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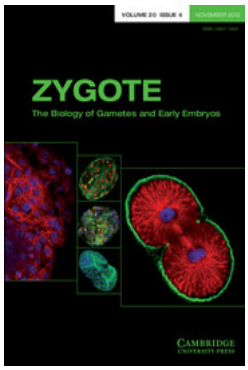

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Stage-dependent sensitivity to ultraviolet radiation in zygotes of the brown alga *Fucus serratus*

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Summary

Sensitivity to ultraviolet (UV) radiation (UV-A, λ = 315–400 nm; plus UV-B, λ = 280–315 nm) of zygotes of the brown alga *Fucus serratus* L. (Phaeophyta) has been assessed through effects on growth of developing germlings. Different stages of development were distinguished by considering 5 h periods of time after fertilisation. Both the stage of the zygote and the UV radiation condition significantly affected growth of developing germlings. The negative response of growth rate of early stages of the zygotes to UV radiation seemed to be caused by UV-B rather than UV-A radiation, as the lowest relative growth rates were always estimated for germlings developed from zygotes irradiated with UV-B radiation. As regards the stage of the zygote, those germlings that developed from zygotes irradiated at 5–10 h after fertilisation showed the strongest inhibition of growth compared with the other stages. These results point to polarisation as the most UV-sensitive process during the first 24 h of the development of the zygote. A non-linear relationship between the developmental stage of the zygote and the sensitivity to UV radiation is suggested.

Keywords: *Fucus*, Growth, Macroalgae, UV radiation, Zygote

Introduction

Stratospheric ozone depletion, which is now a problem not only in the Antarctic atmosphere (Chubachi, 1985) but also in the Northern Hemisphere (Peace, 1996), causes an increase in ultraviolet-B (UV-B, λ = 280–315 nm) radiation reaching the earth's surface (Seckmeyer & McKenzie, 1992). Effects of ultraviolet (UV) radiation (UV-A, λ= 315–400 nm, plus UV-B) in macroalgae have been detected, although primarily in multicelled stages (Wood, 1987; Grobe & Murphy, 1994; Bischof *et al*., 1998; Altamirano *et al*., 2000). However, effects on single- and few-celled stages, which may be considered the most sensitive to any kind of stress, mainly due to their small size and structural simplicity (Hanelt *et al*., 1997; Yakovleva *et al*., 1998), have rarely been assessed (Wiencke *et al*., 2000; Kuhlenkamp *et al*., 2001). For prediction studies of environmental stress factors such as UV radiation, knowledge of the sensitivity of these ontogenetic stages is crucial, since recruitment of the species depends on the survival of these stages, and conclusions obtained with macroscopic stages should not be extrapolated to microscopic ones.

In the present study the sensitivity to UV radiation of growth at the early stages of development of the brown alga *Fucus serratus* L. (Fucales, Phaeophyta) was examined. This species is an important coastal primary producer, widely distributed in the high sublittoral on Atlantic coasts (Lüning, 1990), which has a diplontic monomorphic dioecious life history. The large diploid plant undergoes meiosis at the onset of gametogenesis.

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Production of the haploid male antherozoids and female eggs is followed by germination of the resultant zygote, producing microscopic germlings that will re-establish the diploid macroscopic plant (Lee, 1999). No asexual reproduction is exhibited by this species.

The aims of the present study were to: (1) assess the stage-dependency of the sensitivity to UV radiation of zygotes of *F. serratus*, through the effects on growth of developing germlings; and (2) investigate the possible processes related to the early development of the zygote that may be affected by UV radiation.

Materials and methods

Algal material and sampling site

Fertile receptacles of *Fucus serratus* L. (Fucales, Phaeophyta) were collected during low tide in the intertidal on the Island of Helgoland (North Sea, Germany; 54°11′N 07°53′E). Samples were taken to the laboratory inside plastic bags in an ice-chest and kept in darkness. Receptacles were washed in cold seawater and wiped with paper towel to eliminate gross contaminants and discharged gametes and zygotes. The protocol of McLachlan *et al.* (1971) was followed for the release of gametes. Clean receptacles were placed on dry tissue at room temperature (18 °C, 30–45 min) in order to eliminate surface water. Partially dehydrated receptacles were placed inside 20 cm diameter Petri dishes with sufficient space between the samples that they did not touch each other. The dishes were kept in a culture chamber at 8 °C and in darkness until the release of gametes from conceptacles was observed. After that, receptacles were put inside 8 cm diameter glass Petri dishes, covered with cold sterile seawater and kept inside a culture chamber at 8 °C and in darkness. In less than 1 h, gametes were completely released from the conceptacles and settled on the bottom of the Petri dish, where they could be isolated easily with a Pasteur pipette. Most of the medium which contained mucilage was decanted and replaced by cold sterile seawater and swirled vigorously. The gametes were allowed to settle and the previous procedure repeated several times. Fertilisation was forced by pipetting a suspension of spermatozoids into a suspension of female gametes (McLachlan *et al.*, 1971). Approximately 100 synchronous zygotes were cultured in each separate 5 cm diameter plastic Petri dish with sterile seawater.

