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Article

Effect of Solar Irradiances on Growth and Pigmentation of Antarctic Red Algae, *Kallymenia antarctica* and *Palmaria decipiens*

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Abstract : Growth and pigment responses to different levels of solar radiation with or without ultraviolet (UV)-B component (λ = 280-315 nm) were investigated in Antarctic rhodophytes, *Kallymenia antarctica* and *Palmaria decipiens*, collected around King George Island during the summer of 2000. In *K. antarctica* specific growth rate, based on thallus area or fresh weight, decreased with increasing solar irradiances while *P. decipiens* were relatively insensitive to the effects of light. It is noticeable that the presence or absence of UV-B had no significant effect on growth for either species. However, *K. antarctica* showed a more pronounced reduction in chlorophyll (Chl *a*) concentrations at higher irradiances in the presence of UV-B. In *P. decipiens*, Chl *a* concentrations did not differ despite radiation level fluctuations being lower albeit than initial measurements. Thallus thickness was greater in *K. antarctica* than in *P. decipiens*. There were higher relative amounts of UV-absorbing pigments (UVAPs) in *P. decipiens* than in *K. antarctica*. The single absorbance peak obtained from the methanol extracts was resolved into three (316, 332 and 346 nm) in *K. antarctica* and four peaks (315, 326, 333 and 349 nm) in *Palmaria* as a result of the fourth-derivative. After 7 days exposure to solar radiation, the amount of UVAPs in *K. antarctica* was significantly reduced to a similar degree at all light levels, whereas that of *P. decipiens* remained unchanged except at 5% of surface irradiance. High performance liquid chromatography (HPLC) analysis of purified extracts indicated that *P. decipiens* possesses porphyra-334 in addition to three other mycosporine-like amino acids (MAAs; asterina-330, palythine, shinorine), which are commonly present in *K. antarctica*. Significantly lower tolerance of *K. antarctica* to high levels of solar radiation may be connected with its usual absence in the eulittoral, while the active growth and elastic pigment responses of *P. decipiens* over a wide range of solar irradiance levels up to full sunlight seems to correspond well with its wide vertical distribution from rock pools down to 25-30 m.

Key words : growth, *Kallymenia antarctica*, *Palmaria decipiens*, PAR, pigment, UVAP, UV-B

1. Introduction

Polar environments are characterized by pronounced seasonal variations in the light conditions being one of the most influential factors affecting algal development, whereas Antarctic macroalgae are exposed to relatively constant low water temperatures and high nutrient concentrations over the entire year (Drew and Hastings 1992). Earlier studies have pointed out that Antarctic macroalgae are exposed to high irradiances with the advent of the spring

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season after long-term adaptation to darkness during the winter (Klöser *et al.* 1993) and that the ability to resist high radiation stress may be a determinant factor controlling the algal upper limit (Häder and Figueroa 1997).

There is a spectrum of responses with individual species being more or less able to tolerate high light stress. Some algae can tolerate increasing photon irradiances up to full sunlight with no apparent inhibition of photosynthesis or growth, whereas the same physiological parameters of other species are significantly reduced by high light treatment. In red macroalgae, Herbert and Waaland (1988) found that photoinhibition of *Porphyra perforata* J. Agardh was one-third that exhibited by *P. nereocystis*. Anderson following exposures to 2000 μmol m^{-2} s^{-1} and suggested that the sensitivity to high levels of light corresponded with their ecological habitats, i.e. intertidal for the former species and subtidal for the latter. Thus, adaptation to high irradiance stress may be genetically determined.

Photoinhibition or photodamage also occurs when organisms grown in low light environments are suddenly exposed to higher irradiances. In shallow water, experimental clearance of kelp canopies was found to cause inhibition of growth in the understory red alga *Plocamium cartilagineum* (Linnaeus) Dixon (Kain 1987). Exposure to direct sunlight was lethal to Antarctic deepwater red algae such as *Georgiella confluens* (Reinsch) Kylin and *Pantoneura plocamioides* Kylin (Han *et al.* 2001).

