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Photosynthesis of two moss crusts from the Tengger Desert with contrasting sensitivity to supplementary UV-B radiation

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Abstract

Predicting the effects of increased ultraviolet-B (UV-B) radiation due to stratospheric ozone depletion on temperate desert ecosystems requires better knowledge of the ecophysiological response of common moss species. The aim of the current work was to determine whether elevated UV-B radiation affected photosynthetic performance and chloroplast ultrastructure of two moss crusts and whether response differences were observed between the crusts. In laboratory experiments, *Bryum argenteum* and *Didymodon vinealis*, which show microdistributions and are dominant in soil crusts at the Tengger Desert, Northern China, were subjected to four levels of UV-B radiation of 2.75 (control), 3.08, 3.25, and 3.41 W m^{-2} for 10 days, simulating 0, 6, 9, and 12% of stratospheric ozone at the latitude of Shapotou, respectively. The results showed that chlorophyll *a* fluorescence parameters (*i.e.*, the maximal quantum yield of PSII photochemistry, the effective quantum yield of PSII photochemistry, and photochemical quenching coefficient), pigment contents, soluble protein contents, and the ultrastructure were negatively influenced by elevated UV-B radiation and the degree of detrimental effects significantly increased with the intensity of UV-B radiation. Moreover, results indicated that *B. argenteum* was probably more sensitive to supplementary UV-B radiation than *D. vinealis*. Therefore, we propose the use of *B. argenteum* crusts as a bioindicator of responses to elevated UV-B radiation.

Additional key words: biological soil crusts; chlorophyll *a* fluorescence; photosynthesis; ultraviolet-B.

Introduction

The depletion of stratospheric ozone by the emissions of man-made halocarbons has increased the intensity of UV-B radiation reaching the Earth surface (UNEP 2003). Considerable effort has been invested in determining plant responses to simulated ozone depletion, especially in economically important crops (McKenzie *et al*. 2003, Caldwell *et al*. 2007). Ozone depletion and the associated enhancement of intensity in shortwave UV-B radiation may influence the morphological, reproductive, physiological, and metabolic properties of higher plants, such as biomass and yields, pigment contents, nucleic acids, photosystem II (PSII), thylakoid membranes, and proteins (Reddy *et al*. 2003, Germ *et al*. 2005, Bashandy *et al*. 2009, Newsham and Robinson 2009, Hectors *et al*. 2010).

The effects of UV-B radiation on plants differ among species and are highly dependent on experimental conditions, UV-B radiation dosages, and the duration of exposure (Bassman *et al*. 2003, Bassman and Robberecht 2006). Several studies have found that elevated intensities of UV-B radiation have detrimental effects on

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Abbreviations: BSC – biological soil crusts; Car – carotenoids; Chl – chlorophyll; DE – days of exposure; F_0 – the minimal fluorescence of dark-adapted state; F_m – the maximal fluorescence of dark-adapted state; F_v/F_m – the maximal quantum yield of PSII photochemistry; $^{\bullet}OH$ – hydroxyl radicals; $O_2^{\bullet-}$ – superoxide anions; PAL – phenylalanine ammonia-lyase; PSII – photosystem II; q_P – photochemical quenching coefficient; ROS – reactive oxygen species; Rubisco – ribulose-1,5-bisphosphate carboxylase/oxygenase; TEM – transmission electron microscope; UV-B – ultraviolet-B; Φ_{PSII} – the effective quantum yield of PSII photochemistry.
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photosynthesis in several plant species (Keiller and Holmes 2001, Urban *et al*. 2006, Pradhan *et al*. 2008). It has been shown that a damage to PSII is one of the principal impacts of the reduced rate of photosynthesis under supplemental UV-B radiation (Albert *et al*. 2011). The state of PSII is assessed by the Chl *a* fluorescence parameters, *e.g*. by a decline in the maximal quantum yield of PSII photochemistry (F_v/F_m) that precedes decreases in photosynthetic rates. It has been reported that enhanced UV-B radiation induces reductions in both net photosynthetic rate and Chl content of *Prunus dulcis* (Ranjbarfordoei *et al*. 2011). Shi *et al*. (2004) showed that elevated UV-B radiation increased the photosynthetic rate per unit of leaf area of *Saussrea superba* and *Gentiana straminea*. In contrast, a few studies have reported no significant changes in the photosynthetic activity of other higher plants under elevated UV-B exposure (Chimphango *et al*. 2003, Sullivan *et al*. 2003). In addition, the effects on chloroplast ultrastructure have been observed only in response to UV-B radiation. The reported detrimental effects include a lower chloroplast number, wrinkled thylakoid membranes, and decreased starch grain density in *Brassica napus* and red algae (Fagerberg and Bornman 1997, 2005; Holzinger *et al*. 2004). In theory, these changes in chloroplasts can affect photosynthesis of plants. In contrast, Holzinger *et al*. (2006) concluded that there were no evident changes in chloroplast ultrastructure after short-term exposure to UV-B in green alga (*Prasiola crispa*).

Biological soil crusts (BSC) are the dominant biological surface feature of arid and semiarid zones (Li *et al*. 2011). They are composed primarily of cyanobacteria, green algae, lichens, mosses, and other organisms associated with particles of surface soil (West 1990, Belnap and Lange 2003, Li *et al*. 2010b). The importance of BSC in desert ecosystems has been extensively documented in the literature (Patrick 2002, Li *et al*. 2006b, Bowker 2006, 2007). They are considered desert "ecosystem engineers" (Li *et al*. 2002) as they can reduce the susceptibility of soils to both water and wind erosion (Zhang *et al*. 2006, Jia *et al*. 2012), create favorable habitats for the germination and establishment of vascular plants (Su *et al*. 2007), supply nutrients for fixing nitrogen and carbon (Darby *et al*. 2007), and affect the livelihood and habitation of soil animals (Whitford 2002, Li *et al*. 2006a). Although BSC are critically important in arid and semiarid communities, which account for more than 40% of the terrestrial living surface (Bowker *et al*. 2005), few studies have considered their photosynthetic performance and ultrastructure under elevated UV-B radiation (Csintalan *et al*. 2001, Belnap *et al*. 2007, Chen *et al*. 2009). To date studies on BSC have shown different responses to elevated UV-B radiation, and it remains controversial if they are responsive in terms of photosynthesis (Gehrke 1999, Lud *et al*. 2002, 2003). Niemi *et al*. (2002) reported that exposure to UV-B radiation increased the concentrations of Chl and carotenoids (Car) in *Sphagnum balticum*. In contrast, Martínez-Abaigar *et al*. (2003) showed reductions in the pigment content and in the net photosynthetic rate of *Fontinalis antipyretica* under enhanced UV-B radiation. Haapala *et al*. (2010) found that the moss, *Warnstorfia exannulata*, did not show any significant changes in rates of photosynthesis and in ultrastructure even under the exposure to high levels of UV-B.

