热带亚热带植物学报 2011,19(2): 120~126
Journal of Tropical and Subtropical Botany

多蒴灰藓对强紫外线照射的生理响应

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摘要: 将多蒴灰藓(*Hypnum fertile*)置于紫外辐射下照光 3 周,研究了紫外辐射对多蒴灰藓的损害及其生理响应。结果表明: 与对照(自然环境)相比,多蒴灰藓的叶绿素和类胡萝卜素含量均随紫外辐射时间的延长而减少,MDA 含量却明显增加,SOD、POD 和 CAT 活性也相应增加;增加紫外辐射量会引起多蒴灰藓的氧化胁迫,其能通过增加抗氧化酶的活性来减轻这种胁迫。

关键词: 多蒴灰藓; 叶绿素; 类胡萝卜素; 抗氧化酶; 紫外辐射
中图分类号:Q948.112.1 **文献标识码**:A **文章编号**:1005-3395(2011)02-0120-07
doi: 10.3969/j.issn.1005-3395.2011.02.004

Physiological Responses to Enhanced UV-B Radiation of *Hypnum fertile*

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Abstract: The damages of *Hypnum fertile* (Bryopsida: Musci) and its physiological responses were studied under enhanced UV-B radiation for 3 weeks. The doses of biologically effective UV-B irradiation were 6.93 kJ m^{-2} d^{-1} (ambient UV-B radiation) and 9.01 kJ m^{-2} d^{-1} (enhanced UV-B radiation, about 30% higher than ambient UV-B radiation), respectively. The results showed that the contents of chlorophyll and carotenoid of *H. fertile* both decreased with time under enhanced UV-B radiation, whereas MDA content significantly increased, and the activities of SOD, POD and CAT all increased. It is suggested that enhanced UV-B radiation caused oxidative stress to *H. fertile* and the oxidative stress might be alleviated by increasing the enzymes activities.

Key words: *Hypnum fertile*; Chlorophyll; Carotenoid; Antioxidant enzymes; UV-B radiation

In spite of the current efforts to restrict the production of ozone-depleting substances, thinning of the stratospheric ozone layer and increasing penetration of ultraviolet-B radiation (280-320 nm) to the Earth's surface will continue for decades. Atmospheric ozone remains depleted and the annual average ozone loss is approximately 3% globally[1-2], causing not only the dramatic Antarctic ozone hole but also the general decline at temperate and high latitudes in both hemispheres[3].

An increase in UV-B radiation at Earth's surface will have potentially adverse effects on terrestrial ecosystems include agricultural lands, agro-ecosystems, and less intensively managed lands such as forests, grasslands, savannahs, deserts, tundra, etc[4-5].

Because plant species, even different genotypes of the same species, vary considerably in their sensitivity to this radiation, intensification of solar UV irradiance may alter competitive balance of plants[6-7]. Many studies have shown a deleterious UV-B effect on plant cells such as reduced photosynthesis and

Received: 2010-08-17 **Accepted**: 2010-12-08
Foundation items: Supported by the Science and Technology Commission of Shanghai Municipality (08390513800); Leading Academic Discipline Project of Shanghai Municipal Education Commission (J50401)
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biomass, decreased protein synthesis, impaired chloroplast function, damage to DNA, etc[8–9].

Mosses, though morphological and anatomical simple, are important members of terrestrial ecosystem. In recent years, there are much works refer to the effect of UV-B on mosses[10]. The main variables used to assess the effects of UV-B radiation involved shoot growth, both in length and dry mass, and photosynthesis rates, photosynthetic pigment composition (chlorophylls, carotenoids), chlorophyll fluorescence variables, UV-absorbing compounds, carbohydrates, as well as the morphological and ultrastructural features[11]. However, the present results were somewhat contradictory. No consistent conclusion concerning the susceptibility of moss to UV-B radiation was formed so far[10–12].

