

Effects of ultraviolet radiation on aquatic bryophytes

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ABSTRACT

The depletion of the stratospheric ozone layer as a result of anthropogenic activities increases the ultraviolet-B (UV-B) irradiance at ground level. This may lead to harmful biological consequences affecting photosynthetic organisms. Mountain streams are especially exposed to a UV-B increase, and bryophytes play a key ecological role in them. In this paper, the effects of enhanced UV-B radiation on photosynthetic organisms in general and on bryophytes in particular are described. Hereafter, some results obtained by our group on the effects of UV-B on bryophytes from mountain streams are presented. Laboratory and field experiments show that these effects depend on the species, the environmental factors (such as temperature), and the origin of the samples (sun or shade conditions, low or high altitude). Among the variables measured, the maximum quantum yield of photosystem II (F_v/F_m) and the level of UV-absorbing compounds seem to be the most responsive to enhanced UV-B, but no variable responded in the same manner in every species. The potential use of aquatic bryophytes as bio-indicators of changes in ambient UV-B radiation would require an adequate selection of both variables and species. Promising variables are F_v/F_m , the concentration of UV-absorbing compounds (especially if they are analyzed individually) and DNA damage, whereas the liverwort *Jungermannia exsertifolia* subsp. *cordifolia* has been revealed to be a good bio-indicator species. Globally, the responses of aquatic bryophytes to UV-B radiation and their protecting systems are still poorly characterized, and thus further study is required under both controlled and field conditions.

Keywords: aquatic bryophytes, mosses, liverworts, ultraviolet-B (UV-B) radiation, mountain streams, bio-indicators.

RESUMEN

La degradación antropogénica de la capa de ozono estratosférico provoca un aumento de la radiación ultravioleta-B (UV-B) en la superficie de La Tierra. Esto puede causar consecuencias biológicas nocivas en los organismos fotosintéticos. Los arroyos de montaña están especialmente expuestos al aumento de UV-B, y los briófitos desempeñan un papel ecológico crucial en estos ecosistemas. En el presente artículo, se describen los efectos de un aumento de radiación UV-B sobre los organismos fotosintéticos en general y sobre los briófitos en particular. A continuación, se presentan algunos resultados obtenidos por nuestro grupo de investigación sobre los efectos de la radiación UV-B en briófitos de arroyos de montaña. Los experimentos realizados tanto en campo como en laboratorio muestran que dichos efectos dependen de la especie considerada, de los factores ambientales (como la temperatura) y de la procedencia de las muestras (aclimatadas a condiciones de sol o sombra, provenientes de baja o elevada altitud). Entre las variables analizadas, el rendimiento cuántico máximo del fotosistema II (F_v/F_m) y el nivel de compuestos absorbentes de radiación UV parecen ser las que mejor responden a un aumento de UV-B, pero ninguna variable responde de la misma manera en todas las especies. El uso potencial de los briófitos acuáticos como bioindicadores de cambios en los niveles naturales de radiación UV-B requiere una selección adecuada tanto de las variables analizadas como de las especies empleadas. F_v/F_m y la concentración de compuestos absorbentes de radiación UV (en especial si éstos son analizados individualmente), junto con los daños en el ADN, parecen ser las variables más prometedoras en este campo, mientras que la hepática *Jungermannia exsertifolia* subsp. *cordifolia* podría resultar una buena especie bioindicadora. Desde un punto de vista global, las respuestas de los briófitos acuáticos a la radiación UV-B, y los mecanismos protectores que utilizan para hacerle frente, están todavía poco caracterizados, y en consecuencia se necesita una mayor investigación en condiciones controladas y en campo.

Palabras clave: briófitos acuáticos, musgos, hepáticas, radiación ultravioleta-B (UV-B), arroyos de montaña, bioindicadores.

ULTRAVIOLET RADIATION AND ITS EFFECTS ON PHOTOSYNTHETIC ORGANISMS

Ultraviolet (UV) radiation induces many harmful effects in all living organisms, including humans. UV-C radiation (<280 nm) is ecologically not relevant since it is absorbed by atmospheric oxygen and ozone. However, both UV-B (280-315 nm) and UV-A (315-400 nm) penetrate to the biosphere and have significant biological effects, although only UV-B is absorbed by the stratospheric ozone layer. Biological responses to UV radiation are highly dependent on wavelength, and thus the biologically effective UV (UV_{BE}) can be calculated. UV_{BE} encompasses UV-A and UV-B, but, given the logarithmic increase of its effects with the decrease in wavelength, it is often dominated by UV-B, especially at its shorter wavelengths. Thus, most studies on the effects of UV radiation have dealt with UV-B.

