UV light spectral response of photosynthetic photochemical efficiency in alpine mosses

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Abstract

Aims

Bryophytes play an important role in primary production in harsh alpine environment. As other alpine plants, the alpine bryophytes are often exposed to stronger UV radiation than lowland plants. Plants growing under high UV radiation may differ from those from low UV regimes in their physiological response to UV radiation. We were to (i) test the hypothesis and to address whether and/or how alpine bryophytes differ in photosynthetic photochemical characteristics in response to UV light and (ii) understand the potential effects of UV radiation on photosynthetic photochemical process in alpine bryophytes.

Methods

We examined the maximum quantum efficiency of photosystem II (PSII) photochemistry (F_v/F_m) for two alpine bryophyte species, *Distichium inclinatum* and *Encalypta alpine*, from a *Kobresia humilis* meadow and a *Kobresia tibetica* wetland, respectively, in Haibei, Qinghai (37°29′N, 101°12′E, altitude 3 250 m), and for a lowland bryophyte, *Polytrichum juniperinum,* under different spectrum of UV light. Biological spectral weighting function (BSWF) was obtained to evaluate the effect of UV light on the physiological response in these species.

Important Findings

1) The maximum quantum efficiency of photosystem II photochemistry (F_v/F_m) declined linearly with the increase of radiation dose in wavelengths from 250 to 420 nm. The effect of UV radiation on F_v/F_m decreased with higher rate from 250 to 320 nm and from 400 to 420 nm than in UVA range.
2) The three species from different ecosystems contrasting in altitudes showed similar pattern of UV effectiveness. In comparison with other species reported so far, the moss BSWF was among those with the most modest decrease trend with spectrum effect of UV light 50 times higher at 250 than at 420 nm.
3) Under the scenario of 16% reduction of stratospheric ozone, the integrated effectiveness from 290 to 345 nm increased only 5%, suggesting that the photochemical activity of the bryophyte PSII is likely to insensitive to O_3 depletion.

Keywords: action spectrum • bryophyte • ozone • Tibetan Plateau • ultraviolet radiation

INTRODUCTION

Stratospheric ozone depletion has resulted in increase of UV radiation at Earth's surface (Madronich *et al.* 1998). Solar UV radiation reaching the Earth's surface spans from 280 to 400 nm. The increase of UV radiation in responding to ozone amount variation changes in different wavelengths (Lean and Rind 1998). Because of biological importance of UV radiation, a small change in UV radiation may have large biological and ecological consequences.

The biological effects of elevated ground-level UV radiation have been extensively examined on human health, processes of diverse organisms and ecosystems (Diffey 1991 and references therein; Björn 2007; Björn *et al.* 1999; Häder *et al.* 2007; Laakso and Huttunen 1998; Teramura and Sullivan 1994; Turnbull and Robinson 2009; Turnbull *et al.* 2009; UNEP

1998). In most of these studies, UV lamps and/or filters are used to alter artificially the UV spectrum or the total UV radiation (Björn and Teramura 1993; Musil *et al.* 2002; Qaderi *et al.* 2007; Rousseaux *et al.* 2004; Yao *et al.* 2006). Such experimental methods, however, introduce additional error in simulating UV irradiance change because any current artificial UV light or filter produce unique UV spectrum that differs considerably from the solar UV spectrum (Lean and Rind 1998; Madronich *et al.* 1994). Since biological and chemical photo-processes respond differently to different wavelengths of the UV spectrum, the biological effects of UV sources with the same energy may differ from each other if the spectrum differed. One solution to the spectrum effect of UV radiation of biological response is, perhaps, to use a biological effective dose, but not UV energy in either examination of the biological effects of UV radiation or in simulating the effect of ozone depletion-induced UV radiation change (Flint and Caldwell 2003; Madronich *et al.* 1994).

Biological effective dose of UV radiation is the product of UV energy spectrum and biological spectral weighting function (BSWF), i.e. the biological action spectrum (Flint and Caldwell 2003; Flint *et al.* 2003). Action spectra have long been constructed *in vitro* for biological pigments or molecules including DNA that absorb UV radiation and mediate the effects within an organism (Madronich *et al.* 1994). To evaluate the biological consequences of UV radiation, it is more important to know how the action spectra vary at organism level and/or among species (Björn 2007; Csintalan *et al.* 2001; Yao *et al.* 2006). The action spectra for biological parameters at physiological, population and community levels can provide important insight into our understanding of biological response to change of radiation environments in the future and, thus, are also essential to predict the effects of UV radiation variation on ecosystem functions. Unfortunately, such BSWFs are few terrestrial species and/or ecosystems up to now (Flint and Caldwell 2003).

