudes between 1,300 m and 2,650 m on the Changbai Mountain. After transport to the laboratory, the plants were maintained in an artificial climate room under a simulated alpine environment and cultured in the chamber, respectively. Wild *R. chrysanthum* plants (W type) were grown in an artificial climate room at 18°C (14-h light)/16°C (10-h dark) under white

fluorescent light at 50 μmol(photon) m^{-2} s^{-1}. Domesticated *R. chrysanthum* plants (D type) were grown in the chamber at 24°C under white fluorescent light at 50 μmol(photon) m^{-2} s^{-1}.

Experimental design: To investigate whether there is a difference in the photosynthetic capacity between W type and D type under UV radiation, the experiments were performed by exposing 8-month-old seedlings of two *R. chrysanthum* types to photosynthetically active radiation (PAR), PAR + UVA (PA), and PAR + UVA + UVB (PAB) radiation for 3 d. Plants from each treatment were withdrawn at 24-h intervals in triplicates and tested for their photosynthetic capacity.

PAR and UV radiation exposure: The plants of two *R. chrysanthum* types (W and D) were exposed to artificial radiation of UVB (280–315 nm), UVA (315–400 nm), and PAR (400–700 nm) in replicates (n = 3). To obtain the three desired radiation regimes, long-pass filters of different transmittance characteristics were used. A 400-nm long-pass filter (*Edmund*, *Filter Long 2IN SQ*, NJ, USA) was placed over the culture bottle in the PAR-only treatment. For the PAR + UV treatments 320- or 295-nm long-pass filters (*Edmund*, *Filter Long 2IN SQ*, NJ, USA) were placed over the culture bottles to achieve the PA or PAB regime, respectively. Visible (PAR) light was supplied by warm white fluorescent light lamp (*Philips*, *T5 × 14W*, The Netherlands). UVA radiation was provided by UVA fluorescence tubes (*Philips*, *UVA-340 TL 20W/05*, The Netherlands), and UVB fluorescence tubes (*Philips*, *Ultraviolet-B TL 20W/01 RS*, The Netherlands) were used as a source of artificial UVB radiation. Based on the transmittance function of the long pass filters, the irradiances effectively received by the samples were: 2.3 W m^{-2} UVB, 1.5 W m^{-2} UVA, and PAR of 50 μmol(photon) m^{-2} s^{-1}.

Chl fluorescence measurements: For a 3-d study of UV exposure on *R. chrysanthum*, the 8-month-old seedlings were grown under three radiation conditions (P, PA, and PAB) for 8 h, followed by the illumination under white light for the remaining 16 h daily. During the experimental period, none of the plants experienced any water or nutrient stress. Induction curves and light curves were obtained by using an imaging pulse amplitude modulation fluorometer (*IMAGING PAM M-series*, *Walz*, Effeltrich, Germany). Dark period of the samples was set at least 15 min before Chl fluorescence measurements. From the light curves we obtained the parameters α, $rETR_{max}$, and E_k. Then, we compared the exact photosynthetic performance by analyzing these parameters.

Statistical analysis: One- or two-way analyses of variance (*ANOVA*) were performed using *SPSS 16.0* (NY, USA) to test the single and interactive effects of different light sources used, *i.e.*, PAR, UVA, UVB, and their different sets of combination. When the *ANOVA* results showed a significant difference, the least significant difference (LSD) as a post-hoc test at P<0.05 was calculated to compare the mean values of the various treatment groups. The figures were drawn with *Sigmaplot 12.5* (*Systa Software Inc.*, Chicago, IL, USA).