The objective of this study was to determine the effects of the exposure to elevated UV-B radiation intensities on the photosynthetic performance and ultrastructure of two moss crusts species, *Bryum argenteum* Hedw. and *Didymodon vinealis* (Brid.) Zand. They are both dominant species in moss crusts found within patches of shrubs and herbs in the Tengger Desert of northern China. They exhibit commonly two distinctive microdistributions; *B. argenteum* is mostly distributed in flat areas and *D. vinealis* is usually situated in soil mounds protruding above the soil surface. Compared to *B. argenteum*, *D. vinealis* has longer exposure to higher UV-B radiation due to altitudes of its occurrence. Thus, considering their long-term exposure to different levels of UV-B radiation on account of distinctive microdistributions, we hypothesized that *D. vinealis* may be more tolerant to enhanced UV-B radiation than *B. argenteum*. In this study, we evaluated the effects of supplemental UV-B radiation on the activity of the photosynthetic apparatus as assessed by Chl *a* fluorescence parameters, photosynthetic pigment contents, and observations of chloroplast ultrastructure. Additionally, soluble proteins and UV-B absorbing compounds were simultaneously investigated to determine their possible relationships with photosynthetic parameters. The objectives of this study were to understand photosynthesis and chloroplast ultrastructure of *B. argenteum* and *D. vinealis* under elevated UV-B radiation, to estimate their sensitivity allowing prediction of the effects, and to determine if either moss crusts could be used as a bioindicator of increased UV-B radiation in arid and semiarid areas of China.

Materials and methods

Plant material and UV-B treatments: Well developed samples of *B. argenteum* and *D. vinealis* crusts with 100% coverage were randomly collected in the Shapotou area within the southeastern fringe of the Tengger Desert in Northwestern China (37°32′–37°36′N, 105°02′–104°30′E) in September 2010. The area is a transitional belt from desert steppe to steppified desert and an ecotone between desert and oasis (Li *et al*. 2003), with an elevation of 1,300 m. Mean annual sunshine is 3,264.7 h, mean annual air temperature is –6.9 °C, with extreme

minimum and maximum temperatures of –25.1 °C and 38.1°C, respectively. Mean annual precipitation is 186 mm, 80% of which falls primarily between May and September (the means are from the past 55 years). Dominant natural plants in the study area are *Hedysarum scoparium* Fisch. and *Agriophyllum squarrosum* Moq., with a cover of less than 1%. There are two main types of BSC – moss crusts and algal crusts. The moss crusts are mainly composed of *B. argenteum* and *D. vinealis*, and the algal crusts are mainly comprised of filamentous cyanobacteria, green algae, and diatoms (Li *et al*. 2010a). All crust samples were cleaned with distilled water before extraction with PVC rings (0.1 m in diameter, 0.05 m in height) to ensure sample integrity, after which they were air-dried and stored at the laboratory until the experiments began.

Four of biologically effective UV-B radiation intensities, *i.e*. 2.75 (control), 3.08, 3.25 and 3.41 W m^{-2} were imposed for 10 days, to simulate a depletion of the stratospheric ozone layer by 0, 6, 9, and 12%, respectively, during a clear day on Shapotou summer solstice. The experimental treatments were applied by a set of six 40 W fluorescent lamps (*UV-B 313*, *Chenchen Lighting and Electronics Company*, Shanghai, China) in the laboratory. The lamps were wrapped with 0.13 mm thick cellulose diacetate films (*Courtaulds Chemicals*, Derby, UK) to cut off UV-C radiation below 280 nm (Wang *et al*. 2010). The cellulose diacetate films were regularly replaced every 5 days to ensure the uniformity of UV-B transmission. The UV-B lamps were hung vertically above the moss crusts and the different UV-B radiation levels were obtained by varying the distance between the lamps and the top of the moss crusts. The lamps flanked both sides of cool white fluorescent lamps that provided photosynthetically active radiation. The moss crusts were irradiated from 09:00 to 17:00 h for 10 days and the spectral irradiance from the lamps was determined with a UV digital spectroradiometer (*Photoelectric Instrument Factory*, Beijing Normal University, Beijing, China). Each treatment had three replicates. All moss crusts were watered with distilled water daily and were maintained at 25°C during the experiment. Biological samples were immediately isolated from crusts every 5 d of exposure (DE) during the entire experimental period and frozen in liquid nitrogen and stored at –80°C prior to analysis.

Chl *a* fluorescence parameters were measured after 5 and 10 DE with a pulse amplitude modulated fluorometer (*MFMS-2*, *Hansatech*, UK), as described by Zhao and Wang (2002), in plants that were dark-adapted for 20 min. The minimal fluorescence of the dark-adapted state (F_0), the maximal fluorescence of the dark-adapted state (F_m), and photochemical quenching coefficient (q_P) were recorded. F_v/F_m and the effective quantum yield of PSII photochemistry (Φ_{PSII}) were calculated as $F_v/F_m = (F_m - F_0)/F_m$ and $\Phi_{PSII} = (F_m' - F_t)/F_m'$ (Schreiber *et al*. 1994, Havaux and Kloppstech 2001).

Chl and Car: Photosynthetic pigments were extracted by 100% ice cold ethanol and centrifuged at 12,000 × *g* for 30 min twice at 4°C. The transparent supernatant fractions were combined and used for determination of Chl and Car using a *752N* UV-Vis spectrophotometer (*Shanghai Precision and Scientific Instrument Company Ltd*., Shanghai, China) at 470, 649, and 665 nm, respectively (Lan *et al*. 2011).

Soluble protein content was measured using the Coomassie brilliant blue method (Bradford 1976) and bovine serum albumin as the standard. In short, 0.5 g of *B. argenteum* or *D. vinealis* shoots were homogenized in a cool phosphate buffer solution (*p*H 7.8) containing 1% (w/v) polyvinylpyrrolidone, 1% (w/v) phenylmethanesulfonyl fluoride, 1% (w/v) ascorbic acid, and 1% (v/v) Triton X-100 at 4°C. The mixtures were centrifuged at 15,000 × *g* for 20 min. The supernatants were used for determination of soluble proteins by recording their absorbance at 595 nm (Marshall and Williams 2000).

Total flavonoid content was determined in extracts by the $NaNO_2$-$Al(NO_3)_3$ colorimetric method (Atanassova *et al*. 2011). Fresh samples of 0.3 g were ground to a powder in liquid nitrogen and extracted with 10 mL of 70% (v/v) ethanol in an ultrasonic bath for 20 min at 50°C. The extracts were centrifuged for 15 min at 10,000 × *g* and the supernatants were combined and stored at 4°C. One mL of the supernatant was added to a 10 mL test tube containing 1 mL of 70% (v/v) ethanol and 0.3 mL of 5% (w/v) $NaNO_2$, shaken and then left to stand. After reacting for 6 min, 0.3 mL of 10% (w/v) $Al(NO_3)_3$ was added to each test tube and shaken. After another 6 min, 2 mL of 4% (w/v) NaOH was added. The solution was well mixed and left to stand for 10 min before absorbance was measured at 510 nm with a spectrophotometer. Quantification was done from a calibration curve using rutin (0, 5, 10, 15, 20, 25, 30, 35, 40, 45, and 50 $\mu g \cdot mL^{-1}$) as a standard. The results were expressed as rutin equivalents (RE) per 1 g of the fresh mass [$\mu g(RE)\ g^{-1}(FM)$].

Chloroplast ultrastructure: For transmission electron microscopy (TEM) examinations, small pieces (1–2 mm^2) of *B. argenteum* or *D. vinealis* shoots were cut and soaked in 3% glutaraldehyde solution buffered with 0.2 M sodium phosphate, pH 7.0, for 24 h at 4°C, and then rinsed three times with the same buffer solution, and fixed with 1% osmium tetroxide (OsO_4) for 120 min at 4°C. The samples were dehydrated by a graded series of ethanol solutions (50, 60, 70, 80, 90, and 100%), embedded in araldite resin, cut into ultrathin sections with a *LKB 4800* microtome (*LKB*, Bromma, Sweden) and observed under the *JEM-1230* electron microscope (*JEOL Ltd.*, Tokyo, Japan) with an accelerated voltage of 100 kV (Helliot *et al*. 2003).

