

Iridaea cordata (Gigartinales, Rhodophyta): responses to artificial UVB radiation

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Abstract The effects of UVB radiation on the different developmental stages of the carrageenan-producing red alga *Iridaea cordata* were evaluated considering: (1) carpospore and discoid germling mortality; (2) growth rates and morphology of young tetrasporophytes; and (3) growth rates and pigment content of field-collected plant fragments. Unialgal cultures were submitted to 0.17, 0.5, or 0.83 W m⁻² of UVB radiation for 3 h per day. The general culture conditions were as follows: 12 h light/12 h dark cycles; irradiance of 55 μmol photon per square meter per second; temperature of 9 ± 1 °C; and seawater enriched with Provasoli solution. All UVB irradiation treatments were harmful to carpospores (0.17 W m⁻² = 40.9 ± 6.9%, 0.5 W m⁻² = 59.8 ± 13.4%, 0.83 W m⁻² = 49 ± 17.4% mortality in 3 days). Even though the mortality of all discoid germlings exposed to UVB radiation was unchanged when compared to the control, those germlings exposed to 0.5 and 0.83 W m⁻² treatments became paler and had smaller diameters than those cultivated under control treatment. Decreases in growth rates were observed in young tetrasporophytes, mainly in 0.5 and 0.83 W m⁻² treatments. Similar effects were only observed in fragments of adult plants cultivated at 0.83 W m⁻². Additionally, UVB

radiation caused morphological changes in fragments of adult plants in the first week, while the young individuals only displayed this pattern during the third week. The verified morphological alterations in *I. cordata* could be interpreted as a defense against UVB by reducing the area exposed to radiation. However, a high level of radiation appears to produce irreparable damage, especially under long-term exposure. Our results suggest that the sensitivity to ultraviolet radiation decreases with increased algal age and that the various developmental stages have different responses when exposed to the same doses of UVB radiation.

Keywords Carpospores · Germlings · Morphological alteration · Mortality · UVB effects

Introduction

Artificial UVB radiation (UVBR) affects marine macroalgae in several ways, including effects on photosynthesis, nitrogen metabolism, growth, and DNA damage, as shown in numerous publications reviewed by Franklin and Forster (1997), Xue et al. (2005), and Bischof et al. (2006). Most of these studies focused on the adult stages. Studies on spores, gametes, and the young developmental stages have recently been undertaken (reviewed by Roleda et al. 2007). Early stages are more vulnerable to environmental stresses when compared with juvenile and adult macrothalli, as has been shown for zoospores and germlings of various brown algae (Dring et al. 1996; Wiencke et al. 2000, 2006; Altamirano et al. 2003; Roleda et al. 2007), unicells of Ulvales (Cordi et al. 2001), and early life stages of Gigartinales (Roleda et al. 2004a; Navarro et al. 2008). Recruitment of species depends on the survival of spores and plantlets, and conclusions regarding macroscopic stages should not be extrapolated to microscopic stages (Altamirano et al. 2003).

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However, information on this subject regarding macroalgae, especially red algae, is still limited.

UV radiation effects on macroalgae have primarily been assessed by studying growth rates (GR; Wood 1989; Friedlander and Ben-Amotz 1991; Grobe and Murphy 1998; van de Poll et al. 2001; Roleda et al. 2004b; Mansilla et al. 2006). In contrast to growth, morphology has not been frequently addressed as a parameter influenced by radiation effects (Franklin and Forster 1997), although it can integrate stress effects at several levels. Morphological effects have been studied mainly in higher plants, in which specific receptors for UVBR are activated, producing a subtle alteration in morphological characteristics (e.g., size, number of leaves, degree of bleaching, and stem elongation) (Barnes et al. 1988, 1996).

Iridaea cordata (Turner) Bory de Saint-Vincent is distributed along the Antarctic and sub-Antarctic coasts (Wiencke 1990; Cormaci et al. 1992). This alga is an important carrageenan-producing red alga (Craigie 1990), and it has been harvested in the south of Chile, together with other carrageenan algae.

The aim of this study was to evaluate the effects of different irradiances of artificial UVBR on different developmental stages of *I. cordata*. We assessed (1) carpospore and discoid germling mortality, (2) GR of young tetrasporophytes, and (3) GR and pigment content of fragments from field-collected plants.

Materials and methods

Algal material and general culture conditions

Infertile and cystocarpic plants of *I. cordata* were collected from the intertidal zone of Posesión Bay (52°13' S, 69°17' W), Strait of Magellan (Chile), in January of 2001. They were transported to the laboratory and unialgal cultures were established from fragments, as described by Oliveira et al. (1995). Cultures were maintained in Provasoli's enriched seawater (20 mL L⁻¹; 31 psu salinity), which was prepared without Tris phosphate (Ursi et al. 2008), in a temperature-controlled room at 9±1°C and 55 μmol photons m⁻² s⁻¹ PAR provided by Philips TLT 20 W/54 daylight fluorescent tubes, on a 12 h light/12 h dark cycle. The medium was renewed weekly. Voucher specimens were housed in the phycological herbarium of the University of São Paulo and cryptogamie herbarium of the University of Magallanes.