UV-B irradiance at ground level depends on a number of factors, such as latitude, season, hour of the day, altitude, presence of clouds or aerosols, and surface reflectivity (Björn, 1999). In addition, ozone depletion as a result of anthropogenic emissions of halogenated carbon compounds leads to an increase in UV-B. In mid-latitudes, the ozone loss has led to a 6 to 12 % increase in UV-B radiation above 1980 levels, and predicted changes show the ozone layer will remain vulnerable to further depletion in the near future (McKenzie *et al.*, 2003). Consequently, studies on the effects of ambient and elevated UV-B irradiances are increasingly important. In humans, an excessive exposure to UV-B causes acute and chronic damage to eyes and skin, including sunburn and cancer, and compromises the immune system (Vanicek *et al.*, 1999). In photosynthetic organisms, increased UV-B may cause diverse damage in the photosynthetic apparatus: pigment degradation, photoinhibition, and decreases in quantum yield, photosynthetic rate, and the activity of the Calvin cycle enzymes (Jansen *et al.*, 1998). Also, DNA alterations, oxidative

damage, and changes in mineral absorption can occur. This may lead to alterations in growth and development. However, some controversy about the ecological relevance of these effects still persists (Fiscus & Booker, 1995; Allen *et al.*, 1998; Searles *et al.*, 2001a). At the ecosystem level, UV-B can affect decomposition, nutrient cycling, and trophic interactions (Caldwell *et al.*, 1998). Photosynthetic organisms may develop a number of protection and repair mechanisms against the adverse effects of UV-B (Jansen *et al.*, 1998): production of UV-absorbing compounds (flavonoids, phenyl-propanoids, mycosporine-like aminoacids, etc.), antioxidant and photo-protective mechanisms, and DNA-repairing processes.

Much of the research regarding the effects of UV-B on photosynthetic organisms has focused on terrestrial environments, especially using crop plants, whereas aquatic ecosystems have received less attention. The vast majority of the studies concerning aquatic ecosystems have dealt with marine phytoplankton and macroalgae (Figuerola & Gómez, 2001; Day & Neale, 2002; Häder *et al.*, 2003; Helbling & Zagarese, 2003), while the photosynthetic organisms from freshwater ecosystems have been less studied in line with their minor contribution to the global biomass and primary production of aquatic systems. However, rivers and lakes have an outstanding ecological importance as local systems and, because of their lower depth compared to marine systems, they are highly exposed to the harmful effects of UV-B radiation. In lakes, the penetration of UV radiation and its effects on phytoplankton have been the most studied topics (see for instance Villafañe *et al.*, 1999; Huovinen & Goldman, 2000; Laurion *et al.*, 2000), but macrophytes have also been occasionally considered (Rae *et al.*, 2001). In rivers, scarce work has been done (Rader & Belish, 1997a, 1997b; Kelly *et al.*, 2003), probably due to intrinsic methodological problems derived from their strongly dynamic environmental conditions (depth, discharge, water velocity, chemistry, etc.).

ULTRAVIOLET RADIATION AND BRYOPHYTES

To our knowledge, around 65 papers have been published on the effects of UV-B radiation on bryophytes, among which only 49 contain original data (Table 1). Half of these are strictly bryological, whereas the remaining ones study bryophytes together with other photosynthetic organisms, such as vascular plants or lichens. The research on this topic has focused mainly on terrestrial and semi-aquatic bryophytes from Antarctic habitats and circumpolar heathlands and peatlands. The most used species belong to mosses: several *Sphagnum* species, *Hylocomium splendens* (typical from forest soils), and *Polytrichum commune* (typical from a wide range of acid habitats in damp to wet situations). Liverworts have been notably less studied than mosses, whereas no hornwort has been investigated.

Diverse methodological approaches have been applied. Studies have been conducted under both field and controlled conditions, and in the latter case both in the laboratory and in the greenhouse. The manipulation of UV-B has included the two main experimental options in the context of UV-B research (Rousseaux *et al.*, 2004): exclusion experiments using filters, and supplementation using lamps to simulate ozone depletion. The duration of the experiments has been diverse, from a few hours of UV-B exposure (usually under controlled conditions) to several years (under field conditions). The bryophyte responses have been assessed using morphological and, especially, physiological variables: colour, symptoms of cell degradation, ultrastructural damage, sclerophylly, reproductive effort, growth (both in length and dry mass), photosynthesis and respiration rates, chlorophyll fluorescence variables, photosynthetic pigment composition (chlorophylls, carotenoids), DNA damage (presence of thymine dimers and other photoproducts), protein and glucid concentrations, mineral elements content, and the appearance of UV-absorbing compounds which could serve as a protective mechanism.