Statistical analysis: All experimental results were presented as mean ± standard deviation (SD) of three replicates. One- and two-way analyses of variance (*ANOVA*) were performed using the *SPSS 16.0* statistical package (*SPSS*, Chicago, IL, USA). Where applicable, two-way *ANOVA* was used to evaluate the rates of reduction of species, UV-B radiation, and their combination on Chl *a* fluorescence parameters, photosynthetic pigments, soluble protein content, and total flavonoid content. For each species, one-way *ANOVA* was further used to determine differences among UV-B treatments. In all cases, *Duncan*'s test was used at a significance level of $p<0.05$.

Results

Chl *a* fluorescence: Both species and UV-B level significantly influenced Chl *a* fluorescence parameters though the interaction between species and UV-B level was not significant after 5 DE of UV-B radiation (Table 1). When exposed to UV-B radiation for 10 DE, F_v/F_m and q_P were significantly affected by species and UV-B level, whereas no significant differences in Chl *a* fluorescence parameters were observed in the interaction between species and UV-B level (Table 2). For each species, UV-B radiation significantly declined values of the Chl *a* fluorescence parameters (Fig. 1). In *B. argenteum*, F_v/F_m, Φ_{PSII}, and q_P decreased from 0.694 to 0.329 (Fig. 1*A*), 0.314 to 0.160 (Fig. 1*C*), and 0.739 to 0.456 (Fig. 1*E*), respectively, after 5 DE. Moreover, with the longer exposition period, F_v/F_m, Φ_{PSII}, and q_P showed continuing declines. When exposed to UV-B radiation for 10 DE, F_v/F_m, Φ_{PSII}, and q_P were more markedly inhibited than after 5 DE. Compared with those in the control conditions, F_v/F_m, Φ_{PSII}, and q_P decreased by 58.7% (Fig. 1*B*), 43.6% (Fig. 1*D*), and 40.2% (Fig. 1*F*), respectively, at 3.41 W m^{-2} of UV-B radiation. In *D. vinealis*, the F_v/F_m, Φ_{PSII}, and q_P were consistent with *B. argenteum* under increased UV-B radiation. The lowest values of F_v/F_m, Φ_{PSII}, and q_P were 0.413 (Fig. 1*A*), 0.190 (Fig. 1*C*), and 0.512 (Fig. 1*E*), respectively, and they were observed in *D. vinealis* treated at 3.41 W m^{-2} for 5 DE. In addition, the average values of F_v/F_m, Φ_{PSII}, and q_P were more strongly depressed, by 52.0% (Fig. 1*B*), 46.0% (Fig. 1*D*), and 32.0% (Fig. 1*F*), respectively, after 10 DE. In short, the Chl *a* fluorescence parameters showed that enhanced UV-B was harmful to PSII function of *B. argenteum* and *D. vinealis*, with the latter having higher Chl *a* fluorescence values than the former one.

Chl and Car contents were significantly affected by the species, UV-B level, and the interaction between the two after 5 DE, except for Chl *b* content (Table 1). With supplementary UV-B for 10 DE, all photosynthetic pigment contents differed significantly with regard to species, UV-B level, and the interaction between the two (Table 2). Enhanced UV-B exposure significantly reduced Chl *a* and Chl *b* content of *B. argenteum* and *D. vinealis*. When *B. argenteum* was exposed to 3.41 W m^{-2} UV-B radiation for 5 DE, the content of Chl *a* and Chl *b* decreased by 44.2% (Fig. 2*A*) and 37.7% (Fig. 2*C*), respectively. In *D. vinealis*, the content of Chl *a* and Chl *b* significantly were lowered by 52.5% (Fig. 2*A*) and 37.4% (Fig. 2*C*), respectively. The Chl *a*/*b* ratio in *B. argenteum* and *D. vinealis* declined significantly with increased UV-B dosage (Fig. 2*E*), because the reduction

Table 1. Effects of species and UV-B radiation on chlorophyll *a* fluorescence parameters, photosynthetic pigments, soluble protein content, and total flavonoid content after 5 days based on one-way and two-way *ANOVA*. Each value represents the rates of reduction compared to control (2.75 W m^{-2} UV-B treatments), and it is the mean ± standard deviation (SD, $n\geq3$). The significance of reduction rates was tested with a one-way *ANOVA* comparing different intensity of UV-B radiation, and *different letters* in the same row are significantly different at the 0.05 level according to *Duncan*'s test. Species×UV-B indicates the interactive effect between species and UV-B radiation. The effects are significant at the level of $p<0.05$ with a two-way *ANOVA*, the same is below. Car – carotenoid; Chl – chlorophyll; F_v/F_m – the maximal quantum yield of PSII photochemistry; q_P – photochemical quenching coefficient; Φ_{PSII} – the effective quantum yield of PSII photochemistry.

	Mean ± SD [%]						*p*-value		
	Species		UV-B [W m^{-2}]						
	B. argenteum	*D. vinealis*	2.75	3.08	3.25	3.41	Species	UV-B	Species×UV-B
F_v/F_m	29.6 ± 0.2	21.6 ± 0.2	0	18.2 ± 0.0^b	38.5 ± 0.1^a	45.7 ± 0.096^a	0.008	<0.001	0.341
Φ_{PSII}	30.7 ± 0.2	18.1 ± 0.2	0	20.8 ± 0.1^b	34.8 ± 0.1^a	42.1 ± 0.081^a	0.001	<0.001	0.119
q_P	25.5 ± 0.2	12.2 ± 0.1	0	16.6 ± 0.1^b	27.2 ± 0.1^a	31.6 ± 0.081^a	<0.001	<0.001	0.056
Chl *a*	22.0 ± 0.2	25.5 ± 0.2	0	9.3 ± 0.0^c	37.3 ± 0.0^b	48.3 ± 0.044^a	<0.001	<0.001	<0.001
Chl *b*	18.5 ± 0. 2	16.7 ± 0.2	0	2.9 ± 0.0^c	29.8 ± 0.0^b	37.7 ± 0.017^a	0.019	<0.001	0.158
Chl *a*/*b*	4.80 ± 0.0	12.3 ± 0.1	0	6.6 ± 0.0^c	10.5 ± 0.1^b	17.0 ± 0.075^a	<0.001	<0.001	<0.001
Car	14.1 ± 0.2	7.70 ± 0.1	0	–9.5 ± 0.0^d	22.8 ± 0.1^b	30.2 ± 0.075^a	<0.001	<0.001	<0.001
Soluble protein	20.3 ± 0.2	5.70 ± 0.1	0	6.4 ± 0.0^c	20.0 ± 0.1^b	25.6 ± 0.137^a	<0.001	<0.001	<0.001
Total flavonoid	19.3 ± 0.3	5.60 ± 0.1	0	–13.6 ± 0.1^d	25.2 ± 0.1^b	38.1 ± 0.238^a	<0.001	<0.001	<0.001

Table 2. Effects of species and UV-B radiation on chlorophyll *a* fluorescence parameters, photosynthetic pigments, soluble protein content, and total flavonoid content after 10 days based on one-way and two-way *ANOVA*. Each value represents the rates of reduction compared with control (2.75 W m^{-2} UV-B treatments), and it is the mean ± standard deviation (SD, $n \geq 3$). The significance of reduction rates was tested with a one-way *ANOVA* comparing different intensity of UV-B radiation, and *different letters* in the same row are significantly different at the 0.05 level according to *Duncan*'s test. Species×UV-B indicates the interactive effect between species and UV-B radiation. The effects are significant at the level of $p<0.05$ with a two-way *ANOVA*. Car – carotenoid; Chl – chlorophyll; F_v/F_m – the maximal quantum yield of PSII photochemistry; q_P – photochemical quenching coefficient; Φ_{PSII} – the effective quantum yield of PSII photochemistry.