Experimental irradiance conditions

Four treatments were performed (control and three UVBR levels). PAR treatment (control) was similar to general culture conditions, whereas in other treatments, three irradiances of

UVBR exposure were provided for 3 h per day in the middle of the light period: 0.17, 0.5, and 0.83 W m⁻² (hereafter UVBR1, UVBR2, and UVBR3, respectively). These irradiances were supplied by three artificial UVB tubes (TL 20 W/12RS, Philips) with peak output at 312 nm. UVC light was filtered with cellulose diacetate foil (0.075-mm thick), which displayed 0% transmission below 286 nm. The UVBR values were achieved by varying the distance between the experimental unit (uncovered Petri dishes) and the overhead light source. UVBR and PAR were measured using a photometer/radiometer (Solar Light Company, PMA2200) connected to UVBR and PAR detectors (Solar Light PMA2101 and PMA2132, respectively). Daily doses for all treatments are shown in Table 1.

Carpospore and discoid germling mortality

Carpospores were obtained from field-collected cystocarpic plants. Release of carpospores was induced by stress due to dehydration of the fronds. Carpospores were carefully collected and counted by Pasteur pipettes (under stereoscopy microscope) before transfer to Petri dishes with sterilized seawater. Three hundred carpospores were cultivated in triplicate in each experimental irradiance condition. Carpospore mortality was calculated by percentage of algae alive and settled after 3 days. The live cells were easily distinguishable (pigmented and dividing cells) from the dead cells (no pigment and sometimes not settled). The percentage of dead carpospores for UVBR treatments was calculated using the average number of dead cells as a control value, as described by Wiencke et al. (2000):

$$\text{Dead spores (\%)} = 100 (S_{\text{dead}} - D_C)L_C^{-1},$$

where S_{dead} is the number of dead carpospores under UVBR exposure, and D_C and L_C are the number of dead and living carpospores, respectively, under control treatment.

The total number of survivals at third day was considered as the reference value (100%) to calculate the mortality percentage of young discoid germlings after 4 days. At this point (7 days after release), the diameter of 30 discoid germlings was recorded in triplicate with photographs. These photographs were taken using the stereoscopic microscope and analyzed with Image Pro Plus 4.0 software.

Growth rates of young tetrasporophytes

Young tetrasporophytes were obtained from carpospores cultivated under control conditions in the absence of UVBR for 2 months. After that, 30 tetrasporophytes were cultivated in triplicate in each experimental irradiance condition for GR determination. The surface area was assessed weekly for 28 days, whereas the degree of curling of tetrasporophytes was recorded at the end of the experiment using photographs which were taken using a

Table 1 UVBR and PAR doses during the course of the experiments

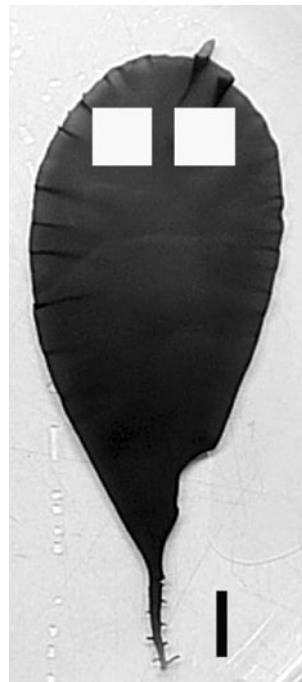
	Intensity (Wm^{-2})	Doses (kJm^{-2})						
		1day	3days	1week	2weeks	3weeks	4weeks	5weeks
PAR (control)	11.95	516	1,549	3,097	7,227	10,841	14,455	18,068
UVBR1	0.17	1.8	5.51	11.0	25.7	38.6	51.4	64.3
UVBR2	0.5	5.4	16.2	32.4	75.6	113.4	151.2	189
UVBR3	0.83	9.0	26.9	53.8	125.5	188.2	251.1	313.7

stereoscopic microscope and analyzed by Image Pro Plus 4.1 software. GRs were estimated from the following equation: $\text{GR} (\% \text{ day}^{-1}) = ((\ln A_f - \ln A_i)t^{-1})100$ where A_i is the initial and A_f is the final area of the young tetrasporophytes after t days of culture under the different treatments.

Growth rates of fragments from field-collected plants

Because the apical sections of *I. cordata* are very irregular, 1-cm² fragments were selected from subapical infertile field-collected plants (Fig. 1) to standardize the biomass and area. Afterwards, these fragments were cultivated for 2 weeks under general culture conditions for acclimatization. Next, four fragments were cultivated in triplicate in each experimental irradiance condition for GR determination. The fresh biomass was recorded weekly for a period of 35 days, and the GRs were estimated with the equation used for young tetrasporophytes, replacing area with biomass.