The moss, *Hypnum fertile,* which has a wide range of geographical distribution, is of medial size and crawl growth type, and may suffer from more UV-B radiation than other mosses. Therefore, *Hypnum fertile* is an ideal experimental material in conducting research on bryophyte physiological responses to enhanced UV-B radiation. The goals of our work were to ascertain the effects of enhanced UV-B radiation on *Hypnum fertile* and its physiological responses to UV-B stress by the variables of chlorophyll and antioxidant enzymes, thus to understand well about the physiological responses of mosses to enhanced UV-B radiation.

1 Material and methods

1.1 Plant material

The samples of *H. fertile* were collected from the same place, the summit of Bei Mountain (alt. 1200 m), 29°06′ N, 119°39′ E in Jinhua, Zhejiang Province, China, on 15 April, 2007. At this place, they grown in an open habitat and no shrubs and arbors shelter from light. The collected material were stored on wet filter papers for 2 days then used to be treated. In the course of treatment, the materials were retained hydrated by keeping the papers wet lest the influence by drought. After 7, 14, 21 days of UV-B radiation, respectively, the materials were collected at 9:00, and apical 3 cm gametophytes were washed in distilled water for three times then used to determine the physiological indices.

1.2 UV-B irradiation and cultivation environment

The experiment was conducted at about 10 m above sea level and the supplemental UV-B_{BE} dose in simulated ambient UV-B irradiation was 6.93 kJ $m^{-2}d^{-1}$ as control. The moss material used in the experiment collected from relatively open habitats at a high sea level (ca. 1200 m). The intensity of ultraviolet radiation increases by 1.3% when the altitude rises 100 m. Considering that the UV intensity of the habitat where the moss material collected was 15% stronger than that of the experimental condition, moreover, the annual rate of ozone destruction is 3%, therefore, we applied a treatment intensity 30% higher than that of the ground, that is to say, the UV intensity of the experimental treatment was actually about 15% stronger than that of the collecting habitat.

Visible radiation (photosynthetic active radiation, PAR from 400 nm to 700 nm) and supplementary UV-B radiation were both supplied for two treatments. Visible radiation was supplied by FSL-T8 lamps (Foshan Electrical and Lighting Co. Ltd. China). Polyester film (Lucky Films Co. Ltd., Baoding, China), 0.125 mm thick, was used to filter both UV-C and UV-B irradiation. The intensity of PAR was 60 μmol m^{-2} s^{-1}. Supplementary UV-B radiation was supplied by UV-B fluorescent lamps (Beijing Institute of Opto-Electronic, Technology, Beijing, China). The lamps were wrapped with 0.125 mm thick cellulose diacetate film (Lucky Films Co. Ltd., Baoding, China) filtering UV-C (<280 nm) irradiation to supply UV-B irradiation. All the lamps were mounted in metal frames. The distance from the lamps to plant was 70 cm. The spectral irradiance was weighted according to the generalized plant action spectrum[13] and normalized at 300 nm to obtain effective radiation (UV-B_{BE}). The supplemental UV-B_{BE} dose in simulated ambient UV-B irradiation was 6.93 kJ $m^{-2}d^{-1}$ using as control and enhanced UV-B radiation was 9.01 kJ $m^{-2}d^{-1}$ UV-B_{BE} (with 30% difference). The polyester and cellulose diacetate films were pre-

solarized for 8 h and changed every 7 days to ensure the uniformity of irradiation. The PAR lamps irradiated for 12 hours from 7:00 to 19:00 per day, and UV-B for 8 hours from 9:00 to 17:00. The treatments were achieved under air temperature of (25 ± 1) ℃.

1.3 Photosynthetic pigments

Gametophytes were homogenized in pre-chilled 95% ethanol, the contents of chlorophyll and carotenoid were determined spectrophotometrically by reading absorbance at 470 nm, 649 nm and 665 nm as described by Bao and Li[14].

