The susceptibility of spores and propagules of Antarctic seaweeds to UV and photosynthetically active radiation – Field versus laboratory experiments

Katharina Zacher, ⁎

Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Am Handelshafen 12, 27570 Bremerhaven, Germany

A R T I C L E   I N F O
Article history:
Received 28 November 2013
Received in revised form 8 May 2014
Accepted 9 May 2014
Available online 24 May 2014

Keywords:
Adenocystis utricularis
Glacial discharge
Global warming
Himantothallus grandifolius
Iridaea cordata
Light climate

A B S T R A C T

The Western Antarctic Peninsula is strongly affected by stratospheric ozone depletion, leading to higher UVR radiation (UVBR) on the Earth surface. It is furthermore experiencing the fastest rates of global warming worldwide, resulting in an increased sediment run-off from glacial melting, altering the underwater light climate. Very little is known of how Antarctic organisms can cope with this rapidly changing environment. Seaweeds play an essential role within the Antarctic coastal ecosystems, building highly complex and productive underwater communities. The unicellular spores are the most sensitive stage in their life-cycle, forming the bottle-neck for successful recruitment. To supplement the very rare field experiments on seaweed propagules, three ecologically important Antarctic seaweeds (Adenocystis utricularis, Himantothallus grandifolius, Iridaea cordata) were investigated. The germination of spores after exposure in the field to different water depths to three light treatments (PAR; PAR + UVA; PAR + UVA + UVB) was recorded. In parallel, spores were exposed to the same treatments under artificial radiation in the laboratory for different periods. Germination of the intertidal species A. utricularis was not affected by the treatments. In spores of I. cordata and H. grandifolius depth was a major factor for successful germination. High PAR fluxes at 1 and 2 m water depth inhibited germination significantly. UVR further lowered germination in H. grandifolius while in I. cordata UVBR had a negative impact only in the laboratory experiment. The results show that already the unicellular life stage expresses strong species-specific susceptibility to changes in the radiation climate. Not only UVR but also the high PAR fluxes in the field are important factors in determining the upper distribution limit of Antarctic seaweeds and laboratory experiments show stronger UVB effects as studies under natural radiation.

© 2014 Elsevier B.V. All rights reserved.

1. Introduction

Ecological effects of global environmental changes on Antarctic organisms, particularly the increase in ultraviolet-B radiation (UVBR, 280–315 nm) caused by stratospheric ozone depletion (Farman et al., 1985; Weatherhead and Andersen, 2006), and rising temperatures due to global warming (IPCC, 2001) are of considerable concern (Roleda et al., 2007a). The Western Antarctic Peninsula (WAP) belongs to the most rapidly warming regions on earth, with a rise of surface air temperature of 3.4 °C (Vaughan et al., 2003) per century, compared to a global mean increase of 0.6 °C (Turner et al., 2007). One of the consequences of the local warming trend is a significant increase in land and sea ice melting, which intensifies the sediment run-off from the glaciers into the oceanic system during the melting season (spring–summer; Cook et al., 2005; Turner et al., 2007), affecting the underwater light climate in the proximity to the glaciers with unknown consequences for the primary producers (Schloss et al., 2002).

At the WAP, seaweeds constitute a year-round essential carbon sink through production of high amounts of biomass with maximum wet biomass in the sublittoral of over 10 kg fresh weight m⁻² (Gómez et al., 2009; Quartino and Boraso de Zaixso, 2008). In some Antarctic areas the phytoplankton productivity is very low and it is postulated that the benthic primary producers (seaweeds and benthic microalgae) form an important food source for the heterotrophic community (Schloss et al., 2002). In this way, seaweeds are crucial for the diversity and stability of the polar coastal ecosystems. Due to retreating glaciers, new areas in the upper subtidal and intertidal will be accessible for seaweed colonization in the future, thereby altering the oceanic food web (Quartino et al., 2013).

