Journal of Ecology 2006
94, 455–463

Susceptibility of zoospores to UV radiation determines upper depth distribution limit of Arctic kelps: evidence through field experiments

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Summary

1 The UV susceptibility of zoospores of the brown seaweeds *Saccorhiza dermatodea*, *Alaria esculenta* and *Laminaria digitata* (Laminariales) was determined in field experiments in June 2004 on Spitsbergen (78°55′ N, 11°56′ E).
2 Freshly released zoospores were exposed for 1 or 2 days at various water depths to ambient solar radiation, ambient solar radiation depleted of UVB radiation (UVBR) and ambient solar radiation depleted of both UVBR and UVAR. Subsequently, germination rates were determined after exposure to favourable light and temperature conditions in the laboratory.
3 The radiation regime was monitored at the water surface and in the water column using data loggers attached adjacent to each experimental platform for the duration of the field exposure.
4 Under ambient solar radiation, the tolerance of zoospores to UVR was highest in the shallow water species *S. dermatodea*, intermediate in the upper to mid sublittoral *A. esculenta* and lowest in the upper to mid sublittoral *L. digitata*. There was, however, no difference in the susceptibility of the zoospores to ambient solar radiation or to solar radiation depleted of UVBR.
5 The water column was relatively UV transparent, especially in the upper water layers. The 1% UVB depth ranged between 5.35 and 6.87 m, although on one stormy day the 1% UVB depth was only 3.57 m, indicating resuspension of sediments.
6 Early developmental stages are most susceptible to environmental stress. Tolerance of zoospores to UVR is a major if not one of the most important factors determining the upper distribution limit of different Laminariales on the shore.
7 Kelps are very important primary producers in inshore coastal ecosystems, serving as food for herbivores and as habitat for many organisms. Enhanced UVBR due to stratospheric ozone depletion may lead to changes in the depth distribution of kelps and may cause significant ecological domino effects.

Key-words: *Alaria esculenta*, depth distribution, germination, *Laminaria digitata*, Laminariales, optical water characteristics, *Saccorhiza dermatodea*, stratospheric ozone depletion, UV radiation, zoospore viability

Journal of Ecology (2006) **94**, 455–463
doi: 10.1111/j.1365-2745.2006.01102.x

Introduction

The depth distribution of seaweeds is governed by a variety of biotic and abiotic factors, among which the radiation regime is very important (Lüning 1990). While the lower depth distribution is determined by the

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need to maintain a positive carbon balance (Gómez *et al*. 1997), the upper limit primarily depends on the capability of seaweeds to sustain high light stress, and especially on the capacity for dynamic photoinhibition of photosynthesis (Sagert *et al*. 1997; Hanelt 1998). In addition to coping with excessive photosynthetically active radiation (PAR), tolerance of UV radiation (UVR) is regarded as a major factor determining the zonation of seaweeds in shallow waters (Maegawa *et al*. 1993; Dring *et al*. 1996; Bischof *et al.* 1998).

Most previous studies on the UV tolerance of seaweeds have focused on their macrothalli (Franklin & Forster 1997). Only a few studies have been performed using the unicellular propagules of seaweeds, the spores, despite the fact that these early developmental stages are regarded as most susceptible to UV stress (Coelho *et al*. 2000). It is known that UVR leads to an inhibition of photosynthesis in zoospores of *Laminaria digitata* and to DNA damage of zoospores of the kelps *L. digitata*, *L. saccharina* and *Alaria esculenta* (Wiencke *et al*. 2000). Both the photosynthetic apparatus and DNA can be repaired in spores of the upper sublittoral species *L. digitata*, and the red algae *Chondrus crispus* and *Mastocarpus stellatus* (Roleda *et al*. 2004), but damage is much less reversible in the mid to lower sublittoral *L. saccharina* and *L. hyperborea* (Roleda *et al*. 2005). Other negative effects of UVR include a decrease of the motility of zoospores from *L. saccharina* (Makarov & Voskoboinikov 2001) and of the phototaxis of spores of *Scytosiphon lomentaria* and *Petalonia fascia* (Flores-Moya *et al*. 2002). Finally, microtubules can be affected by UVR as shown in zoospores of *Macrocystis pyrifera* by Huovinen *et al*. (2000).