Results and discussion

Effect of UVA on F_v/F_m, Φ_{PSII}, $rETR_{max}$, α, and E_k: F_v/F_m of wild *R. chrysanthum* (W-F_v/F_m) depends on the dose of UVA radiation. For example, W-F_v/F_m was significantly inhibited by UVA at 72 h, since P treatment displayed a significant decrease in W-F_v/F_m in comparison with PA treatment only after 72 h (Fig. 1*A*). This is further demonstrated by the fact that W-F_v/F_m at 72 h was significantly lower than that at 24 or 48 h under PA conditions (Fig. 1*A*). However, UVA did not affect Φ_{PSII}, $rETR_{max}$, α, and E_k of wild *R. chrysanthum* (Fig. 1*B–D*). For example, no significant difference in W-$rETR_{max}$, W-α, and W-E_k was found between P and PA treatment (Fig. 1*C–E*). Although W-Φ_{PSII} significantly increased by UVA radiation at 48 h, it was recovered at 72 h (Fig. 1*B*). W-$rETR_{max}$ significantly increased by UVA radiation at 24 h, whereas, it was recovered after 48 h of radiation (Fig. 1*C*). W-α significantly decreased by UVA radiation at 24 h, but it significantly increased at 48 h and recovered until 72 h (Fig. 1*D*). A similar pattern can be seen for W-E_k (Fig. 1*E*).

In domesticated *R. chrysanthum*, UVA did not affect F_v/F_m, Φ_{PSII}, $rETR_{max}$, and E_k regardless of exposure time (Fig. 1*F*,*G*,*H*,*J*). No significant differences in D-F_v/F_m, D-Φ_{PSII}, D-$rETR_{max}$, and D-E_k were found between P and PA treatment regardless of exposure time (Fig. 1*F*,*G*,*H*,*J*). On the contrary, D-α depends on the dose of UVA radiation. For instance, D-α was significantly inhibited by UVA after 48 h of radiation, since P treatment displayed a significant decrease in D-α in comparison with PA treatment after 48 h of radiation (Fig. 1*I*). As a result, wild *R. chrysanthum* was more susceptible to UVA than domesticated *R. chrysanthum* in terms of F_v/F_m and α. For example, W-F_v/F_m was significantly reduced by UVA at 72 h, whereas, no significant difference in D-F_v/F_m was found between P treatment and PA treatment regardless of exposure time (Fig. 1*A*,*F*). In addition, W-α was significantly inhibited by UVA radiation at the first 24 h, but it significantly increased at 48 h and recovered until 72 h (Fig. 1*D*). However, D-α was significantly inhibited by UVA since 48 h post radiation and was not recovered until 72 h (Fig. 1*I*). In addition, Φ_{PSII}, $rETR_{max}$, and E_k of two *R. chrysanthum* types were not susceptible to UVA radiation.

Effect of UVA on q_P and NPQ: The NPQ of the alpine *Rhododendron* was regulated by the light intensity of PAR. When the light intensity was less than 100 μmol(photon) m^{-2} s^{-1}, NPQ of two *Rhododendron* types increased rapidly. After that, the NPQ of the two types of *Rhododendron* tended to be stable with the increase of light intensity (Fig. 2).

Both NPQ and q_P of two *Rhododendron* types were not affected by UVA. For example, there was no significant difference in NPQ between the PA and P for both types of *Rhododendron* after UV-irradiation for 24–72 h (Fig. 2*B–D*).