As the penetration of light into the water column is altered by an accelerated glacial melting due to global warming, both, the upper and lower depth distribution limit of seaweeds might be modified. At the study site King George Island, Antarctica, the number of annual fresh water discharge days and daily discharge volume has doubled within the period from 2002 to 2006 (Eraso and Dominguez, 2007). While the lower depth distribution limit of the seaweeds depends on the capacity of the species to maintain a positive carbon balance (Gómez...
et al., 1997), the upper limit is determined by the capability to cope with excessive photosynthetically active radiation (PAR 400–700 nm) and the tolerance to UV radiation (UVR 280–400 nm, Bischof et al., 2006; Hanelt, 1998; Wiencke et al., 2004, 2006). Negative effects of UVR on seaweeds are, among others, the inhibition of photosynthesis or even photodamage, protein breakdown and the damage of the DNA resulting in lower germination and growth rates (reviewed in Bischof et al., 2006; Karsten et al., 2009; Roleda et al., 2007a).

The upper depth distribution of seaweeds can be determined by the susceptibility of their early life history stages (unicellular spores and propagules) to environmental perturbations (Swanson and Druelh, 2000; Wiencke et al., 2000). These stages are known to be the bottle neck for the successful recruitment of the species because they are more vulnerable to changes in the abiotic environment compared to the mature sporophytes in their life history (Agrawal, 2009; Coelho et al., 2000; Cordi et al., 2001; Roleda et al., 2007a; Veliz et al., 2006; Wiencke et al., 2006). It is therefore necessary to understand the physiological limits of the early developmental stages of the important seaweed species to be able to identify the main factors leading to a successful recruitment.

Most of the studies on young developmental stages have been performed under laboratory conditions with unnatural ratios between PAR, UVA and UVB radiation. Experiments on young developmental algal stages under ambient solar radiation in Antarctica are very rare (but see Zacher et al., 2007a; Zacher and Campana, 2008 working on early successional communities). In laboratory experiments UVR was shown to negatively affect the photosynthetic efficiency of Adenocystis utricularis zoospores, additionally damaging the DNA by forming cyclobutane pyrimidine dimers (CPDs). However, a full recovery is not achieved after 48 h under low light (Zacher et al., 2007a, 2007b). Initial spore densities for brown algae Ascoseira mirabilis were not able to repair their DNA damage completely after 8 h of exposure to 0.4 W m$^{-2}$ UVBR but fully recovered after shorter times of exposure (Roleda et al., 2007b, 2008). In other regions of the Earth some experiments on the high PAR and UV tolerance of young developmental stages have been performed with inconsistent results (Hanelt et al., 1997; Jiang and Gao, 2008; Steinhoff et al., 2011; Wiencke et al., 2006). While Wiencke et al. (2006) and Steinhoff et al. (2011) found a decreased spore germination of subtidal species due to UVR and not under high PAR, Hanelt et al. (1997) and Jiang and Gao (2008) found a strong photoinhibition of photosynthesis due to high PAR and a weaker additional inhibition due to UVR.

To our knowledge, no data have been published so far on the germination of Antarctic seaweeds under ambient solar radiation, even though this region exhibits the strongest degree of stratospheric ozone depletions worldwide. In order to get deeper insights in the high PAR and UV tolerance of Antarctic seaweeds, the spore germination of the inter- to subtidal Halimeda cordata (Rhodophyta), the inter- to upper subtidal Adenocystis utricularis and the Antarctic endemic subtidal Himantothallus grandifolius (both Phaeophyceae) was investigated in Potter Cove, King George Island, Antarctica. Spores were exposed for ~24 h to i) PAR (P), ii) PAR + UVAR (PA) and iii) PAR + UVAR + UVBR (PAB) in different water depths (1, 2, 4 and 8 m) in the field and germination rates were subsequently determined after exposure to low light in the laboratory. For comparative reasons the same species were simultaneously exposed under laboratory conditions, where the different depths were simulated by different periods of exposure (1, 2, 4 and 8 h).

The study aimed at answering several questions:

1. Which wavelength range exerts the strongest effects on the germination of Antarctic propagules?
2. Is there a possible alteration in the upper vertical distribution limit of the subtidal species due to an increased sediment inflow during summer?
3. Are laboratory experiments suitable to provide results which can be used to predict the performance in the field?