	Mean ± SD [%]						*p*-value		
	Species		UV-B [W m^{-2}]						
	B. argenteum	*D. vinealis*	2.75	3.08	3.25	3.41	Species	UV-B	Species×UV-B
F_v/F_m	35.5 ± 0.2	30.9 ± 0.2	0	28.2 ± 0.0^c	49.4 ± 0.0^b	55.3 ± 0.1^a	0.013	<0.001	0.468
Φ_{PSII}	26.1 ± 0.2	27.8 ± 0.2	0	22.4 ± 0.1^b	40.5 ± 0.1^a	44.9 ± 0.1^a	0.641	<0.001	0.991
q_P	25.2 ± 0.2	17.8 ± 0.1	0	20.6 ± 0.1^b	29.4 ± 0.1^a	36.1 ± 0.0^a	0.007	<0.001	0.365
Chl *a* [mg g^{-1}(FM)]	42.5 ± 0.3	30.0 ± 0.2	0	22.6 ± 0.0^c	57.2 ± 0.1^b	65.3 ± 0.1^a	<0.001	<0.001	<0.001
Chl *b* [mg g^{-1}(FM)]	31.2 ± 0.3	23.2 ± 0.2	0	10.6 ± 0.0^c	46.5 ± 0.1^b	51.8 ± 0.1^a	<0.001	<0.001	<0.001
Chl *a*/*b*	21.4 ± 0.1	10.5 ± 0.1	0	13.2 ± 0.1^c	21.5 ± 0.1^b	29.1 ± 0.1^a	<0.001	<0.001	<0.001
Car [mg g^{-1}(FM)]	43.1 ± 0.3	25.6 ± 0.2	0	31.1 ± 0.1^c	49.4 ± 0.1^b	57.0 ± 0.1^a	<0.001	<0.001	<0.001
Soluble protein [mg g^{-1}(FM)]	29.7 ± 0.2	18.0 ± 0.1	0	17.6 ± 0.1^c	35.5 ± 0.1^b	42.3 ± 0.1^a	<0.001	<0.001	<0.001
Total flavonoid [mg g^{-1}(FM)]	35.8 ± 0.3	26.1 ± 0.2	0	22.9 ± 0.0^c	44.8 ± 0.1^b	56.3 ± 0.1^a	<0.001	<0.001	<0.001

in Chl *a* was greater than the reduction in Chl *b*. During exposure to elevated UV-B radiation for 10 DE, the reductions in Chl *a*, Chl *b*, and Chl *a*/*b* were larger than after 5 DE. Chl *a*, Chl *b*, and Chl *a*/*b* ratio in the control were higher than those of all treatments. Specifically, Chl *a*, Chl *b*, and Chl *a*/*b* decreased by 74.9% (Fig. 2*B*), 60.9% (Fig. 2*D*), and 35.3% (Fig. 2*F*) in *B. argenteum* under 3.41 W m^{-2} UV-B, and by 55.6% (Fig. 2*B*), 42.2% (Fig. 2*D*), and 23.0% (Fig. 2*F*) in *D. vinealis*, respectively. On the other hand, Car content was significantly higher by 8.80% in *B. argenteum* and 10.1% in *D. vinealis* when exposed to 3.08 W m^{-2} UV-B radiation for 5 DE, but it decreased with further increases in UV-B radiation (Fig. 2*G*). The reductions in Car content were greater after 10 DE than after 5 DE. The average Car content decreased by 43.87%, 61.40%, and 61.27% in *B. argenteum*, and by 18.22%, 37.38%, and 46.82% in *D. vinealis* under the 3.08, 3.25, and 3.41 W m^{-2} UV-B treatments, respectively (Fig. 2*H*). In contrast, the content Chl *a*, Chl *b*, Chl *a*/*b*, and Car were reduced more in *B. argenteum* than in *D. vinealis* after 10 DE.

Soluble protein content: Significant effects of the species, UV-B level, and the interaction between the two were seen in the soluble protein content after UV-B radiation for 5 and 10 DE (Tables 1,2). Generally, elevated UV-B radiation markedly reduced the soluble protein content in *B. argenteum* after 5 and 10 DE. Compared with the control, the soluble protein content decreased by 10.2, 32.8, and 38.1% after 5 DE (Fig. 3*A*). When treated by UV-B for 10 DE, the soluble protein content was lower than that after 5 DE. Average soluble protein content decreased by 23.1, 43.7, and 52.2% under 3.08, 3.25, and 3.41 W m^{-2} UV-B, respectively (Fig. 3*B*). In *D. vinealis*, the soluble protein content showed similar response patterns when measured after 5 and 10 DE of elevated UV-B radiation. With 5 DE of supplementary UV-B, the soluble protein content declined by 2.67, 7.14, and 13.11% in contrast with the control (Fig. 3*A*). After 10 DE, significant reductions of 12.24% at 3.08 W m^{-2}, 27.16% at 3.25 W m^{-2}, and 32.44% at 3.41 W m^{-2} UV-B were shown (Fig. 3*B*).

Total flavonoid content was significantly affected by the species, UV-B level, and the interaction between the two (Tables 1,2). For each moss species, total flavonoid content showed a significant increase of 13.4% in *B. argenteum* (Fig. 4*A*) and 12.1% in *D. vinealis* (Fig. 4*B*) after 5 DE of UV-B radiation at 3.08 W m^{-2}, but the content of total flavonoid declined significantly with elevated UV-B dose. The total flavonoid content declined further compared with the control, when *B. argenteum* and *D. vinealis* were exposed to UV-B radiation for 10 DE. In *B. argenteum*, the total flavonoid content was significantly reduced by 25.1% at UV-B radiation of 3.08 W m^{-2}, by 51.2% at 3.25 W m^{-2}, and by 67.1% at 3.41 W m^{-2} (Fig. 4*A*). In *D. vinealis*, the total flavonoid content decreased by 20.8, 38.3, and 45.5% for each UV-B radiation treatment compared with the control (Fig. 4*B*), respectively. After 10 DE of UV-B radiation, *B. argenteum* showed the greater total flavonoid content reduction than *D. vinealis* did.

