

VU Research Portal

The effects of UVB radiation on charophycean algae and bryophytes

de Bakker, N.

2011

document version

Publisher's PDF, also known as Version of record

[Link to publication in VU Research Portal](#)

citation for published version (APA)

de Bakker, N. (2011). *The effects of UVB radiation on charophycean algae and bryophytes*. [PhD-Thesis - Research and graduation internal, Vrije Universiteit Amsterdam]. Labor Grafimedia B.V.

General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

E-mail address:

vuresearchportal.ub@vu.nl



Introduction



The sun, ozone depletion and enhanced levels of UVB radiation

The sun provides the earth with energy by radiation, that can be divided into three wavebands: infrared (IF; wavelengths >700 nm), photosynthetically active radiation (PAR; wavelengths from 400-700 nm) and ultraviolet radiation (UV; wavelengths < 400 nm).

The amount of radiation and the wavelengths reaching the earth surface are dependent on scatter and absorption in the atmosphere (atmospheric conditions) and the length of the path that the wavelengths travel through the atmosphere. In the atmosphere solar radiation is scattered and absorbed by particulate matter, water vapour and molecules like oxygen, ozone and nitrogen. The path length is influenced by solar angle and altitude.

Only a limited part of the solar radiative spectrum consists of UV radiation. However, by its shorter wavelengths, it has high energy contents. As a consequence it is more damaging than other wavelengths for life on earth. The UV waveband is generally divided into three bands: UVA (315-400 nm), UVB (280-315 nm) and UVC (wavelengths < 280 nm). The stratospheric ozone layer has a large influence on the UV radiative spectrum reaching the earth: it absorbs all UVC and a large part of the UVB radiation. UVA radiation and longer wavelengths are mostly transmitted.

In the stratosphere a continuous process of production and destruction of ozone takes place. While ozone is formed from oxygen molecules at wavelengths shorter than 240 nm, it is destructed by catalytic reactions with nitric oxide (NO_x), hydroxide (HO_x), and atomic chlorine and bromines. Human activities have influenced the ozone layer negatively, by causing additional ozone depletion due to the emission of ozone depleting catalysts, like CFCs (chlorofluorocarbons). Global circulation patterns affect the concentrations of these compounds in the stratosphere. Moreover, catalytic reactions between ozone and these compounds occur more frequently at very low temperatures. The thickness of the ozone layer, therefore, differs around the world and during the year. Especially in the Antarctic region, the ozone layer is depleted most severely every year. However, also in the northern hemisphere the ozone layer has become thinner since the early 1980s. With a thinner ozone layer, higher levels of UVB radiation and shorter wavelengths reach the earth surface with detrimental effects on various kinds of organisms.

Effects of UV radiation on plants

(Enhanced) levels of UVB radiation may lead to damage for life on earth. Farman *et al.* (1985) discovered the ozone hole and were the first who reported

on a thinning of the ozone layer. Since then much attention has been paid to the effects of UV(B) radiation on terrestrial and marine organisms. Those studies focusing on plants revealed that UVB radiation causes direct damage to DNA, proteins, lipids, pigments and phytohormones (for an overview see Meijkamp 2006). This damage may lead to altered growth and morphology. However, many plants are able to avoid damage or to repair UV-induced damage. Vascular plants and algae, for instance, showed the ability to produce UVB absorbing compounds that filter out UVB radiation (Schnitzler *et al.* 1996, Meijkamp *et al.* 1999, Searles *et al.* 2001). Algae have been shown to produce mycosporine-like amino acids (MAAs), while flavonoids act as UVB screens in vascular plants (Cockell and Knowland 1999). Flavonoids have also been found in some moss species (Markham *et al.* 1990), but in that case, induction by UVB radiation has not been proven yet. In addition, plants avoid UVB damage by altered plant morphology (Meijkamp 2006).

Damage to DNA can be repaired via two ways: in the dark (dark repair) and, more efficiently, by enzymatic photoreactivation in which UVA and blue light play an important role to activate this enzymatic reactions (Sancar and Sancar 1988). Together, the ability to protect against UVB radiation and to repair the damage determines the sensitivity of an organism to UVB radiation.