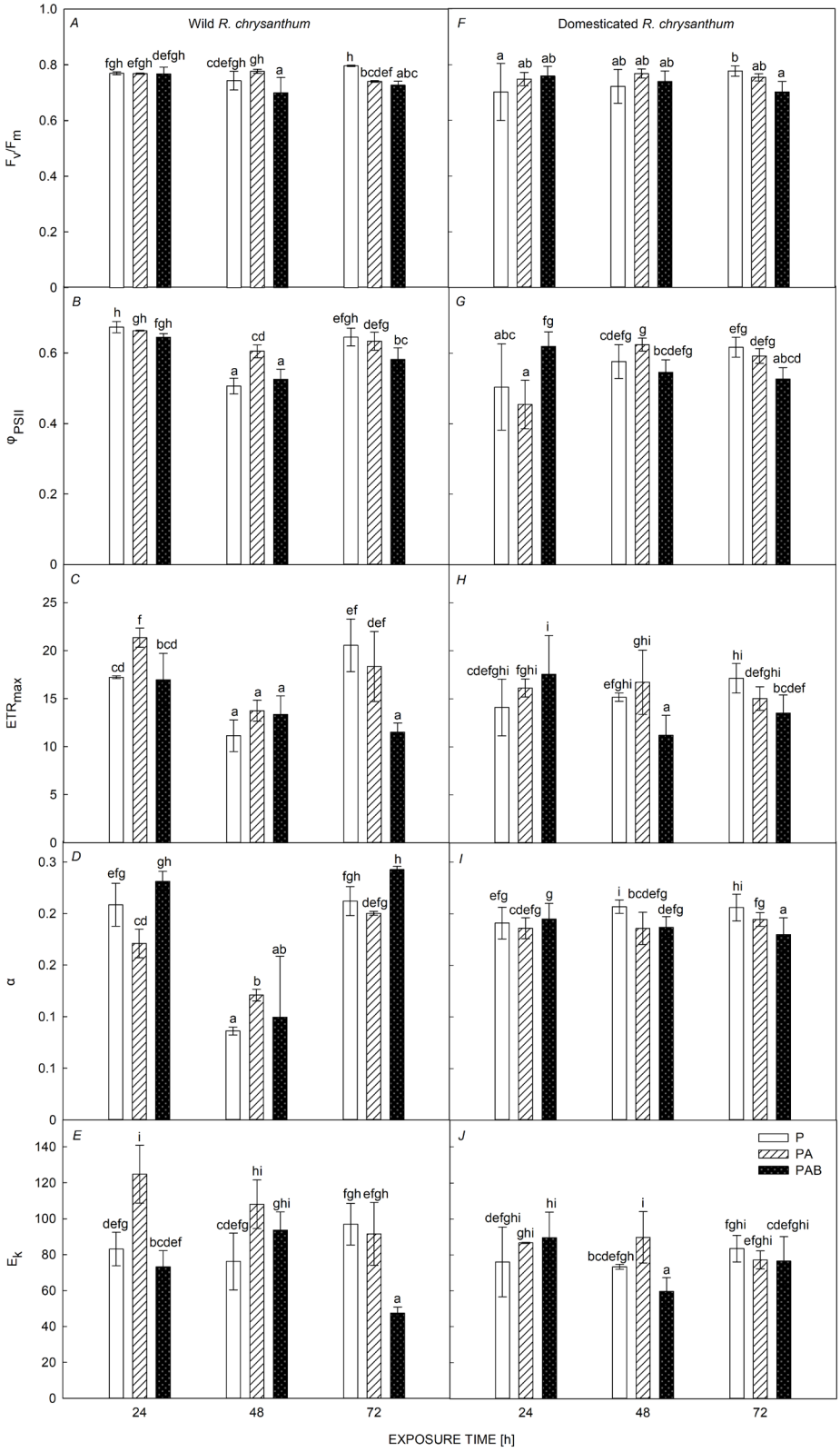

Fig. 1. Maximum quantum yield of PSII (F_v/F_m), effective quantum yield of PSII (Φ_{PSII}), maximum relative electron transport rate ($rETR_{max}$), photosynthetic rate in light-limited region of light curve (α), and minimum saturating irradiance (E_k) of wild and domesticated *Rhododendron chrysanthum* exposed to PAR (P), PAR + UVA (PA) or PAR + UVA + UVB (PAB). Values are means ± SE (n = 3). Different *lowercase letters* indicate statistically significant difference (P<0.05) in the same figure block.

Similar pattern can be seen for q_P (Fig. 3*B–D*). This can be explained by the fact that the intensity of UVA applied in this study did not exceed the photosynthetic capacity of both *Rhododendron* types (Fig. 2). This can be further proved by its habitat environment in nature; the light intensity of UVA applied in this experiment was lower than that in the alpine environment.