2. Materials and methods

2.1. Algal material

Fertile specimens of the brown algae A. utricularis (Bory) Skottsberg, H. grandifolius (A.Gepp and E.S.Gepp) Zinova and the red alga I. cordata (Turner) Bory de Saint-Vincent were collected in November 2008 (A. utricularis and I. cordata) and February 2010 (H. grandifolius) at Potter Cove (King George Island, South Shetland Islands, 62°14.80’S, 58°41.26’W) during two expeditions. Adenocystis utricularis and I. cordata were collected in the intertidal, whereas H. grandifolius grows in the subtidal and was collected by SCUBA diving at approx. 10 m depth. After collection, the specimens were brought immediately to the nearby laboratory and kept at ~2 °C under low light conditions until further processing.

2.2. Spore release

Numerous individuals of each species were divided randomly in 5 replicates and prepared for spore release by blotting with tissue paper and treating the different species in the following ways: I. cordata tetrasporophytes were cut into smaller pieces and put into glass flasks with filtered seawater (0.2 μm) for collection of spores after a few days. Complete thalli of A. utricularis and fertile tissue of H. grandifolius (cut with a razor blade) were kept in darkness in moist chambers overnight or a few days at ~5 °C. Spore release was obtained by flooding the algae with filtered, slightly warmer seawater in photo-dishes according to Clayton and Wiencke (1986). The initial spore density of brown algae was counted by the use of a Neubauer-chamber (Brand, Wertheim, Germany) and of the red alga by a Rafter chamber (Sedgewick-Rafter Cell 550 spore counter, Graticules Ltd., Tonbridge, UK), respectively. Initial spore densities for A. utricularis spore suspension were [zoospore length around 4 μm] approx. $1.8 \times 10^5$ spores ml$^{-1}$, for H. grandifolius spore suspension (zoospore length around 4 μm) approx. $1.42 \times 10^5$ spores ml$^{-1}$ and for I. cordata tetraspore suspension (mean diameter 20 μm) approx. 6000 spores ml$^{-1}$. Spore solutions were then divided and diluted between the field and the laboratory approach. The spore solution of the same species was exposed in the field and under laboratory conditions at the same date, whereas spores of different species were exposed at different dates due to different times of fertility. Himantothallus grandifolius e.g. gets fertile in austral summer to autumn, and was investigated in 2010 whereas fertile I. cordata and A. utricularis were collected in spring 2008.

2.3. Field experiment

The field experimental units consisted of an aluminum frame (~1 m × 1 m) with a black plastic bottom and a top of UV-transparent Plexiglas (GS 2458, Röhm, Darmstadt, Germany). It contained 16 Petri dishes (53 × 12 mm) arranged in a 4 × 4 grid. Petri dishes were filled with the spore solutions and exposed to three different light treatments (PAB, 280 to 700 nm) and PAR + UVAR (P, 530 to 700 nm). Petri dishes were divided into three different light treatments and exposed to three different light treatments and four depths (1, 2, 4 and 8 m) in a two-factorial design (n = 5, L. cordata and A. utricularis and n = 4, H. grandifolius). Three kinds of filter foils were used to obtain the different light treatments (see Bischof et al. 2002 for details): 1. Ultraphan transparent (Digefra GmbH, Germany), 2. Folanorm 320 (Folex GmbH, Germany), and 3. Ultraphan URUV farblos, corresponding to the PAR + UVAR + UVBR (PAB, 280 to 700 nm), PAR + UVAR (PA, 320 to 700 nm) and PAR (P, 400 to 700 nm) treatments, respectively. The cut-off wavelengths of the available filter-material were slightly different from the definition of CIE (Commission Internationale de l’Éclairage, UVB = 280–315 nm, UVA = 315–400 nm) but are for practical reasons commonly used in environmental science (Franklin et al., 2003). Experimental units were
exposed for about 24 h in the field using weights and buoys. Irradiance in the field was measured continuously during the duration of the experiments using UVA and UVB data loggers (X-2000-14, Gigahertz-Optik, Puchheim, Germany) in underwater housings mounted at the experimental units at each depth. PAR profiles were measured once during each experiment around noon between 0 and 10 m depth with a LiCor data logger (LI-1400, Li-Cor, Lincoln, USA) equipped with an underwater PAR sensor (LI-192). Diffuse vertical attenuation coefficients of downward irradiance (Kd) for PAR, UVAR and UVBR during the three field experiments were determined using the following formula (after Kirk, 1994) for the measurement at noon:

$$Kd = \ln \left( \frac{E_d(z_2)}{E_d(z_1)} \right) \times (z_1^{-} - z_2^{-})^{-1}$$

where $E_d(z_1)$ and $E_d(z_2)$ are the respective irradiances at depths $z_1$ (1 m) and $z_2$ (8 m).