The evolution of land plants and the UVAQTER project

While the majority of studies on UVB effects focuses on vascular plants, Rozema *et al.* (1997) put forward that during early land plant evolution the radiation spectrum differed from now, with higher UVB levels than at present, since the stratospheric ozone layer was still developing. Adaptations to UVB were needed to survive these harsh terrestrial conditions. Therefore, Rozema *et al.* (1997) hypothesized that protection to UVB radiation was an important factor in early land plant evolution.

Since firstly UVB levels differed during land plant evolution and, secondly adaptations might be developed via different evolutionary lines, differences in UVB adaptations might be expected between plants which developed early versus later in the evolution of land plants. Terrestrial plant life roughly developed along the line green algae, bryophytes, ferns, gymnosperms and angiosperms.

[¹] UVAQTER is the acronym for 'The role of Ultra Violet-B radiation in Aquatic and Terrestrial ecosystems: an experimental and functional analysis of the evolution of protective and adaptive mechanisms in plants' (project reference ENV4970580).

The European project UVAQTER^[1] focused on the effects of enhanced levels of UVB radiation on plants from marine, freshwater and terrestrial ecosystems, following the evolutionary line of algae, charophycean algae, lichens, bryophytes to vascular plants. The project aimed to analyse, characterize and compare the functioning of UVB screens, i.e. compounds absorbing UVB radiation, in these plant groups, since these compounds were assumed to increase in complexity in accordance with the evolutionary line of vascular plants. This prediction had been made because ancient UVB levels, during land plant evolution, were probably higher than at present (Rozema *et al.* 1997). Within the evolutionary line, specific plant groups were studied by the four different participating research groups. The research presented in this thesis was part of this UVAQTER project and focuses on the effects of UVB radiation on the plant groups charophycean algae and bryophytes.

The effects of UVB on charophytes and bryophytes

From the now living green algae, Charophyceae are most closely related to the vascular land plants. These charophycean algae or charophytes have a common ancestor with vascular land plants. Charophytes are multicellular algae that are found on the entire gradient from shallow to deep (>20 m) freshwater systems. In contrast to plants living on the land, aquatic plants and algae have to cope, amongst other differences, with altered radiation conditions. Several processes, like reflection and attenuation, influence radiation conditions in aquatic systems (Kirk 1994). Dependent on the solar angle part of the solar radiation is directly reflected at the water surface. Subsequently, radiation is attenuated in the water column by absorption and scatter (Kirk 1994). Chemical, biological and physical properties of the water determine the depth each wavelength reaches. As a consequence, reflection and attenuation vary, depending on the conditions, for different wavelengths. An important factor for the penetration depth of UVB radiation is, among other factors, the amount of dissolved organic matter (DOM). Freshwater generally contains higher levels of DOM than marine waters and subsequently UVB radiation is attenuated more quickly in freshwater. Nevertheless it still may penetrate to considerable depths. Therefore, (enhanced levels of) UVB radiation may still be of importance in clear shallow freshwaters and affecting charophycean algae. In addition, submerged vegetation, and especially charophycean algae, contribute to increasing water transparency (references in De Bakker *et al.* 2005) and therefore UVB levels are expected to penetrate deeper as well.

Bryophytes are in the evolutionary line more closely related to vascular

plants than charophycean algae. They occur (mostly) on land and are present in many different habitats worldwide, e.g. in bogs, fens, forests, dunes and grasslands. In contrast to vascular plants, most bryophytes lack vascular tissue and a cuticle on the leaves. Instead, they take up nutrients and water via their leaves and stems (Proctor 2000). In addition, bryophytes are poikilohydric: they depend on sufficient air humidity to be physiologically active. During moist periods they photosynthesise and grow and during times of drought they suspend their metabolism (Proctor 2000) and there is no growth. The ability to survive desiccation and to absorb nutrients from e.g. rain and fog give bryophytes the opportunity to grow in many different habitats. Exposure to UVB radiation and the extent of adaptation by bryophytes thereto, may depend on their habitat characteristics. Obvious are the differences in exposure to different irradiance regimes for forests versus open ecosystems. In addition to different radiation regimes, habitats also differ in the extent to which species are exposed to other stresses, such as drought. Compounds that might reduce effects of drought, like those related to oxidative stress, may additionally act as UVB screen (Smirnoff 1993).

