

THE EFFECTS OF UV-B RADIATION ON AQUATIC AND TERRESTRIAL
PRIMARY PRODUCERS*Mateja GERM*

National Institute of Biology, SI-1000 Ljubljana, Večna pot 111

E-mail: mateja.germ@nib.si

Alenka GABERŠČIK

Department of Biology, Biotechnical Faculty and

National Institute of Biology, SI-1000 Ljubljana, Večna pot 111

Tadeja TROŠT-SEDEJ

Department of Biology, Biotechnical Faculty, SI-1000 Ljubljana, Večna pot 111

Zdenka MAZEJ

ERICO, SI-3320 Velenje, Koroška 58, Slovenia

Jože BAVCON

Department of Biology, Biotechnical Faculty, SI-1000 Ljubljana, Večna pot 111

ABSTRACT

*The effect of enhanced UV-B radiation on aquatic and terrestrial primary producers is reviewed, based on the data from literature and those derived from experiments performed under UV-B doses corresponding to 17% ozone depletion. The changes of the following parameters, i.e. total contents of UV-B absorbing compounds and photosynthetic pigments, terminal electron transport system (ETS) activity and photochemical efficiency of photosystem II, were compared in different species. In some species, UV-B induced synthesis of UV-B absorbing compounds, while the others did not respond to enhanced UV-B or synthesised saturated amounts of these substances, with no respect to UV-B level. It was established that the production of UV-B absorbing compounds demanded additional energy in *Scenedesmus quadricauda*, *Selenastrum capricornutum* and *Ceratophyllum demersum*, since it was correlated to ETS activity. Generally, no effect on potential and actual photochemical efficiencies of photosystem II was observed.*

Key words: UV-B radiation, primary producers, UV-B absorbing compounds, photochemical efficiency of PS II, terminal electron transport activity

EFFETTI DELLA RADIAZIONE UV-B SU PRODUTTORI PRIMARI ACQUATICI E TERRESTRI

SINTESI

*L'articolo presenta una revisione degli effetti di un'aumentata radiazione UV-B su produttori primari acquatici e terrestri, basata su dati di letteratura e su risultati di esperimenti condotti con dosi di UV-B corrispondenti ad un impoverimento in ozono pari al 17%. Le variazioni nei seguenti parametri sono state confrontate per diverse specie: contenuto totale di composti e pigmenti fotosintetici assorbenti raggi UV, attività terminale di trasporto elettroni (ETS) ed efficienza fotochimica del fotosistema II. In alcune specie la radiazione UV-B ha indotto la sintesi di composti assorbenti UV-B, mentre altre specie non hanno manifestato risposta all'aumentata radiazione UV-B o hanno sintetizzato quantità sature di tali sostanze, a prescindere dal livello di UV-B. In *Scenedesmus quadricauda*, *Selenastrum capricornutum* e *Ceratophyllum demersum*, la produzione di composti assorbenti UV-B ha richiesto tassi più elevati di energia, in quanto correlata all'attività ETS. Gli autori non hanno osservato effetti sull'efficienza fotochimica potenziale o effettiva del fotosistema II.*

Parole chiave: radiazione UV-B, produttori primari, composti assorbenti UV-B, efficienza fotochimica di PS II, attività terminale di trasporto elettroni.

INTRODUCTION

The intensive UV research during recent years is the result of our concern regarding the thinning of ozone layer in the stratosphere and consequently increasing ultraviolet (UV) radiation levels that may influence terrestrial as well as aquatic ecosystems (Rozema *et al.*, 1997; Häder *et al.*, 1998; Trošt & Gaberščik, 2001; Gaberščik *et al.*, 2001; Gaberščik *et al.*, 2002a, b; Germ *et al.*, 2002a, b; Rozema *et al.*, 2002). UV-B radiation causes damage to nucleic acids by absorption of UV-B photons by DNA and formation of cyclobutane dimers as well as by formation of free radicals. Membrane damages occur as a consequence of photoabsorption, peroxidation and changes in the membrane lipid composition. UV-B radiation affects photosynthesis by damaging photosystem II (Björn, 1999; Xiong, 2001), disruption of thylakoid membrane, reduction in chlorophyll content, disturbance of membrane permeability and damaging RuBP carboxylase (ribulose-1.5-bisphosphate). It has been established that the activity of respiratory electron transport system (ETS) is enhanced by UV-B (Ferreira *et al.*, 1997; Gaberščik *et al.*, 2002a). UV-B radiation also affected the activity of phytohormones by influencing the synthesis or by inactivation. Plant morphogenetic responses to enhanced solar UV-B radiation are decreases in height, leaf length, leaf area, increases in leaf thickness, altered leaf angle, plant architecture, canopy structure, altered emergence, phenology, senescence, and seed production (Newsham *et al.*, 1996; Rozema *et al.*, 1997; Gaberščik *et al.*, 2002b). Enhanced UV-B results in the disturbance of motility and orientation of phytoplankton (Cullen *et al.*, 1992) decrease cell wall thickness, inhibited enzyme activity and metabolism of nitrogen (Häder, 1996; Nielsen, 1996).