The results obtained are conflicting, since UV-B radiation has been found to either stimulate, to depress, or to have no effect on bryophyte performance. Several studies have found a growth reduction in bryophytes when exposed to UV-B (Sonesson *et al.*, 1996; Gehrke *et al.*, 1996; Markham *et al.*, 1998; Gehrke, 1998, 1999; Ballaré *et al.*, 2001), but this effect seems to depend on the species considered, the experimental design and other additional factors such as water availability and CO₂ concentration. Other harmful effects (chlorophyll degradation, reduction in photosynthesis rates and F_v/F_m) are even less clear, since contradictory results have been found. In addition, the increase in UV-absorbing compounds, which represents the most usual response of vascular plants to enhanced UV-B (Searles *et al.*, 2001a), has only been manifested occasionally in bryophytes (Markham *et al.*, 1990; Ihle & Laasch, 1996; Newsham *et al.*, 2002; Martínez-Abaigar *et al.*, 2003a). Beneficial effects of UV-B radiation on bryophyte growth have also been reported (Johanson *et al.*, 1995; Searles *et al.*, 1999; Phoenix *et al.*, 2001), which further complicates the global interpretation of the results. This controversy contrasts with intuitive thoughts that bryophytes would be strongly sensitive to UV-B radiation, because of their structural simplicity and the consequent lack of defenses commonly found in higher plants: thick cuticles, epicuticular waxes, epidermis (sometimes with several cell layers), hairs on leaf surfaces, etc. It must be taken into account that bryophyte “leaves” are mostly mono-stratified and lack air spaces, which dramatically reduces the radiation pathway and thus its attenuation. Thus, bryophytes (with the exception of thalloid forms, which have been understudied in relation to UV radiation), could only acquire chemical and metabolic defenses through, for instance, UV-absorbing compounds, antioxidant mechanisms, and repairing systems of DNA and photosynthetic machinery. However, the present knowledge on UV-absorbing compounds in bryophytes suggests that this mechanism does not occur in most bryophytes (Arróniz-Crespo *et al.*, 2004), and the rest of

the mechanisms have hardly been tested regarding UV-B radiation. Globally, the responses of bryophytes to UV-B radiation and their protect-

ing systems are still poorly characterized, and thus further study is required both under controlled and field conditions.

Table 1. Original papers on the effects of UV radiation on bryophytes. Key for “Used Species”: L, liverwort; M, moss. Key for “Ambient”: T, terrestrial; P, peatlands; A, aquatic; R, rivers or streams; L, lakes. Key for “Type of Experiment”: F, Field; G, greenhouse; L, laboratory; E, exclusion of UV-B radiation; S, supplement of UV-B radiation; N, samples exposed to natural levels of solar radiation; VSh, very short duration (less than 1 day); Sh, short duration (1-30 days); M, medium duration (longer than one month and shorter than 6 months); Lo, long duration (6 months - 1 year); VLo, very long duration (longer than 1 year); ?, undetermined duration; H, historical study (comparison of samples over a prolonged period). Key for “Variables used”: A, alterations in DNA; Fl, chlorophyll fluorescence; FIS, fluorescence spectra; G, growth; H, hydric relations; M, morphology; Mt1, primary metabolites (glucids, proteins, lipids); Mt2, secondary metabolites, including UV-absorbing compounds; N, mineral nutrients; Ox, variables of oxidative stress (peroxide content, lipid peroxidation, ascorbate, superoxide dismutase, peroxidase, catalase); P, photosynthesis; Ph, phenology; PP, photosynthetic pigments; PS1 and PS2, activity of photosystems I and II, respectively; R, respiration; Rf, reflectance indices; Sc, sclerophylly; U, ultrastructure. *Artículos originales relacionados con los efectos de la radiación UV sobre los briófitos. Clave para “Especies utilizadas”:* L, hepática; M, musgo. *Clave para “Ambiente”:* T, terrestre; P, turberas; A, acuático; R, ríos o arroyos; L, lagos. *Clave para “Tipo de experimento”:* F, campo; G, invernadero; L, laboratorio; E, exclusión de radiación UV-B; S, suplemento de radiación UV-B; N, muestras expuestas a niveles naturales de radiación solar; VSh, duración muy corta (menos de 1 día); Sh, duración corta (1-30 días); M, duración media (mayor de 1 mes y menor de 6 meses); Lo, duración larga (6 meses - 1 año); VLo, duración muy larga (mayor de 1 año); ?, duración indeterminada; H, estudio histórico (comparación de muestras a lo largo de un periodo prolongado). *Clave para “Variables utilizadas”:* A, alteraciones en el ADN; Fl, fluorescencia de clorofila; FIS, espectros de fluorescencia; G, crecimiento; H, relaciones hídricas; M, morfología; Mt1, metabolitos primarios (glúcidos, proteínas, lípidos); Mt2, metabolitos secundarios, incluyendo compuestos absorbentes de UV; N, nutrientes minerales; Ox, variables de estrés oxidativo (contenido de peróxido, peroxidación de lípidos, ascorbato, superóxido dismutasa, peroxidasa, catalasa); P, fotosíntesis; Ph, fenología; PP, pigmentos fotosintéticos; PS1 y PS2, actividad de los fotosistemas I y II, respectivamente; R, respiración; Rf, índices de reflectancia; Sc, esclerofilia; U, ultraestructura.