In recent years, growing attention has been paid to the effects of UV-B radiation on macroalgae since UV-B flux reaching the Earth's surface is increasing due to global depletion of the ozone layer. The ozone hole was first detected over Antarctica and has been deepening with consequent increases in the levels of UV-B radiation (Jones and Shanklin 1995). Research related to UV-B effects has shown that the radiation induces phytotoxic effects such as growth inhibition, destruction of photosynthetic pigments and decline of photosynthesis (Franklin and Forster 1997; Häder and Figueroa 1997; Han *et al.* 1998; Häder 2001). Recent research has also revealed that variability exists among different species or isolates of a single species in response to UV-B radiation (Dring *et al.* 1996; Häder *et al.* 1996; Hanelt *et al.* 1996; Bischof *et al.* 1998; Hanelt 1998; Karsten *et al.* 1999) and even among life-cycle stages (Wiencke *et al.* 2000). The current hypothesis is that UV-B radiation sensitivity may be an important factor controlling the vertical distribution of the species on the shore (Dring *et al.* 1996; Häder *et al.* 1996; Hanelt *et al.* 1996; Bischof *et al.* 1998; Hanelt 1998; Karsten *et al.* 1999). As a consequence, intertidal species that are potentially more exposed to high solar radiation should be more resistant to UV-B radiation than subtidal species.

Despite considerable information on high light effects on macroalgae there have been only a few studies focusing on growth as a physiological parameter (Altamirano *et al.* 2000; Michler *et al.* 2002). Plant growth may be a good indicator of radiation effects since it represents an integration of many inherent variables (Altamirano *et al.* 2000).

In this study, we compare the effects of solar radiation on growth and pigmentation of two species of Antarctic rhodophytes, namely, *Kallymenia antarctica* and *Palmaria decipiens*, collected from different depths based on the supposition that there may be a strong relation between the sensitivity to solar radiation and the distribution of algae.

2. Materials and methods

Algal materials and pretreatment conditions

During the austral summer of 2000 two species of Antarctic red algae were collected from sites at King George Island, Marian Cove (62.3°S, 58.7°W) (Fig. 1). *K. antarctica* were collected by scuba diving at a depth zone of 10-20 m, while *P. decipiens* was collected from within rock pools. The plants were transported in a black vinyl bag to King Sejong Station and maintained for 2-3 days in tanks with ambient seawater inflow at 1-2°C.

Field experiments

Algal discs (12 mm, diam.) were cut from healthy thalli and cultured in outdoor seawater tanks made of Plexiglass. Samples were exposed to three light levels (0.05 I_0, 0.5 I_0, I_0 for 5, 50 and 100% of the surface solar irradiance respectively) in the tanks with continuous inflow of ambient seawater. Sunlight incidence was reduced by a nylon net shade. For comparing the effect of UV-B removal, some culture tanks under 0.5 I_0 and I_0 were covered with acetate filters cutting off the UV-B waveband (< 320 nm). The transmission spectrum of the filter has been published elsewhere (Han *et al.* 2002).

The radiant energy from the total solar spectrum was measured above and in the water column using a Li-1800 UW underwater spectroradiometer with a cosine receptor (Li-Cor, Nebraska, USA). The surface solar radiation varied from 400 to 1540 μmol m^{-2} s^{-1} for PAR, from 44 to 118 μmol m^{-2} s^{-1} for UV-A and from 2.5 to 5.2 μmol m^{-2} s^{-1} for UV-B. Following 7 days of exposure to the solar radiation treatments, the algal samples of each species were harvested for determining the thallus area and fresh