2.4. Laboratory experiments

In the laboratory, light was provided by white fluorescent lamps (Osrám, L65 Watt/255, Germany), emitting background photosynthetically active radiation (PAR) and by UV lamps (Q-Panel UV-A-340, 40 W, Cleveland, USA), emitting a spectrum qualitatively similar to solar radiation in the range of 295 to 340 nm. The same light treatments (PAB, PA and P) as in the field were performed using the same filters material. Irradiation in the laboratory was measured below the cut-off filters using a Solar Light PMA 2100 radiometer equipped with a UVA (PMA 2110) and a UVB broad-band sensor (PMA 2106; Solar Light, Philadelphia, USA). PAR was measured using a flat-head LICOR 190 SA quantum sensor (cosine corrected) connected to a LICOR LI-1400 datalogger. For germination measurements, the spore suspension was put into small Petri dishes ($n = 5$, I. cordata and A. utricularis and $n = 4$, H. grandifolius), which were subsequently exposed to the three radiation conditions for 1, 2, 4 and 8 h at approx. 2 °C.

The doses of the different treatments in the field and in the laboratory are shown in Table 1.

After exposure in the field or in the laboratory the Petri dishes were removed from the treatment and exposed to dim white light (10–15 μmol photons m$^{-2}$ s$^{-1}$) in the laboratory until germination started. Germination rates were determined microscopically by the use of an Axioplan microscope (Zeiss, Göttingen, Germany) equipped with a data logger (LI-1400, Li-Cor, Lincoln, USA) mounted at the experiment, demonstrating a higher turbidity in the experiment with I. cordata compared to the other measurements. At 8 m depth there were still 158, 137 and 184 μmol photon m$^{-2}$ s$^{-1}$ PAR measured around noon. Maximal PAR values in the laboratory experiment were lower than those in the field (constant 51 μmol photon m$^{-2}$ s$^{-1}$).

Fig. 2 shows the underwater UVAR and UVBR at the four depths during the experimental period in the field. There is a clear difference between the radiation regimes at the various depths. Highest values of underwater UVAR and UVBR during the experiments were measured in mid-November at 1 m depth (36.9 W m$^{-2}$ and 1.21 W m$^{-2}$, respectively). In February values were lower, reaching maxima of 15.7 UVAR and 0.6 W m$^{-2}$ UVBR at 1 m depth (Table 1, Fig. 2). Lowest values were measured at 8 m depth with maxima of 4.8 W m$^{-2}$ UVAR and 0.06 W m$^{-2}$ UVBR (Table 1). Total doses of UVAR and UVBR at 1 and 8 m ranged between 605 and 57 kJ and 19 and 0.5 kJ during the field experiments (Table 1). UVA and UVB doses in the field and laboratory experiments differed most strongly in the UVA doses which were lower in the laboratory experiments (Table 1). UVA doses were comparable between the field and laboratory approaches (Table 1).

2.5. Statistics

A two-way ANOVA was performed to test for the interactive effects of depth/dose and light treatment on the germination of the different species. Germination data were arcsin transformed. Prior to analysis, data were tested for homogeneity of variances (Cochran’s test). Heteroscedastic data were analyzed by the non-parametric Kruskal-Wallis test. Post-hoc comparisons were performed with Duncans or Newman–Keuls test. Statistica™ 6.0 software package was used.

