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The effects of UVB radiation on charophycean algae and bryophytes

de Bakker, N.

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General discussion



This thesis analyses the effects of (enhanced) levels of UVB radiation on the fresh water charophyte *Chara aspera* and nine bryophyte species originating from three different habitats. For both plant groups, experiments were conducted under climate controlled conditions. In addition, UVA and UVB effects were studied in the dune bryophyte species *Syntrichia ruralis* under semi-natural conditions. Field measurements were done in the natural charophyte habitats to elucidate the effects of UV radiation under natural conditions. Table 6.1 shortly summarizes the answers to the research questions formulated in Table 1.1 of the general introduction to this thesis (**Chapter 1**). First, the answers will be discussed for charophytes and bryophytes separately. Subsequently, the implications of these results will be discussed within the framework of the evolutionary line of land plants.

UV effects in charophytes

Charophycean algae, or charophytes, have a common ancestor with vascular land plants and are, from an evolutionary point of view, amongst the freshwater green algae the most closely related to vascular land plants. In contrast to land plants, aquatic plants and algae have to cope - amongst others - with a different radiation regime due to attenuation of radiation (including UVB radiation) in the water column. At the same time, charophycean algae are known to contribute to increased water transparency in freshwater systems by accumulating nutrients, preventing resuspension, and by the production of allelopathic substances (references in De Bakker *et al.* 2005, **Chapter 3**). In addition, charophytes also occur in freshwater lakes and pools with a fluctuating water table and are therefore exposed to UVB radiation in the drier periods. These factors make charophycean algae ideal specimens when studying the functioning of UVB screens in an evolutionary line. Still, surprisingly little information is available on the (ecological) effects of UVB radiation on charophytes. The two chapters on charophytes in this thesis (**Chapters 2 and 3**) are among the very few studies of this topic.

The studies presented in this thesis show that the charophyte *Chara aspera* is sensitive to UVB radiation. Under climate controlled conditions (**Chapter 2 and 3**), growth was significantly reduced under (enhanced levels of) UVB radiation. The results of this study indicate that levels of UVB radiation even lower than those tested in this study, may lead to significantly negative plant responses.

This study was also the first to show that UVB exposure leads to DNA damage (i.e. the formation of pyrimidine dimers) in charophytes, as is also the case in other plant groups (**Chapter 3**). More importantly, repair mechanisms in these charophytes were insufficient to reduce the accumulated DNA damage overnight, showing that no detectable repair of this damage takes place in these charophytes. There was a significant positive correlation between the DNA damage levels found and the levels of UVB radiation applied.

More surprising was that, despite the negative effects of UVB exposure, there was no effect of UVB exposure on the amount of UVB absorbing compounds. Charophytes therefore do not seem to have developed protective screens to reduce harmful effects of UVB exposure. This is in contrast to marine algae (having mycosporine-like amino acids; MAAs) or vascular plants (having flavonoids). Instead, the presence of UVA radiation and not UVB radiation caused an increase in (both UVA and) UVB absorption in plant extracts (**Chapter 3**). Most UVB supplementation studies on the effects of UV exposure, so far, did not distinguish among the effects of UVA radiation and UVB radiation and were thus unable to pick up such effects if present.

In vascular plants and algae, several functions have been proposed for the phenolic compounds besides acting as UV screen (references in Day 2001). Thus, there might have been another ecological or physiological function that, associated with UVA radiation that, stimulated the synthesis of compounds that absorb UVB (and UVA) in charophycean algae. The reason for the stimulation of phenolic compounds in charophycean algae by UVA radiation is unknown. It should be noted, however, that the total amount of UVB absorbing compounds found in these charophytes was very low when compared to e.g. those in vascular plants or mosses (e.g. **Chapter 5**). Therefore it might be questionable whether these levels found here function as an ecologically relevant UVB defense mechanism.

Another clue for the absence of expected chemical plant responses to UVB radiation in charophycean algae, was obtained in the field study (**Chapter 3**) that aimed to validate the results of the studies under climate controlled conditions (**Chapter 2**). These field measurements on UVB attenuation in the charophytes' natural habitats by spectroradiometrical measurements and DNA dosimeters showed that UVB radiation was attenuated quickly. DNA damage in DNA dosimeters was significantly correlated with the Setlow weighted daily UVB doses both above water and in the water column. However, in both Lake Veluwe and the dune slack the Buiten Mui, attenuation coefficients were high leading to a 1% depth for UVB radiation of 0.20 to 0.06 cm and a quick extinc-

tion of DNA damage in DNA dosimeters. The charophytes grew at greater depths than the depth where 1% of the harmful UVB radiation was transmitted (as found by Rae *et al.* 2001). Consequently, no DNA damage was found in the charophytes under natural conditions. These results suggest that the water column gives enough protection against UVB radiation, acting as a natural, external UVB screen.