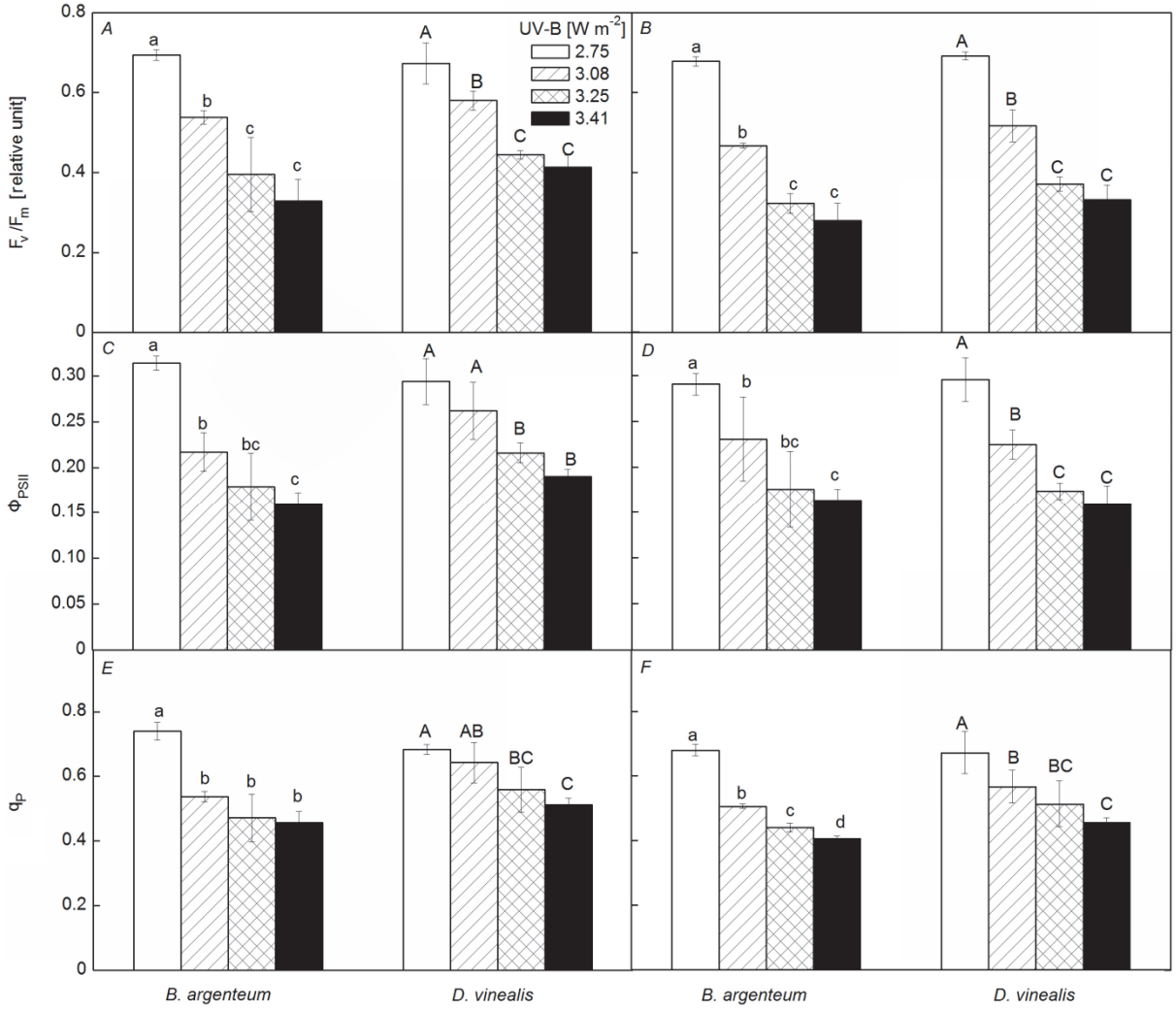

Fig. 1. Changes in F_v/F_m (*A*,*B*), Φ_{PSII} (*C*,*D*), and q_P (*E*,*F*) of *B. argenteum* and *D. vinealis* after 5 (*A*,*C*,*E*) and 10 days (*B*,*D*,*F*) enhanced UV-B radiation treatments of 2.75, 3.08, 3.25, and 3.41 W m^{-2}. Values are means ± standard deviation (SD, $n \geq 3$). Columns with different letters are significantly different at the 0.05 level. F_v/F_m – the maximal quantum yield of PSII photochemistry; q_P – photochemical quenching coefficient; Φ_{PSII} – the effective quantum yield of PSII photochemistry.

Chloroplast ultrastructure: Under ambient UV-B radiation, chloroplasts showed an elliptical shape, thylakoid membranes were intact, stroma thylakoids were parallel to each other and had tightly stacked granal thylakoids, and the lamellar structures of the thylakoids in the chloroplasts were close together (Fig. 5*A*,*E*) in both moss species. When the moss crusts were treated with elevated UV-B radiation, the chloroplasts became rounded instead of elliptical, chloroplast membranes were damaged, lamellar structures of the thylakoids were swollen and dissolved, thylakoids were often greatly distended, leading to the appearance of vesicles in the stroma, and the number of osmiophilic granules increased in the chloroplasts (Fig. 5*B–D*,*F–H*). The cells of both two mosses had lens like oblong shapes and plasmolysis occurred due to protoplast shrinkage outside the cell walls (Fig. 6*B–D*,*F–H*). With the increase in UV-B radiation level, the percentage of the deformed chloroplasts and cells increased and the chloroplasts and cells were seriously damaged in *B. argenteum* and *D. vinealis.* In particular, when the dosage of UV-B increased to 3.41 W m^{-2}, most chloroplast membranes were disrupted and became unidentifiable as a result of osmiophilic granules being released into the stroma, thylakoid structures were much looser, and the thylakoid lamellae were mostly dissolved or even fractured (Fig. 5*D*,*H*). Moreover, the damage to chloroplasts and cells in *B. argenteum* was more serious than that in *D. vinealis*.

Discussion

Our results demonstrated that supplementary UV-B radiation induced detrimental effects in both mosses, and the negative effects on photosynthesis and chloroplast ultrastructures were more serious in *B. argenteum* than that in *D. vinealis*.

Photosynthetic processes in various plants are very sensitive to high UV-B radiation (Xu *et al*. 2009, Zu *et al*. 2010). Many researchers have found that supplementary UV-B radiation causes a wide range of changes in plants (Bassman and Robberecht 2006, Manukyan 2012). However, the reported effects of relatively high UV-B levels on plant photosynthesis and related properties are