Effect of UVB on F_v/F_m, Φ_{PSII}, $rETR_{max}$, α, and E_k: F_v/F_m, Φ_{PSII}, $rETR_{max}$, α, and E_k of wild *R. chrysanthum* depended

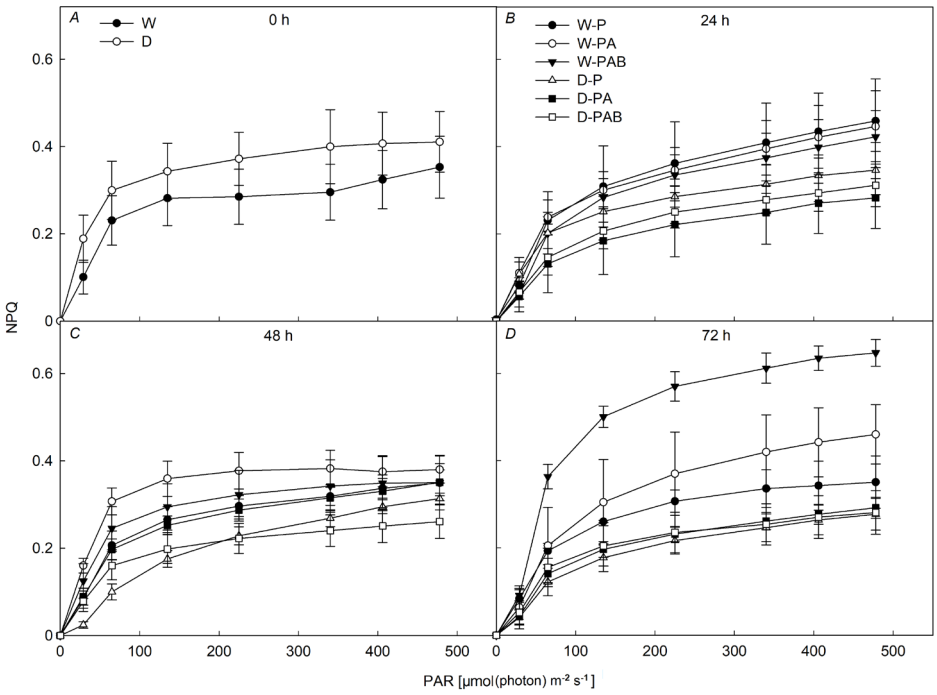

Fig. 2. Mean nonphotochemical quenching (NPQ) as a function of PAR, obtained from wild (W) and domesticated (D) *Rhododendron chrysanthum* leaf exposed to PAR (P), PAR + UVA (PA) or PAR + UVA + UVB (PAB) for 0 h (*A*), 24 h (*B*), 48 h (*C*), and 72 h (*D*). Values are means ± confidence ($n = 3$).