The need for repair processes is reduced if damage to biomolecules, cell structure and cell function can be prevented by the presence of UV-absorbing compounds, such as the phlorotannins in the phenolic vesicles (physodes) that are typically found in kelp zoospores. After exposure to UVR, physodes increase in number and size, particularly in the upper sublittoral *Saccorhiza dermatodea* and *A. esculenta*, and to a lesser degree in kelps from deeper waters (Wiencke, Clayton & Schoenwaelder 2004). This is consistent with the observation that zoospore suspensions of the upper sublittoral *L. digitata* absorb UVBR and UVAR below 360 nm (characteristic of phlorotannins) strongly but *L. saccharina* and *L. hyperborea* from greater water depths do not (Roleda *et al*. 2005). Zoospore suspensions of *A. esculenta*, *L. digitata* and *L. saccharina* can protect cultures of zoospores of other species from the potentially lethal effects of UVAR and UVBR with UV-protection properties varying with the species and, in particular, with the spore density (Clayton & Wiencke 2004).

If the negative effects of UVR are not fully balanced by protective and repair mechanisms, germination is impaired and germination rates decrease. This has been demonstrated clearly in *L. digitata*, *L. saccharina* and *L. hyperborea* growing in this order from the upper to the mid sublittoral on Helgoland (North Sea), with the strongest reduction in *L. hyperborea* (Roleda *et al*. 2005). Similar results were obtained in *S. dermatodea*, *A. esculenta*, *L digitata*, *L. saccharina* and *L. solidungula* growing from low tide level down to about 16 m depth in the middle zone of Kongsfjorden (Spitsbergen, 78°55′ N; Wiencke, Vögele, Kovaltchouk & Hop 2004). Again, the greatest decrease of germination rates was found in the deep water species. In all these studies the strongest effect has been obtained after exposure to both UVBR and UVAR. UVAR alone usually induces more limited effects on photosynthesis, DNA and germination rates (Wiencke *et al*. 2000, 2004; Roleda *et al*. 2005).

Apart from a very limited pilot study performed under natural solar radiation and ambient air temperature (Wiencke, Clayton & Schoenwaelder 2004), all previous studies have been conducted in the laboratory under artificial illumination. Levels of PAR are much lower in the laboratory than in the field, whereas those of UVBR are considerably higher (Wiencke, Clayton & Schoenwaelder 2004). As the effect of UVBR exposure on the performance of brown algal zoospores *in situ* has not been explored, we exposed spores of three kelp species from Spitsbergen for 1 to 2 days at different water depths in Kongsfjorden to the full ambient solar radiation, ambient solar radiation depleted of UVBR and ambient solar radiation depleted of UVBR and UVAR. Radiation regimes were monitored both at the water surface and in the water. Germination rates were subsequently determined after exposure to favourable light and temperature conditions in the laboratory. These studies may cast light on the potential impact of stratospheric ozone depletion, especially over the polar regions (von der Gathen *et al*. 1995; Rex *et al*. 2002), as this process leads to an enhancement of UVB radiation (UVBR) at the earth's surface and in the water column (Groß *et al*. 2001; Dahlback 2002). On Spitsbergen biologically significant UVBR levels are measurable down to about 8 m water depth (Hanelt *et al*. 2001; van de Poll *et al*. 2002) and a UVBR-induced loss of zoospore viability in shallow waters may therefore shift areas of successful kelp recruitment to greater water depths.

Materials and methods

Fertile specimens of *Saccorhiza dermatodea* (Pyl.) J. Ag., *Alaria esculenta* (L.) Grev. and *Laminaria digitata* (Huds.) Lamour. were collected between May and June 2004 by SCUBA divers in Kongsfjorden at Prins Heinrichøya or Blomstrandhalvøya close to Ny Ålesund (Spitsbergen, 78°55′ N, 11°56′ E). For detailed information about the physical environment and the ecosystem of Kongsfjorden in general see Svendsen *et al*. (2002), Hop *et al*. (2002) and Wiencke (2004).

Fertile sori were removed from five different individuals per species using a razor blade, blotted with tissue paper and kept in darkness in a moist chamber at 0 °C overnight or for a few days. Sori were immersed in a small amount of seawater at *c*. 15 °C and placed in the light close to a window to promote the rapid release of zoospores

(Wiencke *et al*. 2000). The initial zoospore density was counted by use of a Neubauer chamber (Brand Germany). Samples taken from this stock suspension were transferred into 5-cm diameter Petri-dishes filled with filtered (0.2 µm pore size) seawater to give spore densities between 35 000 and 60 000 spores cm^{-2}.