1.4 Antioxidant enzyme assays

Enzymes were extracted by grinding 0.5 g of upper gametophytes in a pre-chilled mortar and pestle by liquid nitrogen with 6 ml of 100 mmol/L potassium phosphate buffer, pH 7.8 containing 1% polyvinyl polypryrolidone (PVP). The homogenate was filtered through four layers of cheesecloth and centrifuged at 12000 × *g* at 4℃ for 20 minutes and supernatant was used for enzyme assays.

SOD activity was measured according to Beyer and Fridovich[15] with some modifications, 3 mL reaction medium contained 50 mmol/L K-phosphate buffer, pH 7.8, 14 mmol/L methionine, 75 μmol/L NBT (nitroblue tetrazolium), 0.1 μmol/L EDTA, 2 μmol/L riboflavin. 0.1 mL of enzyme extract was added to start the reaction and incubate at 25℃ under 30 μmol $m^{-2}s^{-1}$ irradiance for 10 minutes. The reaction mixture without enzyme extract developed maximum color due to maximum rate of reduction of NBT. A non-irradiated reaction mixture did not develop color and was used as the control. The formation of blue formazan was monitored by taking the absorbance at 560 nm. One unit of SOD activity was defined as the amount of enzyme required to cause 50% inhibition of the rate of NBT photoreduction.

For the determination of POD activity, an aliquot of the supernatant was diluted 1: 24 with buffer before assay. The reaction medium was formed by 50 mL K-phosphate buffer with addition of 28 μL guaiacol and 19 μL H_2O_2. The reaction was started by adding 100 μL diluted enzyme extract to 3 mL reaction medium. Increase in the absorbance due to guaiacol oxidation was measured at 470 nm. Enzyme activity was defined as the increase in absorbance recorded at one OD value of A_{470} per minute under assay condition[16].

CAT activity was assayed according to the method of Zhang et al.[17]. Two Erlenmeyer flasks numbered were added with 200 μL enzyme extract and 9.8 mL K-phosphate buffer, respectively, then added with 5 mL 1.8 mol/L H_2SO_4 to No. 2 flask to denature the enzyme. Two flasks were incubated at 22℃ for 20 minutes, then respectively added 5 mL 0.02 mol/L H_2O_2 to react for 5 min accurately, later added 5 mL 1.8 mol/L H_2SO_4 to No. 1 flask. Then added 1 mL 20% KI, 3 drops of 10% ammonium molybdate, 5 drops of 1% amylum to the two flasks, the titration was with 0.02 mol/L $Na_2S_2O_3$. The activity of CAT can be calculated by the decomposition of H_2O_2.

1.5 Assay of lipid peroxidation

Oxidative damages to lipids were estimated as the content of total 2-thiobarbituric acid (TBA) reactive substances and expressed as equivalents of MDA according to the method of Zou[18]. Upper gametophytes were (0.8 g) homogenized in 6 mL of 10% (w/v) trichloroacetic acid (TCA), then centrifuged at 10000 × *g* for 10 minutes. An aliquot of 2 mL of supernatant was mixed with 2 mL of 0.6% 2-thiobarbituricacid in 10% TCA. The mixture was heated at 95℃ for 15 minutes and quickly cooled in an ice-water bath, after centrifugation again. The concentration of MDA was calculated from the absorbance at 532 nm (correction was done by subtracting the absorbance at 600 nm for unspecific turbidity) by using extinction coefficient of 155 $mmol^{-1}cm^{-1}$.

1.6 Statistical analysis

Values presented in the text indicate mean values ± S.E. of three independent experiments. The significance of differences between control and UV-B exposed material was analyzed using the Student's *t*-test for comparison of means at the level of

significance of $P<0.05$ or $P<0.01$.