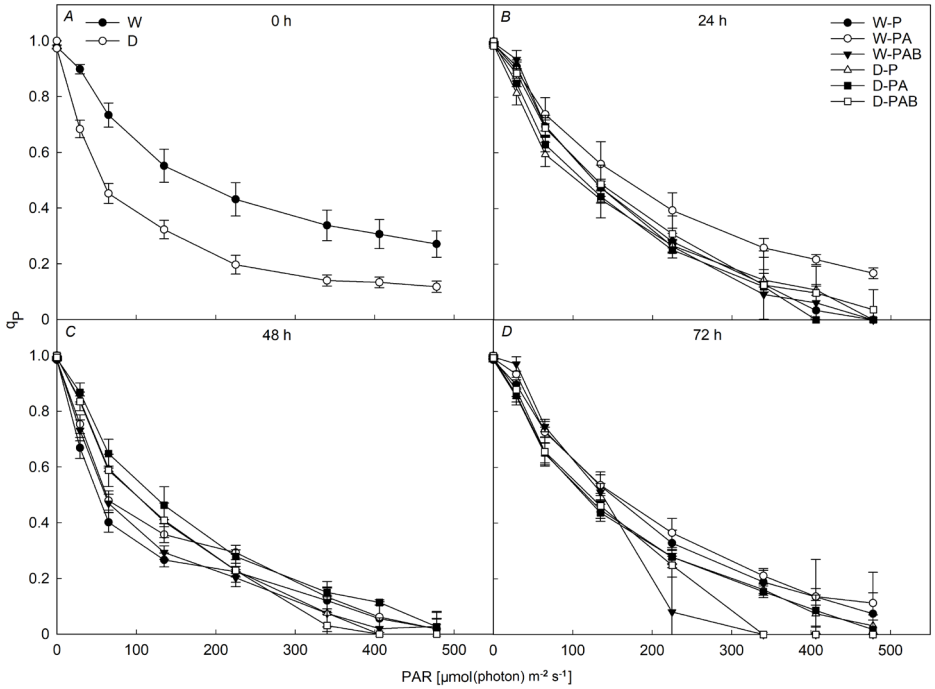

Fig. 3. Mean photochemical quenching (q_P) as a function of PAR, obtained from wild (W) and domesticated (D) *Rhododendron chrysanthum* leaf exposed to PAR (P), PAR + UVA (PA) or PAR + UVA + UVB (PAB) for 0 h (*A*), 24 h (*B*), 48 h (*C*), and 72 h (*D*). Values are means ± confidence ($n = 3$).

on the duration of UVB radiation. For example, W-F_v/F_m significantly decreased by UVB only after 48 h since PA treatment displayed a significant decrease in W-F_v/F_m in comparison with PAB treatment, and it was not affected at either 72 h or the first 24 h (Fig. 1*A*). W-Φ_{PSII} was not affected by UVB in the first 24 h. However, it was significantly inhibited by UVB during the following 2 d, *i.e.*, 48 and 72 h. For example, there was no significant difference in W-Φ_{PSII} between PA treatment and PAB treatment at 24 h, but the former displayed a significant decrease in comparison to the latter after 48-h radiation (Fig. 1*B*). This is further demonstrated by the fact that W-$rETR_{max}$ and W-E_k irradiated by PAB were significantly lower than that irradiated by PA after both 24 and 72 h (Fig. 1*C*,*E*). The opposite trend can be seen for W-α (Fig. 1*D*). This is in accordance with the recent review (Neugart and Schreiner 2018): the effects of UVB and UVA depend on the genotype, the developmental stage of the plant, and the intensity and duration of the UVB or UVA treatment.

For domesticated *R. chrysanthum*, UVB did not affect F_v/F_m regardless of the duration of UVB radiation (Fig. 1*B*). However, Φ_{PSII}, $rETR_{max}$, α, and E_k of domesti-

cated *R. chrysanthum* depended on the duration of UVB radiation. For example, D-Φ_{PSII} was significantly affected only during the first 24 h (Fig. 1*G*). D-rETR$_{max}$ and D-E_k significantly decreased only at 48 h since PA treatment displayed a significant decrease in both D-rETR$_{max}$ and D-E_k in comparison to the PAB treatment only after 48 h (Fig. 1*H*,*J*). Similarly, D-α was significantly inhibited by UVB only after 72 h since PA treatment displayed a significant decrease in D-α in comparison to the PAB treatment only after 72 h (Fig. 1*I*).

Therefore, wild *R. chrysanthum* was more susceptible to UVB radiation than the domesticated type in terms of F_v/F_m, Φ_{PSII}, rETR$_{max}$, α, and E_k. For example, UVB radiation showed significantly inhibiting effects on W-F_v/F_m at 48 h, but not on D-F_v/F_m during the whole 3-d radiation period (Fig. 1*A*,*B*). This is further demonstrated by the fact that Φ_{PSII}, rETR$_{max}$, α, and E_k of wild *R. chrysanthum* was more frequently affected by UVB than that of domesticated *R. chrysanthum* (Fig. 1*B–E*,*G–J*).

Wild *R. chrysanthum* was more susceptible to UVA radiation than the domesticated *R. chrysanthum* in terms of F_v/F_m and α. Furthermore, wild *R. chrysanthum* was more susceptible to UVB radiation than domesticated *R. chrysanthum* in terms of F_v/F_m, Φ_{PSII}, rETR$_{max}$, α, and E_k. This is further demonstrated by the fact that the time for the inhibition of rETR$_{max}$ caused by UVB in W type was 24 h less than that in D type.