3. Results

3.1. Irradiance measurements

Fig. 1 shows the underwater PAR profiles measured during the three field experiments around noon. Although during the experiment with I. cordata maximum values measured in air were much higher than in the other two experiments (1650 μmol photon m$^{-2}$ s$^{-1}$ versus 540 in A. utricularis and 755 μmol photon m$^{-2}$ s$^{-1}$ in H. grandifolius, respectively), PAR values in the water column were very similar from 3 m downwards and lowest in the I. cordata experiment at 10 m depth (Fig. 1). This is also reflected in the Kd values ranging between 0.13 (A. utricularis and H. grandifolius experiment) and 0.21 (I. cordata experiment), demonstrating a higher turbidity in the experiment with I. cordata compared to the other measurements. At 8 m depth there were still 158, 137 and 184 μmol photon m$^{-2}$ s$^{-1}$ PAR measured around noon. Maximal PAR values in the laboratory experiment were lower than those in the field (constant 51 μmol photon m$^{-2}$ s$^{-1}$).

3.2. Germination experiments

Generally, the germination rate of A. utricularis spores was high three days after the release, reaching >80% in all treatments. Germination was not affected by light treatment or depth, even though a higher germination rate after 8 h of exposure was measured in the laboratory experiment (two-way ANOVA, Table 2, Fig. 3a + b). No significant interactions between light treatment and depth/dose were found (Table 2).

The germination rate of H. grandifolius spores was lower compared to A. utricularis five days after release, reaching maximum values of 67% at 8 m depth in the field experiment (Fig. 3c). Lowest germination rates (<15%) were recorded at 1 and 2 m during the field experiment (Fig. 3c). The Kruskal–Wallis test showed a strong influence of the depth on germination. Germination rates were significantly higher at 2 m compared to 1 and at 4 and 8 m depth compared to exposures at 1 and 2 m depth (Newman–Keuls test, Table 2, Fig. 3c). The light treatments with UVAR (PA) and UVAR + UVBR (PAB) showed a significantly

---

Table 1

<table>
<thead>
<tr>
<th>Field</th>
<th>UVA kJ</th>
<th>UVB kJ</th>
<th>UVA W m$^{-2}$</th>
<th>UVB W m$^{-2}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 m</td>
<td>522–605</td>
<td>19–21</td>
<td>15.7–36.9</td>
<td>0.6–1.21</td>
</tr>
<tr>
<td>2 m</td>
<td>442–465</td>
<td>13–14</td>
<td>20.7–22.7</td>
<td>0.03</td>
</tr>
<tr>
<td>4 m</td>
<td>200–263</td>
<td>4.0–5.9</td>
<td>6.6–15.0</td>
<td>0.15–0.35</td>
</tr>
<tr>
<td>8 m</td>
<td>57–105</td>
<td>0.5–1.3</td>
<td>1.9–4.8</td>
<td>0.02–0.06</td>
</tr>
</tbody>
</table>

* In the experiment with H. grandifolius the 2 m logger failed, only values from the other two field experiments are available for this depth.
lower germination rate than the P treatment in the field experiment (Duncan’s test, Table 2). In the laboratory experiment germination was significantly lower under the PAB treatment compared to the P and PA treatments (Table 2, Fig. 3d). Interestingly, germination rates were lower under short term exposure (lower dose) for 2 h than for 4 and 8 h (Fig. 3d). No significant interactions between light treatment and depth/dose were found.

*Iridaea cordata* tetraspores showed lowest germination rates compared to the other two species after 20 d (maximum 47% in the laboratory experiment, Fig. 3f). Germination was significantly reduced at 1 m depth compared to 2, 4 and 8 m and at 2 m compared to 4 and 8 m depth (Kruskal–Wallis and Duncan’s test, Table 2, Fig. 3e). Germination was not significantly affected by the light treatment in the field experiment, but was significantly higher in the P treatments compared to the PAB treatments in the laboratory (two-way ANOVA and Duncan’s test, Table 2, Fig. 3f). No effects of the dose were detected.