2 Results

2.1 Effect of UV-B on photosynthetic pigments

Enhanced UV-B radiation markedly reduced Chl a, Chl b, and Chl (a + b) contents of *Hypnum fertile* (Table 1) compared to control, and the contents decreased with time. After *Hypnum fertile* were exposed for 7 days, 14 days and 21 days, respectively, the content of Chl a reduced by 6.0%, 13.4%, 15.0%; Chl b reduced by 6.2%, 7.0%, 14.6% and total chlorophyll reduced by 6.1%, 11.3%, 14.9%, and carotenoid reduced by 14.3%, 21.0% and 20.9%, respectively.

Table 1 Effects of UV-B radiation on chlorophyll content of *H. fertile*

Radiation days	Treatment	Chlorophyll content (mg g^{-1} FW)			Chl a/b	Carotenoid content (mg g^{-1} FW)
		Chl a	Chl b	Chl (a + b)		
7	Control	0.842 ± 0.012	0.418 ± 0.008	1.261 ± 0.020	2.014 ± 0.012	0.237 ± 0.009
	Treatment	0.794 ± 0.012*	0.408 ± 0.011	1.201 ± 0.011	1.949 ± 0.072	0.203 ± 0.014
14	Control	0.818 ± 0.018	0.400 ± 0.011	1.218 ± 0.014	2.050 ± 0.089	0.219 ± 0.009
	Treatment	0.705 ± 0.024*	0.382 ± 0.013	1.08 ± 0.018**	1.852 ± 0.112	0.173 ± 0.011*
21	Control	0.742 ± 0.018	0.379 ± 0.011	1.121 ± 0.029	1.958 ± 0.015	0.206 ± 0.010
	Treatment	0.63 ± 0.016*	0.324 ± 0.016	1.001 ± 0.022*	1.724 ± 0.088	0.163 ± 0.007*

$n=3$. *, ** indicate significant differences at 0.05 and 0.01 levels by Student's t test, respectively.

2.2 Effect of UV-B on lipid peroxidation

Fig. 1 showed that enhanced UV-B irradiation resulted in significant increase of MDA content of *H. fertile* compared to control. It suggested that membrane was damaged by enhanced UV-B irradiation. The injury aggravated with exposure time. After exposed for 7, 14, and 21 days, MDA content increased by 29.4%, 36.9%, 45.2%, respectively.

2.3 Effect of UV-B on the activities of SOD, POD and CAT

The activities of SOD, POD, and CAT all increased under enhanced UV-B radiation after 7, 14, 21 days of treatment as compared with control (Fig. 2 to 4), but the time for their activities to reach significant difference ($P<0.05$) were different. For SOD activity, enhanced UV-B irradiation for 7 days has no difference from control, after treated for 14 days and 21 days, the difference exhibited significant. For POD activity, after 21 days treatment of enhanced UV-B radiation, the difference exhibited significant ($P<0.05$). CAT activity after treated by UV-B for 7 days increase significantly compared with control. After treated for 7, 14, and 21 days, SOD activity increased by 9.0%, 19.9%, and 17.2%, POD

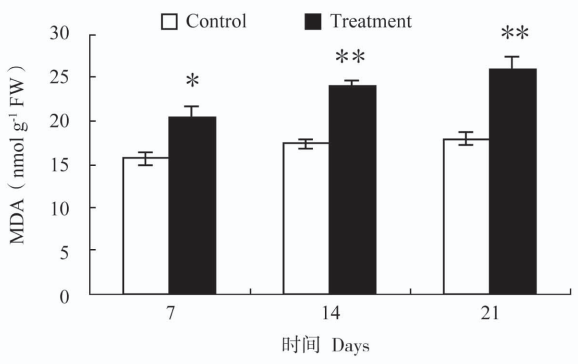

Fig. 1 Effect of UV-B on MDA content of *Hypnum fertile*

$n=3$; *, ** indicate significant differences at 0.05 and 0.01 levels by Student's t test, respectively.