Reference	Used species	Ambient	Type of experiment	Variables used
Arróniz-Crespo <i>et al.</i> (2004)	<i>Chiloscyphus polyanthos</i> (L), <i>Jungermannia exsertifolia</i> subsp. <i>cordifolia</i> (L), <i>Marsupella sphacelata</i> (L), <i>Scapania undulata</i> (L), <i>Brachythecium rivulare</i> (M), <i>Bryum alpinum</i> (M), <i>Bryum pseudotriquetrum</i> (M), <i>Fontinalis antipyretica</i> (M), <i>Palustriella commutata</i> (M), <i>Philonotis seriata</i> (M), <i>Polytrichum commune</i> (M), <i>Racomitrium aciculare</i> (M), <i>Rhynchostegium riparioides</i> (M), <i>Sphagnum flexuosum</i> (M)	A (R)	F, N	Mt2, Sc
Ballaré <i>et al.</i> (2001)	<i>Sphagnum magellanicum</i> (M)	P	F, E, VLo	G, Mt2
Barsig <i>et al.</i> (1998)	<i>Polytrichum commune</i> (M)	P	G, S, M	Mt1, Mt2, PP, U
Björn <i>et al.</i> (1998)	<i>Aulacomnium turgidum</i> (M), <i>Dicranum elongatum</i> (M), <i>Hylocomium splendens</i> (M), <i>Polytrichum commune</i> (M), <i>P. hyperboreum</i> (M), <i>Sphagnum fuscum</i> (M)	T, P	F, S, M-VLo	G, H
Conde-Álvarez <i>et al.</i> (2002)	<i>Riella helicophylla</i> (L)	A (L)	L, E, VSh	Fl, Mt2, P, PP, R
Csintalan <i>et al.</i> (2001)	<i>Dicranum scoparium</i> (M), <i>Leucobryum glaucum</i> (M), <i>Mnium hornum</i> (M), <i>Pellia epiphylla</i> (L), <i>Plagiomnium undulatum</i> (M), <i>Plagiothecium undulatum</i> (M), <i>Polytrichum formosum</i> (M), <i>Sphagnum capillifolium</i> (M), <i>Tortula ruralis</i> (M)	T	L, S, Sh-M	Fl, FIS, Mt2
Gehrke (1998)	<i>Sphagnum fuscum</i> (M)	P	F, S, VLo	G, M, Mt2, P, PP, R
Gehrke (1999)	<i>Hylocomium splendens</i> (M), <i>Polytrichum commune</i> (M)	T, P	F, S, VLo	G, M, Mt2, PP
Gehrke <i>et al.</i> (1996)	<i>Hylocomium splendens</i> (M), <i>Sphagnum fuscum</i> (M)	T, P	F, S, VLo	G, H, Mt2, PP
Huiskes <i>et al.</i> (1999)	<i>Sanionia uncinata</i> (M)	T	-	-
Huiskes <i>et al.</i> (2001)	<i>Sanionia uncinata</i> (M)	T	F, E, Sh	Fl
Huttunen <i>et al.</i> (1998)	<i>Dicranum</i> sp. (M), <i>Hylocomium splendens</i> (M), <i>Polytrichum commune</i> (M)	T, P	G, S, ?	M