Although adaptations to diminish the harmful effects of UVB radiation seem to be absent in charophytes, we found another effect of UVB radiation at climate controlled conditions (**Chapter 2**): UVB radiation led to a significant increase in vegetative reproduction structures (bulbils), while generative reproduction structures (antheridia and/or oogonia or spores) decreased. The decrease in generative reproduction structures is remarkable, because in general -in vascular plants- generative reproduction is stimulated by stressful conditions (Grime 1977) and is therefore expected to be promoted by stress, like UVB radiation. The contrary occurred in these charophytes. They followed a different strategy, which was the stimulation of vegetative reproduction, i.e. bulbils. Bulbils are generally considered to allow rapid re-establishment in fluctuating environments and to survive during winter periods (Krause 1997, Van den Berg *et al.* 2001). This implies that it would be profitable for charophytes to sense fluctuations in their environment, particularly fluctuations in water column levels. Short wavelengths, like UVB radiation, attenuate more quickly than longer wavelengths like photosynthetically active radiation and may thus represent a more sensitive measure of fluctuations in water levels. Such adaptation to UVB radiation may explain why bulbils were stimulated by increasing UVB radiation. So far, there have been no other studies that studied the effects of UV exposure on regeneration in charophytes.

Altogether, the combination of results presented in **Chapters 2 and 3** indicate that charophycean algae are sensitive to UVB radiation, but that UVB radiation has played only a limited role in driving plant adaptations to reduce harmful UVB effects in charophycean algae. Alternatively, the level of UVB radiation may be used as an indicator of the depth of the water column by charophytes and as such may stimulate mechanisms needed to survive dry periods.

UV effects in bryophytes

In the line of evolutionary development bryophytes are more closely related to vascular plants than charophycean algae. Like vascular plants, most bryophytes grow on land. In contrast to vascular plants, most bryophytes lack vascular tis-

sue and a cuticle on the leaves: they take up nutrients and water via their leaves and stems (Proctor 2000). 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. These features of bryophytes may be of importance in the response to UVB radiation (Gehrke 1999) and therefore bryophytes were chosen as a second group of organisms for studying the functioning of UVB screens in an evolutionary line. In addition, most bryophyte studies on UVB effects were conducted in (near) (Ant)Arctic regions with species from open and exposed habitats that were often wet from (snow) melt and with short growing periods. The bryophyte studies in this thesis are among the first that studied effects of UVB radiation on the (eco)physiological responses in temperate bryophytes. In the temperate Atlantic region bryophytes are generally year-round exposed to solar UVB. In bryophytes from temperate regions UVB effects were so far only studied on chlorophyll fluorescence parameters before, as indicator for photosynthetic activity (Takáč et al. 1999, Csintalan et al. 2001). These studies did not quantify growth, DNA damage and UV absorbing compounds yet.

In **Chapter 4**, the effects of enhanced levels of UVB radiation were studied for the bryophyte *Syntrichia ruralis*, in a 13 months lasting UV supplementation outdoor experiment. *S. ruralis* is a colonizer from open dune areas and is fully exposed to solar radiation under natural conditions. During the experiment net length growth showed a strong seasonal character with hardly any growth in spring and summer, and a slow growth in autumn that ceased again in winter. Height growth of *S. ruralis* was significantly reduced under enhanced UVB exposure, like in other studies (references in **Chapter 5**). Total specific weight (gram per cm plant length) was positively affected by UVB radiation (marginally significant). At the same time, coinciding with the results obtained for charophycean algae (**Chapter 2**), there was no significant effect of the different UV treatments on the amount of UVB absorbing compounds, unlike effects found for vascular plants upon UVB exposure (references in Meijkamp 2006). Independent of UV exposure, however, the levels of UVB absorbing compounds were significantly lower in autumn compared to those in spring. In the Netherlands higher UVB levels are found in spring (due to low ozone values), compared to autumn (data RIVM 1996-2006). Correspondingly, Newsham et al. (2002) and Newsham (2003) found that the ratio of UVB to PAR irradiance was a good predictor for the concentrations of UVB screening compounds in bryophyte species in Antarctica. This suggests that the background UVB to PAR irradiance ratio levels were an important factor determining the levels of UVB absorbing compounds. Still, this explanation does not match with the lack of re-

sponse of UVB absorbing compounds to the different treatments in the 13 months lasting UVB supplementation experiment. That finding suggests that UVB radiation was not the trigger for the observed levels. Indeed, while the level of total phenolic compounds was affected by UV exposure, this was not related to UVB radiation. Instead, and remarkably but again in coincidence with the results obtained for charophycean algae (**Chapter 2**), the presence of UVA radiation supplied simultaneously with UVB radiation led to a higher level of total phenolic compounds. As for charophycean algae, this points to another driver than the need of a UVB screen that leads to a change in the amount of phenolic compounds in bryophytes.