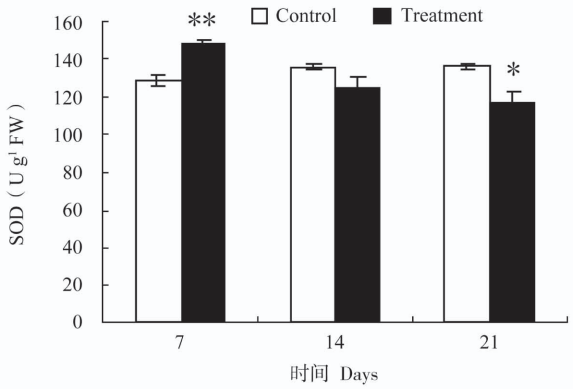

Fig. 2 Effect of UV-B on SOD activity of *Hypnum fertile*

$n=3$. *, ** indicate significant differences at 0.05 and 0.01 levels by Student's t test, respectively.

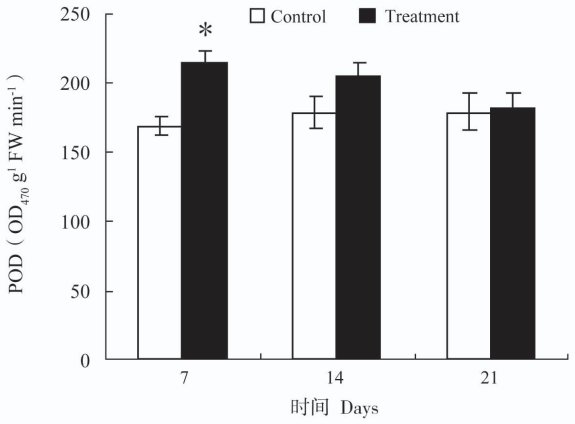

Fig. 3 Effect of UV-B on POD activity of *Hypnum fertile* $n=3$. *, ** indicate significant differences at 0.05 and 0.01 levels by Student's *t* test, respectively.

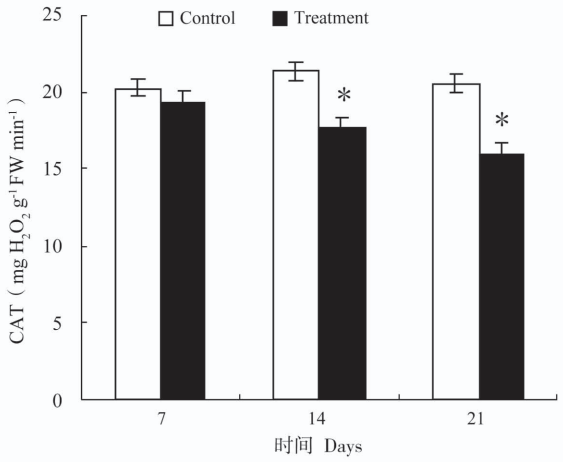

Fig. 4 Effect of UV-B on CAT activitiy of *Hypnum fertile* $n=3$. *, ** indicate significant differences at 0.05 and 0.01 levels by Student's *t* test, respectively.

activity increased by 1.1%, 15.2% and 26.8%, and POD activity increased by 11.5%, 15.3%, 34.2%, respectively.

3 Discussion and conclusions

The effects of UV-B on chlorophyll contents varied among different mosses. In the majority of the bryophytes investigated, chlorophyll concentrations are not influenced by UV-B exposure. However, after exposure to supplemental UV-B radiation, *Sphagnum fuscum* exhibited decreasing of chlorophyll a concentration, while chlorophyll levels in *Sphagnum balticum* increased[12]. In this study, Chl a, Chl b, total Chl, and Car contents all gradually reduced under enhanced UV-B radiation compared to simulated ambient UV-B radiation. Similar results were also reported in previous studies of other higher plants[1,8,19]. Such reduction in the level of Chl under UV-B enhanced radiation may be due to inhibition in their biosynthesis or breakdown of pigments or their precursors[19]. Moreover, Chlorophylls exist in a highly organized state by forming complexes with proteins and lipids; therefore, the UV-B induced degradation of protein and lipids complexes associated with pigments in the thylakoid membrane resulted in the decrease of Chl a[20]. The decreases of chlorophyll may protect the rest of the cell[8]. Several studies showed that Chl a content reduced more quickly than Chl b and Car contents, and resulted in the decrease of Chl a/b[3,21], which is not observed in our experiments. Since carotenoids protect chlorophyll from photooxidative destruction, therefore, any reduction in carotenoids could have serious consequences on chlorophyll[3,20]. However, we can explain the phenomenon in other way, the quick reduction of carotenoide content because the absorbance of UV-B radiation by its conjugated double bonds, thus protecting its chlorophylls from the UV-B radiation.

