BRIEF COMMUNICATION

Photosynthetic responses to solar UV-A and UV-B radiation in low- and high-altitude populations of *Hippophae rhamnoides*

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Abstract

Two contrasting sea buckthorn (*Hippophae rhamnoides* L.) populations from the low (LA) and high (HA) altitudinal regions were employed to evaluate the plant physiological responses to solar UV-A radiation and near-ambient UV-B radiation (UV-B+A) under the sheltered frames with different solar ultraviolet radiation transmittance. LA-population was more responsive to solar UV-A. Some modification caused by UV-A only existed in LA-population, such as significant reduction of leaf size, relative water content, and chlorophyll (Chl) *b* content as well as $\delta^{13}C$ elevation, coupled with larger increase of contents of total carotenoids (Cars). This higher responsiveness might be an effective pre-acclimation strategy adapting for concomitant solar UV-B stress. Near-ambient UV-B+A radiation caused significant reduction of leaf size and Chl content as well as slight down-regulation of photosystem 2 activity that paralleled with higher heat dissipation, while photosynthetic rate was modestly but significantly increased. The higher photosynthesis under near-ambient UV-B+A radiation could be related to pronounced increase of leaf thickness and effective physiological modification, like the increase of leaf protective pigments (Cars and UV-absorbing compound), constant high photochemical capacity, and improved water economy.

Additional key words: abscisic acid; carotenoids; chlorophyll content and fluorescence; intra-specific response; photosystem 2; quenching photochemical and non-photochemical; sea buckthorn; relative water content; stomatal conductance; water use efficiency.

Ultraviolet radiation (UV) striking the earth's surface is comprised by approximately 95 % UV-A (315–400 nm) and 5 % UV-B radiation (280–315 nm) (White and Jahnke 2002). Exposure to UV-B radiation at ambient or enhanced levels elicits a variety of responses in plant photosynthesis, such as CO_2 uptake, photosynthetic electron transport chain, dark respiration, stomatal behaviour, pigment contents, and endogenous content of phytohormones (Jansen *et al*. 1998). However, only a few researches were conducted on plant responses to UV-A band (White and Jahnke 2002, Close *et al*. 2007). UV-A radiation may have little biological effectiveness according to the commonly used biological spectra weighting functions (BSWF) (Green *et al*. 1974), but some indoor and field studies suggest that UV-A alone inhibits plant growth and development, *e.g.* hypocotyl elongation (Ballaré *et al*. 1991), leaf expansion (Häder 1996), inflorescence emerging and flower opening (Day *et al*. 1999). The positive effects of UV-A were also observed in protection of the photosynthetic apparatus against UV-B-induced damage by restoring photosystem 2 (PS2) activity and facilitating energy dissipation through xanthophyll cycle (Gartia *et al*. 2003), and were widely evidenced in photo-repair processes for DNA damage (Takeuchi *et al*. 1996).

Woody plants exhibit various morphological and physiological responses to UV radiation. Such responses differ between tree species originating from different UV habitats, which may have developed differing UV tolerances (Ren *et al*. 2006). In the southeast of the Qinghai-Tibetan Plateau of China, sea buckthorn (*Hippophae rhamnoides* L.), a thorny nitrogen-fixing deciduous perennial shrub, is naturally distributed from 1 700 to 3 500 m altitude (Yang *et al*. 2005). Owing to its strong

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resistance to environmental stresses such as cold and drought, sea buckthorn has been widely used in forest restoration as the pioneer species (Li *et al*. 2005). In our study, two contrasting populations of sea buckthorn from the high (HA) and low (LA) altitudes were pot-grown under sheltered environments with different solar ultraviolet radiation transmittance. Our aims were to evaluate their physiological responses, in particular photosynthetic response, to ambient UV-A and UV-B as well as to test the intra-specific differences in these responses.