Fig. 1 *Iridaea cordata* collected from intertidal zone of Posesión Bay, Strait of Magallanes (Chile). White squares indicate the subapical region where fragments were excised. Scale bar=1 cm



Pigment analysis

The pigment analysis was carried out on fragments from subapical infertile field-collected plants cultivated for 35 days in each experimental irradiance condition. Both phycobiliprotein and chlorophyll-a (Chl-*a*) were analyzed from the same sample by spectrophotometry using an HP8452 A spectrophotometer. Pigment extractions were carried out at 4°C, according to Kursar et al. (1983) as modified by Plastino and Guimarães (2001). Briefly, 250 mg of tissue from fragments cultivated for GR determination were disrupted by grinding with liquid nitrogen and 50 mmol L⁻¹ phosphate buffer, pH5.5. Crude extracts were centrifuged at 36,000×*g* for 25 min to obtain the phycobiliproteins. Chl-*a* was extracted after dissolving the pellet in 90% acetone and centrifuged at 12,000×*g* for 15 min. Pigment concentration was calculated according to Kursar et al. (1983) for phycobiliproteins [phycoerythrin (PE), phycocyanin (PC), and allophycocyanin (APC)] and according to Jeffrey and Humphrey (1975) for Chl-*a*. All pigment extractions were performed in triplicate.

Data analysis

Data were tested for homogeneity of variances and normality (Kolmogorov–Smirnov test). Corresponding transformations were performed for data that were heteroskedastic (unequal variances) and non-normal. The arcsine transformation was applied to percentage data of carpospore mortality. Data (UVB irradiance treatment) were compared by one-way analysis of variance (ANOVA). Time series measurements on the GR of the young tetrasporophytes and adult segments were subjected to repeated measures ANOVA to determine the effects of treatments across the sampling days. In all cases, a posteriori Newman–Keuls test was used to establish statistical differences. Statistical analyses were done using the Statistica 7 program.

Results

Under control conditions *Iridaea cordata* carpospores developed into small red multicellular basal disks, with a diameter

of 0.089 ± 0.005 mm at 2 weeks of culture. At this time, a small primary erect cylindrical axis was initiated from the central area of the disk. The erect frond continued to elongate (2 mm at 2 months) and formed a foliose thallus.

Carpospore and discoid germling mortality

A higher percentage of mortality was observed in carpospores exposed to UVBR treatments (UVBR1 = $40.9 \pm 6.9\%$, UVBR2 = $59.8 \pm 13.4\%$, and UVBR3 = $49 \pm 17.4\%$) compared with carpospores exposed to control conditions ($6 \pm 3.0\%$) after 3 days (Fig. 2). ANOVA showed a significant effect of treatment ($df=3$, $F=8.33$, $P=0.007$). Mortality of carpospores was significantly different between control and all UVBR treatments, but there was no significant difference between individual UVBR treatments.

Discoid germlings that originated from carpospores were observed in all tested conditions. Considering the total number of discoid germlings that had settled 4 days after the first observation (7 days from release), mortality was similar in all treatments ($df=3$, $F=0.91$, $P=0.48$; Fig. 3). Diameter varied among treatments ($df=3$, $F=5.26$, $P=0.02$). Those discoid germlings exposed to UVBR2 and UVBR3 treatments became paler and exhibited smaller diameters than those germlings cultivated under control conditions (Fig. 4). Germlings could be separated into two groups based on diameter; the UVBR2- and UVBR3-treated germlings formed one group defined by small

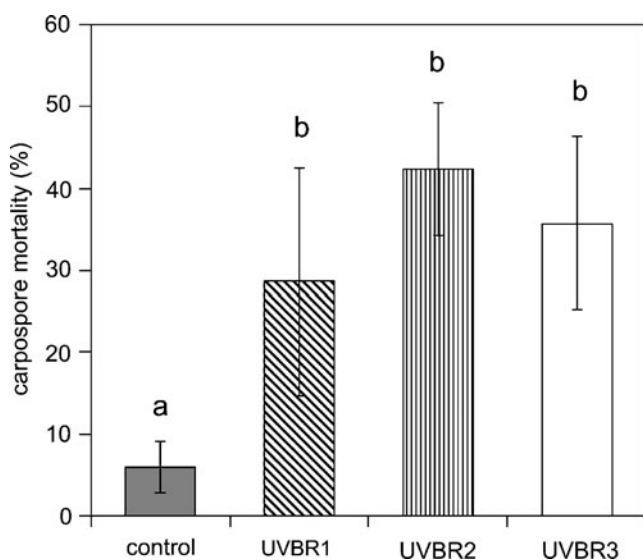


Fig. 2 Carpospore mortality of *Iridaea cordata*. Data were calculated as percentage of carpospores alive and settled after a 3-day culture period, after release in different conditions (UVBR1= 0.17 Wm^{-2} , UVBR2= 0.5 Wm^{-2} , UVBR3= 0.83 Wm^{-2} , and control=PAR). Bars indicate standard deviation ($n=3$). Treatments with different letters indicate significant differences according to one-way ANOVA and Newman-Keuls test ($P<0.05$)