Experimental conditions: controlled or field experiments

Studies on the effects of UVB radiation in plants have been conducted in growth chambers, greenhouses and under (semi-)natural conditions. Each of these methods has advantages and disadvantages. In general, growth chambers and greenhouses give researchers the ability to manipulate each environmental variable separately, e.g. radiation, temperature, or humidity. Often higher numbers of replicates can be used and side effects can be minimized by rotating the experimental units. However, the manipulated environmental conditions often differ from the field conditions. Simulating solar radiation spectra in growth chambers and greenhouses is difficult. Due to technical constraints, UVA and visible radiation (PAR) are often low compared to natural conditions, while these are important in mitigating UVB effects on plants (Caldwell *et al.* 1994).

In contrast to controlled conditions, seldom plants are exposed to a single stress factor under natural conditions. More often several factors influence plant performance at the same time, like e.g. water stress, nutrient availability and temperature (Caldwell *et al.* 1998). The effects of UVB radiation under field conditions may therefore be influenced by these additional stressors. Plant performance under these circumstances may be different from those under controlled conditions. In this thesis, therefore a combination of different methods has been applied.

Research questions and thesis outline

Given the importance of bryophytes and charophycean algae in the evolutionary line of land plant development, the overall aim of this thesis is to study the effects of UVB radiation on growth, DNA damage and induced UVB absorbing compounds in charophytes and bryophytes. In addition, the effects found in charophytes and bryophytes are placed in an ecological framework by analysing charophycean algae under both controlled and field conditions, and by including a comparison of the UVB effects in bryophytes from three contrasting habitats. The research questions addressed in each chapter are listed in Table 1.1. Although many studies determined the effects of UVB radiation on different organisms, only a limited number so far focused on the effects of UVB radiation on bryophytes and even fewer on the effects on charophytes. For charophycean algae this study was actually one of the first. Bryophyte UVB studies have been conducted mainly on species from bog habitats with short summer periods (as snow covered them in winter) in the Arctic and Antarctic region. In the Netherlands, situated in the temperate Atlantic region, bryophytes are mostly year-round exposed to UVB radiation and much less information was available for bryophytes growing under these conditions.

Thus, **Chapters 2 and 3** focus on the effects of UV radiation on charophycean algae. **Chapter 2** reports on the effects of UV on growth, DNA damage and UVB absorbing compounds under climate controlled conditions. Subsequently, in **Chapter 3**, the actual effects of UVB radiation under natural conditions are shown, measured by a combination of *in situ* UV measurements and DNA dosimeters, and sampling of charophytes. **Chapters 4 and 5** focus on bryophytes. **Chapter 4** presents the effects of UVB radiation on the dune moss species *Syntrichia ruralis* under semi-natural conditions. Bryophytes occupy many different habitats with different UVB exposure. In **Chapter 5**, nine bryophyte species from three different habitats (forests, dunes and fens/bogs) are compared in their response to UVB radiation in an experiment with standardized climate controlled conditions. In **Chapter 6**, the results are summarised and discussed.

References

- Caldwell MM, Flint SD, Searles PS. 1994. Spectral balance and UV-B sensitivity of soybean: a field experiment. *Plant Cell & Environment* 17: 267-276.
- Caldwell MM, Björn LO, Bornman JF, Flint SD, Kulandaivelu G, Teramura AH, Tevini M. 1998. Effects of increased solar ultraviolet radiation on terrestrial ecosystems. *Journal of Photochemistry and Photobiology B: Biology* 46: 40-152.