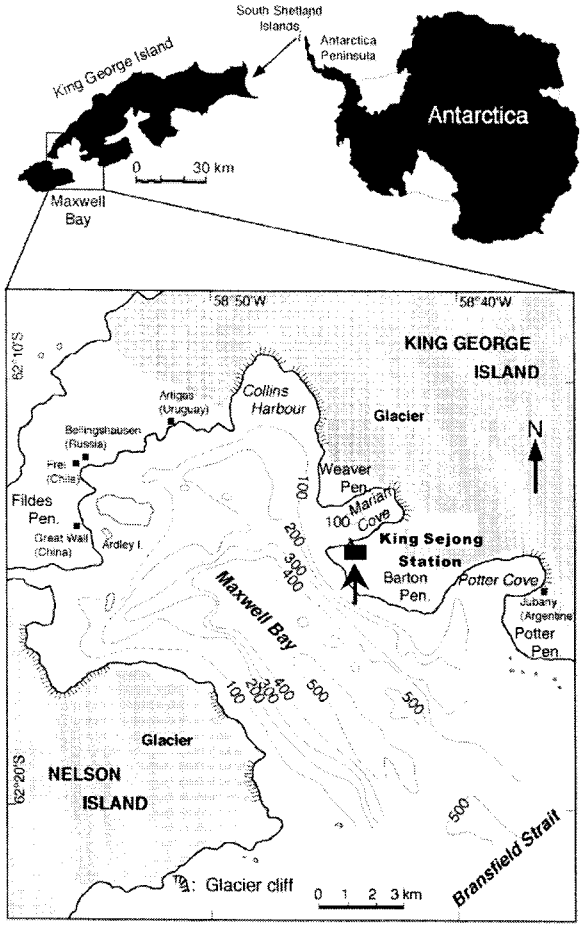

Fig. 1. Location of the study site (King Sejong Station) at Marian Cove, King George Island, Antarctica.

weight. The surface areas of the thallus discs were measured using a computer-assisted image analyzer (MV 200, Samsung, Korea) and the fresh weight of harvested samples was measured by weighing them following the removal of surface water with paper tissue. The specific growth rate (SGR) was calculated as follows:

$$SGR_{area}\ (\%\ day^{-1}) = 100 \times \ln (A_7 - A_0)/7$$
$$SGR_{FW}\ (\%\ day^{-1}) = 100 \times \ln (W_7 - W_0)/7$$

(ln: natural logarithm, A_7: final area after 7 days, A_0: initial area, W_7: final fresh weight after 7 days, W_0: initial fresh weight)

Pigment extraction and quantification

For Chl *a* and UV-absorbing pigment extraction, the weighed thalli were immersed in 99.9% methanol for at least 24 h at 5°C in the dark and the absorption spectra of thalli was determined using a spectrophotometer (Specord S 10, Zeiss). Chl *a* concentrations were calculated following the equation given by Lichtenthaler and Wellburn (1983). For determination of the amount of UVAPs the same extract was scanned for absorbance between 250 and 400 nm and the amount was expressed as a ratio of the absorbance maximum in the UV range to the chlorophyll absorbance maximum at 665 nm (Post and Larkum 1993). To clarify sample-specific absorption fourth-derivative spectra involving 13 point intervals were generated with algorithms after Savitzky and Golay provided by the manufacturer (Zeiss, Germany) (Butler and Hopkins 1970).

High performance liquid chromatography (HPLC) analysis

Samples were dried, pulverized and extracted in 20 vol. (w/v) 80% methanol at 45°C for 2 h. The methanol solution was then evaporated to the point of dryness *in vacuo*. The extract was redissolved in 10 vol. (w/v) distilled water and the supernatant was filtered through 0.45 μm pore-sized membrane filters (Gelman, USA). UV-absorbing pigments were separated and identified by high performance liquid chromatography equipped with a dual absorbance detector (Waters, USA). The analytical column used was CAPCELLPAK C18 UG120 (5 μm, 4.6 × 250 mm, Shiseido, Japan) protected by a UG 120 guard (4.6 × 10 mm, Shiseido, Japan). The samples were eluted isocratically with a mobile phase of 0.2% acetic acid in water at a flow rate of 0.5 m*l* /min. Separation was carried out at 40°C maintained by a constant temperature column heater. The wavelength for detection was 330 nm. Identification of MAAs was done by comparing the absorption spectra and retention times with those of a standard based on *Porphyra yezoensis* Ueda collected in Korea.

Statistical analysis

Main and combined effects were tested by the appropriate analyses of variance (ANOVA). Differences between the levels of a factor were further analyzed by the Least Significance Difference (LSD) (Sokal and Rholf 1969).