Sample holders for the field experiments consisted of an aluminium frame (0.25 × 0.40 m) with a black plastic bottom and a top of UV-transparent Plexiglas 'GS 2458' (Röhm, Darmstadt, Germany: mean transmission 93% of PAR, 92% of UV-A and 86% of UV-B), and accommodated 15 Petri-dishes (53 × 12 mm) arranged in a 3 × 5 grid. To determine the effect of different radiation treatments, the Plexiglas above each Petri-dish was covered either with Ultraphan URUV farblos (Digefra GmbH, Munich, Germany), Folex PR Montage (Dr Schleussner, Dreieich, Germany) and Ultraphan URT 300 (Digefra GmbH, Munich, Germany) foil to give three treatments: photosynthetically active radiation (PAR) = P, PAR + UV-A = PA, and PAR + UV-A + UV-B = PAB. The spectral properties of the foils used are published elsewhere (Bischof *et al*. 2002). Treatments were assigned randomly. Two to five drops of zoospore suspension from different sporophytes were added to each dish, before filling to the top with filtered seawater. They were then covered by UV-transparent Plexiglas, such that each dish was water-tight and free of air bubbles. Several sample holders were prepared and deployed at five depths (0.25 m, 0.5 m, 1 m, 2 m and 4 m) in the fjord between the old and the new pier in Ny Ålesund using anchors and buoys. They were exposed for about 24 hours in the field. One experiment was run for 45 hours due to very low light conditions and corresponding low UV doses.

An ELUV 14 datalogger was fixed close to each sample holder, to determine the UV-B doses (erythema weighted, UV_{ery}; El Naggar *et al*. 1995) at the different depths. The sensitivity of the datalogger was calibrated to the standard CIE-87 erythemal response after McKinlay & Diffey (1987). We used this datalogger as it is, to our knowledge, the only submersible field datalogger available. Surface PAR was measured throughout the experimental period using a cosine quantum sensor attached to a LI-COR datalogger (LI-1000, LI-COR Biosciences, Lincoln, Nebraska, USA). Diffuse vertical attenuation coefficients of downward irradiance of UVBR were determined after Kirk (1994) using the UV_{ery} data determined at different depths.

After exposure, the sample holders were recovered from the fjord and the individual Petri-dishes were covered with lids and exposed to dim white light (10 µmol photons^{-2} s^{-1}) using daylight fluorescent tubes (Osram Daylight Lumilux De Luxe L36W/12–950) at a temperature of 10 °C for 3 days. Germination rates were determined microscopically by use of an Axioplan microscope (Zeiss, Göttingen, Germany) equipped with a 25× seawater immersion objective. A spore was classified as germinated if at least a germ-tube was formed. We did not distinguish between dead spores and those that were living, but not germinated. Approximately 300 spores were examined per sample.

Germination data were tested for homogeneity of variances (Levene Statistics) and normality (Kolmogorov-Smirnov test). Due to different environmental conditions during each field experiment, statistical tests were conducted separately on each species. The response of the dependent variable was tested using multiple analyses of variance (MANOVA, $P < 0.05$) to determine the interaction between the effects of irradiance and depth. This was followed by Duncan's multiple range test (DMRT, $P = 0.05$) to determine which groups were homogeneous or significantly different from each other. Statistical analyses were done using the SPSS program (SPSS, Chicago, IL, USA).

Biologically effective UV-B doses (UV_{ery}) resulting in a 50% inhibition in germination were determined from all germination data (expressed as percentage of the value in treatment P) using non-linear regression ($y = a + bx + cx^2$), corresponding to the best fit curves.

Results

Throughout the investigation period, the weather was relatively bright, with a mixture of sunny and cloudy periods. Even during the polar day there is a clear variation between low light conditions at midnight and high light conditions at noon (see Fig. 1a). Midnight photon fluence rates (PFR) were between about 100 and 200 µmoles photons m^{-2} s^{-1}, whereas maximum PFRs of about 1200–1400 µmoles photons m^{-2} s^{-1} were measured at noon. PAR values at the surface were

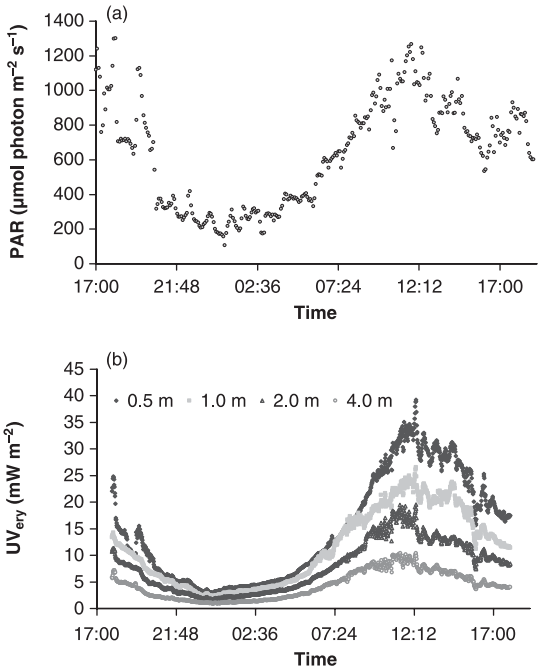

Fig. 1 Variation in radiation during a typical polar day showing (a) 24-hour surface photosynthetically active radiation and (b) corresponding Erythema-weighted UV-B radiation (UV_{ery}; El Naggar *et al*. 1995) at 0.5, 1.0, 2.0 and 4.0 m water depth.