Table 1. Continued. *Continuación.*

Reference	Used species	Ambient	Type of experiment	Variables used
Huttunen <i>et al.</i> (2005a)	<i>Dicranum scoparium</i> (M), <i>Funaria hygrometrica</i> (M), <i>Hylocomium splendens</i> (M), <i>Pleurozium schreberi</i> (M), <i>Polytrichum commune</i> (M), <i>Polytrichastrum alpinum</i> (M), <i>Sphagnum angustifolium</i> (M), <i>S. capillifolium</i> (M), <i>S. fuscum</i> (M), <i>S. warnstorfi</i> (M)	T, P	N, H	M, Mt2
Huttunen <i>et al.</i> (2005b)	<i>Hylocomium splendens</i> (M), <i>Pleurozium schreberi</i> (M)	T	N, H	M, Mt2
Ihle (1997)	<i>Conocephalum conicum</i> (L)	T	L, S, VSh	Mt1
Ihle & Laasch (1996)	<i>Conocephalum conicum</i> (L)	T	L, S, VSh-Sh	Fl, Mt1, Mt2, P
Johanson <i>et al.</i> (1995)	<i>Hylocomium splendens</i> (M)	T	G, S, ?	G, Ph
Lewis Smith (1999)	<i>Bryum argenteum</i> (M), <i>Bryum pseudotriquetrum</i> (M), <i>Ceratodon purpureus</i> (M)	T	F, E, M	G
Lovelock & Robinson (2002)	<i>Bryum pseudotriquetrum</i> (M), <i>Ceratodon purpureus</i> (M), <i>Grimmia antarctici</i> (M)	T	F, N, ?	Mt2, PP, Rf
Lud <i>et al.</i> (2002)	<i>Sanionia uncinata</i> (M)	T	F, L, E, S, VSh-VLo	A, G, Fl, M, P, Mt2, PP
Lud <i>et al.</i> (2003)	<i>Sanionia uncinata</i> (M)	T	F, E, S, VSh-Sh	A, Fl, Mt2, P, PP, R
Markham <i>et al.</i> (1990)	<i>Bryum argenteum</i> (M)	T	N, H	Mt2
Markham <i>et al.</i> (1998)	<i>Marchantia polymorpha</i> (L)	T	G, S, M	G, M, Mt2, Ph
Martínez-Abaigar <i>et al.</i> (2003a)	<i>Jungermannia exsertifolia</i> subsp. <i>cordifolia</i> (L), <i>Fontinalis antipyretica</i> (M)	A (R)	L, S, M	Fl, Mt2, P, PP, R, Sc
Martínez-Abaigar <i>et al.</i> (2003b)	<i>Jungermannia exsertifolia</i> subsp. <i>cordifolia</i> (L), <i>Fontinalis antipyretica</i> (M)	A (R)	L, S, M	G, M
Montiel <i>et al.</i> (1999)	<i>Sanionia uncinata</i> (M)	T	F, S, ?	Fl
Newsham (2003)	<i>Andreaea regularis</i> (M)	T	F, N, M	Mt2, PP
Newsham <i>et al.</i> (2002)	<i>Sanionia uncinata</i> (M), <i>Cephaloziella varians</i> (L)	T	F, N, Sh-M	Fl, Mt2, PP
Newsham <i>et al.</i> (2005)	<i>Cephaloziella varians</i> (L)	T	F, N, E, M	Mt2, PP
Niemi <i>et al.</i> (2002a)	<i>Sphagnum angustifolium</i> (M), <i>S. papillosum</i> (M), <i>S. magellanicum</i> (M)	P	F, S, M	G, Mt2, PP
Niemi <i>et al.</i> (2002b)	<i>Sphagnum balticum</i> (M), <i>Sphagnum papillosum</i> (M)	P	F, S, M	G, Mt2, PP
Núñez-Olivera <i>et al.</i> (2004)	<i>Jungermannia exsertifolia</i> subsp. <i>cordifolia</i> (L), <i>Fontinalis antipyretica</i> (M)	A (R)	L, S, M	Fl, G, Mt1, Mt2, P, PP, R, Sc
Núñez-Olivera <i>et al.</i> (2005)	<i>Jungermannia exsertifolia</i> subsp. <i>cordifolia</i> (L), <i>Fontinalis antipyretica</i> (M)	A (R)	L, S, Sh	Fl, Mt1, Mt2, P, PP, R, Sc
Phoenix <i>et al.</i> (2001)	<i>Hylocomium splendens</i> (M)	T	F, S, VLo	G, H
Post & Vesik (1992)	<i>Cephaloziella exiliflora</i> (L)	T	F, N, Sh	M, Mt2, P, PP, U
Prasad <i>et al.</i> (2004)	<i>Riccia</i> sp. (L)	T	L, S, VSh	Ox, PP, PS1, PS2
Rader & Belish (1997a)	<i>Fontinalis neomexicana</i> (M)	A (R)	F, E-S, M	G
Robinson <i>et al.</i> (2005)	<i>Grimmia antarctici</i> (M)	T	F, E, VLo	Fl, H, M, Mt2, P, PP, Rf
Robson <i>et al.</i> (2003)	<i>Sphagnum magellanicum</i> (M)	P	F, E, VLo	G, M
Robson <i>et al.</i> (2004)	<i>Sphagnum magellanicum</i> (M)	P	F, E, VLo	G, M
Rozema <i>et al.</i> (2002)	<i>Tortula ruralis</i> (M)	T	F, E, ?	G, Mt2
Schipperges & Gehrke (1996)	<i>Hylocomium splendens</i> (M), <i>Sphagnum fuscum</i> (M)	T, P	F-L, S, M- VLo	G, H, P
Searles <i>et al.</i> (1999)	<i>Sphagnum magellanicum</i> (M)	P	F, E, Lo	G, Mt2, PP
Searles <i>et al.</i> (2001b)	<i>Sphagnum magellanicum</i> (M)	P	F, E, VLo	G, M, Mt2
Searles <i>et al.</i> (2002)	<i>Sphagnum magellanicum</i> (M)	P	F, E, VLo	G, M, Mt2, PP
Sonesson <i>et al.</i> (1996)	<i>Hylocomium splendens</i> (M)	T	L, S, M	G, P
Sonesson <i>et al.</i> (2002)	<i>Dicranum elongatum</i> (M), <i>Sphagnum fuscum</i> (M)	P	F, S, VLo	G, H
Taipale & Huttunen (2002)	<i>Hylocomium splendens</i> (M), <i>Pleurozium schreberi</i> (M)	T	F, S, M	Mt2
Takács <i>et al.</i> (1999)	<i>Dicranum scoparium</i> (M), <i>Leucobryum glaucum</i> (M), <i>Mnium hornum</i> (M), <i>Pellia epiphylla</i> (L), <i>Plagiothecium undulatum</i> (M), <i>Polytrichum formosum</i> (M), <i>Tortula ruralis</i> (M)	T	G, S, Sh-M	Fl