Experimental design

Six different stages in the early development of the zygote were considered as time in hours after fertilisation (0, 5, 10, 15, 20, 25 h). Zygotes of different stages were exposed for 5 h to three different UV radiation conditions at 15 °C, which were obtained using three kinds of blocking filters placed at the top of the Petri dishes: two types of Ultraphan filters (Digefra, Munich, Germany) with transmission at λ >395 nm and λ >295 nm for the photosynthetically active radiation (PAR, λ = 400–700 nm) only (P) and PAR+UV+A+UV-B (PAB) conditions, respectively, and a Folex filter (Folex, Dreieich, Germany) with transmission at λ >320 nm for the PAR+UV-A (PA) condition. The transmission spectra of the blocking filters are shown in Figueroa *et al.* (1997). The light source consisted of six UVA-340 (Q-Panel, Cleveland, OH, USA) lamps placed at 10 cm above the Petri dishes. The spectral irradiances under each UV radiation condition were measured with a spectroradiometer (LI-1800UW, Li-Cor, Lincoln, NE, USA). To estimate the wavelength-dependent effectiveness of the UV irradiances applied in each treatment (biologically effective dose, BED), spectral irradiances in the range 300–400 nm were weighted using an effective biological spectrum for inhibition of photosynthesis in the diatom *Phaeodactylum* (Cullen *et al.*, 1992). The biologically effective spectral irradiance (BESI) was calculated according to Madronich & Flocke (1997), as follows:

$$\mathrm{BESI} = \int_{300\ \mathrm{nm}}^{400\ \mathrm{nm}} I(\lambda)\, \varepsilon(\lambda)\, \mathrm{d}\lambda$$

where $I(\lambda)$ and $\varepsilon(\lambda)$ are the spectral irradiance and biological response at λ nm, respectively. Time integration (from initial (t_0) to final (t_f), the time period of exposure) of this quantity gives the BED:

$$\mathrm{BED} = \int_{t_0}^{t_f} \int_{300\ \mathrm{nm}}^{400\ \mathrm{nm}} I(\lambda)\, \varepsilon(\lambda)\, \mathrm{d}\lambda\, \mathrm{d}t$$

Both unweighted doses and BEDs are compiled in Table 1. Weighting of irradiances in the range 280–300 nm could not be done due to limitations of the spectroradiometer, so BEDs were underestimated.

Table 1 Unweighted doses (kJ m^{-2}) of PAR, UV-A and UV-B radiation, and biologically effective dose (BED) (kJ m^{-2}) (Cullen *et al.*, 1992), under each UV radiation condition

	PAB	PA	P
Unweighted			
PAR	1.9	1.8	1.1
UV-A	590.1	479.2	5.5
UV-B	24.0	0.7	0.0
BED	22.0	13.0	0.1

PAB, PAR+UV-A+UV-B; PA, PAR+UV-A; P, PAR.

After irradiation, zygotes were post-cultivated for 10 days under 120 µmol m^{-2} s^{-1} PAR and at 15 °C. Culture medium was renewed every third day. Relative growth rate (RGR) of the germlings was estimated by changes in length of the major axis without considering the primary rhizoid, using the following equation:

$$\text{RGR (\% day}^{-1}) = 100 \times (\ln L_f - \ln L_0) \times t^{-1}$$

where L_0 is the initial overall mean diameter of the zygote (57 µm) and L_f is the length after t = 10 days. Length of germlings was measured with the ocular micrometer of an inverted microscope (Leitz Labovert, Germany). From each of the three Petri dishes incubated under each UV radiation condition, 10 germlings were randomly chosen and measured.

Statistical analysis

Relative growth rate data were compared by a two-way (UV radiation condition and stage of the zygote) model I ANOVA. In order to study differences among means within each factor *t*-tests have been performed among treatments. The arcsine transformation was applied to the RGR percentages. The homoscedasticity was checked by the F_{max} test. For limiting the overall experiment-wise error rate ($p < 0.05$) each comparison was tested using a lower comparisonwise error calculated by the Bonferroni method. For each treatment, the number of replicates was always three, as the mean RGR value of an individual Petri dish was considered as a simple replicate. All the statistical tests were performed in accordance with Sokal & Rohlf (1995).