Table 1 Surface levels of photosynthetically active radiation (PAR) and of weighted UV-B radiation (UV_{ery}; El Naggar *et al.* 1995) at different water depths during field experiments performed in Kongsfjorden (Spitsbergen). Values corresponding to different treatments of PAR = P, PAR + UV-A = PA, and PAR + UV-A + UV-B = PAB were extrapolated from the percentage transmission of UV dose (UV_{ery}) using the same cut-off filter foils in the laboratory (ND = not determined)

	Experimental duration			PAR ($J\ m^{-2}$)	UV_{ery} ($J\ m^{-2}$)			
Species	Date	Total time h:min	Treatment	Surface	0.5 m	1.0 m	2.0 m	4.0 m
Saccorhiza dermatodea	09.06.04 17.37 to 10.06.04 18.18	24:41	No filter	1.06×10^7	1.34×10^3	9.49×10^2	5.81×10^2	ND
			PAB		9.35×10^2	6.63×10^2	4.06×10^2	
			PA		3.46×10^1	2.46×10^1	1.51×10^1	
			P		0.00×10^0	0.00×10^0	0.00×10^0	
Saccorhiza dermatodea	21.06.04 16.30 to 23.06.04 13.30	45:00	No filter	1.73×10^7	8.18×10^2	3.99×10^2	1.35×10^2	ND
			PAB		5.72×10^2	2.79×10^2	9.44×10^1	
			PA		2.12×10^1	1.04×10^1	3.49×10^0	
			P		0.00×10^0	0.00×10^0	0.00×10^0	
Alaria esculenta	04.06.04 08.40 to 05.06.04 09.26	24:46	No filter	1.26×10^7	1.38×10^3	1.02×10^3	6.77×10^2	3.39×10^2
			PAB		9.67×10^2	7.16×10^2	4.73×10^2	2.37×10^2
			PA		3.58×10^1	2.65×10^1	1.75×10^1	8.77×10^0
			P		0.00×10^0	0.00×10^0	0.00×10^0	0.00×10^0
Alaria esculenta	14.06.04 18.35 to 15.06.04 16.15	21:40	No filter	8.23×10^6	6.78×10^2	5.96×10^2	3.89×10^2	1.85×10^2
			PAB		4.74×10^2	4.16×10^2	2.72×10^2	1.30×10^2
			PA		1.76×10^1	1.54×10^1	1.01×10^1	4.80×10^0
			P		0.00×10^0	0.00×10^0	0.00×10^0	0.00×10^0
Laminaria digitata	07.06.04 17.34 to 08.06.04 18.02	24:32	No filter	1.17×10^7	1.28×10^3	9.74×10^2	6.86×10^2	3.72×10^2
			PAB		8.95×10^2	6.81×10^2	4.79×10^2	2.60×10^2
			PA		3.32×10^1	2.52×10^1	1.78×10^1	9.62×10^0
			P		0.00×10^0	0.00×10^0	0.00×10^0	0.00×10^0
Laminaria digitata	17.06.04 16.10 to 18.06.04 16.10	24:00	No filter	1.33×10^7	6.98×10^2	5.06×10^2	2.50×10^2	7.85×10^1
			PAB		4.88×10^2	3.54×10^2	1.75×10^2	5.49×10^1
			PA		1.81×10^1	1.31×10^1	6.49×10^0	2.03×10^0
			P		0.00×10^0	0.00×10^0	0.00×10^0	0.00×10^0

relatively similar in all experiments and varied between 8.23×10^6 J m^{-2} and 1.73×10^7 J m^{-2} (Table 1).

Figure 1(b) shows the UV_{ery} values obtained in a typical experiment (7–8 June). There is a clear differentiation of the underwater radiation regime at the various depths. Minimum levels of UVB radiation (UVBR, determined as UV_{ery}) at midnight were between 2 and 5 mW^{-2} at all depths, whereas maximum values between 18 and 45 mW^{-2} were recorded at noon at 0.5 m water depth (data not shown).