An LA-population (Maoxian, 32°20'N, 103°52'E, 1 700 m a.s.l.) and a HA-population (Daofu, 30°59′N, 101°07'E , 3 300 m a.s.l.) of *H. rhamnoides* from Qinghai-Tibetan Plateau of China were selected. The local UV-B intensities of the LA and HA habitats under clear sky at the summer solstice, which was the summer's maximum, were about 0.83 and 1.03 μmol m^{-2} s^{-1} (equivalent to approximately 9.5 and 11.8 kJ m^{-2} d^{-1} of 8 h), and the mean annual precipitation was 486.3 and 652.6 mm, respectively. The uniform seedlings of the two populations were chosen and transferred to 5 000 cm^3 pots containing homogeneous natural soil grown in sheltered frames. The sheltered frame was made up of four sticks (deep into soil) and roof with parallel rails spaced 0.75 m as described by Searles *et al*. (1999) and Yao *et al*. (2006a). The frame roof was covered either with 3.12 mm polycarbonate sheet to eliminate all UV radiation (<400 nm) for –UV treatment (control), or with 0.08 mm polyester film to eliminate UV-B radiation (<315 nm) for UV-A treatment, or with 0.038 mm *Teflon* plastic film to transmit UV-B and UV-A for near-ambient UV treatment [UV-B+A, 0.74 μmol m^{-2} s^{-1} (equivalent to approximately 8.5 kJ m^{-2} d^{-1})] (Papadopoulos *et al*. 1999). The PAR under the sheltered filters was *ca*. 85–93 % of ambient for the sheet as well as plastic films. The spectra of –UV, UV-A, and UV-B+A radiation are shown in Fig. 1. The sheet and film were cleaned every week and replaced every six weeks throughout the growing seasons. Totally nine frames were set up for those three UV treatments with three replication in each treatment. The seedlings of each population were randomly distributed to the sheltered frames, with four seedlings in each replication.

After 90 d of treatment, gas exchange measurements were taken on fully expanded, exposed leaves using an open system, with a portable photosynthesis measurement system (*CI-301PS*, *CID*, USA). The measurements took place under optimal summer conditions (28–30 °C and 36–55 % relative humidity in the air of leaf chamber) between 08:00 and 11:00 h for each day, total one week. Half of seedlings per replication were randomly selected for this measurement. The intrinsic water use efficiency (WUEi) was calculated by dividing the net photosynthetic rate (P_N) by stomatal conductance (g_s). Chlorophyll (Chl) fluorescence measurements were taken on the same leaves using a modulated fluorometer (*PAM 2100*, *Walz*, Effeltrich, Germany) as described by Schreiber *et al*. (1994). The plant leaves, darkened for 40 min, were irradiated with a strong beam of "white light" (PPFD = 8 000 μmol m^{-2} s^{-1}, 1.0 s) to determine the maximum (F_m) and the minimum (F_0) fluorescence as well as F_v/F_m. The actual quantum yield (Y) was measured under saturating irradiance (600 μmol m^{-2} s^{-1}). The photochemical (q_P) and non-photochemical (q_N) quenching coefficient were also calculated.

For the determination of photosynthetic pigment concentration, leaf discs (1.0 cm^2) were excised from exposed and fully expanded leaves in the same position and extracted by dimethyl sulphoxide (DMSO) according to Yao *et al*. (2005). The absorbance of the extract was measured spectrophotometrically at 480, 665, and 649 nm, and the turbidity of the extract was checked at 750 nm (always less than 0.01). Contents of Chl *a*, Chl *b*, and carotenoids (Cars) were calculated using equations of Wellburn (1994). The UV-absorbing compounds were extracted from fully expanded leaves (0.1 g fresh mass) with 10 cm^3 of acidified methanol (methanol/water/HCl, 79/20/1) and measured spectrophotometrically at 300 nm.

The youngest fully expanded leaves were sampled at 08:00 h in the morning to determine the relative leaf water content (RWC) according to Yang *et al*. (2005).