ULTRAVIOLET RADIATION AND AQUATIC BRYOPHYTES FROM MOUNTAIN STREAMS

Before our studies, only two other ones had been conducted on the effects of UV radiation on truly aquatic bryophytes (see Table 1), despite the interest of how diverse organisms from different habitats respond to this environmental factor. In Conde-Álvarez *et al.* (2002), samples of the thalloid liverwort *Riella helicophylla* from a saline lake were cultivated throughout a natural daily light cycle under two radiation treatments: solar radiation (UV + photosynthetically active radiation or PAR) and solar radiation deprived of UV (PAR treatment). There were significant differences between the two treatments in the maximum quantum yield of photo-system II (F_v/F_m), the effective quantum yield of photosynthetic energy conversion of PSII (Φ_{PSII}), the electron transport rate (ETR) and the initial slope of ETR vs. irradiance curve (all higher in PAR plants than in UV+PAR plants throughout the day), photosynthetic capacity (higher in PAR plants only at noon), chlorophyll *a* (lower in UV+PAR only at 11.00), and phenolic compounds (higher in UV+PAR only at 13.30). No differences between treatments were found in dark respiration, photochemical quenching, and carotenoid concentration, and only slight ones in non-photochemical quenching (higher in UV+PAR only in the morning). Thus, UV radiation (particularly UV-B) caused some damage to the photosynthetic apparatus. Recovery of inhibited photosynthesis took place in the afternoon, therefore solar UV radiation did not cause irreversible damage in the short term. Rader & Belish (1997a) carried out a ten-week field experiment in which samples of the moss *Fontinalis neomexicana* were transplanted from a reference site to both a shaded and an open section of a mountain stream and were irradiated with enhanced levels of UV-B radiation. The transplants from the open site showed an important, although non-significant, reduction in dry biomass with respect to those growing under ambient conditions. However, the moss in this experiment failed to grow in any site and under

any treatment condition, and there was a loss of material in all samples from the beginning to the conclusion of the experiment, which casts doubt on the significance of the results.

For several reasons, we circumscribe our research interest to the effects of UV-B radiation on aquatic bryophytes from mountain streams. Firstly, these ecosystems might be particularly exposed to the effects of UV-B radiation, since 1) the biologically active UV-B radiation increases between 5 % and 20 % per 1000 m altitudinal increase (Björn *et al.*, 1998); 2) UV-B radiation can easily reach the organisms because they live at relatively low depths or even emersed, and UV-B radiation can penetrate into the oligotrophic waters typically occurring in mountain streams; and 3) the low temperatures which prevail during most of the year may limit the development of protection and repairing mechanisms against UV-B radiation. Secondly, bryophytes are the most abundant primary producers in mountain streams and are also important in nutrient cycles and food webs (Bowden *et al.*, 1999; Núñez-Olivera *et al.*, 2001). This domination suggests that they can withstand present levels of UV-B radiation, but the underlying physiological mechanisms are unknown and the structural protections against UV-B are lacking (as it was mentioned above for bryophytes as a group). Thirdly, bryophytes have an outstanding bio-indication ability in a number of pollution processes and environmental changes (see a recent review in Ah-Peng & Rausch de Traubenberg, 2004), which could suggest their potential use as bio-indicators of changes in UV-B levels. And finally, the scarcity of studies existing on this particular topic recommends increasing our knowledge on it, especially considering the present social interest on the causes and consequences of global climate change.

In our work, we have conducted both laboratory and field studies. In the laboratory, we have cultivated bryophytes under enhanced UV-B simulating a 20 % ozone depletion, with the aim to characterize bryophyte responses to higher than present UV-B levels. The applied biologically effective UV-B ($UV-B_{BE}$) was 0.67 W m^{-2} , equivalent to an exposure of $9.6 \text{ kJ m}^{-2} \text{ d}^{-1}$,

which was calculated using the generalized plant damage action spectrum of Caldwell (1971). We established three general radiation regimes (PAR, PAR + UV-A, and PAR + UV-A + UV-B) to distinguish the effects of UV-A and UV-B radiations separately. Bryophyte responses were analyzed in terms of sclerophylly, the photosynthetic pigment composition, the rates of net photosynthesis and dark respiration, some variables of chlorophyll fluorescence, and the UV-absorbing compounds. In addition, we occasionally measured DNA damage (through the appearance of thymine dimers), protein concentration, length growth and morphological symptoms (both macro- and microscopic). The duration of the experiments was diverse, from 3 days to 4 months. We have concentrated our studies on two species, the moss *Fontinalis antipyretica* and the foliose liverwort *Jungermannia exsertifolia* subsp. *cordifolia* (hereafter *J. cordifolia*), which were always collected from streams between 1300 and 2000 m altitude.