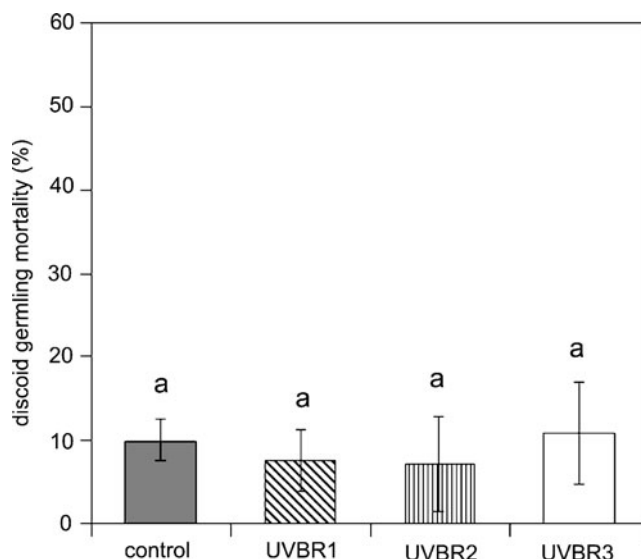


Fig. 3 Discoid germling mortality of *Iridaea cordata*. Data were calculated after a culture period of 7 days in different conditions (UVBR1= 0.17 Wm^{-2} , UVBR2= 0.5 Wm^{-2} , UVBR3= 0.83 Wm^{-2} , and control=PAR). The total number of surviving germlings on the third day after release was considered as the initial value (100%). Bars indicate standard deviation ($n=3$). ANOVA results are as in Fig. 2

diameters, whereas the PAR-treated germlings was defined by large diameters (Fig. 4).

Growth rates of young tetrasporophytes

A higher GR was observed in young tetrasporophytes exposed to control and UVBR1 treatments when compared with young tetrasporophytes cultivated under UVBR2 and

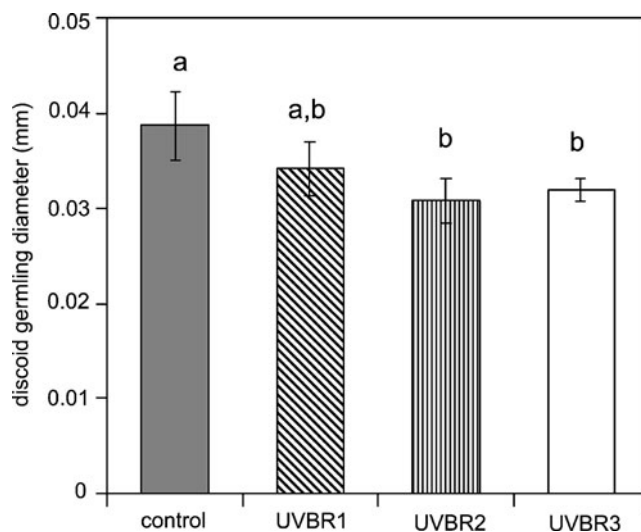


Fig. 4 Diameter of 7-day-old *Iridaea cordata* discoid germlings, cultivated in different conditions (UVBR1= 0.17 Wm^{-2} , UVBR2= 0.5 Wm^{-2} , UVBR3= 0.83 Wm^{-2} , and control=PAR). Bars indicate standard deviation ($n=3$). ANOVA results are as in Fig. 2

Table 2 Repeated measures analysis of variance and significance values for main effects and interactions of treatment and exposure time on growth rates of young and adult fragments of *Iridaea cordata*

Variable	Source of variation	df	F	P value
Young tetrasporophytes				
GR	Treatment (A)	3	11.81	0.000*
	Exposure time (B)	3	12.81	0.000*
	A×B	9	4.25	0.002*
Adult fragments				
GR	Treatment (A)	3	303.94	0.000*
	Exposure time (B)	4	42.87	0.000*
	A×B	12	18.99	0.000*

*P<0.05

UVBR3 treatments ($df=3$, $F=19.03$, $P=0.00$). Detailed analysis of the GR of all data collection dates (days 7 to 28) showed that there was daily variation (Table 2 and Fig. 5). After 7 days, higher GRs were observed in young tetrasporophytes cultivated under control conditions when compared with those tetrasporophytes exposed to UVBR treatments. Meanwhile, there were no differences among any of the treatments at 14 and at 21 days. However, at 28 days, young tetrasporophytes grown under UVBR1 showed higher GRs when compared with those tetrasporophytes that were exposed to UVBR2 and UVBR3 treatments but similar GRs when compared with control tetrasporophytes.

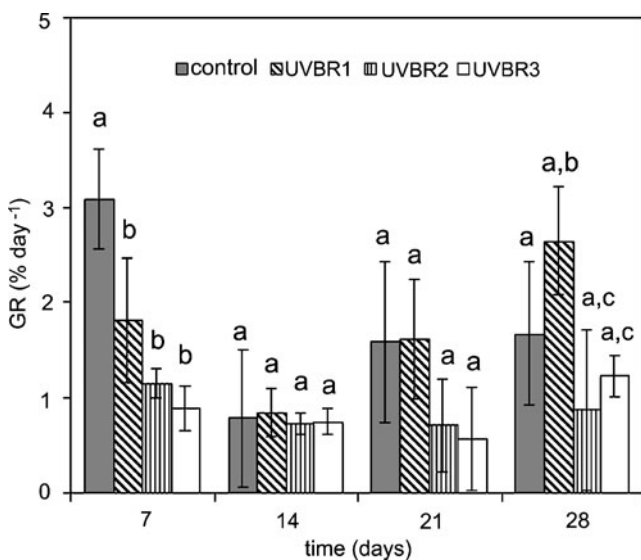


Fig. 5 Relative growth rates of young tetrasporophytes of *Iridaea cordata* cultivated in different conditions (UVB1=0.17 Wm⁻², UVB2=0.5 Wm⁻², UVB3=0.83 Wm⁻², and control=PAR) showing all data collection dates (days 7–28). Bars indicate standard deviation ($n=3$). ANOVA results are as in Fig. 2