For the measurement of abscisic acid (ABA), the

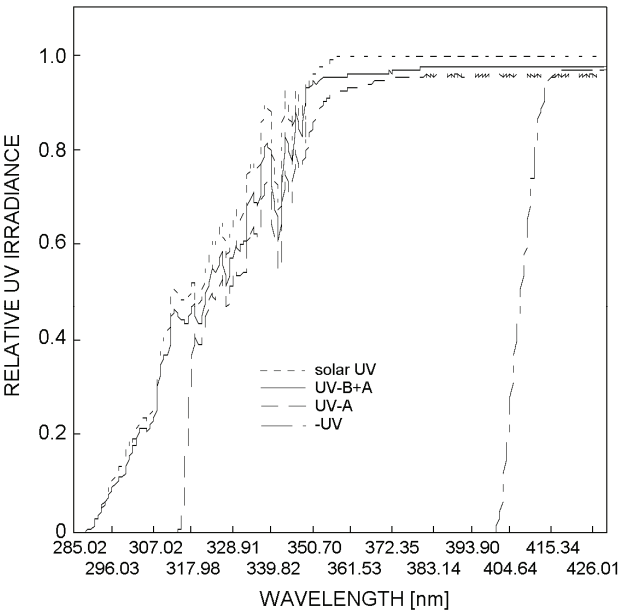

Fig. 1. Spectral irradiance for different solar UV radiation in sheltered frame (relative values, all measurements were determined at plant level). Solar UV – solar UV radiation without shelter and film (as spectral control of the three treatments); UV-B+A – solar UV-B and UV-A radiation transmitted by *Teflon* film; UV-A – solar UV-A radiation transmitted by polyester film (UV-B exclusion); –UV – no UV radiation eliminating all UV radiation (<400 nm) by polycarbonate sheet.

youngest fully expanded leaves were excised and placed in liquid nitrogen. Samples were stored at –70 °C until analysed for abscisic acid (ABA) as described by Yang *et al*. (2005). Leaf samples used for the carbon isotope analysis were oven-dried for 24 h at 80 °C and homogenized by grinding in a ball mill. The carbon isotope composition ($\delta^{13}C$) in combusted samples was measured with a mass spectrometer (*Finnegan MAT Delta-E*), as described by Hubick *et al*. (1986) and Li *et al*. (2000). After 5 months, all seedlings of each treatment were harvested. Leaf area for each seedling was determined by a *CI-202*-scanning planimeter (*CID*, Camas, WA, USA). Leaf biomass samples were dried to constant mass, and then areal leaf mass (ALM) was calculated.

The effects of the treatments on the parameters were tested using two-way ANOVA. Within each population, pair-wise comparisons between different treatments were made using Tukey's Student Range (HSD) Test at $p<0.05$.

Leaf size and thickness were affected by UV radiation (Table 1). Compared with –UV treatment, leaf size of LA-population was significantly decreased by UV-A, and additionally reduced by UV-B+A, while in HA-population the leaf size was decreased only under UV-B+A exposure. As an indicator of leaf thickness, ALM was enhanced by UV-B+A treatment but not affected by UV-A in both populations. Such leaf responses could be explained as an important acclimation mechanism to UV radiation. The reduction of leaf size could help reduce the amount of UV interception, and the leaf thickening help block and prevent the harmful UV-B radiation from reaching the sensitive photosynthetically active mesophyll (Ren *et al*. 2006).

The reduction of Chl content by UV-B was well documented in previous study (Yao *et al*. 2006b), as similar with our result (Table 1). Compared with –UV, UV-A induced significant reduction of Chl *b* content only in LA-population. Under UV-B+A, Chl *a* experienced little change in LA-population and modest reduction in HA-population, but pronounced decrease of Chl *b* content occurred in both populations, which resulted in higher Chl *a*/*b* ratio than in –UV treatment. Similar results were also observed in beech under UV-B (Láposi *et al*. 2002) and in four tropical woody species under high irradiance (Kitajima and Hogan 2003), but the underlying reasons need to be further elucidated. On the other hand, total Cars content was evidently increased by UV-A and UV-B+A treatments in LA-population compared with –UV. Considering the alteration of Chl content, the total Car/Chl ratio was increased by about 23.0 % ($p<0.05$) under UV-A and UV-B+A exposure in LA-population and increased by 20.6 % ($p<0.05$) under UV-B+A in HA-population. The enhancement of total Car/Chl ratio