Protection against UV-B radiation is of primary importance for photosynthetic organisms, which depend on solar radiation as the primary source of energy. Organisms have evolved different strategies and mechanisms to cope with UV-B stress. The general response found in the majority of primary producers is enhanced production of UV-absorbing compounds, which provide a protection screen filtering out harmful UV radiation (Sommaruga, 2001; Xiong, 2001; Gaberščik *et al.*, 2002b, Germ *et al.*, 2002a). The concentration and type of these compounds generally depends on the group of organisms and the level of UV-B radiation (Holm-Hansen *et al.*, 1993; Hannach & Sigleo, 1998; Sommaruga & Garcia-Pichel, 1999). Defence mechanisms of higher plants against UV-B damage also include scattering and reflection of UV-B radiation by epidermal and cuticular structures, photoreactivation enzymes, excision of DNA damage and scavenging of radicals, while polyamines may additionally ameliorate UV-B damage to membranes (Stapleton, 1992; Mitchell & Karentz, 1993; Runeckles & Krupa, 1994). Phytoplankton pro-

tects itself by forming cenobia or relative larger cell size and shading vital cellular structure (Nielsen, 1996; Xiong *et al.*, 1999; Xiong 2001). The net effect of UV-B on organisms is the result of damage and repair processes and depends on the type of the environment.

Aquatic and terrestrial environments differ in many parameters essential for plant survival. Terrestrial plants have evolved structures like cuticle and stomata, which on the one hand reduce the loss of water, while on the other hand they limit uptake of carbon dioxide (CO₂) from the air. The important role of epidermal and cuticular structures and other leaf properties, such as waxy layer, leaf hairs and leaf bladders, is also scattering and reflection of UV-B radiation. The main factors limiting growth and development of aquatic plants are variable light intensity and slow diffusion of CO₂ (Frost-Christensen & Sand-Jensen, 1992; Clevering *et al.*, 1996; Vadstrup & Madsen, 1996). Plants in aquatic and terrestrial environment are exposed to different radiation conditions, including those in the UV range. The UV-B penetration in water may vary from only few centimetres in highly humic lakes to dozen of meters in clear oceanic waters (Smith & Baker, 1981). Optical properties of water depend on water itself, dissolved organic matter (DOM), the photosynthetic biota and particulate matter (Nielsen, 1996; Williamson *et al.*, 1996; Sommaruga & Psenner, 1997; Huovinen *et al.*, 2003). Aquatic plants could be therefore partly protected from direct UV-B radiation by water filter. Phytoplankton populations are exposed to high solar UV-B level, when they are close to the water surface and when the water transparency for UV-B is high. Higher aquatic plants thriving in the littoral are exposed to UV-B when water level decreases. Amphibious plants deserve special attention in UV-B research, since they thrive at the water/land interface and therefore in contrasting environments regarding availability of water, gas and radiation (Madsen & Breinholt, 1995).

The publications on UV-B research experiments are numerous (Rozema *et al.*, 1997, 2002), but in many cases the results are not comparable due to different methodological approaches. The major problem was the radiation conditions with unrealistic UV-B doses and low ratio of photosynthetic active radiation. The aim of the present article is to compare selected responses of different primary producers exposed to the level of UV-B radiation doses based on expected future scenarios.

MATERIAL AND METHODS

The data on the following plant species were reviewed: *Scenedesmus quadricauda* (Turp.) Bréb., *Selenastrum capricornutum* Prinz, *Sphagnum magellanicum* Brid., *Ranunculus trichophyllus* Chaix [*Batrachium trichophyllum* (Chaix) van den Bosch], *Myosotis scorpioides* L. [*M. palustris* (L.) Hill], *Ceratophyllum demersum* L., *Myriophyllum spicatum* L., *Potamogeton alpinus* Bal-

bis, *Picea abies* (L.) Karst, *Fagopyrum esculentum* Moench [*F. vulgare* T. Nees, *Polygonum fagopyrum* L.], *Pulmonaria officinalis* L. [*P. officinalis* L. subsp. *maculosa* (Hayne) Gams], *Tropaeolum majus* L. and *Picea abies* (L.) Karst. Plants were treated under similar conditions in outdoor and indoor experiments.

Higher plants were exposed to enhanced level of UV-B radiation in the semi-controlled conditions in field and indoor experiments. Phytoplankton was treated with enhanced level of UV-B in indoor experiments. Plants from the natural environment were transplanted into natural sediment in semi-controlled conditions in the Botanical Garden of Ljubljana University (46°35'N, 14°55'E), Slovenia. An UV-B supplement system was designed as described by Björn & Teramura (1993). Three different treatments were applied: simulation of 17% ozone depletion (UV-B(+)) using Q-Panel UV-B 313 lamps, filtered with cellulose diacetate filters, which cut the UV-C range (wavelengths lower than 280 nm). The second treatment reduced the ambient level of UV-B radiation (UV-B(-)) for 50% using Mylar foil, which blocks wavelengths below about 320 nm (Geirke et al., 1996). Finally, control treatment was ambient radiation and Q-Panel UV-B 313 lamps, filtered with Mylar foil, to correct for effects of the UV-A radiation (control). The doses simulating 17% ozone depletion were calculated and adjusted weekly using the program published by Björn & Murphy (1985), based on the generalized plant action spectrum (Caldwell, 1968). Ambient UV-B radiation was measured using the European Light Dosimeter Network (ELDONET, Real Time Computer, Möhrendorf, Germany) measuring system, which also monitors UV-A radiation and PAR.

Cell suspensions of *S. quadricauda* and *S. capricornutum* were cultured in polyethylene (PE) open-top (200 ml, less than 4 cm suspension layer) vessels in Jaworski medium at 23±2°C. Light sources were GROLUX lamps, which provided 200 µmol m⁻² s⁻¹ of PAR (12/12 hours, light/dark). The UV-B doses varied from 0.8 to 12.3 kJ m⁻²/day, using the lamps and filters mentioned above.