3. Results

The surface area growth rates of Antarctic red algae cultured at the three solar irradiances are shown in Fig. 2. The irradiance levels were similar to those found at the surface (I_0), 1 m (0.5 I_0) and 15 m depth (0.05 I_0). In *K. antarctica* the SGR_{area} recorded was highest (2.1% d^{-1}) at 0.5 I_0, and decreased with an increase in irradiance levels. The shallow water *P. decipiens* showed growth rates

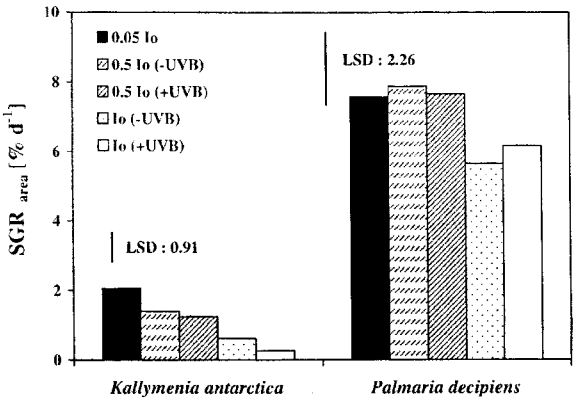

Fig. 2. Specific growth rate (% d^{-1}) of *K. antarctica* and *P. decipiens* calculated from thallus disc area measurements. The two species were cultured in outdoor tanks for 7 days under different levels of solar irradiances. Some culture tanks under 50 and 100% of surface solar irradiance were covered with acetate filters cutting off UV-B waveband (< 320 nm). Io represents the amount of solar irradiance reaching the water surface. Data are presented as the mean of the samples (n=6), and each bar represents the least significant difference (LSD) value at P=0.05.

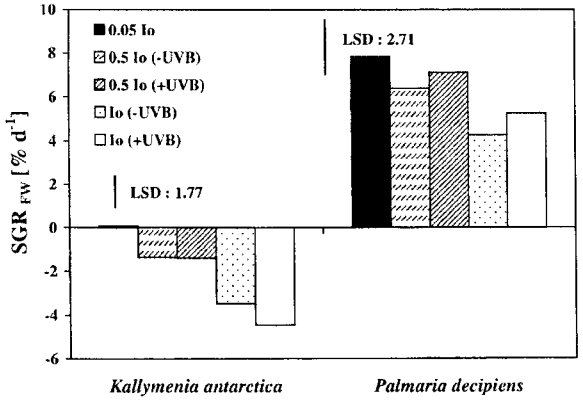

Fig. 3. The fresh weight-based specific growth rate (% d^{-1}) of *K. antarctica* and *P. decipiens* treated for 7 days under different solar radiation conditions. See the legend for Fig. 2 for details.

ranging from 5.7 to 7.9% d^{-1} with no significant difference between light levels ($p > 0.05$). The presence or absence of the UV-B component did not have a significant effect on growth.

No change in fresh weight relative to the initial was observed over the 7 days in *K. antarctica* grown at 0.05 I_0, but there was a significant reduction in SGR_{FW} with increasing irradiances (Fig. 3). *P. decipiens* from tide pools

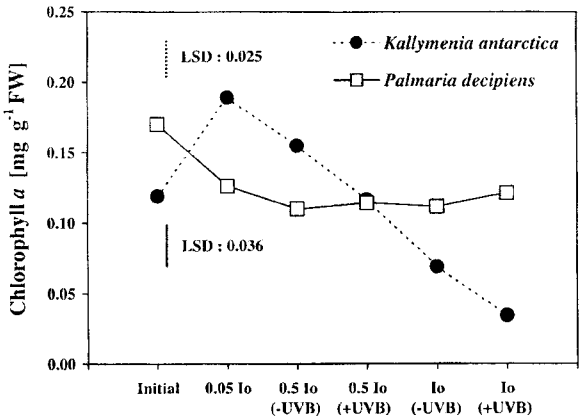

Fig. 4. Chlorophyll *a* concentrations of *K. antarctica* and *P. decipiens* exposed for 7 days to different levels of solar radiation with or without UV-B. The dotted and solid horizontal lines represent the initial Chl *a* content for *K. antarctica* and *P. decipiens* respectively. See the legend for Fig. 2 for details.