In order to test whether the results of **Chapter 4** obtained for a single temperate bryophyte species indicate a more general behavior of bryophytes from different habitats towards UVB radiation, a similar experiment was conducted under climate controlled conditions. In this experiment nine bryophyte species from three different habitats (forests, dunes and bogs/fens) were exposed to three UVB levels (and their (UVA) control treatments) for ten weeks (**Chapter 5**). In this experiment we analysed species' responses to UVB radiation. The results obtained in this study largely confirmed the results obtained for *S. ruralis* over a wider range of species: UVB radiation led in most species to significant levels of UV induced DNA damage (except for *Dicranum scoparium* and *Polytricum formosum*). In most species the highest dose, but often also a lower UV dose led to significant levels of DNA damage. Growth was significantly affected in some species, mainly in the highest treatment. UVB absorbing compounds were not significantly affected in most species, except in *Sphagnum fallax* and *S. ruralis* where ambient and/or enhanced UVB levels even decreased the levels of UVB absorbing compounds (while no effect of UVB radiation on UVB absorbing compounds had been found for *S. ruralis* in **Chapter 4**). Also, when all species and all treatments were analysed together, a significant decrease in UVB absorbing compounds after UVB exposure was found. These results contrast previously found correlations between concentrations of UVB absorbing compounds and surface UVB radiation levels (Markham *et al.* 1990), indicating that such correlations cannot be used as proof of induction of these compounds by UVB radiation. In coincidence with a lack of induction, no dose-response relations between methanol extractable UVB absorbing compounds and past UVB radiation had been found in other studies with terrestrial and aquatic bryophytes and liverworts (Huttunen *et al.* 2005ab, Arroniz-Crespo *et al.* 2008). Together, like in **Chapter 4**, the results of **Chapter 5** suggest another driver than UVB radiation inducing UVB absorbing compounds.

To understand which driver this could be, in **Chapter 5** we also tested whether habitat origin consistently affected the UVB response among the nine species. Analysis of the effects of exposure to (increasing levels of) UVB radiation among the species from different habitats revealed that DNA damage was least in forest species. Moreover, in contrast to dune and bog/fen species, DNA damage did not increase with increasing UVB exposure in forest species. Moreover, forest species were only negatively affected in their growth rates at the highest UVB levels, whereas dune species were affected at the middle and highest UV levels and bog/fen species were significantly affected at all UV treatments. Even so, there was no difference in the level of UVB absorbing compounds among the species from the different habitats, while differences among species within a habitat were large. Likewise, notwithstanding the different sensitivities of bryophytes from different habitats to UV exposure, there was no dose-response relation in UVB absorbing compounds for any of the habitats.

Together, these results show that bryophyte species from more extreme environments (dunes and bog/fens) are most sensitive to UVB radiation, while there seems only limited influence of UV exposure on bryophyte adaptations. Takáč *et al.* (1999), Csintalan *et al.* (2001) and Dunn and Robinson (2006) pointed out that adaptations to other stresses in bryophytes might interfere with the UVB tolerance in bryophytes. If this is a general rule, not the habitat types but the ability to cope with different stresses may determine the differences in tolerance to UVB radiation. Both desiccation and UVB radiation may lead to oxidative stress (references in **Chapter 5**). Fen and bog bryophytes are always wet and during natural UV exposure physiologically active. These were also the most sensitive species to UV exposure. The fact that these species survive in nature probably lies in the fact that they are by far better competitors to other stresses induced by the extreme environment they live in, e.g. nutrient competition. Based on a similar line of reasoning, it would be expected that dune species would be much less sensitive since they are able to cope with desiccation. Under high UV exposure levels at field-conditions dune species are often in a dry state in which the curled leaves, waxes and/or glass hairs might reduce the direct impact of UV on plant cell damage. This contrasts Gehrke's (1998) argument that being physiologically active is an advantage for bryophytes to repair incurred damage immediately. Still, at the greenhouse conditions during the experiment with high humidity levels, dune species were found to be sensitive as at these conditions they were unable to use their natural adaptations to reduce oxidative stress. The greenhouse experiment might therefore have shown an exaggeration of the UV response of these dune species. The co-

incidence between the sensitivities of bryophytes to harmful effects of UVB radiation and the ability to cope with other stresses like desiccation makes it hard to prove whether UVB radiation itself or other stresses that occur simultaneously with UVB radiation play a role in bryophytes under natural conditions.