### 4. Discussion

The main results of this first field study on the light susceptibility of Antarctic macroalgal spores demonstrate the extreme tolerance of the intertidal *A. utricularis* zoospores to high PAR and UV radiation and a lower tolerance of the upper to lower subtidal *I. cordata* and *H. grandifolius* spores. The results reflect the actual position of these algae on the shore and confirm that the PAR and UV tolerance of the

![Fig. 1. Underwater PAR (photosynthetic active radiation, 400–700 nm) profiles (0 to 10 m) from the three field experiments measured around noon in μmol photon m\(^{-2}\) s\(^{-1}\) (logarithmic scale).](image-url)

![Fig. 2. Underwater UVA and UVB radiation during the field experiments A-UVA + A-UVB *A. utricularis* (15.–16.11.2008), H-UVA + H-UVB *H. grandifolius* (13.–14.02.2010) and I-UVA + I-UVB *I. cordata* (10.–11.11.2008) at 1, 2, 4 and 8 m depth. The 2 m sensor in the experiment with *H. grandifolius* failed after some hours.](image-url)

### Table 2

<table>
<thead>
<tr>
<th>Species</th>
<th>Source of variation</th>
<th>Field experiment</th>
<th>Laboratory experiment</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F-value</td>
<td>P-value</td>
<td>F-value</td>
</tr>
<tr>
<td><em>A. utricularis</em></td>
<td>Light treatment (A)</td>
<td>0.518 ns</td>
<td>2.241 ns</td>
</tr>
<tr>
<td></td>
<td>Depth/dose (B)</td>
<td>2.786 ns</td>
<td>3.174 0.032429</td>
</tr>
<tr>
<td></td>
<td>A × B</td>
<td>0.888 ns</td>
<td>0.558 ns</td>
</tr>
<tr>
<td><em>H. grandifolius</em></td>
<td>Light treatment (A)</td>
<td>3.739 0.033464</td>
<td>30.660 &lt;0.00001</td>
</tr>
<tr>
<td></td>
<td>Depth/dose (B)</td>
<td>129.950 0.00001</td>
<td>0.983 &lt;0.00001</td>
</tr>
<tr>
<td></td>
<td>A × B</td>
<td>0.939 ns</td>
<td>2.201 ns</td>
</tr>
<tr>
<td><em>I. cordata</em></td>
<td>Light treatment (A)</td>
<td>3.120 ns</td>
<td>3.490 0.038462</td>
</tr>
<tr>
<td></td>
<td>Depth/dose (B)</td>
<td>23.722 &lt;0.00001</td>
<td>0.983 ns</td>
</tr>
<tr>
<td></td>
<td>A × B</td>
<td>2.335 nt</td>
<td>0.146 ns</td>
</tr>
</tbody>
</table>
unicellular developmental stages is one important factor (among others) for the successful recruitment of the algae at a certain depth, thereby participating in the determination of the vertical distribution of the species.

In contrast to other field studies performed on Arctic seaweeds (Steinhoff et al., 2011; Wiencke et al., 2006) germination was strongly inhibited by high PAR in the subtidal species (*H. grandifolius* and *I. cordata*). PAR intensities during the field studies could reach maximum values of ~600 μmol m⁻² s⁻¹ at 2 m water depth (experiment with *I. cordata*) when the vertical attenuation coefficient (*Kd*) as an indicator of water turbidity was quite low, meaning that PAR could penetrate relatively deep into the water column. In the studies on Arctic spores PAR values and doses were lower. In the study by Wiencke et al. (2006) with much higher *Kd* values (between 0.67 and 1.28 for UVBR) and by Steinhoff et al. (2011) the high PAR treatment was around 400 μmol m⁻² s⁻¹ during the day, possibly leading to the different results for the subtidal species. High PAR intensities are known to exert negative effects on the photosynthesis and growth of sporophytes and gametophytes of seaweeds (Aguilera et al., 1999; Dring et al., 2001; Hanelt et al., 1997) in *Saccharina latissima* (formerly *Laminaria saccharina*) exposure to 500 μmol m⁻² s⁻¹ PAR for 2 h led to a severe photoinhibition of photosynthesis in sporophytes and gametophytes (Hanelt et al., 1997). Young sporophytes did not recover under low light, indicating photodamage. Spores were not tested in this study, but as the resistance to high light levels was related to changes in the thallus structure during the development of the sporophytes (Hanelt et al., 1997), the photosynthesis of the unicellular spore is considered even more vulnerable to high PAR than the one of gametophytes and sporophytes. It was high PAR as well that accounted for most of the reduction of the effective quantum yield in the conchocelis phase of *Porphyra haitanensis* (Jiang and Gao, 2008). During laboratory exposure to relatively low PAR the optimum quantum yield (*Fv/Fm*) of *A. utricularis* zoospores did not change (Zacher et al., 2007b), whereas in *I. cordata* spores a decrease of *Fv/Fm* was measured over time (Zacher et al., 2009). This confirms a stronger sensitivity of *I. cordata*.