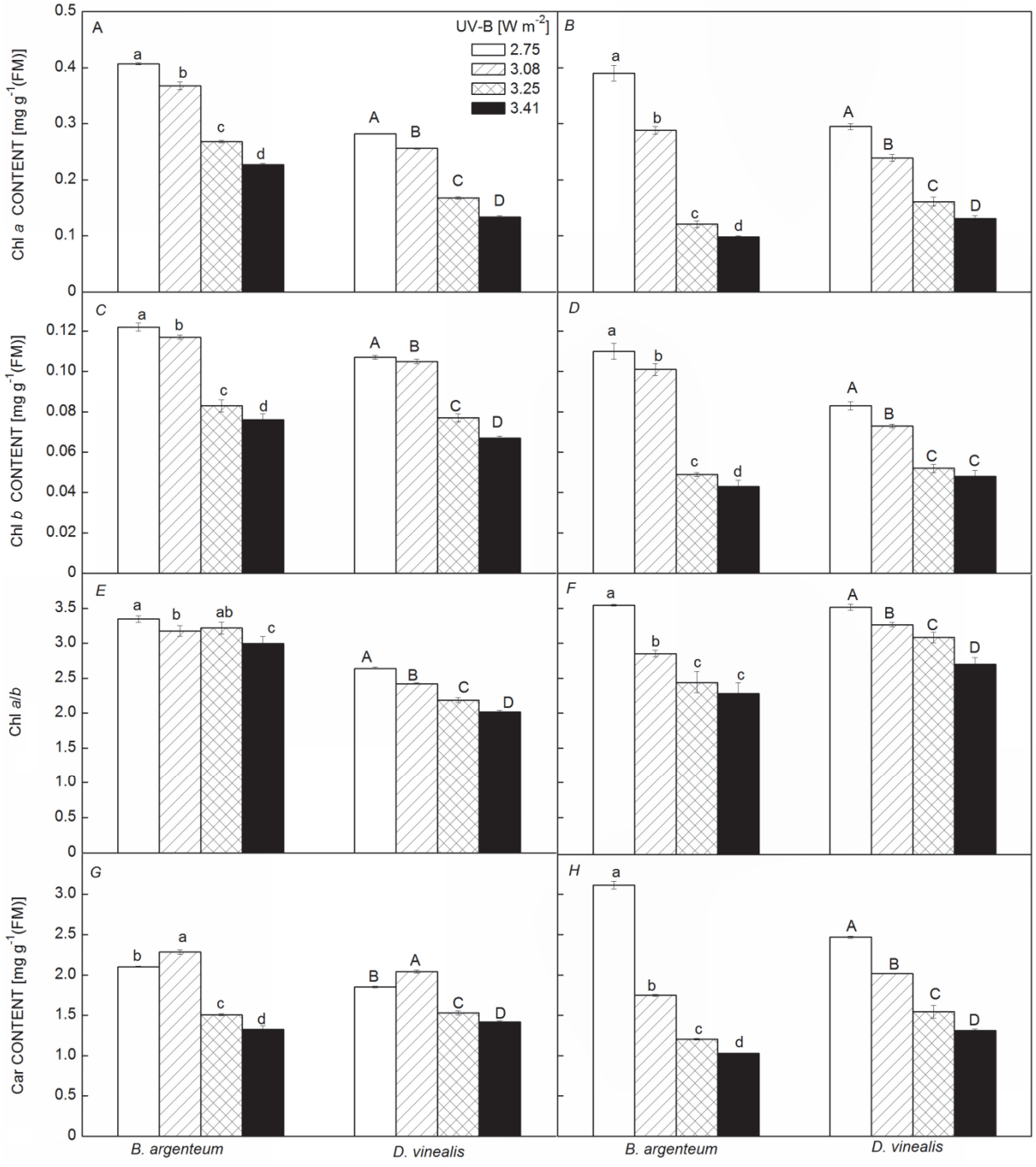

Fig. 2. Changes in Chl *a* (*A*,*B*), Chl *b* (*C*,*D*), Chl *a*/*b* (*E*,*F*), and Car (*G*,*H*) contents of *B. argenteum* and *D. vinealis* after 5 (*A*,*C*,*E*,*G*) and 10 days (*B*,*D*,*F*,*H*) of enhanced UV-B radiation of 2.75, 3.08, 3.25, and 3.41 W m^{-2}. Car – carotenoid; Chl – chlorophyll.

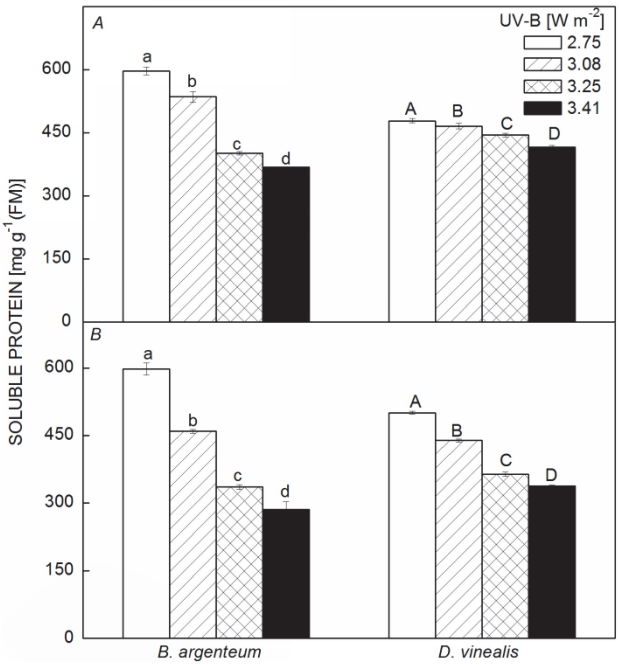

Fig. 3. Changes in soluble protein content of *B. argenteum* and *D. vinealis* after 5 (*A*) and 10 days (*B*) of enhanced UV-B radiation treatments with 2.75, 3.08, 3.25, and 3.41 W m^{-2}.

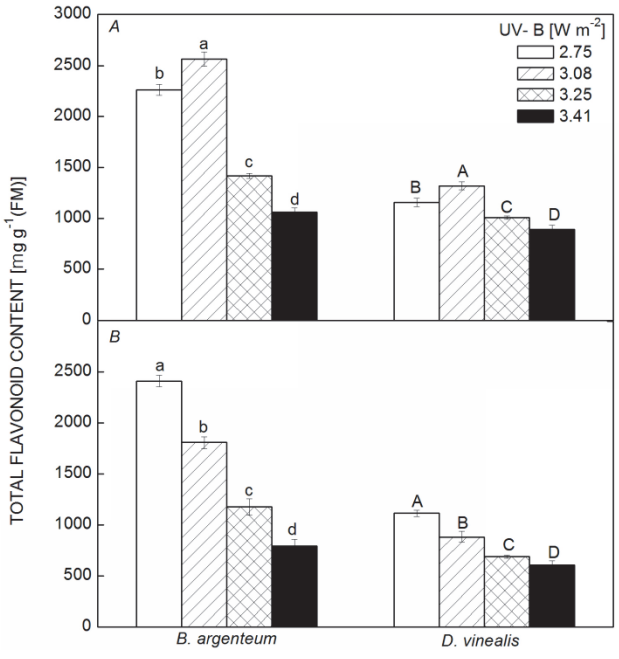

Fig. 4. Changes in the total flavonoid content of *B. argenteum* and *D. vinealis* after 5 (*A*) and 10 days (*B)* of enhanced UV-B radiation treatments with 2.75, 3.08, 3.25, and 3.41 W m^{-2}.

variable, and may differ even between genotypes of species (Kakani *et al*. 2003). Our results demonstrated that elevated intensities of UV-B radiation caused obvious reduction in Chl *a* fluorescence parameters and of Chl content in both two mosses. Moreover, the inhibitory effect of UV-B on the mosses was promoted as the dosage of UV-B increased (Figs. 1, 2).

Regarded as the most sensitive photosynthetic target, PSII is often susceptible to UV-B (Bornman 1989, Joshi *et al*. 2011). The UV-B induced inhibition of photosynthesis may be caused by the loss of photochemical efficiency of PSII. As the most used Chl *a* fluorescence parameter, F_v/F_m represents the conversion efficiency of primary light energy and PSII capture efficiency of primary light energy (Guo *et al*. 2005, Guidi *et al*. 2007), and it is widely used to evaluate effects of environmental stress on plants (Kummerová *et al*. 2006). In our experiment, increased UV-B radiation induced the linear decrease in F_v/F_m in *B. argenteum* and *D. vinealis* (Fig. 1*A*,*B*). q_P is used to assess the actual utilization of energy absorbed by PSII antennae and as an indicator of the proportion of open PSII centers (Wilson and Jacobs 2012). In the present study, sustained declines in q_P induced by relatively high UV-B levels in *B. argenteum* and *D. vinealis* (Fig. 1*G*,*H*) suggests that both two moss crusts failed to keep PSII centers in an open state, thus the excitation energy could not be used for the electron transport. The elevated UV-B radiation decreased drastically Φ_{PSII} in *B. argenteum* and *D. vinealis* (Fig. 1*C*,*D*), which might be linked to changes in the overall activity of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) (Bischof *et al*. 2000). This suggests that the photochemical efficiency of open PSII reaction centers declined. Similarly to this study, Surabhi *et al*. (2009) demonstrated that q_P declined in the sensitive cultivar of cowpea (*Vigna unguiculata* (L.) Walp.) as UV-B exposure increased. The changes in photosynthetic parameters were greater in *B. argenteum* than those in *D. vineali*, and the decline in the Chl *a* fluorescence parameters depended on the period of UV-B exposure.