The UV_{ery} doses shown in Table 1 clearly reflect the spectral properties of the different cut-off filters used. No UVBR was measured under the filter used for the P treatment. The UVAR values reflect both the UVA transparency of the used filter and the relatively low sensitivity of the ELUV-14 datalogger in the UVA region of the spectrum. The filter used for the PAB treatment has a UV_{ery} transmission of about 70%.

Although the surface radiation regime was similar during the various experiments (Table 1), the underwater radiation regime exhibited clear differences, with water being UV transparent at some times and more turbid at others (7–8 June, see Fig. 1, Table 1, and 9–10 June vs. 17–18 June; 4–5 June, 21–23 June and 14–15 June represent intermediate situations). This is also reflected in Kd values ranging between 0.67 and 1.28 and 1% UVB-depths between 6.87 and 3.57 m (Fig. 2).

In the first experiment with *S. dermatodea* (9–10 June), germination rates between 66 and 78% were determined at 1 and 2 m depth under all of the three exposure conditions (Fig. 2a). At 0.5-m depth germination rates under full ambient solar radiation (PAB) and under solar radiation depleted of UVBR (PA) did not differ significantly (Table 2) from those under solar radiation depleted of both UVBR and UVAR (P). In the second experiment with this species (on 21–23 June), germination rates under all three conditions and at all depths were very similar and ranged between 17 and 30% (Fig. 2a).

UVR had no significant effect on the germination capacity of *S. dermatodea* in either field experiment. In the first, however, depth had a significant effect on germination (ANOVA, $P = 0.003$, see Table 2). Regardless of light quality, Duncan's multiple range test (DMRT, $P = 0.05$) showed significantly higher germination rate at 1.0 m depth compared with 0.5 m and 2.0 m depths.

In the first experiment with *A. esculenta* (4–5 June), germination rates of about 50% were measured under the P condition in all four tested depths (Fig. 2b). Low germination rates of 15–20% were determined under the PAB and PA condition at 0.5 and 1 m depth. These were not, however, significantly different from the rates measured under the P condition (Table 2). At 2 and 4 m depth germination rates were all very similar. In the second experiment with this species (14–15 June),

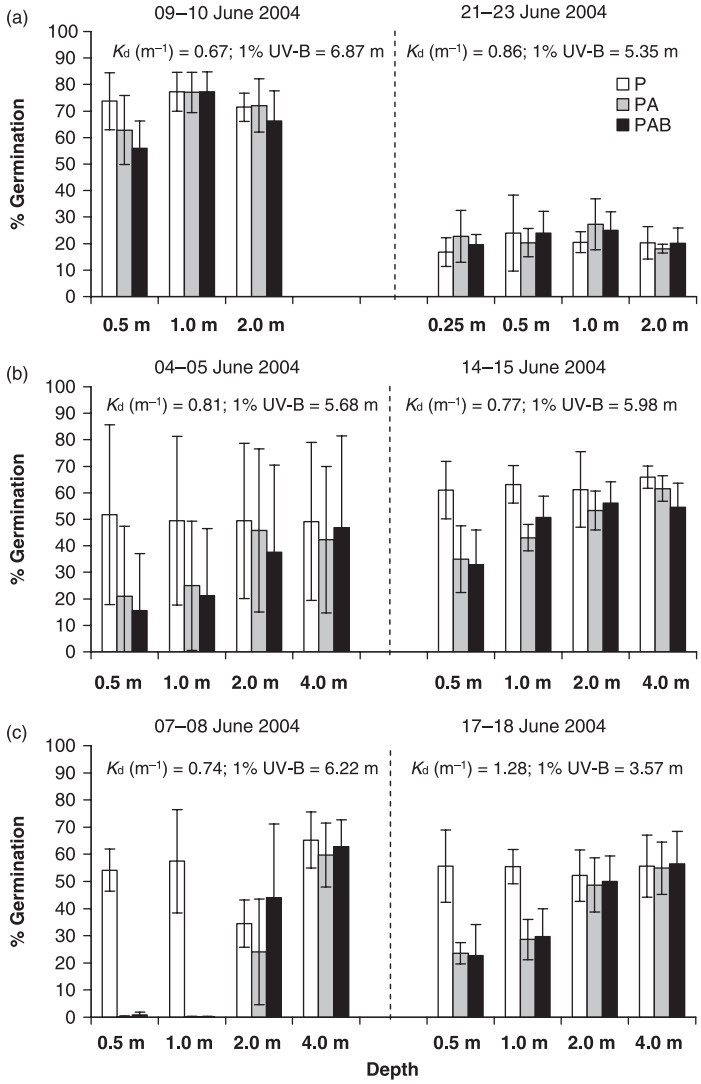

Fig. 2 Spore germination in (a) *Saccorhiza dermatodea*, (b) *Alaria esculenta* and (c) *Laminaria digitata*, 3 days after exposure to ambient solar radiation treatments consisting of photosynthetically active radiation (PAR = P), PAR + UV-A (PA) and PAR + UV-A + UV-B (PAB) at different depths and exposure times (see Table 1) and post-cultivated at 10 µmole photons m^{-2} s^{-1}. Inset values are corresponding average attenuation coefficients (K_d) and depth of 1% UV-B penetration. Vertical bars are standard deviations (SD, n = 5).