Photosynthetic pigments and UV-B absorbing substances

Carotenoids and chlorophyll *a* and *b* were determined according to Jeffrey & Humphrey (1975). The procedure for the extraction of UV-B absorbing substances followed the method described by Caldwell (1968). UV-B absorbing substances were extracted with an extraction medium (methanol:distilled water:HCl = 79:20:1) and centrifuged. The supernatants of the samples were scanned in the range from 280-320 nm. The extinction values were corrected for dry weight of the sample.

Physiological parameters

The quantum efficiency of PS II (photosystem II) was

measured using the fluorometer OS-500 (Opti-Science, USA). The optimal quantum efficiency was calculated as F_v/F_m . Plants were kept in cuvettes for dark adaptation for 15 min before the measurements at ambient temperature. The effective quantum efficiency of PS II (yield - Y) was measured under actual light conditions, described by the expression $Y = (F_m' - F)/F_m'$. The yield was measured under full light conditions (from 1500 to 2000 µmol m⁻² s⁻¹) at the prevailing ambient temperature (Schreiber et al., 1995).

Respiratory potential was estimated via measuring the potential electron transport system (ETS) activity of mitochondria as reported in detail by Packard (1971) and modified by Kenner & Ahmed (1975). The material was homogenized in ice-cold homogenizing buffer and centrifuged in a refrigerated ultracentrifuge (500 g, 4 min, 0°C). The supernatant of the homogenate was mixed with substrate solution, INT solution and incubated for 40 min at room temperature. During incubation, the INT (instead of oxygen) was reduced to formazan. The absorption of formazan was measured with UV/VIS Spectrometer System (Lambda 12, Perkin-Elmer, USA) at 490 nm. The absorption was converted to the amount of oxygen utilized per dry mass per time.

Statistical analysis

All measurements were conducted on 4-10 parallel samples respectively. The significance of the differences was indicated as follows: (+) stands for positive trend, (++) indicates significant positive effect, (x) indicates no clear effect, and (-) negative effect. Differences were tested by two-way Student's t-test.

DISCUSSION

According to data from many researches, UV-B induces the bleaching of photosynthetic pigments (Strid et al., 1990; Holm-Hansen et al., 1993; Bischof et al., 1998). Even though accessory pigments appear to be more sensitive than chlorophylls (Tevini, 1993), the destructive effect on chlorophyll has been reported by Jansen et al. (1996), Olsson (1999) and Demmig-Adams & Adams (1992). The latter suggest that the decrease in chlorophyll *a* is related to a kind of excess-light stress avoidance mechanism. The effect of UV-B on the content of chlorophyll *a* seems to be species specific. Several researchers (Tosserams & Rozema, 1996; Antonelli et al., 1997; Garde & Cailliau, 1998) support the results obtained in our laboratory under the 17% depletion of ozone layer (Tab. 1), which showed no effect of UV-B radiation on chlorophyll *a* content. In some cases, the contents of chlorophyll *a* even increase under UV-B radiation (Liu et al., 1995). Beardall et al. (1997) and De Lange et al. (2000) report a negligible effect on chlorophyll *a* in UV-B treated cells of *A. flos-aquae* and *Sele-*

nastrum, respectively. Veen *et al.* (1997) find a stimulation of chlorophyll *a* and *b* production in green alga *S. capricornutum*. The same effect was also found in *S. quadricauda* and *S. capricornutum* in our laboratory (Germ *et al.*, 2002a). The increase of chlorophyll *a* in *P. abies* was observed in emergent needles in spring only, when the protective mechanisms were not fully developed (Trošt & Gaberščik, 2001). The fact that the production of chlorophyll *a* was not depressed but slightly stimulated could also be explained as a protective strategy of cells. By "multiplication" of target sites, an organism avoids disturbances in the activity. Karentz *et al.* (1991) also point out the protective role of chloroplasts in the cell. Their position in the cell could provide the protection of nucleus against strong radiation.

The increase of UV-B absorbing compounds with increasing UV-B radiation dose (Shick *et al.*, 1996) suggests that UV-B induces synthesis of these substances for protection of the photosynthetic apparatus in primary producers (Hunt & McNeil, 1999; Karsten *et al.*, 1999; Turunen *et al.*, 1999). Synthesis of UV-B absorbing compounds was induced by UV-B radiation in *S. quadricauda* and in *S. capricornutum* (Tab. 1) as it had been observed for many other algae (Karentz *et al.*, 1994; Häder, 1996; Xiong *et al.*, 1999; Sommaruga, 2001; Xiong, 2001; Germ *et al.*, 2002a). Enhanced UV-B radiation also increased the production of UV-B absorbing compounds in *C. demersum* and *F. esculentum* (Gaberščik *et al.*, 2002a, b). In many cases, the production of UV-B absorbing compounds does not necessarily depend on UV-B dose (Rau & Hofmann, 1996). No correlation with the UV-B dose and synthesis of UV-B absorbing compounds was found in *R. trichophyllus*, *M. scorpioides*, *P. alpinus*, and *M. spicatum* (Germ *et al.*, 2002b). Some plants, such as those from tropical and high altitude environments, contain saturated amounts of flavonoids, and enhanced doses do not exert an increased production (Teramura & Sullivan, 1994). It is hypothesized (Sullivan *et al.*, 1996) that the receptors triggering the synthesis of UV-B absorbing compounds are saturated in plants growing in an open environment so that they provoke maximal synthesis at all irradiances. In *P. abies*, the protective mechanisms also appeared to be dependent more on the developmental state of leaf than induced by enhanced UV-B radiation. In emergent needles only, where UV-B radiation could penetrate into the mesophyll, biosynthesis of UV-B absorbing compounds was related to UV-B radiation dose (Trošt & Gaberščik, 2001). It seemed that in the studied plants the amount of UV-B absorbing compounds was sufficient, since we detected no disturbances in plant physiology (Tab. 2). None of the studied species exposed to UV-B radiation corresponding to 17% ozone depletion showed decrease of Fv/Fm ratio or Y that would reflect disturbance in photosynthesis. It is also likely that the damage caused by UV-B radiation is efficiently repaired (Rozema *et al.*, 1997). On the contrary, many authors re-

port about the effects of UV-B radiation on photochemical efficiency of PS II (Schoefield *et al.*, 1995; Häder *et al.*, 1996; Xiong *et al.*, 1999; Xiong, 2001.)

