## The effects of UVB radiation on charophycean algae and bryophytes


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This thesis reports on the effects of UVB radiation on charophycean algae and bryophytes. Due to thinning of the ozone layer, more UVB radiation is reaching the earth surface. UVB radiation affects life on earth. Since the discovery of the ozone hole many studies focused on the effects of UV(B) radiation on terrestrial and marine organisms. Studies that focused on the effects on plants showed direct UVB damage to DNA, proteins, lipids, pigments and phytohormones, which may lead to altered growth and morphology. However, many plants are able to avoid damage due to harmful UVB radiation (e.g. by production of UV screens) or to repair the UV-induced damage that had occurred, thus decreasing the sensitivity of an organism to UVB radiation.

It is expected that the sensitivity of organisms to UVB radiation differs depending on its evolutionary position. During land plant evolution the radiation spectrum differed from current conditions, 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 and this might have been 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. The European project UVAQTER[1] aimed to analyse, characterise and compare the functioning of UVB screens, i.e. compounds absorbing UVB radiation, in algae, charophycean algae, lichens, bryophytes to vascular plants, since these compounds were assumed to increase in complexity in accordance with the evolutionary line of vascular plants. The research presented in this thesis was part of UVAQTER. Given the importance of bryophytes and charophycean algae in the evolutionary line of land plant development, the overall aim of this thesis was 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 were 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 bry-

[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).

ophytes from three contrasting habitats.

Effects of UVB radiation on both bryophytes and charophycean algae had been studied only to limited extents before; for charophycean algae the studies in this thesis were even the first. Charophycean algae, are -of all currently living green algae- the most closely related to vascular land plants. Charophytes live in shallow to deep fresh water systems. In these aquatic environments several processes, like reflection and attenuation, alter radiation conditions (including UVB). In fresh water systems, UVB is generally more quickly attenuated than in marine systems, by among others the higher amounts of dissolved organic matter. However, UVB may still penetrate to considerable depths and be of importance in fresh water systems. In addition, submerged vegetation, and especially charophycean algae, contributes to increasing water transparency facilitating a deeper penetration of UVB radiation. Ozone depletion may further increase UVB radiation in these ecosystems.

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. Bryophytes depend on sufficient air humidity to be physiologically active. In contrast to vascular plants, most bryophytes lack vascular tissue and a cuticle on the leaves: they take up nutrients and water via their leaves and stems. Their 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. In addition, most bryophyte studies on UVB effects had been conducted in the (near) (Ant)Arctic regions where UVB levels changed most, and only with a limited number of species, all from open and exposed habitats that were often wet from (snow) melt and with short growing periods. Exposure to UVB radiation and the extent of adaptation by bryophytes thereto, may, however, depend on their habitat characteristics. In the temperate Atlantic region bryophytes are generally year-round exposed to solar UVB radiation. Adaptations to several stresses may coincide. The bryophyte studies in this thesis are among the first that studied effects of UVB radiation on the growth, DNA damage and UV absorbing compounds in temperate bryophytes. Next to differences in (UVB) irradiance regimes in e.g. forests versus open ecosystems, habitats also differ in the extent to which species are exposed to other stresses (like drought). A comparison of UVB responses from several bryophytes from different habitats is a first critical test to understand the variability in UVB sensitivity of bryophytes through their habitat preferences.

Greenhouse experiments presented in this thesis showed that the charophycean alga *Chara aspera* was sensitive to UVB radiation (chapters 2 and 3). UVB radiation negatively affected growth, while it increased levels of DNA damage which were not repaired over night. Moreover, the charophytes did not seem to develop UVB screens to protect against UVB radiation since no increase in UVB absorbing compounds was found. Remarkable was that the vegetative reproduction (bulbils) increased in the presence of UVB radiation, while generative reproduction (antheridia and oogonia) decreased (chapter 2).

The effects of UVB radiation on charophycean algae found at greenhouse conditions were verified by field measurements in two charophytes-dominated fresh water systems in The Netherlands to elucidate whether charophytes are affected by UVB radiation under natural conditions (chapter 3). At field conditions, both spectroradiometrical measurements and DNA dosimeters showed that UVB radiation was attenuated quickly in both freshwater systems and penetrated to shorter depths than where the charophytes grew. This indicated that UVB radiation did not reach the submerged charophyte vegetation. In addition, no DNA damage was found in charophytes under natural conditions. This suggests that the water column gives enough protection against UVB radiation, acting as a natural, external UVB screen. However, one of the fresh water systems was a dune slack with fluctuating water levels during the year. Such specific conditions may result in UVB exposure to charophytes for certain periods annually.

The second part of this thesis (chapters 4 and 5) focusses on the effects of UVB radiation on bryophytes. Enhanced UVB exposure reduced net growth in the bryophyte *Syntrichia ruralis* var. *arenicola*, a species from open dune areas, under semi-natural outdoor conditions (chapter 4). At the end of the 13 months lasting experiment, total plant length was significantly decreased by UVB exposure, while there were no significant differences in branching pattern or length of the side branches among the different treatments. Since total dry weight was not affected by the treatments, plants under enhanced UVB exposure tended to be more compact. The concentration of phenolic compounds was significantly increased by UVA exposure, but was not affected by enhanced UVB radiation. No differences were found in concentrations of UVB absorbing compounds among the different treatments in *S. ruralis*. However, the levels of UVB absorbing compounds changed significantly within a growing season, independent of UV exposure levels. This indicates that these substances are constitutively abundant and that UVB exposure (alone) does not affect the amount of UVB absorbing compounds in this bryophyte. This suggests that no or an-other UVB defense mechanism might be acting in bryophytes than in higher plants.

In chapter 5, we investigated whether habitat origin affects the sensitivity to UVB radiation in bryophytes. Nine species were selected from three contrasting habitats - forests, bogs/fens and dunes - within the Netherlands. In forests, UVB exposure levels are generally low, while in bog/fen and dune systems plants are exposed to high UVB levels under sunny conditions. However, under these sunny conditions, plants in bog/fens are generally physiologically active due to higher moisture levels, while in the dunes bryophytes are at high UVB levels mostly physiologically inactive. Growth rates, DNA damage and UVB absorbing compounds were measured in all species after exposure to different levels of UVB radiation and their control treatments in a climate-controlled greenhouse for ten weeks. UVB radiation significantly increased DNA damage in most species and negatively affected growth rates in several species. UVB absorbing compounds decreased in some of these temperate bryophytes. UVB responses were consistent within species from the same habitats: species from the dune and the bog/fen habitat appeared to be more sensitive to UVB radiation, compared to species from the forest habitat in this experiment. Habitat origin thus seemed to influence the sensitivity of species against UVB radiation with, paradoxically, increased sensitivity in species from those habitats that experience higher exposure to UVB under natural conditions. Experimental conditions resembled natural conditions for bog and fen species most. The outcome of this study indicates that adaptations to UVB lack in these species. Dunes species are at sunny weather conditions often dry and inactive. This experiment provides a measure of potential sensitivity to UVB for these species, while they may be less sensitive to UVB at natural conditions. This may be related to the fact that other stresses than UVB may interfere with UVB tolerance. Several studies pointed out that adaptations to other stresses, like the ability to cope with desiccation, might interfere with the UVB tolerance in bryophytes. Both UVB and desiccation may lead to oxidative stress, therefore defence mechanisms against desiccation may also give protection to UVB.

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.