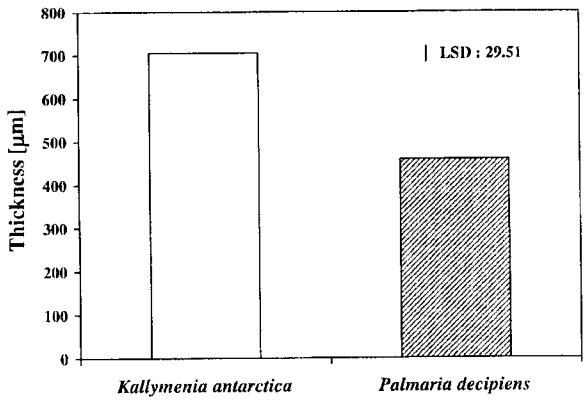

Fig. 5. Thallus thickness of the field-collected samples of *K. antarctica* and *P. decipiens*.

increased its fresh weight at rates of 4.3-7.8% d^{-1} with no differential effects by either irradiance or UV-B.

The Chl *a* content of *K. antarctica* was significantly affected by changes in solar irradiance with a greater reduction occurring at higher irradiance levels (Fig. 4). In addition, the damaging effects were greater in the presence of UV-B. The pigment content did not vary in the shallow water *P. decipiens* as a result of the treatments, although the amount was smaller than that of the initial.

The thallus of field samples was thicker in *K. antarctica* (704.4 μm) than in *P. decipiens* (458.7 μm) (Fig. 5).

Methanol extracts of the field materials had absorbance peaks in the range of 300-360 nm (Fig. 6). Relative

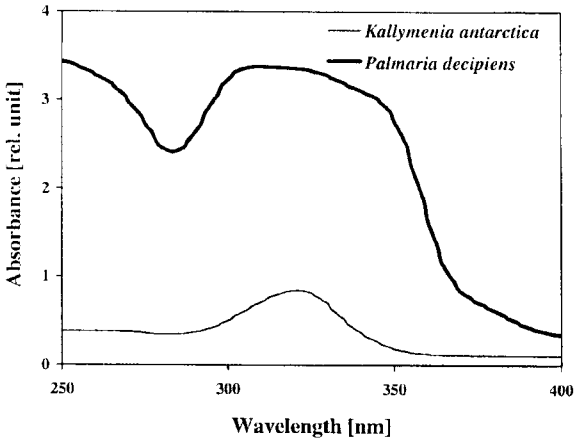

Fig. 6. UV absorption spectra normalized with the chlorophyll absorbance maxima of the methanol extracts of the field-collected samples of *K. antarctica* and *P. decipiens*.

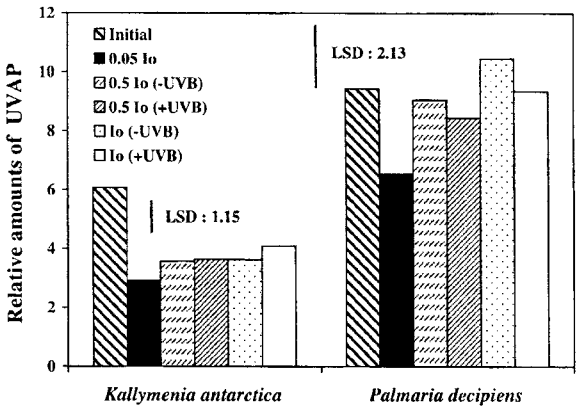

Fig. 7. Relative amount of UV-absorbing pigments in *K. antarctica* and *P. decipiens* after a 7 day culture under different solar radiation conditions. See the legend for Fig. 2 for details.

concentrations of UVAPs were considerably higher in *P. decipiens* from shallow water than in *K. antarctica* collected in deep water. When cultured in outdoor tanks the amount of UVAPs in both species did not differ between the treatments (Fig. 7). It was however noted that a significant reduction in the UVAPs as compared with the initial was found in *K. antarctica* over all light levels, while being recognized in *P. decipiens* at 0.05 I_0.

The fourth derivative spectrum for *K. antarctica* resolved the UVAP maximum at 316, 332 and 346 nm while the broad UV peak for *P. decipiens* split into bands of 315, 326, 333 and 349 nm (Fig. 8).