Tab. 1: The influence of enhanced UV-B radiation content of chlorophyll *a*, carotenoids and UV-B absorbing compounds (UV-B AC). Legend: + indicates positive trend, ++ indicates significant positive effect, x indicates no clear effect, - stands for negative effect (n = 4-10, p < 0.05).

Tab. 1: Vpliv povečanega UV-B sevanja na vsebnost klorofila *a*, karotenoidov in UV-B absorbirajočih snovi (UV-B AC). Legenda: + označuje pozitivno težnjo, ++ označuje značilno pozitiven vpliv, x označuje nejasen vpliv, - označuje negativen vpliv (n = 4-10, p < 0,05).

Species	Chl a	Carotenoids	UV-B AC	Source
<i>S. quadricauda</i>	+		++	Germ <i>et al.</i> , 2002a
<i>S. capricornutum</i>	+		++	not published
<i>S. magelanicum</i>	x	x	x	not published
<i>R. trichophyllus</i>	x	x	x	Germ <i>et al.</i> , 2002b
<i>C. demersum</i>	+ /		+ + / +	not published / Gaberščik <i>et al.</i> , 2002a
<i>M. spicatum</i>	x	x	x	not published
<i>P. alpinus</i>	x	x	x	Germ <i>et al.</i> , 2002b
<i>M. scorpioides</i>	x	x	x	not published
<i>F. esculentum</i>	x	+	+	Gaberščik <i>et al.</i> , 2002b
<i>P. officinalis</i>	x	x	x	Gaberščik <i>et al.</i> , 2001
<i>T. majus</i>	x	x	+	not published
<i>P. abies</i>	+ , x		+ , x	Trošt & Gaberščik, 2001

Tab. 2: The influence of enhanced UV-B radiation on Fv/Fm ratio, yield and ETS activity. Legend: + indicates positive trend, ++ indicates significant positive effect, x indicates no clear effect, - stands for negative effect (n = 4-10, p < 0.05).

Tab. 2: Vpliv povečanega UV-B sevanja na razmerje Fv/Fm, učinkovitost in aktivnost ETS. Legenda: + označuje pozitivno težnjo, ++ označuje značilno pozitiven vpliv, x označuje nejasen vpliv, - označuje negativen vpliv (n = 4-10, p < 0,05).

Species	Fv/Fm	Yield	ETS	Source
<i>S. quadricauda</i>			++	Germ <i>et al.</i> , 2002a
<i>S. capricornutum</i>			++	not published
<i>S. magelanicum</i>	x	x	x	not published
<i>R. trichophyllus</i>	x	x	x	Germ <i>et al.</i> , 2002b
<i>C. demersum</i>	x /	x /	++	not published / Gaberščik <i>et al.</i> , 2002a
<i>M. spicatum</i>	x	x	x	not published
<i>P. alpinus</i>	x	x	x	Germ <i>et al.</i> , 2002b
<i>M. scorpioides</i>	x	x	x	not published
<i>F. esculentum</i>	x	x		Gaberščik <i>et al.</i> , 2002b
<i>P. officinalis</i>	x	x		Gaberščik <i>et al.</i> , 2001
<i>T. majus</i>	x	x		not published
<i>P. abies</i>	x	x	+ , x	Trošt & Gaberščik, 2001

The production of photosynthetic pigments and UV-B absorbing compounds demanded an additional supply of energy, which was provided by increased respiratory

potential. The relation between the amount of UV-B absorbing compounds and ETS activity was significantly positive as reported for *S. quadricauda* and *C. demersum* (Tab. 2) (Gaberščik et al., 2002a). Increased ETS activity under enhanced UV-B radiation therefore augmented the energetic cost involved in generating the internal mechanisms of photoprotection (Ferreira et al., 1997; Scott et al., 1999; Gaberščik et al., 2002a).

SUMMARY

Enhanced UV-B radiation due to thinning of the stratospheric ozone layer affects primary producers. The research carried out on many species under similar experimental conditions, i.e. doses corresponding to 17% ozone depletion, showed species specific responses. Data from literature are very controversial. The contents of chlorophyll a were increased in algae *S. quadricauda* and *S. capricornutum* and in submersed macrophyte *C. demersum*. The increase of chlorophyll a in *P. abies* was observed in spring only, when the protective mechanisms were not fully developed. Other species showed no evident changes in chlorophyll content. The increase of UV-B absorbing compounds with increasing UV-B radiation dose is the most frequent reaction to UV-B radiation reported in literature. It has been observed for many algae, as well as for *S. quadricauda* and *S. capricornutum*. UV-B radiation also induced production of UV-B absorbing compounds in higher plants *C. demersum* and *F. esculentum*. In many cases, the production of UV-B absorbing compounds does not necessarily depend on UV-B dose. No correlation with the UV-B dose was detected in aquatic plants *R. trichophyllus*, *M. scorpioides*, *P. alpinus*, and *M. spicatum*. It was hypothesized that the receptors triggering the synthesis of UV-B absorbing compounds are saturated in plants growing in