INTRODUCTION

Table 1.1: The research questions that were studied in this thesis

Plant group	
Charophytes:	
<i>Chara aspera</i>	<p>What are the effects of enhanced levels of UVB radiation on growth, morphology, and amounts of UVB absorbing compounds under climate controlled conditions? (Chapters 2, 3)</p> <p>What are the UVB radiation patterns in waters with natural charophyte dominance? (Chapter 3)</p> <p>What are the effects of UVB radiation under natural conditions? (Chapter 3)</p>
Bryophytes:	
<i>Syntrichia ruralis</i>	<p>What are the effects of enhanced levels of UVB radiation on growth, morphology, and amounts of UVB absorbing compounds and total phenolic compounds under semi-natural conditions? (Chapter 4)</p>
<i>Syntrichia ruralis</i> , <i>Dicranum scoparium</i> , <i>Mnium hornum</i> , <i>Polytrichum commune</i> , <i>Polytrichum juniperinum</i> , <i>Polytrichum formosum</i> , <i>Campylopus introflexus</i> , <i>Sphagnum magellanicum</i> , <i>Sphagnum fallax</i>	<p>What are the effects of enhanced levels of UVB radiation on DNA damage, growth, and amounts of UVB absorbing compounds in different bryophytes in a climate controlled greenhouse? (Chapter 5)</p> <p>Does habitat origin affect the bryophyte UVB responses? (Chapter 5)</p>

- Cockell CS, Knowland J. 1999. Ultraviolet radiation screening compounds. *Biological reviews* 74: 311-345.
- De Bakker NVJ, van Bodegom PM, van de Poll WH, Boelen P, Nat E, Rozema J, Aerts R. 2005. Is UV-B radiation affecting charophycean algae in shallow freshwater systems? *New Phytologist* 166: 957-966.
- Farman JC, Gardiner BG, Shanklin JD. 1985. Large losses of total ozone in Antarctica reveal seasonal ClO_x/NO_x interaction. *Nature* 315: 207-210.
- Kirk JTO. 1994. *Light & Photosynthesis in Aquatic Ecosystems*. Cambridge, UK: Cambridge University Press.
- Markham KR, Franke A, Given DR, Brownsey P. 1990. Historical Antarctic ozone level trends from herbarium specimen flavonoids. *Bull. Liaison-Groupe Polyphenols* 13: 230-235.
- Meijkamp BB. 2006. *Multilevel UV-B attenuation. Morphological and chemical adaptations of Vicia faba to ultraviolet-B radiation*. Doctoral thesis VU University Amsterdam, The Netherlands.
- Meijkamp B, Aerts R, Van de Staaij J, Tosserams M, Ernst W, Rozema J. 1999. Effects of UV-B on secondary metabolites in plants. In: Rozema J. (ed.) *Stratospheric ozone depletion, the effects of enhanced UV-B radiation on terrestrial ecosystems*, pp. 39-59. Backhuys Publishers, Leiden.

- Proctor MCF. 2000. Physiological ecology In: Shaw AJ, Goffinet B (eds) *Bryophyte biology*. University Press Cambridge, United Kingdom.
- Rozema J, van de Staaij J, Björn LO, Caldwell M. 1997. UV-B as an environmental factor in plant life: stress and regulation. *Trends in Ecology and Evolution* 12: 22-28.
- Sancar A, Sancar GB. 1988. DNA repair enzymes. *The Annual Review of Microbiology* 57: 29-67.
- Schnitzler JP, Jungblut TP, Heller W, Kofferlein M, Hutzler P, Heinzmann U, Schmelzer E, Ernst D, Langebartels C, Sandermann H. 1996. Tissue localization of UV-B screening pigments and of chalcone synthase mRNA in needles of Scots pine seedlings. *New Phytologist* 132: 247-258.
- Searles PS, Flint SD, Caldwell MM. 2001. A meta-analysis of plant field studies simulating stratospheric ozone depletion. *Oecologia* 127: 1-10.
- Smirnoff N. 1993. The role of active oxygen in the response of plants to water deficit and desiccation. *New Phytologist* 125: 27-58.