Bryophytes are widely distributed on the earth. They are important pioneer species and even dominant species in polar, subpolar and alpine ecosystems, where the depletion of stratospheric ozone concentration is often larger and the UV radiation increase tends to be higher than other regions (Boelen *et al.* 2006; Gornall *et al.* 2007; Newsham *et al.* 2002). Lichens, bryophytes, high vascular plants and even soil microorganisms in these ecosystems have been found to respond significantly to artificial exclusion or supplementation of UV radiation (Johnson *et al.* 2002; Turnbull *et al.* 2009). In most of these experiments, only the total UV radiation has been considered in order to simulate the decrease of ozone column (most commonly in equivalent to 15–20% ozone depletion scenarios), few dealt with the spectral composition. BSWF is not the same for different genera or even congener species (Miller *et al.* 2009). However, within our knowledge, no action spectrum observation for UV radiation has been reported for bryophytes.

Chlorophyll fluorescence has been widely used in characterizing physiological effects of and adaptation to environmental stresses, including UVB increase (e.g. Csitalan *et al.* 1999; Newsham *et al.* 2002; Szôllôsi *et al.* 2008). Examining the chlorophyll fluorescence can be especially useful in photosynthetic studies of bryophytes that are often difficult for photosynthetic gas exchange methods because of their small size. Chlorophyll fluorescence reflects the fraction of absorbed light energy by light-harvesting pigments that are not used in chloroplast photochemistry or in thermal dissipation (Baker 2008). Photosynthesis, mass production and growth parameters are among the most commonly studied traits in UV manipulation experiments (Björn 2007; Boelen *et al.* 2006; Flint and Caldwell 2003; Teramura and Sullivan 1994; Turnbull and Robinson, 2009). Despite the extensive application of chlorophyll fluorescence, little information is available for BSWF based on chlorophyll fluorescence, in particular for bryophytes.

Bryophyte species can contribute to as high as 35% of primary production in an alpine shrub meadow on Tibetan Plateau (Li and Qi 1993), where mini-hole of stratospheric ozone layer is observed (Zhou and Luo 2004). Despite signs of ozone layer recovery have been captured, it is believed that it still needs a long time for total restoration (Son *et al.* 2009; Weatherhead and Andersen 2006; Yang *et al.* 2006). Therefore, it is interesting to know whether the productivity of bryophyte species will be affected by any change of UV radiation in the future. To address such issues, any knowledge about the photosynthetic response to UV radiation in these species would be necessary. In this study, we examined the maximum quantum efficiency of PSII photochemistry (F_v/F_m) at different doses of UV radiation from 250 to 400 nm for three bryophyte species, two from the Tibetan Plateau and the other one from a low altitude in Japan. The primary aims of the study include: (1) to construct the first BSWF of UV radiation for alpine bryophyte species based on the chlorophyll fluorescence and (2) to compare BSWF of F_v/F_m among the three species, as well as to BSWF of some other action spectra reported so far.

MATERIALS AND METHODS

Plant materials

Two bryophyte species, *Distichium inclinatum* and *Encalypta alpine*, were taken, respectively, from a *Kobresia humilis* meadow and a *Kobresia tibeica* wetland at Haibei Alpine Meadow Ecosystem Research Station of the Chinese Academy of Sciences (37°29′N, 101°12′E) in the northeast part of the Qinghai–TibetanPlateau. The altitude is ~3 250 m. Annual mean air temperature is –2°C and annual precipitation is 500 mm. The details for the alpine meadow and wetland can be found elsewhere (Hirota *et al.* 2004; Klein *et al.*, 2001). The sampled mosses were cultured in a growth chamber at 20°C/5°C (day/night) with 14-h day length and PPFD 620 μmol m^{-2} s^{-1} for ~5 months before we conducted the following measurements.