an open environment, thus provoking maximal synthesis at all irradiances. In *P. abies*, the production of UV-B absorbing compounds appeared to be dependent more on the developmental state of leaf than induced by enhanced UV-B radiation. In emergent needles only, where UV-B radiation could penetrate into the mesophyll, biosynthesis of UV-B absorbing compounds was related to UV-B radiation. Many authors report about the effect of UV-B radiation on photochemical efficiency of PS II. None of the studied species exposed to UV-B radiation corresponding to 17% ozone depletion showed decrease of Fv/Fm ratio or Y, which would reflect disturbance in photosynthesis. The production of UV-B absorbing compounds demanded an additional supply of energy, which was provided by higher respiratory potential. The relation between the amount of UV-B absorbing compounds and ETS activity was significantly positive, as reported for *S. quadricauda*, *S. capricornutum* and *C. demersum*. The increased ETS activity under enhanced UV-B radiation therefore provided additional energy needed for the establishment of photoprotection and photorepair mechanisms.

ACKNOWLEDGEMENTS

This research was part of the project "The role of UV-B radiation on aquatic and terrestrial ecosystems: an experimental and functional analysis of the evolution of protective and adaptive mechanisms in plants, environment and climate" (Pl. 970637) supported by the EU (DGXII, Environmental Programme, ENV4-C197-0580), and part of St.O Alpe2 (3311-01-2183388) financed by Ministry of Education, Science and Sport of the Republic of Slovenia. Their financial support is gratefully acknowledged.

VPLIV UV-B SEVANJA NA VODNE IN KOPENSKKE PRIMARNE PROIZVAJALCE

Mateja GERM

Nacionalni inštitut za biologijo, SI-1000 Ljubljana, Večna pot 111

E-mail: mateja.germ@nib.si

Alenka GABERŠČIK

Oddelek za biologijo, Biotehniška fakulteta in

Nacionalni inštitut za biologijo, SI-1000 Ljubljana, Večna pot 111

Tadeja TROŠT-SEDEJ

Oddelek za biologijo, Biotehniška fakulteta, SI-1000 Ljubljana, Večna pot 111

Zdenka MAZEJ

ERICO, SI-3320 Velenje, Koroška 58

Jože BAVCON

Oddelek za biologijo, Biotehniška fakulteta, SI-1000 Ljubljana, Večna pot 111

POVZETEK

Povečano UV-B sevanje, ki je posledica tanjšanja ozonske plasti, vpliva na primarne proizvajalce. Raziskave

kažejo, da so se različne vrste, izpostavljene odmerkom, ki ustrezajo približno 17% stanjšanju ozonske plasti, odzvale različno. Rezultati o vplivu UV-B sevanja na primarne proizvajalce si pogosto nasprotujejo. Vsebnost klorofila a je pod vplivom UV-B sevanja narasla pri algah vrste *Scenedesmus quadricauda* in *Selenastrum capricornutum* ter pri podvodni rastlini navadni rogolist *Ceratophyllum demersum*. Narasčanje vsebnosti klorofila a pri navadni smreki *Picea abies* smo opazili samo spomladi, ko zaščitni mehanizmi še niso bili popolnoma razviti. Druge vrste, ki smo jih preučevali, niso kazale jasnega vpliva UV-B sevanja na vsebnost klorofila a. Glede na podatke v literaturi je narasčanje UV-B zaščitnih snovi najbolj pogost odziv primarnih proizvajalcev na povečano UV-B sevanje. UV-B sevanje je vplivalo na izgradnjo UV-B zaščitnih snovi tudi pri vrstah *S. quadricauda* in *S. capricornutum* in višjih rastlinah, kot sta navadni rogolist *C. demersum* in navadna ajda *Fagopyrum esculentum*. V mnogih primerih pa izgradnja UV-B zaščitnih snovi ni odvisna od odmerka UV-B sevanja. Korelacije med vsebnostjo UV-B zaščitnih snovi in odmerkom UV-B sevanja ni bilo pri lasastolistni vodni zlatici *Ranunculus trichophyllus*, alpskem dristavcu *Potamogeton alpinus* in klasastem mnanu *Myriophyllum spicatum*. Predpostavljamo, da so receptorji, ki vplivajo na izgradnjo UV-B zaščitnih snovi, nasičeni pri rastlinah, ki rastejo na odprtih rastiščih in tako omogočajo maksimalno izgradnjo pri različni intenziteti obsevanja. Pri navadni smreki *P. abies* je videti, da je bila izgradnja UV-B zaščitnih snovi bolj odvisna od razvojnega stanja iglic kot od povečanega UV-B sevanja. Izgradnja UV-B zaščitnih snovi je bila povezana z UV-B sevanjem samo pri nerazvitih iglicah, kjer je UV-B sevanje prodiralo do mezofila. Mnogi avtorji so dokazali vpliv UV-B sevanja na fotokemično učinkovitost fotosistema II (FS II). V naši raziskavi nobena od preučevanih vrst ni pokazala vpliva UV-B sevanja, ki ustreza 17% simulaciji tanjšanja ozonske plasti, na zmanjšanje potencialne fotokemične učinkovitosti (Fv/Fm), ali dejanske fotokemične učinkovitosti (angl. yield), ki kažejo na motnje v procesu fotosinteze. Izgradnja UV-B zaščitnih snovi zahteva dodatno zalogo energije, ki si jo organizmi zagotovijo s povečanim dihalnim potencialom (aktivnost ETS). Razmerje med vsebnostjo UV-B zaščitnih snovi in aktivnostjo ETS je bila značilno pozitivna pri vrstah *S. quadricauda*, *S. capricornutum* in navadnem rogolistu *C. demersum*. Povečana aktivnost ETS pri organizmih, ki so bili izpostavljeni povečanemu UV-B sevanju, je zagotovila dodatno energijo za vzpostavitev fotozaščite in fotopopravljajnih mehanizmov.