Additional UV radiation did not significantly affect the germination of *A. utricularis* and *I. cordata* spores in the field reconfirming former studies on the photosynthetic performance of spores from these species (Zacher et al., 2007b, 2009) and of adult field material (Hanelt et al., 1994; Rautenberger and Bischof, 2008). An initially lower optimum quantum yield (*Fv/Fm*) under the UV treatment was followed by a complete recovery, suggesting that photosynthesis is down-regulated (dynamic photoinhibition) and no photodamage of photosystem II occurred (Hanelt et al., 1994).

On the other hand the germination of *H. grandifolius* spores was negatively affected by UV radiation in the field experiments. However, no additional UVB radiation effect on germination in comparison with the UVA treatment is detectable, a fact consistent to the study on Arctic zoospore germination (Wiencke et al., 2006). Apparently, the strong UVB effects found in many laboratory studies are most likely caused by

---

**Fig. 3.** Germination of *A. utricularis* (AF + AL), *H. grandifolius* (HF + HL) and *I. cordata* (IF + IL) after exposure in the field in different water depths (AF, HF, IF = field) and in the laboratory for different periods (AL, HL, IL = lab). P = PAR, PA = PAR + UVA, PAB = PAR + UVA + UVB. Shown is the mean germination ± SD. Letters indicate significant differences between the depth/doses (two-way ANOVA).
by the unnatural PAR to UVA to UVB ratios (e.g. Roleda et al., 2005; Wiencke et al., 2000). In contrast to our field study H. grandifolius and I. cordata germination was negatively affected by UVB radiation in the laboratory experiments. While in the laboratory experiment the UVA to UVB ratio was 10–12 to 1, in the field the UVA is much higher in relation to the UVB part of the spectrum. It was even increasing with depth due to a higher UVB attenuation in the water column (between 24 and 95 to 1 in our experiment). Furthermore the PAR radiation in the laboratory experiment was much lower than that in the field. That fact generally leads to an overestimation of UVB effects in laboratory studies which in the field are masked or overrun by PAR and/or UVA effects. Another reason of not detecting UVB effects in the field might be a better stimulation of the blue-light dependent photolyase, repairing UV induced DNA lesions by absorbing light between 350 and 450 nm (Hada et al., 2000; Pakker et al., 2000).

Although Antarctic seaweeds are characterized as low light adapted (Wiencke et al., 1993) and show strong photoinduction during high light stress, A. utricularis sporophytes were shown to be able to cope with excessive light and optimize their photosynthesis under these conditions (Hanelt et al., 1994). The responses of A. utricularis to a changing light regime during the study by Hanelt et al. (1994) were very fast even under low temperatures, thereby making this alga well adapted to its intertidal habitat with extreme alterations in temperature and light. The different PAR susceptibilities of the investigated species might be explained by a higher content of xanthophyll cycle pigments in A. utricularis in comparison with the other two species (Hanelt et al., 1994). In the intertidal brown alga Dictyota dichotoma the conversion of violaxanthin to zeaxanthin is responsible for an increase in thermal energy dissipation as a protection from excessive irradiation (Uhrmacher et al., 1995). Whether this is also true for the zoospores of the species in our study remains to be tested.