For comparison with lowland mosses, the third species was collected on the northern slope of an aqueduct in National Institute for Environmental Studies in Tsukuba, Japan (36°N, 140°E). The altitude is ~50 m. Intact patches of moss that lived

vigorously in open habitat were taken to laboratory the day before experiment. They were fully watered to maintain moist.

Instruments

A large spectrograph manufactured and installed specially made by JASCO corporation was used to generate UV light with a continuous spectrum from 250 to 1 100 nm, in which only the light with wavelengths shorter than 420 nm was used in this study. The focuses of the light with different wavelengths formed an arc at 20 cm high above a table. The spectrum was marked at 10-nm interval with lines along the radiation direction on the table. We made a wooden shelf for holding the moss. On the shelf, there are holes each with depth of 15 cm and inner diameter of 1 cm, equivalent to bandwidth of 2.5 nm. The holes were at the same height of light focuses, and each right above the corresponding lines marked on the table. The spectrometer was calibrated by the manufacturer before carrying out the experiment. The energy of UV light was listed in Table 1.

Chlorophyll *a* fluorescence was measured using a PAM-2000 fluorometer (Heinz Walz GmbH, Germany). The distance from the head of optical fiber to moss thallus, intensity and lasting time of saturation pulse light, signal gain and damp were pre-tested and adjusted to suit for moss measurement.

Experimental protocol

Patches of uniformly grown mosses were divided into small clusters. Rhizoid and part of the stems of these moss clusters were inserted into 15-ml plastic test tubes. The tubes were filled with tap water. A roll of paper towel was placed in each tube with one end touching moss rhizoid and the other end reaching the bottom of the tube. After the paper towel was fully wetted, part of free water was then poured and only 2 ml water remained at the tube bottom. The paper towel also prevented water from flowing out when the tubes were inserted into the holes horizontally. A preliminary experiment showed that moss samples maintained high water content (604 ± 238%, $n = 11$) after 2 h of UV exposure with this method. F_v/F_m of mosses was not negatively affected under the high water content (Cui *et al.* 2009).

The moss clusters were kept in darkness for at least 2 h before chlorophyll *a* fluorescence parameter F_v/F_m was measured. The tubes were then inserted into the holes of the wooden shelf and moss samples were exposed to UV radiation. They were taken out and F_v/F_m was measured in darkness at ~30-min interval. UV radiation exposure was lasted for ~4 h.

Data analysis

Fluorescence parameter calculation was based on the methods of Adams *et al.* (1999). F_v/F_m was estimated from $(F_m - F_0)/F_m$, where F_m was the maximum fluorescence after a saturating flash and F_0 was minimum fluorescence in total darkness.

Linear regression was used to fit the data of F_v/F_m to irradiance dose at each wavelength. When the linear correlation was statistically significant at the level of $P < 0.1$, the slope was adopted to characterize the dose-response of F_v/F_m for individual irradiance. The significant slopes contained three to nine replicate data for different wavelength in each species.

RESULTS

Dose–response relationships were produced for all wavelengths by expressing the magnitude of the F_v/F_m against the level of irradiance received from the UV light source. Examples of dose–response relationships at 250 and 280 nm were shown in Fig. 1. The response of F_v/F_m to UV light was linear within the range of used light dose (Fig. 1). For all the replicates of each wavelength, the linear relationships showed higher significant level in shorter wavelength in both UVB (from 280 to 320 nm) and UVA (>320 nm, Fig. 2). The linear relationship for the dynamics of the bryophyte F_v/F_m in the complete darkness was less significant and only 18% of the total replicates showed statistically significant linear correlation (CK, total 155 replicates). The significant slopes in controls (total darkness) were not uniformly negative, with 44.4% positive ones. The mean was also positive and was an order lower than those under light exposure, indicating that the bryophyte samples did not experience additional stress during the experiment.