The curling of tips was observed among young tetrasporophytes exposed to UVBR treatments after 14 days, but this morphological alteration was more evident after 21 days. This morphological alteration was more evident in plantlets cultivated under the UVBR2 and UVBR3 treatments (Fig. 6), where the curling degree of thalli reached $192\pm15^\circ$ and $209\pm36^\circ$, respectively (Fig. 7).

Growth rates of fragments from field-collected plants

The GRs of fragments from field-collected plants cultivated under control, UVBR1, and UVBR2 treatments were similar. However, the GRs were higher when compared with GRs of plants cultivated under UVBR3 ($df=3$, $F=229.78$, $P=0.00$). Analysis of the GRs at all data collection dates (days 7–28) showed that the plants exposed to UVBR3 presented a sustained GR decrease after 21 days (Table 2 and Fig. 8). Moreover, changes in morphology were observed after 7 days among fragments exposed to UVBR treatments. These changes appeared as a curling of fragments from field-collected plants and were more evident after 14 days. After UVBR3 treatment, the margins of fragments became pale, and a necrotic process was observed afterwards (Fig. 9).

Pigment analysis

The phycobiliprotein extracts of fragments from plants cultivated in each experimental irradiance condition had absorption peaks at 498, 560, and 620 nm, whereas the Chl-*a* extract had absorption peaks at 430 and 664 nm. Plants exposed to UVBR3 showed considerable changes in pigment concentrations when compared with plants cultivated under control, UVBR1, and UVBR2 treatments, such as less PE and PC (Fig. 10). However, AFC and Chl-*a* concentrations were similar among all tested conditions. Pigment concentrations among plants exposed to control, UVBR1, and UVBR2 treatments were similar.

PE/PC, PE/APC, and APC/Chl-*a* ratios were similar among all treatments (Table 3). However, the PE/Chl-*a*, PC/APC, and PC/Chl-*a* ratios were lower in UVBR3 when compared with the control, UVBR1, and UVBR2 treatments. Among those three treatments, all pigment ratios were similar.

Discussion

Mortality, growth, and morphology

Results obtained in *Iridaea cordata* corroborate the hypothesis that sensitivity to UVR decreases with increases in the age of the algae (Dring et al. 1996). Carpospores were