In a recently reported experiment using grapevine (*Vitis vinifera* L. cv. Chardonnay), Majer and Hideg (2012) showed a similar effect of UVB radiation on photochemical yields as we observed in wild *Rhododendron*, namely the decrease in F_v/F_m and Φ_{PSII}. The stimulated photoprotective mechanisms and reduced photosynthetic activities of the wild type in our study may contribute to limitation of photosynthesis observed by Majer and Hideg (2012). A decrease in F_v/F_m, ETR, and also photosynthesis reflects the loss of PSII activity, usually (but not always) following the degradation of D1 and D2 proteins induced by UVB. The proteins D1 and D2 of PSII RC play a great role in the sensitivity of PSII to UVB radiation; their degradation occurred at the UVB intensity of 0.53 W m^{-2} (Jansen *et al*. 1996). The key effect is the damage of PSII Mn-containing cluster (Melis *et al*. 1992, Vass *et al*. 1996, Tyystjarvi 2008, Kreslavski *et al*. 2009, Wei *et al*. 2011, Hou and Hou 2013). It is just this damage that promotes destruction of D1 protein (Kosobryukhov *et al*. 2015). In our experiment, a much higher intensity of UVB (8-h exposure to 2.3 W m^{-2} UVB) was applied to two *R. chrysanthum* types, causing a decrease in F_v/F_m and rETR$_{max}$ in both of them after 48-h exposure, however, the decrease disappeared in the domesticated type after 72-h exposure (Table 1). This may suggest that degradation of proteins D1 and D2 occured in the wild types since 48 h, but not in the domesticated type. Our ongoing research is characterizing the related proteins in two *R. chrysanthum* types, thereby to help understand the defense mechanism of the plant against UV radiation. This will be demonstrated in our future proteomic study.

Effect of UVB on q_P and NPQ: NPQ in the wild type was affected by the dose of UVB more than that in the domesticated type. For example, after exposition of the wild type to UVB radiation for 24–48 h, there was no significant change in NPQ (Fig. 2*B*,*C*), but it significantly increased after 72 h (Fig. 2*D*). However, there was no significant change in NPQ of the domesticated type during the whole period (24–72 h) of UVB radiation (Fig. 2*B–D*). This suggests that the range of photosynthetic capacity is ranked as follows: 24–48 h of UVB dose < wild type < 72 h of UVB dose < domesticated type. These results demonstrate that, compared to the domesticated type, the wild type showed higher photoprotective function in response to UVB, which was due to its lower photosynthetic capacity. This is further demonstrated by the fact that in the absence of UVB, a photoprotective function, indicated as NPQ, of the wild type was slightly lower than that of

Table 1. Changes in photosynthetic capacity of wild (W) and domesticated (D) *Rhododendron chrysanthum* under UV radiation. E_k – minimum saturating irradiance; F_v/F_m – maximum quantum yield of PSII; NPQ – nonphotochemical quenching; q_P – photochemical quenching; rETR$_{max}$ – maximum relative electron transport rate; α – photosynthetic rate in light-limited region of light curve; Φ_{PSII} – effective quantum yield of PSII. *Green color* indicates increase, *red color* indicates decrease, *gray color* indicates no change.

Radiation	*Rhododendron*	Exposure time [h]	F_v/F_m	Φ_{PSII}	rETR$_{max}$	Ek	α	NPQ	q_P
UVA	W	24	-	-	↑	↑	↓	-	-
		48	-	↑	-	↑	↑	-	-
		72	↓	-	-	-	-	-	-
	D	24	-	-	-	-	-	-	-
		48	-	-	-	↑	↓	-	-
		72	-	-	-	-	↓	-	-
UVB	W	24	-	-	↓	↓	↑	-	-
		48	↓	↓	-	-	-	-	-
		72	-	↓	↓	↓	↑	↑	↓
	D	24	-	↑	-	-	-	-	-
		48	-	-	↓	↓	-	-	-
		72	-	-	-	-	↓	-	-

the domesticated type (Fig. 2*A*). Furthermore, in present experiment, q_P in the wild type was affected by the dose of UVB rather than that in the domesticated type. For example, after 24–48 h of UVB radiation, there was no significant change in q_P in the wild type (Fig. 3*B*,*C*), but it was significantly reduced after 72 h (Fig. 3*D*). However, there was no significant difference in q_P between PAB and PA in the domesticated type during the 24–72 h of UVB irradiation (Fig. 3*B–D*).