The two bryophytes mentioned above responded differently to the enhancement in UV-B radiation under controlled conditions, while UV-A radiation had a scarce biological effect (Martínez-Abaigar *et al.*, 2003a), as it occurred in other experiments using bryophytes (Niemi *et al.*, 2002a, 2002b). The samples of the moss which were irradiated with UV-B showed, with respect to the control, decreases in the chlorophyll and carotenoid concentration, the chlorophyll *a/b* quotient, the chlorophylls/phaeopigments ratios, the net photosynthesis rates, the light saturation point, F_v/F_m and ETR. They also showed increases in the sclerophylly index ("leaf" mass per area) and the dark respiration rates. The majority of these changes were indicative of plant stress and some of them had been previously found in bryophytes exposed to enhanced UV-B radiation. However, the UV-B-irradiated samples of the liverwort only showed a decrease in F_v/F_m , which might be the most sensitive physiological variable to UV-B, together with a 20 % increase in the concentration of UV-absorbing compounds. This defense mechanism, rarely described in bryophytes, would enable the liverwort to have a higher tolerance than the

moss against UV-B radiation, at least under the specific experimental conditions used. Also, the increment of UV-absorbing compounds in the liverwort might be a useful ecophysiological tool in the bioindication of UV-B.

The different response of the two studied species to UV-B radiation was also evident in their morphological features (Martínez-Abaigar *et al.*, 2003b). When exposed to enhanced UV-B, the moss showed brown colour, depressed growth, development of the central fibrillar body in the cells, chloroplast disappearance and presence of protoplasts progressively vesiculose, vacuolized and finally hyaline. These symptoms are little specific and have been described in several pleurocarpous mosses as a response to diverse processes of senescence and stress (both natural and anthropogenic). The uniquely specific response of the moss to enhanced UV-B was a colour change in the cell walls, from yellow to orange-brown. In contrast, the exposed samples of the liverwort looked healthy and their macro- and microscopic appearances were quite similar to those of control samples.

In the laboratory, we also examined the influence of temperature (2 °C vs. 10 °C) on the physiological and morphological responses of *Fontinalis antipyretica* and *Jungermannia cordifolia* to enhanced UV-B (Martínez-Abaigar *et al.*, 2003b; Núñez-Olivera *et al.*, 2004). The influence of temperature on the effects of UV-B radiation depended on the species: the higher the UV-B tolerance, the lower the influence of temperature. Also, different morphological and physiological variables showed varied responses to this influence. Particularly, the lower temperature used in our study enhanced the adverse effects of UV-B radiation on several important physiological variables (F_v/F_m , growth and chlorophylls/phaeopigments ratios) in the UV-B-sensitive *F. antipyretica*, but not in the more UV-B-tolerant *J. cordifolia*. Thus, the adverse effects of cold and UV-B radiation were apparently additive in the moss (probably because the development of protection mechanisms was limited by cold), whereas this additiveness was lacking in the liverwort. We conducted a Principal Components Analysis (PCA) for both species using

the physiological data obtained in the experiments and confirmed their different response to the concomitant action of UV-B and cold.

Another environmental factor that can influence the response of different species to UV-B radiation is their previous field acclimation to sun or shade conditions (Núñez-Olivera *et al.*, 2005). Shade samples of *Fontinalis antipyretica* were more sensitive to the UV-B treatment than sun samples, and F_v/F_m was the physiological variable which better discriminated both types of samples, since it decreased 42 % in the shade samples and only 27 % in the sun samples at the end of the culture period. In *Jungermannia cordifolia*, controls and UV-B-treated samples were not significantly different in either the sun or the shade samples. PCAs for each species, ranking the physiological results along the culture period, strongly supported these points. In conclusion, the shade samples were more sensitive to UV-B than the sun samples, but only in the more UV-B-sensitive species.

We also determined that the sensitivity of bryophyte species to artificially enhanced UV-B could be tested without having to cultivate the samples for a long period. A continuous UV-B exposure of 78 h reproduced the differences in the responses of *Fontinalis antipyretica* and *Jungermannia cordifolia*, which had been previously found in longer experiments lasting 36-82 days (Núñez-Olivera *et al.*, 2005). For this short-term test, several culture conditions, which were known to accelerate the appearance of damage, were imposed: high ratio UV-B/PAR, continuous UV-B exposure, and cold temperature. This type of fast test may therefore be used instead of long-duration tests to evaluate the UV-B tolerance of bryophytes.