The dose–response relationships were used to produce the action spectra (Fig. 3). The action spectrums of F_v/F_m in relation to the energy of different spectrum UV could be fitted to an exponential function. The decrease of F_v/F_m with the increase of UV light energy was 'slower' in UVA than in UVC and UVB (Fig. 3a and b). The effect of UV radiation on F_v/F_m decreased

Table 1: spectral energy of the spectrometer

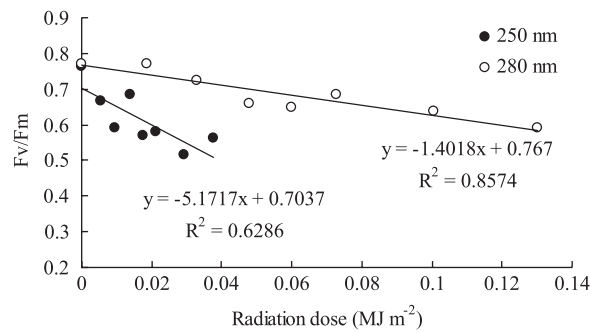| Wavelength (nm)	Energy (W m^{-2})	Photo flux density (µmol m^{-2} min^{-1})
250	2.18	2.74×10^2
260	4.56	5.94×10^2
270	6.32	8.55×10^2
280	7.53	1.06×10^3
290	8.52	1.24×10^3
300	10.58	1.59×10^3
310	11.85	1.84×10^3
320	13.41	2.15×10^3
330	14.05	2.33×10^3
340	15.05	2.57×10^3
350	15.88	2.79×10^3
360	16.01	2.89×10^3
370	15.88	2.95×10^3
380	16.56	3.15×10^3
390	17.85	3.49×10^3
400	18.23	3.66×10^3
410	18.11	3.72×10^3
420	18.78	3.95×10^3

Figure 1: response of the maximal quantum efficiency of photosystem photochemistry F_v/F_m to the dose of UV light of wavelength 250 and 280 nm in *Distichium inclinatum*
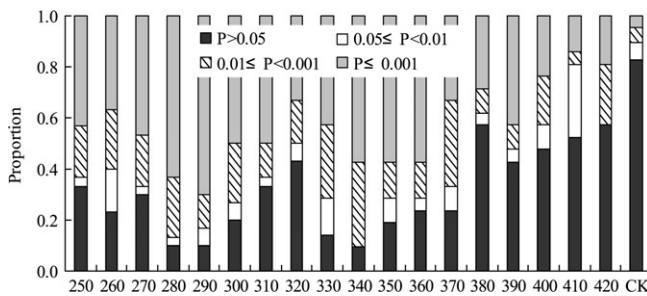

Figure 2: proportion of statistically significant levels for regression slope of the effect-dose lines.
At each wavelength, all the replicates for the three species were pooled.

Figure 3: action spectrum for UV radiation effect on F_v/F_m.
Data of three moss species were pooled. In (a), exponential regression curves were $y = 2290.66 \times 10^{-0.02542x}$ ($R^2 = 0.9482$) for absolute effect and $y = 1298.13 \times 10^{-0.02513x}$ ($R^2 = 0.9409$) for relative effect that all were normalized to 1.0 at 300 nm. In (b), the solid and dash lines were exponential regression for absolute and relative effects, respectively.

roughly 50 times from 250 to 420 nm. The pattern of the UV effect on F_v/F_m was similar in the three bryophyte species from contrasting elevation (Fig. 4). Compared with the action spectra for other physiological responses, the BSWF showed the mildest reduction of UV effect with the increment of wavelength (Fig. 5). Based on the BSWF obtained in the study, the integrated UV light effect on the bryophyte fluorescence increased only 5% under the same scenario of 16% reduction of stratospheric ozone, while it increased ~20% on growth of higher plants, 43% on Commission Internationale de l'Éclairage (CIE) erythemal dose and 95% on DNA damage (Fig. 6).