Studies showed that UV-B radiation produces oxidative stress, it is generally accepted that the mechanism of UV-B toxicity involves oxidative damage[22]. An efficient antioxidant defense system is present in plants to counteract oxidative stress. It is composed by enzymatic and non-enzymatic mechanisms. The former includes superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), etc. The non-enzymatic mechanisms consist of antioxidants such as ascorbate, glutathione, tocopherol and carotenoids[23]. Superoxide dismutase accelerates the conversion of superoxide to hydrogen peroxide, catalase and peroxidase catalyse H_2O_2 breakdown[22]. In regard to the activities of defense enzymes in higher plants to enhanced UV-B radiation, there still exist contradictory results[8,22,24]. This study showed hat the activities of SOD, POD, and CAT all increased in the moss of *H. fertile* under enhanced UV-B

radiation compared with the control. Our results suggested that enhanced UV-B radiation induced the enzymatic antioxidant defense system, which help the moss in acclimation to the stress.

MDA is an indicator of lipid peroxidation of membrane, and can be used to evaluate the impairment of lmembrane. MDA content in *H. fertile* increased with stress time under enhanced UV-B radiation, this indicated the membrane was damaged by active oxygen. The increase of MDA content may be due to the content of active oxygen exceeded the scavenge capability of antioxidant defense system in despite of the activities of SOD, POD, CAT all increased.

Concerning the susceptibility of moss to light radiation, one may assumed that the majority of mosses are susceptible to UV-B radiation. Because of their simple structure, only one cell layer of a leave, lacking protection by a cuticle, an undifferentiated leaf anatomy, leaf water content depends on air humidity and they are rootless and thus lack buffering against aboveground stress[25]. The nutrition of *Hypnum fertile* is mainly from atmospheric deposition and rain. The factor effected the growth of bryophyte is mainly humidity. Culturing moss with wet filter paper, not only form the same background for different treatments, but also provide humidity to maintain the vitality of moss.

Whereas the hitherto studies indicated the bryophytes are not more susceptible than vascular plants. Having studied the effects of enhanced UV-B radiation on *Hylocomium splendens* and *Polytrichum commune*, Gehrkel suggested that morphological and functional complexity of a species may not enhance the ability of individuals to cope with disturbances initially or on a short-term scale[25]. Photosynthetic and photoprotective pigments are often used to assess the effects of UV-B radiation on plants, but changes of these pigments in mosses under UV-B radiation are also exist contradictory results[11]. Our results suggested that enhanced UV-B radiation caused oxidative stress, the moss of *H. fertile* could alleviated stress by increasing the cell protective enzymes activities. Though the activities of SOD, POD, and CAT all increased under enhanced UV-B radiation, but the time for their activities to reach significant difference varied much, which may result from the difference of their sensitivity to oxidative stress from enhanced UV-B radiation.

This experiment was manipulated in laboratory with certain PAR and UV-B radiation and the material was keeping wet all alone. In natural conditions, mosses often suffer from drought, the PAR/UV-B ratio is different, there are many other factors could influence the results. Furthermore, the materials were irradiated for only three weeks, hence, different responses are likely to be appear under long-term UV-B irradiation. Further studies should consider these factors.

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