Consistent with the photosynthetic activity (q_P) results, many other photosynthetic parameters of wild type decreased by UVB at 24 h ($rETR_{max}$ and E_k), 48 h (F_v/F_m and Φ_{PSII}), and 72 h (Φ_{PSII}, $rETR_{max}$, and E_k), respectively. However, minor photosynthetic parameters of domesticated type decreased at 48 h ($rETR_{max}$ and E_k), and 72 h (α) (Table 1). Taken all the given data together, we can conclude that the wild type was more sensitive to UV stress, but it possesses more effective mechanisms to counteract it.

Yang *et al*. (2007) applied enhanced-UVB radiation on winter wheat (*Triticum aestivum* L.) seedlings at different growth temperature, and found that decreased F_v/F_m and increased minimum fluorescence (F_0) were observed under high UVB (0.119 W m^{-2}) at both temperatures (25/20 or 10/5°C) and low UVB (0.049 W m^{-2}) at 10/5°C. They concluded that low temperature intensified UVB-induced photoinhibition and damage by weakening the antioxidant system (Yang *et al*. 2007). Huang *et al*. (2016) reported that moderate photoinhibition of PSII protects PSI from photodamage under chilling stress in tobacco leaves. In this study, the wild type was grown in an artificial climate room at 18°C (14 h)/16°C (10 h), while the domesticated type was grown in the chamber at 24°C. Based on the literature above and our results, we suggest that low temperature is the reason why intensified UVB-induced photoinhibition (decreased q_P, $rETR_{max}$, E_k, F_v/F_m) was observed in the wild type rather than in the domesticated type. Furthermore, stomatal response to increased UV radiation can be a regulator of photosynthetic apparatus activity (Kosobryukhov *et al*. 2015). Majer and Hideg (2012) applied UVB of 0.84 W m^{-2} to supplement 50 µmol(photon) m^{-2} s^{-1} PAR daily, between 9–15 h. These conditions, much lower doses than those in our experiment (8-h exposure to 2.3 W m^{-2} UVB for 3 d), resulted in intense stomata closure and strong limitation of photosynthesis and decreased the photochemical yield (Φ_{PSII} and F_v/F_m). Stomata in abaxial epidermal strips of *Arabidopsis* ecotype Landsberg *erecta* closed in response to increasing UVB rates, with maximal closure after 3-h exposure to 2.89 W m^{-2} UVB (Tossi *et al*. 2014). Although the three experiments cannot be compared directly, due to differences in plant material (species, age), it is possible to hypothesize that stomata closure may occur in *Rhododendron* (especially in the wild type) because of much higher dose of UVB used in our study. Li *et al*. (2017) found that UVB-induced stomatal closure was promoted by mitogen-activated protein kinase phosphatases *via* modulating hydrogen peroxide-induced nitric oxide production in *Arabidopsis* guard cells.

UVB-induced limitation of photochemistry was not solely due to stomata closure which does not affect F_v/F_m, but internal PSII factors could also be involved (Majer and Hideg 2012). Although with the same PAR irradiances accompanying UVB [50 µmol(photon) m^{-2} s^{-1}], the two experiments cannot be compared directly due to UVB conditions [lower UVB used by Majer and Hideg (2012) and much higher UVB in our study]. However, both experiments showed the decrease of the photochemical yields indicated y F_v/F_m and Φ_{PSII}. In accordance with this, a significant decrease in F_v/F_m was observed in a 8-d study of grapevine (*Vitis vinifera* L.) applying 0.081 W m^{-2} UVB radiation with 165 µmol(photon) m^{-2} s^{-1} from 13:00 to 20:00 h (Schoedl *et al.* 2013), though two experiments cannot be compared directly, due to differences in plant material, PAR/UVB ratio [higher PAR/UVB ratio used by Schoedl *et al*. (2013) and much lower PAR/UVB ratio in our study].

Conclusion: From this study, we can conclude that the wild type was more sensitive to UV stress, but has more effective mechanisms to counteract it. The next challenge is a characterization of the differential proteins in two *R. chrysanthum* types after 48-h UV exposure, which could bring more information about the defense mechanism of the plant against UV radiation.

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