Results

Both the stage of the zygote and the UV radiation conditions, as well as the interaction between these two factors, significantly affected growth of developing germlings of *F. serratus* (Table 2). The harmful effects of UV radiation on the early stages of the zygote of *F. serratus* seemed to be caused by UV-B rather than UV-A radiation, as observed from results of growth rates of developing germlings. Within the same stage, i.e. the same 5 h periods after fertilisation, the lowest RGR value was always found for those germlings from zygotes irradiated with UV-B radiation (PAB) (*t*-tests, $p < 0.025$) (Fig. 1). However, those germlings from zygotes treated with UV-A radiation but without UV-B (PA) showed significantly lower RGR than those under the P treatment only up to the 15 h stage (*t*-tests, $p < 0.025$), after which no significant differences were observed between these two treatments (PA and P). Germlings that developed from zygotes irradiated with UV-B radiation (PAB) in the stages from 5 to 10 h after fertilisation showed the strongest inhibition of growth, followed by germlings developed from zygotes irradiated during their first 15–20 h after fertilisation (*t*-tests, $p < 0.025$). The least sensitive stages to UV-B were 0 and 25 h after fertilisation (*t*-tests, $p < 0.025$).

Table 2 Two-way (UV radiation condition and stage of the zygote) ANOVA for RGR (% of control) values after the arcsine transformation

Factor	d.f.	% SS	*p*
UVR	2	44.4	< 0.0001*
SZ	5	45.5	< 0.0001*
UVR × SZ	10	6.4	< 0.0001*
Error	36	3.7	< 0.0001*

d.f., degrees of freedom; % SS, percentage of the total sum of squares [% SS= (factor SS/total SS)/100]; UVR, UV radiation condition; SZ, stage of the zygote.
*Significant at $p < 0.05$.

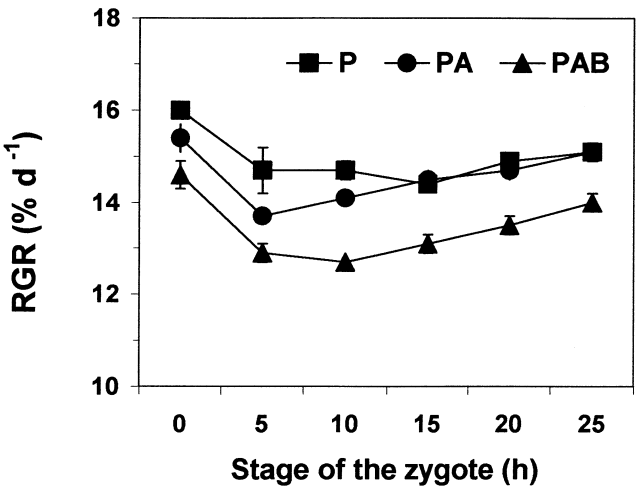

Figure 1 Relative growth rate (RGR) (% day^{-1}) of germlings of *Fucus serratus* after exposure of zygotes of different stages to three different UV radiation conditions. Data are expressed as mean value ± standard deviation (n=3). When error bars do not appear; it is because they are smaller than the size of the symbol. PAB, PAR+UV-A+UV-B; PA, PAR+UV-A; P, PAR.

Discussion

Until recently, effects of UV radiation in macroalgae have been investigated exclusively in macroscopic stages. However, recent evidence has shown that the microscopic stages may produce a 'bottleneck' effect in the adaptation process of macroalgal communities in a scenario of enhanced UV radiation (Dring *et al.*, 1996;

Yabe *et al*., 1997; Wiencke *et al*., 2000). Dring *et al*. (1996) and Yakovleva *et al*. (1998) suggested that tolerance to UV radiation depends on the stage of the life history in brown and red macroalgae respectively, with a higher sensitivity found in microscopic stages. Cordi *et al*. (2001) observed that reproductive cells of the green alga *Enteromorpha intestinalis* L. (Link) were up to six-fold more sensitive to UV-B radiation than macroscopic stages. Furthermore, they observed that sexual reproductive phases of the life cycle of this species (gametes fusing to form a zygote and developing into a sporophyte) exhibited a greater sensitivity to UV-B radiation compared with the asexual phase (zoospores developing into gametophytes), which could lead to a decreased genotypic variability in the population. Thus, harmful effects of UV-B radiation on microscopic stages of macroalgae may have different implications according to whether they are linked to the asexual or the sexual generation. Many species of macroalgae exhibit an alternation of sexual and asexual generations, such as the brown algal species *Scytosiphon lomentaria* (Lyngb.) Link and *Petalonia fascia* (O.F. Müll.) Kuntze. Zooids of these species can be isogametes, anisogametes or non-sexual (parthenogenetic or neutral) gametes. Flores-Moya *et al*. (2002) suggested that if zooids function as gametes, fertilisation may not take place under UV-B radiation, blocking the life history; on the other hand, if they function as non-sexual gametes, the recruitment of new thalli by asexual reproduction could be decreased. Because *F. serratus* has a zygotic meiosis, with only one generation in its life history, the harmful effects of UV radiation on early developmental stages of the zygote, which lead to a decrease in growth of developing germlings, may have more serious negative consequences for this species. *Fucus* species do not show asexual reproduction, and recruitment of new plants is based only on sexual reproduction and successful development of zygotes and germlings. Due to this any damage to these microscopic stages may have important negative consequences for the populations of this species on the shoreline.