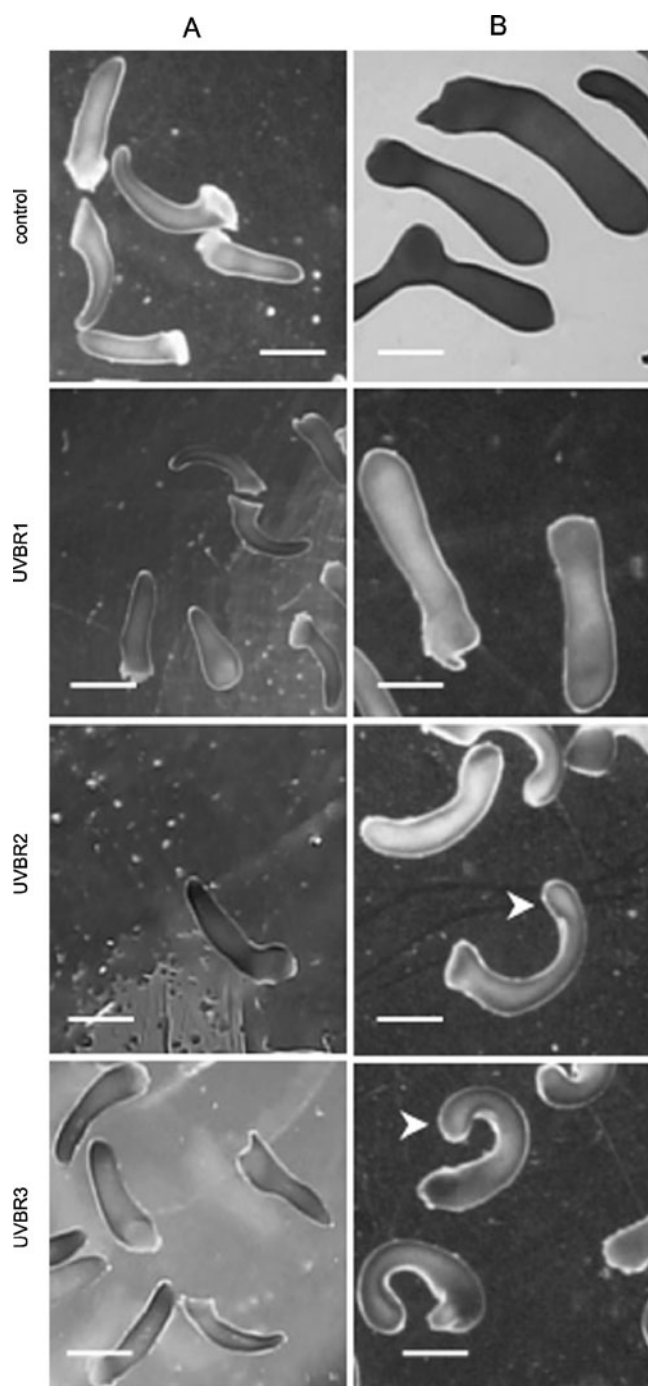


Fig. 6 Young tetrasporophytes of *Iridaea cordata*. **a** Plants before experiments. **b** Plants cultivated in different conditions (UVBR1=0.17 Wm⁻², UVBR2=0.5 Wm⁻², UVBR3=0.83 Wm⁻², and control=PAR) after a period of 28 days. Arrowheads indicate curling tips. Scale bar=0.1 cm

the most harmed stage after all UVBR-tested treatments, whereas discoid germlings and young tetrasporophytes showed lower GRs only when cultivated with UVBR2 and UVBR3 treatments. The sensitivity of carpospores can be explained by the smaller size and structural simplicity of

this microscopic stage and also by the lack of a cell wall, as suggested by other early stages in seaweeds (Lobban and Harrison 1997; Cordi et al. 2001). In this way, these characteristics would allow UVBR to easily penetrate to the UV-sensitive cellular molecules. Furthermore, the spores still do not possess a developed physiological capacity for protection against stress factors (Franklin and Forster 1997). The absence of UVAR in our study may also have contributed to mortality. This radiation increases the induction of mechanisms for repairing damage and protecting algae against UVBR (Takayanagi et al. 1994; van De Poll et al. 2001).

Despite the fact that UVBR damaged *I. cordata* carpospores, those carpospores that did survive and settle originated discoid germlings, regardless of the treatment. This fact shows that surviving germlings were able to acclimatize to UVBR because the differences in mortality among the treatments were only observed for the first 3 days.

The harmful effects on *I. cordata* germlings increased with the dose of UVBR, as previously observed in germlings of other seaweeds (Makarov and Voskoboinikov 2001; Altamirano et al. 2003). However, low doses of UVBR did not provoke the effect in discoid germlings of *I. cordata*, which did not show growth suppression when carpospores were treated with lower UVBR (UVBR1). These results can be partially explained by the presence of mycosporine-like amino acids because the presence of shinorine and palythine has already been reported from *I. cordata* (Hoyer et al. 2001).

Decreases in the GRs in the beginning of experiments, as verified in young tetrasporophyte of *I. cordata*, have been reported for other species (Grobe and Murphy 1998; Altamirano et al. 2000; Cordi et al. 2001; Mansilla et al. 2006) and could be interpreted as a period of acclimatization to the new irradiance condition. During the following weeks of cultivation, the GRs of young tetrasporophytes under UVBR treatment were similar to those tetrasporophytes cultivated under control conditions, even though tip-curling was observed. Curling was also evident in adult fragments exposed to UVBR. Similar results have been reported for some Laminariales (Michler et al. 2002; Roleda et al. 2004b; Navarro et al. 2008). This curling could be considered an acclimation that aims to reduce the area exposed to UVBR, thus acting as a protective factor against radiation (Navarro et al. 2008). This mechanism was not related to the energy available for growth because the adult and early stage morphological alterations took place when GR had not yet been affected, as was reported for higher plants exposed to UVBR (Rozema et al. 1997; Greenberg et al. 1997).

Decreases in the GRs and necrosis process at final of experiment, as verified in adult segments of *I. cordata*, may

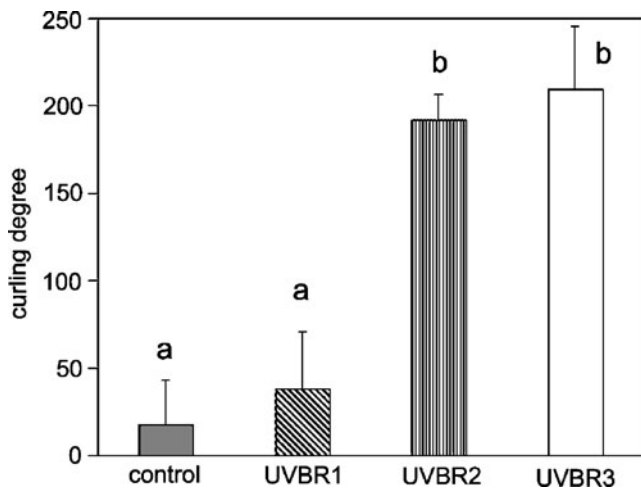


Fig. 7 Curling degree of young tetrasporophytes of *Iridaea cordata* cultivated in different conditions (UVB1=0.17 Wm⁻², UVB2=0.5 Wm⁻², UVB3=0.83 Wm⁻², and control=PAR) after a 28-day period. Bars indicate standard deviation (n=3). ANOVA results are as in Fig. 2

be related to DNA damage. UVBR damages DNA by forming cyclobutane–pyrimidine dimers. These photoproducts inhibit transcription and replication of DNA and consequently disrupt cell metabolism and division (Buma et al. 1995, 2000), directly constraining cell viability and growth (Roleda et al. 2005a).