DISCUSSION

Wavelength-dependent responses to solar UV radiation have been reported for diverse plant parameters, including photosynthetic O_2 evolution and CO_2 uptake (Miller *et al.* 2009), UV-absorbing compounds (Zheng and Gao 2009), stomatal openness (Eisinger *et al.* 2000) and growth (Flint and Caldwell 2003). Chlorophyll fluorescence measurements suggested that the photochemical efficiency of chloroplast photosystems can be inhibited by broadband UV radiation (UVB only or UVB + UVA) in many species (Joshi *et al.* 2007). Chlorophyll fluorescence is an important indicator in characterizing plant physiological responses to environmental stresses, and particularly useful for plant species with small leaf or body size, such as like
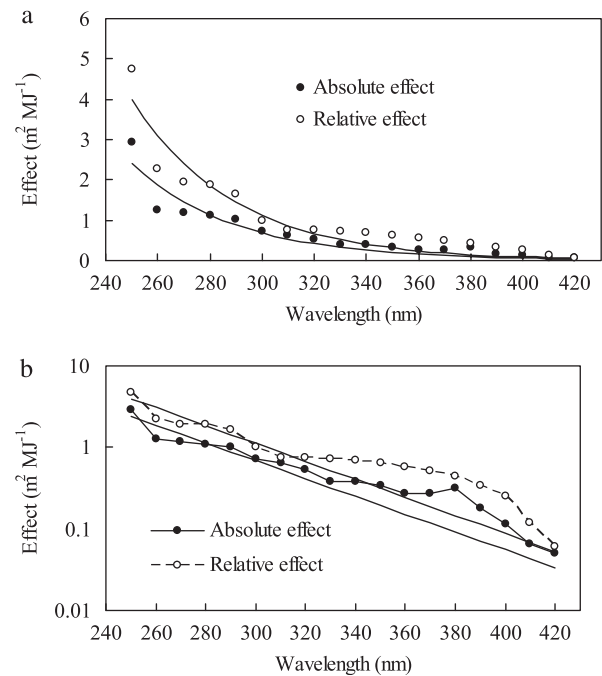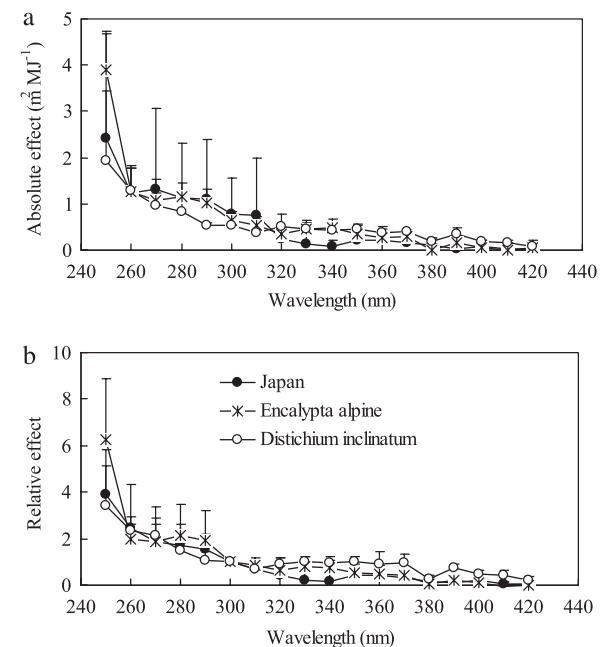

Figure 4: action spectrum of UV radiation induced F_v/F_m depression in three moss species *Distichium inclinatum, Encalypta alpine* and *Polytrichum juniperinum*
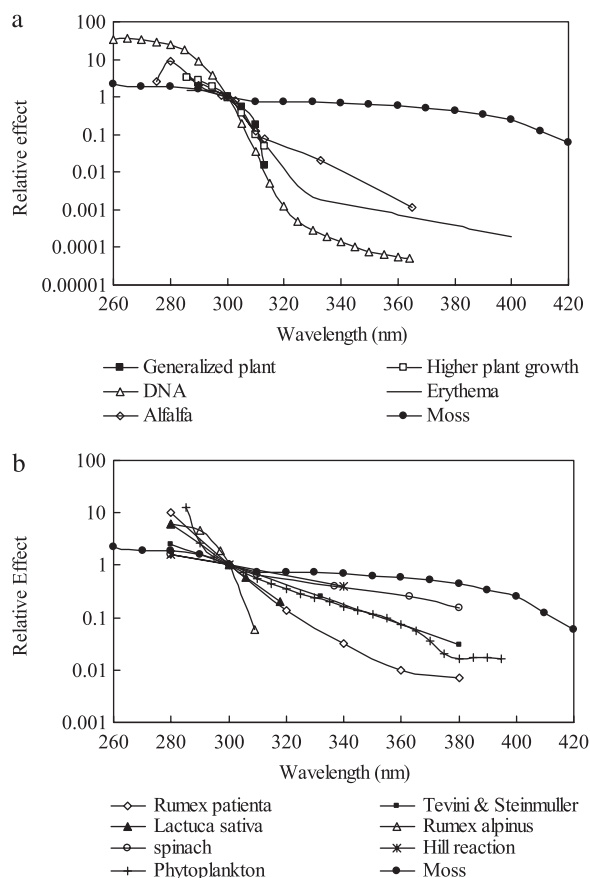
a