Ključne besede: UV-B sevanje, primarni proizvajalci, UV-B absorbirajoče snovi, fotokemična učinkovitost FS II, aktivnost terminalnega elektronskega transporta

REFERENCES

- Antonelli, A., D. Grifoni, F. Sabatini & G. Zipoli (1997): Morphological and physiological response of bran plants to supplemental UV radiation in Mediterranean climate. In: Rozema, J., W. W. C. Gieskes, S. C. van den Geijn, C. Nolan & H. de Boois (eds.): UV-B and Biosphere. Kluwer Academic Publishers, Dordrecht, Boston, London, p. 127-136.
- Beardall, J., T. Berman, S. Markager, R. Martinez & V. Montecino (1997): The effects of ultraviolet radiation on respiration and photosynthesis in two species of microalgae. *Can. J. Aquat. Sci.*, 54, 687-696.
- Bischof, K., D. Hanelt & C. Wiencke (1998): UV-radiation can affect depth-zonation of Antarctic macroalgae. *Mar. Biol.*, 131(4), 597-605.
- Björn, L. O. (1999): Effects of ozone depletion and increased ultraviolet-B radiation on terrestrial plants. In: Baumstark-Khan, C. (ed.): Fundamentals for the assessment of risks from environmental radiation. Kluwer Academic Publishers, Dordrecht, p. 463-470.
- Björn, L. O. & T. M. Murphy (1985): Computer calculation of solar ultraviolet radiation at ground level. *Physiol. Veg.*, 23(5), 555-561.
- Björn, L. O. & A. H. Teramura (1993): Simulation of daylight ultraviolet radiation and effects of ozone depletion. In: Young, A. R., L. O. Björn, J. Moan & W. Nultsch (eds): Environmental UV Photobiology. Plenum Press, New York, p. 41-71.
- Caldwell, M. M. (1968): Solar ultraviolet radiation as an ecological factor for alpine plants. *Ecol. Monogr.*, 38, 243-268.
- Clevering, O. A., C. W. P. M. Blom & W. Van Vierssen (1996): Growth and morphology of *Scirpus lacustris* and *S. maritimus* seedlings as affected by water level and light availability. *Funct. Ecol.*, 10, 286-296.
- Cullen, J. J., P. J. Neale & M. P. Lesser (1992): Biological Weighting Function for the Inhibition of Phytoplankton Photosynthesis by Ultraviolet Radiation. *Science*, 258, 646-650.
- Demmig-Adams, B. & W. W. Adams (1992): Photoprotection and other responses of plants to high light stress. *Annu. Rev. Plant Physiol. Plant Mol. Biol.*, 43, 599-626.
- De Lange, H. J., E. Van Donk & D. O. Hessen (2000): *In situ* effects of UV radiation on four species of phytoplankton and two morphs of *Daphnia longispina* in an alpine lake (Finse, Norway). *Verh. int. Verein. Limnol.*, 27, 1-6.
- Ferreira, G. A., S. Demers, P. Del Giorgio & J. P. Chanut (1997): Physiological responses of natural plankton communities to ultraviolet-B radiation in Redberry Lake (Saskatchewan, Canada). *Can. J. Fish. Aquat. Sci.*, 54(3), 705-714.