germination rates of about 60–65% were obtained under the P condition at all depths. Under the PAB and PA conditions a depression to about 35% was apparent at 0.5 m water depth.

In *A. esculenta*, significant effects of irradiance and dose (as a function of depth) (ANOVA, $P < 0.001$) were only observed in the second field experiment (Table 2). DMRT ($P = 0.05$) showed that the P condition is significantly different from PA and PAB conditions but PA and PAB conditions are not significantly different from each other. Values at 0.5 m were significantly different from the other depths. Depths 1 and 2 m are homogenous subsets, as were 2 and 4 m, although 1 m was significantly different from 4 m.

In the first experiment with *L. digitata* (7–8 June, Fig. 2c) almost no germination was observed under the PAB and PA condition at 0.5 m and 1 m depth, whereas a germination rate of about 55% was obtained under the P condition at these depths. At 4 m depth germination rates of about 60% were measured under all three conditions, whereas at 2 m very variable values between 25 and 45% were determined under all radiation conditions. During the second experiment with this species (17–18 June) germination rates exhibited little variation under the P condition at all depths studied, with values around 55% (Fig. 2c). UVBR and UVAR had no effect on the germination rate at 2 and 4 m depth. However, at 0.5 and 1 m depth there was a clear decrease of germination rates down to 22–27% under both PA and PAB.

In both field experiments with *L. digitata* there were significant effects of irradiance and depth as well as an interaction between these variables (ANOVA, $P = 0.001$). DMRT ($P = 0.05$) showed that, in both experiments, the P condition is significantly different from the PA and PAB conditions but PA and PAB conditions are not significantly different from each other. In the first experiment, depths 1 m and 2 m belong to a homogenous subset and are significantly different from depths

Table 2 Multiple analysis of variance (MANOVA) and significance values for the main effects and interactions of irradiance (PAR = P; PAR + UV-A radiation = PA; PAR + UV-A + UV-B radiation = PAB) and depth on germination of zoospores in three species of Laminariales from Spitsbergen. *Significant; NS, not significant

Date of experiment	Species	Source of variation	d.f.	*F*-value	*P*-value
9–10 June 2004	*S. dermatodea*	UV treatment (A)	2	2.412	0.104^{ns}
		Depth (B)	2	7.053	0.003*
		A × B	4	1.289	1.289^{ns}
21–23 June 2004	*S. dermatodea*	UV treatment (A)	2	0.312	0.734^{ns}
		Depth (B)	3	1.257	0.301^{ns}
		A × B	6	0.583	0.742^{ns}
4–5 June 2004	*A. esculenta*	UV treatment (A)	2	2.599	0.085^{ns}
		Depth (B)	3	1.261	0.298^{ns}
		A × B	6	0.431	0.855^{ns}
14–15 June 2004	*A. esculenta*	UV treatment (A)	2	16.195	< 0.001*
		Depth (B)	3	10.177	< 0.001*
		A × B	6	2.327	0.047*
7–8 June 2004	*L. digitata*	UV treatment (A)	2	35.096	< 0.001*
		Depth (B)	3	39.256	< 0.001*
		A × B	6	10.428	< 0.001*
17–18 June 2004	*L. digitata*	UV treatment (A)	2	16.326	< 0.001*
		Depth (B)	3	16.085	< 0.001*
		A × B	6	4.646	0.001*

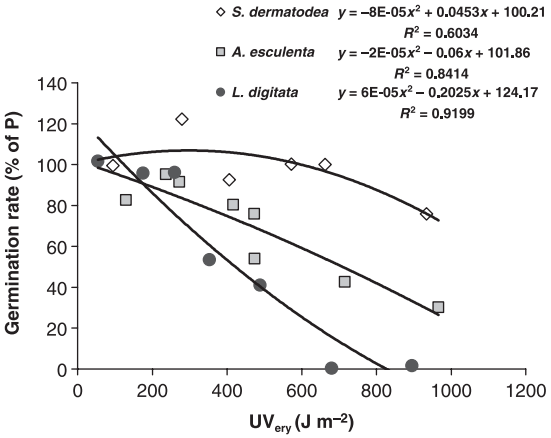

Fig. 3 Relationship between effective UV-B dose measured as UV_{ery} and germination rate expressed as percentage of PAR. Non-linear regression was used to obtain dose–response relationship. Biological effective doses needed to achieve 50% inhibition of germination BED50 are > 1000 J m^{-2}, 700 J m^{-2} and 418 J m^{-2} for *S. dermatodea*, *A. esculenta* and *L. digitata*, respectively.