Different development stages showed varying responses when exposed to the same UVBR doses. At 7 days (see total doses in Table 1), the germlings and young tetraspor-

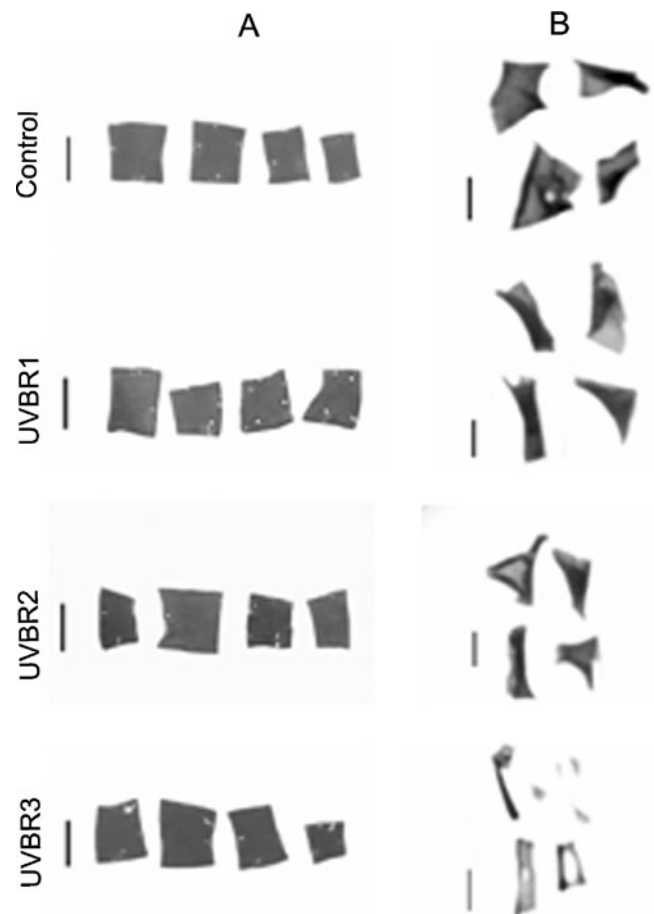


Fig. 9 Fragments of *Iridaea cordata*. **a** Plants before experiments. **b** Plants cultivated in different conditions (UVBR1=0.17 Wm⁻², UVBR2=0.5 Wm⁻², UVBR3=0.83 Wm⁻², and control=PAR) after a 35-day period. Scale=1 cm

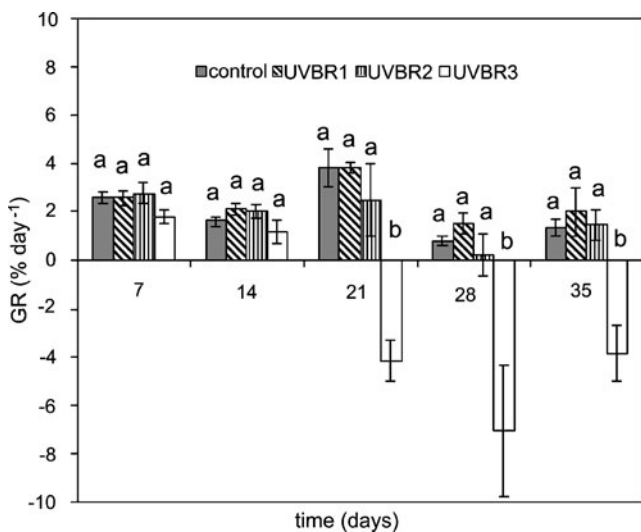


Fig. 8 Relative growth rates of *Iridaea cordata* fragments cultivated in different conditions (UVB1=0.17 Wm⁻², UVB2=0.5 Wm⁻², UVB3=0.83 Wm⁻², and control=PAR) showing all data collection dates (days 7–35). Bars indicate standard deviation (n=3). ANOVA results are as in Fig. 2

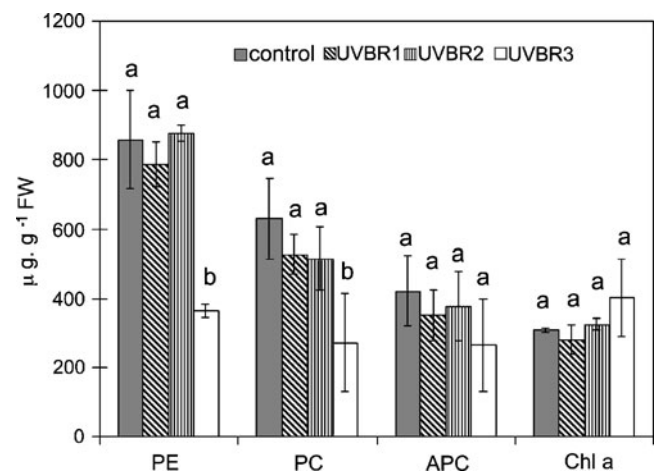


Fig. 10 Pigment concentrations of fragments of *Iridaea cordata*. Data were obtained from algae cultivated in different conditions (UVBR1=0.17 Wm⁻², UVBR2=0.5 Wm⁻², UVBR3=0.83 Wm⁻², and control=PAR) after a 35-day period. Data are expressed as mean values±SD (n=3). ANOVA results are as in Fig. 2