- Frost-Christensen, H. & K. Sand-Jensen (1992):** The quantum efficiency of photosynthesis in macroalgae and submerged angiosperms. *Oecologia*, 91, 377-384.
- Gaberščik, A., M. Novak, T. Trošt, Z. Mazej, A. M. Germ & L. O. Björn (2001):** The influence of enhanced UV-B radiation on the spring geophyte *Pulmonaria officinalis*. *Plant Ecol.*, 154(1/2), 49-56.
- Gaberščik, A., M. Germ, A. Škof, D. Drmaž & T. Trošt (2002a):** UV-B radiation screen and respiratory potential in two aquatic primary producers: *Scenedesmus quadricauda* and *Ceratophyllum demersum*. *Verh. int. Verein. Limnol.*, 27, 1-4.
- Gaberščik, A., M. Vončina, T. Trošt, M. Germ & L. O. Björn (2002b):** Growth and production of buckwheat (*Fagopyrum esculentum*) treated with reduced, ambient and enhanced UV-B radiation. *J. Photochem. Photobiol. B.*, 66, 30-36.
- Garde, K. & C. Cailliau (1998):** The impact of UV-B radiation and different PAR intensity on growth, ¹⁴C-uptake, DOC excretion, cell morphology and pigmentation in the marine prymnesiophyte, *Emiliania huxleyi*. Ph.D. Thesis. University of Copenhagen and VKI, Denmark, p. 32-52.
- Gehrke, C., U. Johanson, D. Gwinn-Jones, L. O. Björn, T. V. Callaghan & J. A. Lee (1996):** Single and interactive effects of enhanced ultraviolet-B radiation and increased atmospheric CO₂ on terrestrial and subarctic ecosystems. *Ecol. Bull.*, 45, 192-203.
- Germ, M., D. Drmaž, M. Šiško & A. Gaberščik (2002a):** Effects of UV-B radiation on green alga *Scenedesmus quadricauda*: growth rate, UV-B absorbing compounds and potential respiration in phosphorus rich and phosphorus poor medium. *Phyton*, 42, 25-37.
- Germ, M., Z. Mazej, A. Gaberščik & D. P. Häder (2002b):** The influence of enhanced UV-B radiation on *Batrachium trichophyllum* and *Potamogeton alpinus*-aquatic macrophytes with amphibious character. *J. Photochem. Photobiol. B.*, 66, 37-46.
- Häder, D. P. (1996):** Effects of enhanced solar UV-B radiation on phytoplankton. *Sci. Mar.*, 60(1), 59-63.
- Häder, D. P., H. Herrmann & R. Santas (1996):** Effect of solar radiation and solar radiation deprived of UV-B and total UV on photosynthetic oxygen production and pulse amplitude modulated fluorescence in the brown alga *Padina pavonia*. *FEMS Microbiol. Ecol.*, 19, 53-61.
- Häder, D. P., H. D. Kumar, R. C. Smith & R. C. Worrest (1998):** Effects on aquatic ecosystems. *J. Photochem. Photobiol. B.*, 46, 53-68.
- Hannach, G. & A. C. Sigleo (1998):** Photoinduction of UV-absorbing compounds in six species of marine phytoplankton. *Mar. Ecol. Prog. Ser.*, 174, 207-222.
- Holm-Hansen, O., N. D. Lubin & E. W. Helbling (1993):** Ultraviolet radiation and its effects on organisms in aquatic environments. In: Young, A. R., L. O. Björn, J. Moan & W. Nultsch (eds.): *Environmental UV Photobiology*. Plenum Press, New York, p. 379-425.
- Hunt, J. & D. L. McNeil (1999):** The influence of present-day levels of ultraviolet-B radiation on seedlings of two Southern Hemisphere temperate tree species. *Plant Ecol.*, 143(1), 39-50.
- Huovinen, P. S., H. Penttillä & M. R. Soimauo (2003):** Spectral attenuation of solar ultraviolet radiation in humic lakes in Central Finland. *Chemosphere*, 3, 205-214.
- Jansen, M. A. K., B. M. Greenberg, M. Edelman, A. K. Mattoo & V. Gaba (1996):** Accelerated degradation of the D2 protein of PS II under ultraviolet radiation. *Photochem. Photobiol.*, 63, 517-522.
- Jeffrey, S. W. & G. F. Humphrey (1975):** New Spectrophotometric Equations for determining Chlorophylls a, b, c1 and c2 in Higher plants, Algae and natural Phytoplankton. *Biochem. Physiol. Pflanzen*, 167(8), 191-194.
- Karentz, D., J. Cleaver & D. L. Mitchell (1991):** Cell survival characteristics and molecular responses of Antarctic phytoplankton to ultraviolet-B radiation. *J. Phycol.*, 27, 326-341.
- Karentz, D., M. L. Bothwell, R. B. Coffin, A. Hanson, G. J. Herndl, S. S. Kilham, M. P. Lesser, M. Lindell, R. E. Moeller, D. P. Morris, P. J. Neale, R. W. Sanders, C. S. Weiler & R. G. Wetzel (1994):** Impact of UV-B radiation on pelagic freshwater ecosystems: Report of working group on bacteria and phytoplankton. *Ergeb. Limnol.*, 43, 31-69.
- Karsten, U., K. Bischof, D. Hanelt, H. Tug & C. Wiencke (1999):** The effect of ultraviolet radiation on photosynthesis and ultraviolet-absorbing substances in the endemic Arctic macroalga *Devaleraea ramentacea* (Rhodophyta). *Physiol. Plant.*, 105 (1), 58-66.
- Kenner, R. A. & S. I. Ahmed (1975):** Measurements of electron transport activities in marine phytoplankton. *Mar. Biol.*, 33, 119-127.
- Liu, L., D. C. Gitz III & J. W. McLure (1995):** Effects of UV-B on flavonoids, ferulic acid, growth and photosynthesis in barley primary leaves. *Physiol. Plant.*, 93, 725-733.
- Madsen, T. V. & M. Breinholt (1995):** Effect of air contact on growth, inorganic carbon sources, and nitrogen uptake by an amphibious freshwater macrophyte. *Plant Physiol.*, 107, 149-154.
- Mitchell, D. L. & D. Karentz (1993):** The Induction and Repair of DNA photodamage in the Environment. In: Young, A. R., L. O. Björn, J. Moan & W. Nultsch (eds.): *Environmental UV Photobiology*. Plenum Press, New York, p. 345-376.
- Newsham, K. K., A. R. McLeod, P. D. Greenslade & B. A. Emmet (1996):** Appropriate controls in outdoor UV-B supplementation experiments. *Global Change Biol.*, 2, 319-324.
- Nielsen, T. (1996):** Effects of ultraviolet radiation on marine phytoplankton. Ph.D. Thesis. Lund University, Section of plant physiology, Lund.
- Olsson, L. (1999):** Modification of flavonoid content and photosynthesis by ultraviolet-B radiation. Atrazine toler-