2 m and 4 m, which are also significantly different from each other. In the second experiment, both 0.5 m and 1.0 m and 2.0 m and 4.0 m are homogenous subsets. The two subsets are significantly different from each other.

Overall, the most UV-sensitive species was therefore *L. digitata*, the least sensitive *S. dermatodea*, and *A. esculenta* occupied an intermediate position. The dose–response curves for the three species (Fig. 3) clearly show that the 50% biologically effective dose (BED50) for *S. dermatodea* was as high as > 1000 J m^{-2} UV_{ery}, for *A. esculenta* 700 J m^{-2} UV_{ery} and for *L. digitata* as low as 418 J m^{-2} UV_{ery}.

Discussion

The main result of this first field study of UV-effects on brown algal zoospores is that, under ambient solar radiation, the UVR tolerance is highest in the shallow water species *S. dermatodea*, intermediate in the upper to mid sublittoral *A. esculenta* and lowest in the upper to mid sublittoral *L. digitata*. Clearly, the viability of the zoospores of the species studied depends on the UV exposure and is a major if not the most important factor determining their upper distribution limit as proposed by Wiencke *et al*. (2000) and Wiencke *et al.* (2004). However, there is no additional UVBR effect on the viability of the zoospores compared with the PA condition.

Indoor and outdoor radiation conditions mainly differ in the much higher PAR levels in the field compared with the laboratory. Whereas in laboratory studies (e.g. Wiencke, Clayton & Schoenwaelder 2004) PFRs < 30 μmoles photons m^{-2} s^{-1} were applied, surface field PFRs in this study ranged between 100 and 1400 μmoles photons m^{-2} s^{-1}. A somewhat unexpected result is that high PAR values do not inhibit germination in the field, as shown by similar germination rates in the P treatment at different water depths in all species. Moreover, parallel laboratory experiments under dim light conditions with the same spore material gave similar germination rates to those in the field (data not shown). This result is in contrast to previous observations that, in addition to the inhibitory effect of UVR, high levels of PAR exert strong negative effects on photosynthesis and on the growth of seaweed macrothalli (Hanelt *et al*. 1997; Aguilera *et al*. 1999). Such patterns may, however, be confined to the sun-adapted macrothalli of seaweeds with highly active photosynthetic tissues, and may not

be appropriate for the spores of Laminariales, which are shade adapted, contain only a single chloroplast with few thylakoids (Henry & Cole 1982) and exhibit only very low photosynthetic rates (Kain 1964; Amsler & Neushul 1991).

Another important difference is the much higher UVBR levels in the laboratory compared with the field. Under ambient solar radiation, over various time intervals, about 10 times lower UVBR doses were recorded compared with those in standard laboratory experiments (data taken from Wiencke, Clayton & Schoenwaelder 2004), probably explaining lower laboratory germination under PAB filters than under PA conditions (Wiencke *et al*. 2000; Wiencke, Clayton & Schoenwaelder 2004; Roleda *et al*. 2005). Another possibility may be a better stimulation under field conditions of the blue-light dependent photolyases that remove the cyclobutane pyrimidine dimers resulting from UV-induced DNA damage (Pakker, Beekman & Breeman 2000; Pakker, Martins, Boelen, Buma, Nikaido & Breeman 2000). In higher plants, photolyase enzymes recognize UV-induced DNA lesions and reverse dimerization by absorbing light between 350 and 450 nm (Hada *et al*. 2000).

The UVR-tolerance of zoospores may be partly explained by increased activity of the repair mechanisms, which apparently operate best in the shallow water species *S. dermatodea*, to a lesser degree in the upper to mid sublittoral *A. esculenta* and least in the upper to mid sublittoral *L. digitata*, as observed in laboratory studies (Wiencke, Clayton & Schoenwaelder 2004). Repair of DNA damage has been demonstrated in a variety of seaweeds (van de Poll *et al*. 2002) and also in zoospores of *L. digitata*, *L. saccharina and L. hyperborea* (Roleda *et al*. 2005). In the latter study, efficient repair was observed in the upper sublittoral *L. digitata*, but not in species occurring in greater water depths. Although the recovery of photosynthesis after UVR exposure has been documented, repair processes have so far not been shown in macroalgae, despite the fact that such processes must be involved.