UV effects in relation to the evolutionary line of land plants

The research presented in this thesis was part of the European project UVAQTER^[1]. This EU project focused on the role of enhanced levels of UVB radiation on aquatic and terrestrial ecosystems and aimed to analyse, characterise and compare the functioning of UVB screens in plants from marine, fresh water and terrestrial ecosystems. The project assumed that exposure to UVB radiation would induce UVB absorbing compounds in plants from marine algae to vascular plants. These UVB inducible UV screens had already been found in algae and cyanobacteria (MAAs) and in vascular land plants (flavonoids), but not yet in the other plant groups. Based on these studies it was assumed that the complexity of UV screens would increase with the evolution of land plants, following the evolutionary line from green algae via bryophytes, ferns and gymnosperms to angiosperms. This prediction had been made because ancient UVB levels, during land plant evolution, were probably higher than at present (Rozema *et al.* 1997). Adaptations against UVB radiation, like protective UVB absorbing compounds, might therefore have played an important role in the land plant evolution and the transition from water to land. However, it remained uncertain whether the increase of thickness in the protective stratospheric ozone layer as an external UV screen or the (evolution of) plant UV screens made this transition possible.

The research presented in this thesis focused on the effects of UVB radiation on the least evolutionary developed groups: charophycean algae and bryophytes. As shown in the previous sections and contrary to the above-mentioned assumptions, none of the bryophyte and charophyte species studied in this thesis had UVB inducible UV screens, notwithstanding that all species were to some degree negatively affected by UVB radiation. This indicates that

[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).

there was no increase in the complexity of UV screens with the evolution of land plants. On the contrary; in some of the bryophyte species examined even a decrease in UVB absorbing compounds was found after UVB exposure. Although within the EU project the presence of UV screens in all plants had been assumed, the outcome of this thesis does not give evidence for presence of this type of substances acting as inducible UV screens in any of the bryophytes and charophytes studied.

One important remark should be made in relation to this conclusion: other types of UV screens, e.g. cell-wall substances that exclude or reduce UV radiation were not quantified in our studies. At the time this research was conducted the appropriate methods were not available to us to study presence of these substances. In a recent study, Clarke and Robinson (2008) showed the presence of cell-wall bound UV screens in Antarctic bryophytes. In most of their studied species, the fraction of cell-wall bound UV screens was at least as large as the methanol soluble fraction (used in our studies). Likewise, Rozema *et al.* (2009) indicate that UVB absorbing monomers in cell walls may prevent damage to the cellular metabolism. Neither of these studies showed that these substances were UVB inducible. Searles *et al.* (1999, 2002), however, did not find any significant difference in UVB absorbing compounds, including cell-wall bound compounds, in bryophytes exposed to different UVB levels. As long as it has not been shown that cell-wall bound UVB absorbing compounds are UVB inducible, this does not change the conclusion drawn above.

In vascular plants, algae and cyanobacteria, flavonoids and MAAs are induced by UVB radiation (Cockell and Knowland 1999). In contrast, in charophytes, UVB absorbing compounds seemed close to absent. The absence of an induction of UVB absorbing compounds in bryophytes points to a potentially different role of these compounds in these species. Polyphenolic UVB absorbing compounds often serve other functions than screening UV alone, e.g. radical scavenging, anti-freeze, anti-herbivory, signal transducer etc. (Rozema *et al.* 1997, Cockell and Knowland 1999). Given the different responses to UVB radiation found in **Chapter 5** for different bryophytes, it may be that coping with desiccation could be one of those other functions.