- ant and sensitive cultivars of *Brassica napus*. Ph.D. Thesis. Lund University, Section of plant physiology, Lund.
- Packard, T. T. (1971):** The measurement of respiratory electron-transport activity in marine phytoplankton. *J. Mar. Res.*, 29, 235-243.
- Rau, W. & H. Hofmann (1996):** Sensitivity to UV-B of Plants Growing in Different Altitudes in the Alps. *J. Plant Physiol.*, 148, 21-25.
- Rozema, J., J. van de Staaij, L. O. Björn & M. Caldwell (1997):** UV-B as an environmental factor in plant life: stress and regulation. *Tree*, 12, 22-28.
- Rozema, J., L. O. Björn, J. F. Bornmann, A. Gaberščik, D. P. Häder, T. Trošt, M. Germ, M. Klisch, A. Gröninger, R. P. Sinha, Y. Y. He, M. Lebert, R. Buffoni-Hall, N. V. J. De Bakker, J. van De Staaij & B. Meijkamp, (2002):** The role of UV-B radiation in aquatic and terrestrial ecosystems - an experimental and functional analysis of the evolution of UV-B absorbing compounds. *J. Photochem. Photobiol. B.*, 66(1), 2-12.
- Runekles, V. C. & S. V. Krupa (1994):** The impact of UV-B radiation and ozone on terrestrial vegetation. *Environ. Pollut.*, 83, 191-213.
- Schoefield, O., B. M. A. Kroon & B. B. Prézelin (1995):** Impact of ultraviolet-B radiation on photosystem II activity and its relationship to the inhibition of carbon fixation rates for antarctic ice algae communities. *J. Phycol.*, 31, 703-715.
- Schreiber, U., W. Bilger & C. Neubauer (1995):** Chlorophyll fluorescence as a noninvasive indicator for rapid assessment of *in vivo* photosynthesis. In: Schulze, E. D. & M. M. Caldwell (eds.): *Ecophysiology of Photosynthesis*. Springer-Verlag, Berlin, Heidelberg, New York, p. 49-61.
- Scott, J. D., L. Chalker-Scott, A. E. Foreman & M. D'Angelo (1999):** *Daphnia pulex* fed UVB-irradiated *Chlamydomonas reinhardtii* show decreased survival and fecundity. *Photochem. Photobiol.*, 70, 308-313.
- Shick, J. M., M. P. Lesser & P. L. Jokie (1996):** Effects of ultraviolet radiation on corals and other coral reef organisms. *Global Change Biol.*, 2, 527-545.
- Smith, R. C. & K. S. Baker (1981):** Optical properties of the clearest natural waters (200-800 nm). *Appl. Optics*, 2, 177-184.
- Sommaruga, R. (2001):** The role of solar UV radiation in the ecology of alpine lakes. *J. Photochem. Photobiol. B.*, 1-2, 35-42.
- Sommaruga, R. & R. Psenner (1997):** Ultraviolet radiation in a high mountain lake of the Austrian Alps: air and underwater measurements. *Photochem. Photobiol.*, 65(6), 957-963.
- Sommaruga, R. & F. Garcia Pichel (1999):** UV-absorbing mycosporine-like compounds in planktonic and benthic organisms from a high-mountain lake. *Arch. Hydrobiol.*, 144(3), 255-269.
- Stapleton, A. E. (1992):** Ultraviolet radiation and Plants: Burning Question. *Plant Cell*, 4, 1353-1358.
- Strid, A., W. S. Chow & J. M. Anderson (1990):** Effects of supplementary UV-B radiation on photosynthesis in *Pisum sativum*. *Biophys. Biochem. Acta.*, 1020, 260-268.
- Sullivan, J. H., B. W. Howells, C. T. Ruhland & T. A. Day (1996):** Changes in leaf expansion and epidermal screening effectiveness in *Liquidambar styraciflua* and *Pinus taeda* in response to UV-B radiation. *Physiol. Plant.*, 98, 349-357.
- Teramura, A. H. & J. H. Sullivan (1994):** Effects of UV-B radiation on photosynthesis and growth of terrestrial plants. *Photosynthesis Res.*, 39, 463-473.
- Tevini, M. (1993):** Effects of enhanced UV-B radiation on terrestrial plants. In: Tevini, M. (ed.): *UV-B radiation and ozone depletion: Effects on humans, animals, plants, microorganisms, and materials*. Lewis Publishers, Boca Raton, FL, p. 125-153.
- Tosserams, M. & J. Rozema (1996):** Effects of ultraviolet-B radiation (UV-B) on growth and physiology of the dune grassland species *Calamagrostis epigeios*. *Environ. Pollut.*, 89, 209-214.
- Trošt, T. & A. Gaberščik (2001):** The effect of enhanced UV-B radiation on Norway spruce (*Picea abies* (L.) Karst.) needles of two different age classes. *Acta Biol. Slov.*, 44(3), 13-25.
- Turunen, M., W. Heller, S. Stich, H. Sandermann, M. L. Sutinen & Y. Norokorpi (1999):** The effects of UV exclusion on the soluble phenolics of young Scots pine seedlings in the subarctic. *Environ. Pollut.*, 106(2), 219-228.
- Vadstrup, M. & T. V. Madsen (1996):** Growth limitation of submerged aquatic macrophytes by inorganic carbon. *Freshw. Biol.*, 34, 411-419.
- Veen, A., M. Reuvers & P. Roncak (1997):** Effects of acute and chronic UV-B exposure on green algae: a continuous culture study using a computer-controlled light regime. *Plant Ecol.*, 128, 28-40.
- Williamson, C. E., R. S. Stemberger, D. P. Morris, T. M. Frost & S. G. Pausen (1996):** Ultraviolet radiation in North American lakes. Attenuation estimates from DPC measurements and implications for plankton communities. *Limnol. Oceanogr.*, 40(15), 1024-1034.
- Xiong, F. (2001):** Evidence that UV-B tolerance of the photosynthetic apparatus in microalgae is related to the D1-turnover mediated repair cycle *in vivo*. *J. Plant Physiol.*, 158, 285-294.
- Xiong, F., L. Nedbal & A. Neori (1999):** Assessment of UV-B sensitivity of photosynthetic apparatus among microalgae: Short-term laboratory screening versus long-term outdoor exposure. *J. Plant Physiol.*, 155(1), 54-62.