Loss of Chl is a negative effect of UV-B and may be an indication of ongoing senescence (Weichmann 2000). Many reports have shown that one of the most common symptoms of elevated UV-B exposure is a decrease in Chl concentration (Medina *et al*. 2010, Zu *et al*. 2011). Declines in Chl concentration in UV-B treated shoots have been related to the suppression of aminolevulinic acid synthesis or a reduction in protochlorophyllide (Choi and Roh 2003). In our study, the content of Chl *a* and Chl *b* decreased significantly in *B. argenteum* and *D. vinealis* with supplementary UV-B radiation (Fig. 2). Reductions in Chl content induced by exposure to relatively high UV-B levels were probably due to the destruction of chloroplast structures, which inhibited the synthesis of new Chl and stimulated the degradation of the existing Chl (Niemi *et al*. 2002, Peng and Zhou 2009). These results are in agreement with those for cyanobacterial soil crusts reported by Bowker *et al*. (2002), which showed that UV-B augmentation resulted in a decline in Chl *a* content. Furthermore, our results supported the conclusions of Xie *et al*. (2009) who reported that exposure to UV-B resulted in photoinhibition

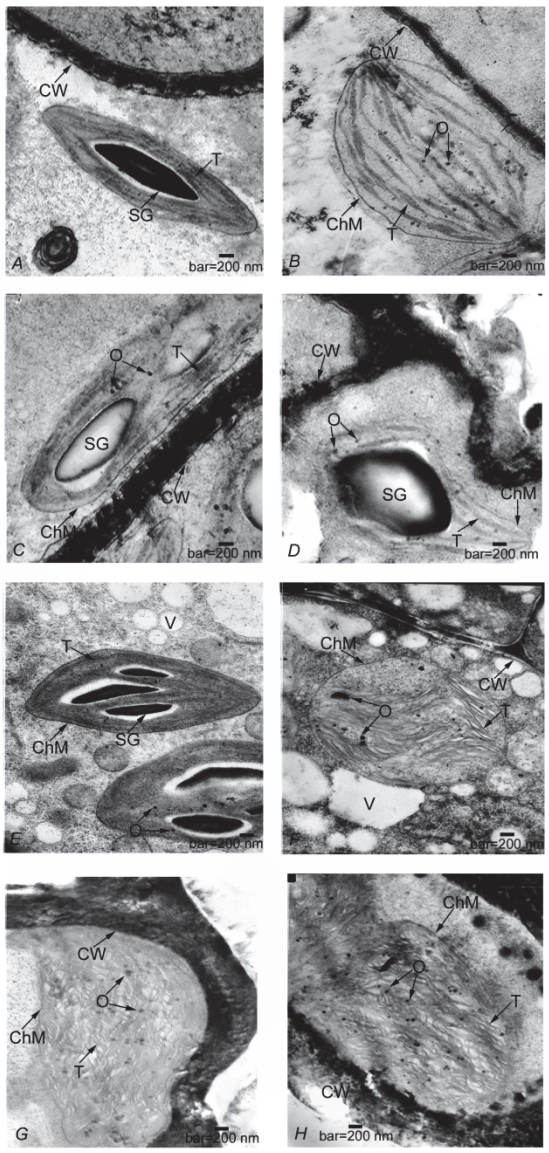

Fig. 5. Chloroplast ultrastructure of *B. argenteum* (*A*,*B*,*C*,*D*) and *D. vinealis* (*E*,*F*,*G*,*H*) at 2.75 (*A*,*E*), 3.08 (*B*,*F*), 3.25 (*C*,*G*), and 3.41 W m^{-2} (*D*,*H*) of UV-B after 10 days of radiation. Bars indicate 200 nm. ChM – chloroplast membrane; CW – cell wall; O – osmiophilic granule; SG – starch grain; T – thylakoid; V – vesicle.

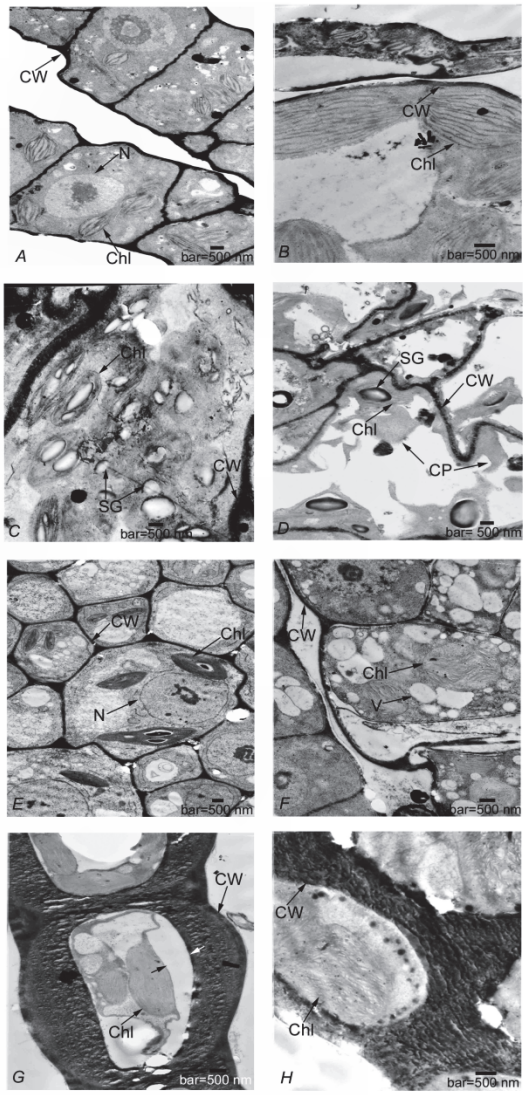

Fig. 6. Ultrastructure of *B. argenteum* (*A*,*B*,*C*,*D*) and *D. vinealis* cell (*E*,*F*,*G*,*H*) at 2.75 (*A*,*E*), 3.08 (*B*,*F*), 3.25 (*C*,*G*), and 3.41 W m^{-2} (*D*,*H*) after UV-B radiation for 10 days. Bars indicate 500 nm. Chl – chloroplast; CP – cytoplasm; CW – cell wall; N – nucleus; SG – starch grain.

of *Microcoleus vaginatus* soil crusts. The ratio of Chl *a*/*b* was significantly lowered in both two mosses due to a stronger reduction in the content of Chl *a* under elevated UV-B radiation. Similarly, Liu *et al*. (2012) reported that UV-B radiation reduced the ratio of Chl *a*/*b*. However, contradictory results for the responses of the Chl *a/b* to supplementary UV-B radiation have been reported. For example, Zhao *et al*. (2003) found that the Chl *a*/*b* ratio significantly increased in cotton plants under elevated UV-B. In addition, several studies have reported that pigment content is related to the photosynthetic membrane; thus, a loss of membrane integrity causes a loss in the balance of the photosystem pigment pool (Çakirlar *et al*. 2008).