The different nature of the protection mechanisms between mosses and liverworts, which had been previously pointed out for *Fontinalis antipyretica* and *Jungermannia cordifolia* under laboratory conditions, was tested in a field survey conducted for 14 aquatic bryophytes from mountain streams, 10 mosses and 4 liverworts (Arróniz-Crespo *et al.*, 2004). The diverse species showed significantly different levels of methanol-extractable UV-absorbing compounds

(MEUVAC) and also different forms in their absorbance spectra in the UV band. The high levels of MEUVAC and the clearly hump-shaped spectra in the UV-B and UV-A wavelengths (280-400 nm), which were found in the liverworts, contrasted with the low levels and non hump-shaped spectra generally found in the mosses (except for *Polytrichum commune*). Thus, the accumulation of MEUVAC might represent a frequent and constitutive a protecting mechanism against UV-B radiation in liverworts, but not in mosses.

In another field experiment, we tested the effects of a natural altitudinal gradient of ultraviolet-B (UV-B) radiation, from 1140 to 1816 m altitude, on the physiology of 11 populations of *Jungermannia cordifolia* (Arróniz-Crespo, 2005). Several physiological variables showed significant linear relationships with altitude: global MEUVAC levels, the concentrations of two phenolic derivatives, ETR_{max} and NPQ_{max} increased with altitude, whereas photoinhibition percentage and respiration rates decreased. This was also confirmed by a PCA, since most of these variables represented significant loading factors ordinating populations by altitude. The characteristics shown by high-altitude populations may confer tolerance to high UV-B levels, and the specific response to UV-B of the two phenolic derivatives suggests that they could be used as indicators of the spatial changes in UV-B radiation. In addition, the concentrations of these two phenolic derivatives increased specifically under artificially enhanced UV-B radiation (unpublished results). An interesting question remains to be solved: could these compounds be used as indicators of temporal changes in UV-B, which could be related to ozone depletion?

CONCLUSIONS AND PERSPECTIVES

1. Our results demonstrate that the effects of UV-B radiation on aquatic bryophytes depend primarily on the species, and thus they do not constitute a single functional group in this respect. The different responses to UV-B are revealed not only by changes in colour or in

- key physiological variables, such as growth, chlorophyll concentration, photosynthesis rates or chlorophyll fluorescence parameters, but also by variables responsible for protecting mechanisms, such as the concentration of UV-absorbing compounds. In particular, the constitutive presence and/or inducible enhancement of UV-absorbing compounds depend strongly on the species and, outstandingly, on the type of bryophyte (moss or liverwort) considered.
2. It is recommendable to evaluate UV-B sensitivity in sufficiently prolonged experiments, however short-term (72 h) tests may render comparable results.
 3. The responses of aquatic bryophytes to UV-B radiation depend not only on specific genetic factors, but also on environmental factors (such as temperature) and the origin of the samples (sun or shade conditions, low or high altitude). The effects of these factors depend on the species: in the UV-B sensitive ones, both cold and previous shade acclimation may exacerbate the harmful effects of enhanced UV-B.
 4. Among the variables measured under laboratory conditions, the maximum quantum yield of photo-system II (F_v/F_m) and the level of UV-absorbing compounds seem to be the most responsive ones to enhanced UV-B. However, no variable responds in the same manner in every species, which still limits our global comprehension on the effects of UV-B on bryophytes. The positive thing here is that a "UV-B syndrome" may be identified by the treatment of physiological data of control and UV-B-exposed samples through multivariate analyses (such as PCA), since both types of samples usually appear clearly separated in the generated plots.
 5. The noteworthy variability of the results reported in the literature on the effects of UV radiation on bryophytes may be due to the above-mentioned diversity of species, environmental factors, variables and experimental conditions used in the different studies. Thus, it is necessary to take into account the methodological approaches to appropriately interpret the results obtained.
 6. The use of aquatic bryophytes as bio-indicators of changes in UV-B radiation requires an adequate selection of both variables and species. Promising variables regarding this point are F_v/F_m , because of its sensitivity to UV-B, and the concentration of UV-absorbing compounds, due to its remarkable specificity of response. The analysis of individual UV-absorbing compounds may have a stronger ecological and physiological relevance than the usual global analysis of these compounds, since each one may respond in a different manner to UV-B. Thus, a previous identification of the compounds occurring in the different species is clearly needed. A third variable potentially useful for bio-indication purposes could be the evaluation of DNA damage caused specifically by UV-B radiation. Regarding the species selection, our results point at *Jungermannia cordifolia* because of its good responsiveness to UV-B, availability of healthy biomass throughout the year (if populations are selected properly), and wide distribution range over mountain streams of the northern hemisphere.
 7. Two phenolic derivatives from *Jungermannia cordifolia* which absorb UV radiation have shown their ability to increase in response to a field spatial gradient of UV-B. The future combination of laboratory and field works studying the behaviour of these compounds under different UV treatments, and particularly the field assessment of their seasonal and inter-annual variations in response to temporal changes in ambient UV-B, could allow for the development of a protocol of bio-indication of the potential increase in UV-B radiation due to ozone depletion.

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