In addition to the observed absence of (UVB inducible) UV screens in our studies, there are other arguments to question the general hypothesis that UV screens increased in complexity with the evolution of land plants. First, after species and plant groups separate evolutionarily, they continue adapting to the environmental conditions they face. Species split when two populations are physically isolated and exposed to different environmental and biotic selection

Table 6.1: Overview of the answers to the research questions that were studied in this thesis

Plant group	Research Question
Charophytes:	
<i>Chara aspera</i>	<p data-bbox="447 352 1049 435"><i>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)</i></p> <p data-bbox="447 456 1049 586">Enhanced levels of UVB led to significantly:</p> <ul data-bbox="447 482 1049 586" style="list-style-type: none"> • decreased plant length • increased DNA damage • increased numbers of bulbils, while plants with generative reproduction structures decreased <p data-bbox="447 609 1049 664"><i>What are the UVB radiation patterns in waters with natural charophyte dominance (Chapter 3)</i></p> <ul data-bbox="447 687 1049 743" style="list-style-type: none"> • UVB attenuation was high in Lake Veluwe and the Buiten Muy <p data-bbox="447 765 1049 821"><i>What are the effects of UVB radiation under natural conditions? (Chapter 3)</i></p> <ul data-bbox="447 843 1049 927" style="list-style-type: none"> • There were no detectable levels of DNA damage in charophytes • Charophytes grew deeper than the 1% UVB depth

Table 6.1: continued

Plant group	Research Question
Bryophytes:	
<i>Syntrichia ruralis</i>	<p><i>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)</i></p> <p>Enhanced levels of UVB radiation led to:</p> <ul style="list-style-type: none"> • significantly negatively affected plant height • positively affected total specific weight (marginally significant) • no effects on the amount of UVB absorbing compounds
<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>	<p><i>Assessing 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)</i></p> <p>Enhanced UVB radiation levels led to significantly:</p> <ul style="list-style-type: none"> • increased DNA damage in most species (except in <i>D. scoparium</i> and <i>P. formosum</i>) • negatively affected plant growth in species from bog/fen habitat; ambient UVB levels affected growth positively in two species (<i>S. ruralis</i> and <i>D. scoparium</i>) • decreased UVB absorbing compounds in <i>S. recurvum</i> and <i>S. ruralis</i> at ambient and/or enhanced UVB levels, but no effects in other species <p><i>Does habitat origin affect the bryophyte UVB responses? (Chapter 5)</i></p> <p>UVB radiation:</p> <ul style="list-style-type: none"> • significantly increased DNA damage in all UVB treatments and habitats; for dune and bog/fen species a significant dose-response relation of DNA damage with increasing UV levels was found. • significantly decreased growth rates in all habitats, though UVB levels leading to significant effects differed among habitats: significantly reduced growth rates at all UVB levels in bog/fen species, middle and highest UVB levels in dune species and only at the highest UVB level in forest species • did not differently affect the amount of UVB absorbing compounds in the species depending on habitat origin and UVB levels, except for the ambient UVB level in forest species (UVB absorbing compounds reduced). • significantly decreased UVB absorbing when all species and treatments were combined

stresses. Charophytes and bryophytes share a common ancestor and may have split under influence of a stressor in the past. Solar UVB radiation could have been such a stressor, but this has never been proven, e.g. it is unclear whether UVB radiation is strong enough to allow selection upon this factor. Other stressors, upon which selection may have occurred, will have been acting simultaneously and might have been more important in determining the occurrence of UVB absorbing compounds. Moreover, even if UVB radiation has been a dominant stressor, other adaptations than the induction of UVB absorbing compounds could have taken place instead. For instance, charophytes seem to survive high UVB radiation levels by the formation of bulbils, while some bryophytes are inactive during periods of high UVB radiation. Second, even within a plant group, species experience very different conditions. For instance, within bryophytes, species occur from more open and UV exposed to more shaded, some at humid conditions, whereas other prosper at dry conditions etcetera. Under these different conditions they may need different adaptations to UVB radiation. Third and finally, even if UVB radiation drove the occurrence of UV screens, the possibly higher levels of UVB radiation during land plant evolution (Rozema *et al.* 1997), might make that 'early land plants' needed more extensive UV screens than species that adapted to land conditions later during evolution. It is unknown if UV protection mechanisms in e.g. cyanobacteria and lichens have been maintained until recent times. They might have been lost, recovered again or developed further (Rozema *et al.* 2002). Together, these arguments show that there might not be a 'chronological and steady' increase in complexity of UV screens during the evolution of the plant groups.

In conclusion, this thesis showed that increased UVB radiation leads to reduced growth and enhanced DNA damage in bryophytes and charophytes, but not to the induction of UV screens. Charophytes live in the water and thereby have an external UV screen and might opt for a strategy of increased vegetative reproduction through the formation of bulbils when UVB levels are too high. In bryophytes, UVB absorbing compounds occur, but the combined responses to UVB radiation seems to be related to other drivers than UVB exposure levels, like desiccation.

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