Table 1. Effects of solar UV radiation on leaf morphological, pigment, photosynthetic, and chlorophyll fluorescence properties in two contrasting *H. rhamnoides* populations. In each population, values followed by the same letter in the same line do not differ significantly at $p<0.05$ by LSD pair-wise comparisons. Means of at least 3 replicates. –UV – no UV radiation (absence of solar UV-A and UV-B); UV-A – solar UV-A radiation (UV-B exclusion); UV-B+A – solar UV-B and UV-A; ALM, areal leaf mass; A_{300} – UV-absorbing compound; WUEi – intrinsic water use efficiency; C_i – intercellular CO_2 concentration; RWC – leaf relative water content; ABA – abscisic acid; $\delta^{13}C$ – carbon isotope composition; F_0 – minimum fluorescence; F_m – maximum fluorescence; F_v/F_m – potential quantum yield; *Y* – actual quantum yield; q_P – photochemical quenching coefficient; q_N – non-photochemical quenching coefficient.

Leaf parameter	Maoxian population			Daofu population		
	–UV	UV-A	UV-B+A	–UV	UV-A	UV-B+A
Leaf size [cm^2]	2.92a	2.44b	2.13b	2.32a	2.03ab	1.73b
ALM [$g\ m^{-2}$])	64.54b	66.46b	85.21a	74.34b	74.19b	94.48a
Chl *a* [$g\ kg^{-1}$(FM)]	2.218a	2.139a	2.201a	2.238a	2.220a	2.066b
Chl *b* [$g\ kg^{-1}$(FM)]	0.734a	0.643b	0.628b	0.738a	0.721a	0.623b
Chl *a*/*b*	3.022b	3.343ab	3.521a	3.045b	3.083ab	3.317a
Cars [$g\ kg^{-1}$(FM)]	0.323b	0.372a	0.384a	0.303a	0.324a	0.332a
Car/Chl	0.109b	0.134a	0.136a	0.102b	0.110ab	0.123a
A_{300}	1.12c	1.55b	1.80a	1.42c	1.76b	2.58a
P_N	13.14b	13.81b	15.24a	11.27b	11.68ab	12.59a
g_s	278.78a	282.56a	274.80a	275.96a	274.22a	270.80a
WUEi	0.047b	0.049ab	0.055a	0.040b	0.043ab	0.047a
C_i	290.12a	292.06a	290.68a	292.70a	294.00a	295.38a
RWC [%]	72.04a	66.52b	64.20c	69.87a	68.51a	62.69b
ABA [$\mu g\ kg^{-1}$(FM)]	162.51a	256.81a	139.37a	219.16a	168.45a	104.34a
$\delta^{13}C$	–28.35b	–27.55a	–27.48a	–28.10b	–28.35b	–26.88a
F_0	0.261a	0.267a	0.227b	0.272a	0.289a	0.234b
F_m	1.737a	1.755a	1.427b	1.813a	1.910a	1.661b
F_v/F_m	0.852a	0.850a	0.842a	0.850a	0.849a	0.859a
Y	0.523a	0.481ab	0.424b	0.509a	0.524a	0.424b
q_P	0.647a	0.660a	0.582a	0.671a	0.689a	0.570b
q_N	0.400a	0.418a	0.405a	0.444b	0.434b	0.521a

was commonly observed in the study of field UV-exclusion or indoor studies with low UV/PAR ratio in the plant species such as *Colobanthus quitensis* and *Deschampsia antarctica* (Xiong and Day 2001), and *Cucumis sativus* and *Glycine max* (Yao *et al*. 2006b). Cars usually protect from photo-oxidative destruction in high UV/blue/"white" radiation conditions. Therefore, the elevation of Car content was very important for acclimation to UV radiation. In addition, UV-A and UV-B+A caused profound elevation of content of UV-absorbing compounds (Table 1), which improved the leaf capacity to screen UV radiation and shield the underlying tissues (Yao *et al*. 2006a).