The different UV susceptibilities of the investigated species could have been caused by an uneven increase of the activities of repair mechanisms. DNA damage can be repaired under the influence of photolyase enzymes (light-dependent), nucleotide excision and recombination repair (light-independent; van de Poll et al., 2002). The dimerization of the DNA due to UVB radiation and its repair was found in many seaweeds and their spores (Roleda et al., 2007a, 2007b; van de Poll et al., 2002; Zacher et al., 2007b, 2009). It was shown that haploid spores are very efficient in DNA damage repair and that the most efficient repair occurred in eulittoral species in comparison to sublittoral ones (Roleda et al., 2006, 2007a, 2008). Another reason for the different tolerances for PAR and UV radiation within the different species might be the ability of producing photoprotective substances. For kelp zoospores from the Northern Hemisphere it was shown that the mother plant exudates phlorotannins (polyphenolic substances) during the release of the spores (Müller et al., 2009; Steinhoff et al., 2011). Because phlorotannins absorb in the UVB range, UV protective environments can be formed, preventing UV induced cell damage (Roleda et al., 2006; Swanson and Druehl, 2002). Phlorotannins were found in both brown algal species tested here (A. utricularis and H. grandifolius) (Iken et al., 2007). However, whether an exudation during spore release really takes place remains to be tested for these species. The red alga I. cordata on the other hand, contains UV absorbing mycosporine-like amino acids (MAAs; Hoyer et al., 2001). In the spores of this species the MAAs shionine (λmax = 334 nm) and palythine (λmax = 320 nm) were determined and higher concentrations of palythine compared to shionine were found (Zacher et al., 2009). Under natural solar radiation, the UVA wavelengths were shown to exhibit the highest efficiency on the synthesis of both MAAs in the red alga Chondrus crispus (Kråb et al., 2002), possibly explaining our findings of UV effects in the laboratory (with less UVA) but not in the field.

A. utricularis and I. cordata are fertile during the whole Antarctic spring/summer (Müller, 1984), whereas H. grandifolius releases spores mostly in summer (Wiencke, 1996; Wiencke and Clayton, 1990), when water turbidity due to melt water is usually higher at coastal areas and UVB radiation is lower than in spring during the time of strongest stratospheric ozone depletion (Weatherhead and Andersen, 2006). At Potter Cove, King George Island, H. grandifolius is usually observed to grow from 7 to 10 m downwards (Quartino et al., 2001; Wiencke and Clayton, 2002), while in the current experiments it was already able to successfully germinate at 4 m water depth. A successful recruitment is also dependent on other factors such as interspecific competition with other dominant Antarctic species. Klöser et al. (1994) found H. grandifolius only below a Desmarestia belt at the mouth of Potter Cove whereas in areas inside Potter Cove H. grandifolius is more abundant than Desmarestia (Quartino et al., 2013) and already found together with Desmarestia species at 3 m water depth where turbidity is high (Quartino, personal communication). This is an indication that a change in abiotic conditions may lead to changes in the community structure especially at more affected sites and that a recruitment higher up the shore is possible at turbid sites. Surely, other abiotic and biotic factors despite the light climate such as substrate, slope and ice disturbance affect the survival of the species at a specific site.

In conclusion, photosynthetically active radiation (400–700 nm) was mainly responsible for the germination success of the species at a certain depth, whereas the UV part of the spectrum had no or only a minor impact.

Our results further show the importance of field experiments to get ecologically relevant results. Laboratory experiments tend to overestimate UVB effects but can serve as mechanistic studies. While a change in depth distribution of A. utricularis due to a change in the light regime is unlikely, the upper distribution limit of I. cordata and H. grandifolius is a function of both, PAR and UVR. A changing underwater light climate due to increasing sedimentation will allow an upward shift of these species at the shore (as already observed in the inner Potter Cove (Quartino, personal communication)).

Global change, however, will have multiple effects on the marine ecosystems interacting in a manifold and yet mostly unknown way. There is a special need for experiments on multiple stressors, such as temperature, light, disturbance and sedimentation combined with biotic factors such as grazing and competition which are simultaneously acting on organisms. These data are urgently needed in order to get more realistic results to fit future models calculating the outcome of global climate change on the coastal ecosystems.

Acknowledgments

The work has been performed at Dallmann Laboratory, annex to Carlini (formerly Jubany) Station, within the frame of the scientific collaboration existing between Instituto Antártico Argentino/Dirección Nacional del Antártico and Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research. Special thanks are due to Hannah Schmidt and Claudia Daniel for helping in the laboratory and performing the light measurements. I am grateful to the members of the dive group led by Max Schwanitz for collecting the algae and Christian Wiencke, Cornelia Buchholz and an unknown reviewer for improving the manuscript. [SS]

References