Very few attempts have been made to elucidate the possible target molecules and processes that determine the UV radiation sensitivity of microscopic stages of macroalgae. In the brown algae *Scytosiphon lomentaria* and *Petalonia fascia* UV radiation affected movement patterns of zooids, possibly through damage to the photosensing pigments (Flores-Moya *et al*., 2002). Damage to DNA molecules is a well-known target of UV radiation in living organisms, also in microscopic stages of macroalgae, as a direct relationship between DNA damage and mortality in zoospores of kelp species has been shown (Wiencke *et al*., 2000). However, no information is available on the sensitivity to UV radiation of the cellular processes related to the development of the microscopic stages of macroalgae. The UV radiation dose used in the present experiment was not able to inhibit germination of zygotes completely, but was sufficient to distinguish differences in the susceptibility to UV radiation of the stages studied. In zygotes of *Fucus*, during the first 24 h after fertilisation of the eggs, several important processes related to the future development of the germlings occur, i.e. polarisation, germination, mitosis and cytokinesis (Quatrano, 1972, 1978; Kropf, 1992, 1997). Polarisation is the process by which zygotes acquire a developmental axis. It can be further subdivided into two events: axis formation and axis fixation (Kropf, 1989). In fucoids zygotes, axis formation occurs from 5 to 9 h post-fertilisation (Kropf, 1989), although this first axis is labile and can be changed by gradients of different kinds (Quatrano, 1973; Nuccitelli, 1978). Between 8 and 12 h the axis becomes irreversibly fixed in space and can no longer be repositioned; this denotes axis fixation (Quatrano, 1973). Germination occurs between 13 and 17 h and marks the initiation of tip growth (Kropf, 1989), and mitosis begins approximately a few hours later (Kropf, 1992).

Distinguishing developmental stages as 5 h periods from fertilisation, as has been done in this study, allows it to be established which of these processes may be affected by UV radiation. For *F. serratus*, results of this experiment show that all these processes are negatively affected by UV radiation, although that occurring between 5 and 10 h after fertilisation, i.e. polarisation, seems to be more sensitive to UV-B radiation compared with germination and mitosis, which occur later. The essence of polarity is the redistribution and localisation of macromolecules, organelles and metabolic processes within the cytoplasm, plasmalemma and cell wall. The axis is established by cytoplasmic components such that the two ends of the zygote differ structurally and physiologically, so that a polarised cell is formed (Kropf, 1992). The rhizoidal pole shows an accumulation of mitochondria and ribosomes, and the thallus pole an accumulation of chloroplasts (Jaffe, 1968; Quatrano, 1972). This redistribution of organelles during polarisation may be the possible target of UV radiation during the first 24 h of the development of the zygotes in *F. serratus*, as well as damaging DNA during mitosis.

Previous references have shown that sensitivity to UV radiation may be a function of the life history stage in macroalgae, with microscopic stages being more sensitive than macroscopic ones (Dring *et al*., 1996; Yakovleva *et al*., 1998). However, this simple relationship is not so intuitive when considering different developmental stages within the same microscopic stage. In a laboratory study with zygotes of various species of *Fucus*, Bird & McLachlan (1974) found that cold-hardiness during early embryogenesis

appeared to be a non-linear function of age. Furthermore, Brawley & Johnson (1991) reported that survival of germlings of the fucoid *Pelvetia fastigiata* (J. Ag.) DeToni in the intertidal zone was age-specific, because embryos at 24–48 h post-fertilisation were more vulnerable to the physical stress of emersion than those at 6 h and 1 week, but these authors could not find any explanation for these results. In the present study the relationship between sensitivity to UV radiation and age of the zygote is non-linear; on the contrary, the most sensitive processes have been recognised to occur several hours after fertilisation of the egg. It could be hypothesised that sensitivity to any kind of stress in the development of the zygotes in fucoid species is stage-dependent.

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