When HPLC was performed on the Antarctic red algal

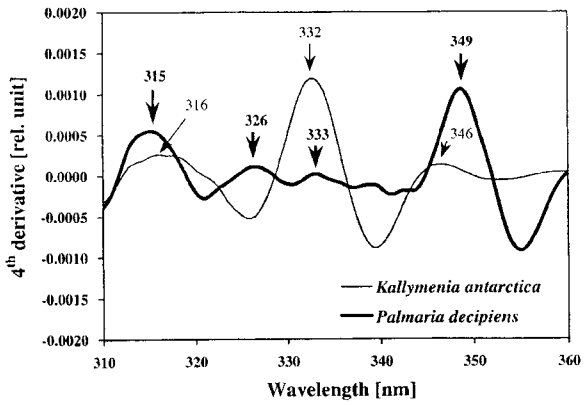

Fig. 8. Fourth-derivative spectra of the UV absorption spectra of the field-collected samples of *K. antarctica* and *P. decipiens*.

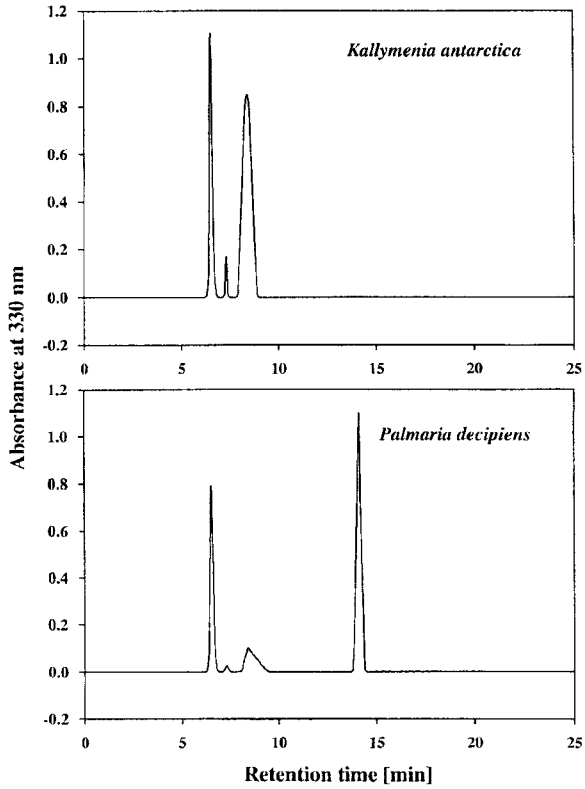

Fig. 9. High performance liquid chromatography separation of MAAs in *K. antarctica* and *P. decipiens* (first peak: palythine, second peak: asterina-330, third peak: shinorine, fourth peak: porphyra-334).

tissues both species were found to have asterina-330, palythine and shinorine in common. Porphyra-334 was additionally observed in *P. decipiens* (Fig. 9).

4. Discussion

Thallus expansion is a consequence of cell division and cell enlargement, and the reduced growth rate in the area of *K. antarctica* by high irradiances could be attributed to some disturbances in these processes. An irradiance dependence of cell division rates has been reported in Antarctic benthic microalgae, showing a remarkable inhibition of cell division at high light levels (Rivkin and Putt 1987). It is interesting to note that UV-B irradiance had no additional effects on the growth of *K. antarctica*. In field studies on Arctic macroalgae, the UV-A component of natural sunlight has been pointed out as a main cause for the negative effects on growth (Aguilera *et al.* 1999). High PAR rather than UV-B has also been suggested to be preponderantly responsible for the photoinhibition of photosynthesis of temperate subtidal macroalgae (Dring *et al.* 2001). The present study simply indicates that PAR and UV influences equivalent to those found at 0-5 m depths would adversely affect subtidal *K. antarctica*.

On the other hand, the sustained growth response of *P. decipiens* to high irradiances may be related to the fact that this species is known to be physiologically fit for making high photon irradiance available in spring (Weyman *et al.* 1997).