Another explanation for the differential UV tolerance is the presence of protective mechanisms. UV-absorbing compounds, in particular phlorotannins are present in kelp zoospores, with higher concentrations in upper compared with mid sublittoral species (Roleda *et al*. 2005). Moreover, an increase in the number and diameter of phlorotannin-containing physodes has been described in *S. dermatodea* and in *A. esculenta* (Wiencke, Clayton & Schoenwaelder 2004), another reason for the success of these species in shallow waters.

Beside the incident surface radiation, an important factor governing the underwater radiation regime in polar regions is the presence of sea ice, which attenuates both PAR and UVBR very strongly (Hanelt *et al*. 2001). By the time the break-up of ice occurs in spring, the solar angle is already relatively high and algae are therefore suddenly exposed for long daily periods to very high PFRs. Moreover, the water is very clear and biologically relevant UVBR penetrates the water column down to about 5–8 m depth (Fig. 2; Hanelt *et al*. 2001; van de Poll *et al*. 2002). From the end of June onwards, however, attenuation increases due to a strong inflow of turbid melt water from then until mid August (Svendsen *et al*. 2002), after which the water transparency increases again (Hanelt *et al*. 2001).

This change in the underwater radiation may be reflected also in the UVR susceptibility of algal spores. Germination is clearly inhibited in spores from *L. saccharina*, *L. digitata* and *A. esculenta* collected in spring and exposed to PA (Wiencke *et al*. 2000), but there is no equivalent UVAR effect on autumn-collected spores (Wiencke, Clayton & Schoenwaelder 2004). In our opinion, the inhibition of germination after UVAR exposure in spring is related to the fact that material is not yet acclimated to high radiation conditions. In a marine diatom, damage to carbon fixation in the cells was found to be higher under UV-A, which also induces localized loss on the acceptor side of the PSII reaction centres (Grzymski *et al*. 2001; Turcsányi & Vass 2002).

All the species studied here develop their sori in summer. *A. esculenta* and *L. digitata* are fertile between May and September, whereas young specimens of *S. dermatodea* become fertile in August and September (C. Wiencke & M. N. Clayton, unpublished data) and 18-month-old specimens in May and June. The spores of the studied species were therefore exposed to the described radiation conditions at an appropriate time, underlining the ecological relevance of our data.

In the field, *S. dermatodea* is common at depths between 0.5 and 5.5 m, *A. esculenta* at depths between 1.5 and 12.5 m and *L. digitata* grows between 1.5 and 13.5 m (Wiencke, Vögele, Kovaltchouk & Hop 2004; C. Wiencke unpublished data). The known depth distribution pattern therefore mostly reflects the data obtained here on UV tolerance of the zoospores. The only misfit is the overlap in the distribution between *A. esculenta* and *L. digitata* in shallow water. However, in such situations, *L. digitata* may grow below *A. esculenta* (C. Wiencke, unpublished observations) and settling in the shade of *A. esculenta* may allow the very UV sensitive zoospores of *L. digitata* to establish. The adult macrothalli of *L. digitata* are clearly sun adapted and can cope very well both with high PAR and with UVBR (Hanelt *et al*. 1997; Bischof *et al.* 1998). Additional biotic factors, such as competition or grazing, as exemplified by Wahl *et al*. (2004), require further investigation.

The results suggest the need for studies of the protective and repair mechanisms in the most UV-tolerant species, *S. dermatodea* and *A. esculenta*. The question remains whether they will be able to cope with the increase of harmful UVBR due to stratospheric ozone depletion. A 10% decline in ozone concentration results in a doubling of irradiance at 300 nm (Frederick *et al*. 1989). In the Ny Ålesund area a 12% increase in irradiance at 300 nm was already measured as a

consequence of a relatively minor reduction in ozone concentration of 10 Dobson units (Groß *et al*. 2001). Enhanced UVBR certainly will influence the viability of brown algal zoospores and, hence, the zonation of seaweeds around Spitsbergen.

Acknowledgements

This work was performed at the Ny Ålesund International Research and Monitoring Facility on Spitsbergen (Svalbard). The authors are grateful to M. Schwanitz, C. Daniel, A. Chapman, S. Kremb and C. Wanke for providing samples by SCUBA diving, as well as to the staff at Koldewey Station. Thanks go to M. Molis for help with the design of the experiment. The experiments comply with the current laws of Germany and Norway.

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Received 27 June 2005
revision accepted 15 November 2005
Handling Editor: Malcolm Press