P_N was increased by UV-B+A treatment (Table 1). Considering the unaffected g_s (Table 1), WUEi was increased under UV-B+A exposure. Previous study confirmed that P_N and g_s were closely related to UV-B intensity, markedly reduced by high-level of enhanced UV-B radiation, but not affected by low level of UV-B radiation (Moorthy and Kathiresan 1997). Šprtová *et al*. (2003) proposed that higher P_N under UV-B could be partially related to larger amount of photosynthetic tissue per leaf area due to increased leaf thickness, which was evidenced by our results (Table 1). Johnson and Day (2002) also found that the absorption of UV-induced blue fluorescence and the direct absorption of UV (>311 nm) by photosynthetic pigments maximally enhanced photosynthesis of *Sorghum bicolor*. In addition, little UV-A and UV-B+A effects on C_i (Table 1) and g_s showed that UV radiation did not cause stomatal limitation.

Although leaf RWC was decreased by UV-A and additionally reduced by UV-B+A, the ABA content and g_s were not affected in both treatments. In this case, the reduction of RWC did not influence plant photosynthesis in the two populations. As a tool to measure long-term WUE (Farquhar *et al*. 1989), $\delta^{13}C$ value was significantly increased by UV-A and UV-B+A in LA-population but only increased by UV-B+A in HA-population (Table 1), which was consistent with enhanced WUEi under UV exposure. Reduction of RWC as well as increased WUE (long-term and intrinsic) showed that UV radiation improved the water economy of sea buckthorn, as reported by Manetas *et al*. (1997).

Chl fluorescence is a sensitive general biomarker to UV exposure (Cordi *et al*. 1997). We found little effect by UV-A in all Chl fluorescence parameters compared with –UV treatment. Under UV-B+A, although F_v/F_m remained unaffected, F_0, F_m, Y, and q_P were significantly decreased in two populations, with increased q_N in HA-population. As shown by Praxedes *et al*. (2006), constant F_v/F_m implied that photoinhibition did not occur in both populations under UV-B+A exposure. However, the decline of F_0, F_m, and elevation of q_N showed that there existed more excitation energy under UV-B+A exposure *via* dissipation of q_N, in particular thermal dissipation, and this is also reinforced by enhanced content of total Cars (Table 1) that contribute to thermal dissipation and quenching of reactive oxygen species (Ort and Baker 2002). The increased excitation energy induced slight pressure on PS2 (indicated by the decrease in q_P), implying that a fraction of the PS2 traps was closed, thus bringing about a decrease in Y. Considering the constant F_v/F_m, Y reduction was likely related with PS2 down-regulation, which served as a photo-protective mechanism by adjusting the rate of photochemistry to match ATP and NADPH consumption (Praxedes *et al*. 2006).

Significant intra-specific differences of plant responses to UV-A existed in these two contrast populations (Table 1), although such effects were observed very rarely under UV-B+A. We found some modifications caused by UV-A radiation only existed in LA-population, such as significant reductions of leaf size, RWC, and Chl *b* content as well as $\delta^{13}C$ elevation, coupled with greater increase of total Car content. In this case, the LA-population was more physiologically responsive to UV-A, which might be a pre-acclimation strategy of LA-population to UV stress upon UV-A signal perception. These responses help plant seedling retain constant photochemical capacity and high P_N under UV-A. The HA-population, originating from colder conditions with high ambient UV radiation, has higher constitutive value of leaf thickness, UV-absorbing compound (Table 1), and ascorbic acid as found in our previous study (Yang *et al*. 2005), which make it much more tolerant to UV radiation. For this reason, UV-A intensity in our study seemed to be very small to incur those physiological modifications in HA-population. On the other hand, near-ambient UV-B+A caused significant reduction of leaf size and Chl content as well as slight down-regulation of PS2 that paralleled with higher heat dissipation, while P_N was modestly, but significantly increased. We suggest that the higher P_N under near-ambient UV-B+A radiation may be related to pronounced increase of leaf thickness and effective physiological modification, like the increase in contents of leaf protective pigments (Cars and UV-absorbing compound), constantly high photochemical capacity, and improved water economy.

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