b

Figure 5: comparison of action spectrum for UV effect on F_v/F_m in moss with that for generalized higher plant (Caldwell 1971), growth of higher plants (Flint and Caldwell 2003), generalized DNA damage (Setlow 1974), CIE erythema (McKinlay and Diffey 1987) and DNA damage in alfalfa in (a), as well as some action spectra for photosynthesis in (b), including Hill reaction (Caldwell et al. 1986), spinach chloroplast suspension (Jones and Kok 1966), *Rumex alpinus* and *Lactuca sativa* (Bogenrieder 1982), *Rumex patienta* (Caldwell et al. 1986), average effect in Antarctic phytoplankton (Neale and Kieber 2000) and cucumber (Coohill 1989).

cryptogams (Pfundel 2003; Joshi *et al.* 2007). Despite its wide application in UV radiation researches, action spectrum of UV on fluorescence parameters had not been constructed in any species before. As the first BSWF of UV on chlorophyll fluorescence, this study showed a gradual decline of action effect on photosystem photochemical efficiency with the increase of UV wavelength (Figs 3 and 4). The decline was sharp from UVC to UVB and in violet region. In UVA region, the action effect decreased much slowly. The three-phase pattern was similar to some other UV action spectra, such as for erythema (McKinlay and Diffey 1987), for DNA damage (Setlow 1974), for depression of higher plant growth (Flint and Caldwell 2003), for inhibition of phytoplankton photosynthesis (Neale and Kieber 2000) and for macroalgal photosynthesis (Miller *et al.* 2009). However, the turning points and specific slopes of each phase varied greatly for these action spectra (Fig. 6a). Other action spectra had simpler shapes, either two-phase curves or lines
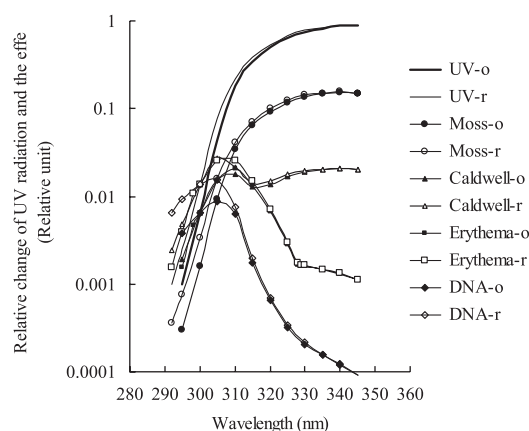

Figure 6: comparison of the change of UV effectiveness in different action spectra under the scenario of a 16% decrease of stratospheric ozone (Caldwell et al., 1989).
'o' and 'r' denoted original and final amount of UV radiation or relative effect. 'Caldwell' represented action spectrum for higher plant growth (Flint and Caldwell 2003), 'Erythema' was CIE erythemal action spectrum (McKinlay and Diffey 1987) and 'DNA' was generalized DNA damage (Setlow 1974).

(Bogenrieder 1982; Boucher and Prezelin 1996; Caldwell 1971; Caldwell *et al.* 1986; Coohill 1989; Jones and Kok 1966; Quaite *et al.* 1992). The large difference among these action spectra reconfirmed that no common spectrum has been found that can substitute for any specific spectrum (Coohill 1989). The result obtained in the current study also hints that changes in the spectrum of UV radiation due to changes of ozone concentration, cloudiness and other atmospheric conditions may have markedly different effect on photosynthetic photochemical response even the total UV energy are the same.

The bryophyte BSWF showed the most modest decline of UV inhibition effect among the photosynthetic relative action spectra (Fig. 6b). Such pattern indicated that UVA played an important role in integrated inhibition effect on the bryophyte photosystem photochemistry as UVA radiation was generally several times higher than UVB on the plateau (Cui *et al.* 2008). The bryophyte BSWF further suggested that the shorter wavelength UV light would contribute much less to the integrated UV inhibition effect on moss F_v/F_m, despite much larger increase in the shorter wavelength irradiation under stratospheric ozone depletion (Madronich *et al.* 1998; Björn *et al.* 1999). The result was in accordance with the effects of UV increase on Hill reaction (Caldwell *et al.* 1986), DNA damage in alfalfa (Quaite *et al.* 1992), phytoplankton biology (Helbling *et al.* 1992) and growth of higher plants (Flint and Caldwell 2003). The large contribution of longer wavelength counteracted with the higher relative change in shorter wavelength. Therefore, the bryophyte BSWF should be insensitive to the increase of UV radiation induced by ozone depletion (Fig. 7). Its sensitivity to O₃ decrease was much lower than generalized plant spectrum and inhibition of growth of cress seedlings and even lower than Hill reaction (Madronich *et al.*