Soluble proteins in plants are closely related to metabolic activity and strongly influenced by enhanced UV-B radiation. In our study, supplementary UV-B radiation markedly decreased the soluble protein content in *B. argenteum* and *D. vinealis* (Fig. 3). This might be due to diverse modifications including photooxidation and photodegradation of amino acid residues in proteins as amino acids absorbed at 280 nm, which may change the molecular structure of proteins, leading to protein inactivation (Aráoz and Häder 1997). The degradation or inactivation of soluble proteins may be related to the fixation of CO_2, especially to the content of Rubisco and the D1 protein of PSII (Lee and Correia 2005, Kadur *et*

al. 2007), which should be reflected in a reduction of photosynthesis. The UV-B-induced inhibition of photosynthesis might be caused by the decreased photochemical efficiency, and this detrimental effect may be related to the content or activity of Rubisco, a key regulatory enzyme in the Calvin cycle (Bischof *et al*. 2000, Mishra *et al*. 2008). These results are in accordance with those of Yu *et al*. (2004), who found that supplementary UV-B radiation significantly reduced the content of soluble protein in *Platymonas subcordiformis*. In contrast, Liu *et al*. (2005) found that UV-B radiation significantly increased soluble protein synthesis. The increase in soluble proteins may be attributed to strengthening of aromatic amino acids synthesis, and hence to the acceleration of flavonoids biosynthesis to protect the organism from UV-B damage (Mackerness *et al*. 2001, Ryan *et al*. 2002).

UV-B absorbing compounds are the "first line of defense" against UV-B radiation damage induced in plants. Bieza and Lois (2001) reported that increased levels of UV absorbing compounds provide a shield against UV before reaching a sensitive target. Car and flavonoids have effective radical scavenging capabilities and they can strengthen photoprotection to reduce the effects of enhanced UV-B radiation (Flint *et al*. 2004, Kumari and Agrawal 2010). Our results suggest that the UV-B induced increase in the content of Car and total flavonoids was transitory in *B. argenteum* and *D. vinealis*, with maximal values after 5 DE to 3.08 W m^{-2} UV-B radiation (Fig. 2*G*,*H*,4). This might be an ecological adaption for both mosses under enhanced UV-B radiation. This was identical with the findings of Newsham *et al*. (2002), who found that total Car concentrations increased in bryophyte tissues in response to elevated UV-B radiation exposure. Furthermore, it supports the conclusions of Sangtarash *et al*. (2009), who observed supplementary UV-B radiation induced increases in Car concentrations in canola (*Brassica napus*). The significant increase in the content of flavonoids in wheat seedlings were reported by Yao *et al*. (2011). Promotion of the phenylpropanoid pathway genes is a common response to abiotic and biotic environmental stresses including UV-B in plants (Ryan and Hunt 2005, Caldwell *et al*. 2007). This pathway produces phenolic compounds, such as flavonoids, tannins, and anthocyanins (Cerovic *et al*. 2002). UV-B radiation induces production of several key phenylpropanoid pathway enzymes (Bieza and Lois 2001, Pluskota *et al*. 2005), leading to increased production of flavonoids (Roberts and Paul 2006, Vogt 2010). Therefore, we assumed that enhanced UV-B radiation leading to the flavonoid biosynthesis might be actually strengthened by 3.08 W m^{-2} of UV-B after 5 DE, while high levels of UV-B irradiation might contribute to the inhibition of phenylpropanoid pathway enzymes. This hypothesis is supported by the Eichholz *et al*. (2012), who demonstrated that low UV-B dosage resulted in a stimulation of phenylalanine ammonia-lyase (PAL) activity in white asparagus (*Asparagus officinalis* L.). Zu *et al*. (2011) found that supplementary UV-B radiation significantly inhibited synthesis of flavonoid in Korean pine needles. However, Car and total flavonoid content decreased with UV-B radiation intensity and irradiation time because the generating way of protective pigments induced by UV-B may have already been saturated (Deckmyn *et al*. 1994). Zheng *et al*. (2008) found that low intensity and short period of UV-B radiation induced the accumulation of catechins in tea (*Camellia sinensis*), while excessive UV-B radiation suppressed their accumulation. Our findings suggest that there was a depression in flavonoids under high levels of UV-B radiation, which was in accordance with the change in the soluble protein content.

In plant cells, photosynthesis occurs in chloroplasts (Allen *et al*. 2011), and our results showed that chloroplast and cell developments were defective in *B. argenteum* and *D. vinealis,* when exposed to elevated UV-B. Chloroplast membranes were disrupted and swollen, and the lamellar structures of thylakoids in cells were loose and obscured under supplementary UV-B radiation (Figs. 5, 6). TEM indicated that the inhibition of enhanced UV-B radiation on the photosynthetic parameters closely correlated with the damage of the chloroplast ultrastructure in cells. The damaged chloroplasts and cell membranes in both mosses might be associated with the PSII function, as significant decrease in F_v/F_m and Φ_{PSII} (Fig. 1) was observed. The destruction of thylakoid membranes leads to deterioration of chloroplast protein stability of and it accelerates the decomposition of Chl under elevated UV-B radiation (Bray *et al*. 2000). Protein and Chl contents in *B. argenteum* and *D. vinealis* showed the additional decline with enhanced levels of UV-B radiation, which supported the above conclusion. In addition, the irregular arrangement of granal thylakoids resulted in the decline in Chl content and depression in Chl *a* fluorescence. More serious damage to the membranes of chloroplasts, granal thylakoids, and lamellae structures was observed in *B. argenteum*, which confirmed the greater decrease in the photosynthetic parameters. In addition, the degree of damage to chloroplast ultrastructure depended on the dosage of UV-B radiation, similarly to the changes in the photosynthetic parameters.

In this study, *B. argenteum* and *D. vinealis* were particularly sensitive to elevated UV-B radiation, possibly due to their simple structure. In both moss species, the shoots have only one layer of cells, which may result in the high internal UV-B flux. Yoshimura *et al*. (2010) showed that solar ultraviolet radiation caused transmittance to be greater in thin structures rather than in thick leaf structures of vascular plants. In the mosses, only the cell walls provide UV-B shielding because they lack the protection of a cuticle. In addition, both moss species are rootless and therefore they lack ability to protect themselves from increasing UV-B radiation

(Gehrke 1999). However, the ability of both two moss crusts to resist UV-B radiation was not identical. Results showed that *D. vinealis* exhibited usually greater resilience than *B. argenteum* under supplementary UV-B radiation, especially under higher doses of UV-B. Specifically, UV-B radiation expanded the discrepancy in the Chl *a* fluorescence parameters, Chl and Car contents, and soluble protein content between both moss crusts, with *D. vinealis* showing higher values than *B. argenteum* did. This might result in greater competitive advantages of *D. vinealis* than of *B. argenteum* under elevated UV-B exposure.

In summary, elevated UV-B radiation induced significant damage to *B. argenteum* and *D.vinealis* in terms of Chl *a* fluorescence parameters, pigments, soluble protein contents, UV-B radiation absorbing ability, and chloroplast and cell ultrastructure. Although UV-B absorbing compounds in both two mosses could protect them against elevated UV-B damage, the protective mechanism was not efficient enough to prevent UV-B induced damage. This observation indicated that *B. argenteum* and *D.vinealis* exhibited significant sensitivity to increased UV-B radiation. Moreover, the damage was greater in *B. argenteum* than in *D. vinealis*. Therefore, we propose to use *B. argenteum* crusts as a bioindicator of responses to elevated UV-B radiation.

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