Table 3 Ratios of pigment concentration in fragments of subapical infertile field-collected plants of *Iridaea cordata* cultivated for 35 days in different conditions (UVBR1=0.17 Wm⁻², UVBR2=0.5 Wm⁻², UVBR3=0.83 Wm⁻², and control=PAR). Data are means of three

replicates; within each column, treatments with asterisk indicate significant differences according to one-way ANOVA and a posteriori Newman–Keuls test ($P<0.05$)

	PE/PC	PE/APC	PE/Chl- <i>a</i>	PC/APC	PC/Chl- <i>a</i>	APC/Chl- <i>a</i>
Control	1.36	2.06	2.78	1.51	2.04	1.36
UVBR1	1.49	2.27	2.83	1.51	1.89	1.25
UVBR2	1.74	2.45	2.71	1.39	1.57	1.15
UVBR3	1.55	1.59	0.96*	1.03*	0.67*	0.66

ophytes exhibited altered growth, whereas only morphology was affected in the adult plants. If we analyzed the effects of the highest UVBR treatment used in all development stages, we observed that carpospores and adult stages were the most damaged compared with intermediate stages. In the highest UVBR treatment, we observed mortality in carpospores and fragments of adult plants. These varying responses between young tetrasporophytes and segments of adult plants could be related to diverse morphological characteristics. Young tetrasporophytes have a cylindrical thallus, whereas the adult stages are laminar. In this way, more area is directly exposed to UVBR in the latter. The morphology may explain why adult thalli segments presented partial necrosis under UVBR3. According to Roleda et al. (2005b), not only is thallus thickness sufficient to minimize deleterious UVR effects, but also the optical property of the thallus is important. Optical properties can influence reflection, attenuation, scattering, absorption, and transmittance of UV radiation in plant tissues (Caldwell et al. 1983).

The use of morphological changes as biological parameters to examine UVR effects is limited due to the long time required to observe responses (Roleda et al. 2004b). Another challenge involves the best way to reliably evaluate morphological change. Here, we present a simple way to measure morphological effects in *I. cordata* young tetrasporophytes: the degree of curling. Our analyses showed that the higher UVBR (UVBR2 and UVBR3) can be detrimental for thallus morphology, especially during long-term exposure.

Pigment

Pigments represent critical targets of UVBR as well. UVBR has already been demonstrated to be effective in reducing the concentrations of pigments in different macroalgae and cyanobacteria (Häder and Häder 1989; Döhler et al. 1995). In this context, Chl-*a* and phycobiliprotein were severely affected by UVBR in *Eucheuma striatum* (Wood 1989), *Gracilaria cornea* (Sinha et al. 2000), and *Gracilaria*

edulis (Eswaran et al. 2002). The concentration of Chl-*a* was increased in *Leptosomia simplex* (Döhler 1998), *Mastocarpus stellatus*, and *Chondrus crispus* (Roleda et al. 2004a), and *Ulva* sp. (Grobe and Murphy 1998; Altamirano et al. 2000) when exposed to UVBR. In *I. cordata*, reduced PE and PC contents were observed at high doses of UVBR. These results corroborate observations of bleaching, which occurred on the thalli. The UVBR3 could have degraded pigments in a differential way, based on the spatial distribution of these pigments in the chloroplast. PE was bleached first because it is located in the peripheral part of the hexameric disks of the phycobilisomes (Talarico 1996), while chlorophylls were more resistant (Gerber and Häder 1993; Sinha et al. 1995). This pigment destruction pattern agrees with results observed in *Porphyra umbilicalis*, in which the PE was first affected when the alga was exposed to UVR, but the concentration of Chl-*a* was not changed (Aguilera et al. 1999).

The synthesis and reposition of PE, aside from its capacity for disassociation, favors the acclimatization of the phycobilisomes to radiation changes (Algarra and Rüdiger 1993), creating a photoprotective function of this pigment (Sinha et al. 1995) because the PE/PC ratio can be re-established in short periods of time (Beach et al. 2000). *I. cordata* cultivated under UVBR3 exhibited a PE/PC ratio similar to that of plants cultivated in control conditions, suggesting that PC and PE levels decreased at similar rates. The PC/APC ratio was lower when *I. cordata* was cultivated under UVBR3, while the PE/APC rate was similar to that observed under control conditions. These results suggest that PC was more sensitive to UVBR than PE, as reported for *Kappaphycus alvarezii* (Eswaran et al. 2001).

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