1998). Our result was consistent with the field observation that F_v/F_m was unaffected by ozone depletion in two Antarctic bryophytes (Newsham *et al.* 2002) and in bipolar moss *Sanionia uncinata* (Lud *et al.* 2002).

The BSWF indicates also the importance to consider the relative effectiveness of UVA and UVB. Most researches focused on change of UVB and ignored the effects of UVA. Limited literatures reported highly various UVA effects and those relative to UVB. UVA accounted for more than half of the total inhibition of UV radiation on tropical phytoplankton photosynthesis (Helbling *et al.* 1992). UVA reduced the alternative respiration more than UVB (Mulley *et al.* 2001) and that the inhibition of UVA on the carbon uptake of phytoplankton was greater than UVB at upper water layer (Nielsen and Ekelund 1995). Moreover, UVB produced more serious damage to DNA than UVA, while UVA can ameliorate the effect of UVB because it could be used as energy source for photorepair of UVB-induced DNA damage by enzyme photolyase (Joshi *et al.* 2007; Menck 2002; Newsham *et al.* 2005). These results suggested that the relative effectiveness of UVB and UVA seemed biological trait dependant. The higher radiation amplification factor (Madronich *et al.* 1994) and the larger relative effectiveness of UVB to UVA (Fig. 5a) in plant growth traits than leaf photosynthesis, indicating that growth relevant processes other than leaf photosynthesis are more vulnerable or sensitive to UVB than UVA, thus more sensitive to the ozone depletion. Leaf photosynthesis, as the result of a series of physiological and biochemical processes, showed a higher vulnerability to UVB than UVA as compared with chloroplast suspension, thylakoid membrane, Hill reaction and F_v/F_m (Fig. 5b). It seemed that photo-physical and photochemical processes were effectively protected *in vivo*, probably by other pigments like xanthophylls. Stomatal opening is reported to be more sensitive to UVB than to UVA (Eisinger *et al.* 2000). The higher depression of leaf photosynthesis may be caused by UV damage to photosynthetic machinery, RUBISCO activation (Björn 2007) or by interaction of UV radiation with other stresses (Szôllôsi *et al.* 2008; Turnbull and Robinson 2009).

The three bryophyte species were taken from alpine meadow, alpine wetland and a lowland opening site. The response pattern of F_v/F_m to the UV spectrum was similar within the three species (Fig. 4a and b), i.e. a single BSWF can be used for these bryophytes. Other studies showed that different species of phytoplanktons, lichens, bryophytes or higher plants may have different responses to UVB, UVA or total UV radiation (Björn 2007; Csintalan *et al.* 2001; Dunn and Robinson 2006; Yao *et al.* 2006). The similarity of BSWF within the three bryophytes may be partly due to the instability of PSII D1 protein. The loss of PSII function was dependent on photon dose but less on wavelength. Photoinactivation of individual PSII reaction centers was inevitable after 10^6–10^7 photons had been absorbed (Park *et al.* 1995). Therefore, with the background of ambient visible light, UV radiation did not induce further decline of photochemical fluorescence parameters in bryophytes or algae (Robinson *et al.* 2003 and references therein). Pfündel

(2003) also showed that natural UV can produce inactivated PS II exhibiting relatively high F_v/F_m, and it was F_0 increase but not F_v/F_m decrease that indicated photoinactivation in grapevine plant leaves. In this study, F_0 did not exhibit regular change with the increase of radiation dose (data not shown). Nevertheless, the similarity of action spectra for the three mosses did not imply that stratospheric ozone depletion would affect plant species in the same manner. Other processes may respond divergently as available studies indicated that different species had different sensitivities toward UV radiation and a shift in species composition was a likely consequence of increased UV radiation (Björn 2007; Björn *et al.* 1999; Robinson *et al.* 2003).

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