Algal biomass may be a good indicator of radiation effects since it represents an integration of many inherent variables (Altamirano *et al.* 2000; Michler *et al.* 2002). In the present study, solar radiation at ambient levels had depressive effects on the growth of *K. antarctica,* while *P. decipiens* showed a significant accumulation of biomass, indicating again a differing sensitivity to high irradiances between the species inhabiting different ranges of depth. One possible mechanism that explains the reduction of biomass may be the reduced photosynthetic rate due to photoinhibition resulting from high irradiances although destruction of pigments or morphological alteration may also be another explanation. The inhibition of photosynthesis by excess light may be the result of multiple processes of damage and inactivation leading to inefficiency in solar energy conversion, lower carbon acquisition and reduced growth in plants (Osmond 1994). It is noticeable that *P. decipiens* grows well both in terms of thallus area and biomass over a relatively wide range of irradiance in contrast to the notion that red algae generally has a narrow range of optimum irradiances (Gantt 1990). State transitions might be a possible means of avoiding damaging photoinhibition, by diverting excess energy harvested by phycobilisomes to PS I before photooxidation takes place in PS II (Gantt 1990). Recently, two forms of phycobilisomes have been isolated from the Antarctic *P. decipiens* and have been proposed as playing an ecophysiological role in rapid acclimation due to changes in ambient light conditions (Lüder *et al.* 2001).

Irradiance-caused pigment destruction was found in *K. antarctica*, but there was no significant difference in Chl *a* contents in *P. decipiens* exposed to solar radiation effects. The photosynthetic pigments have been recognized as a possible target for high PAR and UV-B radiation (Bischof *et al.* 2002). Antarctic red algal species such as *Georgiella confluens* (Reinsch) Kylin and *Pantoneura plocamioides* Kylin dwelling in deep waters were found to be subject to complete bleaching when exposed for 5 days to ambient levels of solar radiation, while no significant reduction in Chl *a* contents was noted for two red algae varieties, *Iridaea cordata* (Turner) Bory de Saint-Vincent and *Porphyra endiviifolium* (A & ES Gepp) Chamberlain, growing mainly in shallow waters (Han *et al.* 2001). The Chl *a* response to solar UV-B radiation shown by *K. antarctica* is in agreement with previous reports regarding UV-B effects on various macroalgae, in which chlorophyll content was adversely affected by artificial or solar UV radiation (Franklin and Forster 1997; Häder and Figueroa 1997; Han *et al.* 1998) although UV-B radiation had no significant effect on Chl *a* content in some long-term cultivation studies (Grobe and Murphy 1998; Altamirano *et al.* 2000). The reason for the UV-induced decrease in Chl *a* content might be due either to a decline in pigment synthesis through physical disturbances in chloroplast thylakoids or an increase in pigment destruction upon absorption of high energy quanta (Han *et al.* 1998). It has been suggested that UV-B radiation may influence down-regulation of the expression of genes crucial for chlorophyll-binding proteins leading to chlorophyll degradation (Mackerness *et al.* 1996).

The decrease in Chl *a* content of *P. decipiens* plants relative to the initial may be due either to a dilution effect parallel with growth (Altamirano *et al.* 2000) or to a regulatory function to avoid photodamage caused by excess light energy (Lüder *et al.* 2002).

The Chl *a* content of *K. antarctica* plants grown at 0.05 I_0, which is significantly higher than that initially measured might imply an induction of chlorophyll production at this irradiance level. When light penetrates a water column, total irradiance diminishes and some wavelengths are filtered out more rapidly than others as a function of increasing depth (Jerlov 1966). As the irradiance level is similar to that recorded at the depth of growth in *K. antarctica*, the result might be due to a spectral component missing at

such depth but present in the culture system, inducing that of chlorophyll production. Lower Chl *a* concentration was also recognized in *P. decipiens* grown at 0.05 I_0. The pigment levels of *P. decipeins* are known to decline even under dim light and this behavior is considered a season-anticipating response (Aguilera *et al.* 2002).

Morphological characteristics of macroalgae have been reported to affect their physiological responses to light stress implying that algal species with thin thalli are generally more susceptible to high irradiance damage than those with thick thalli (Franklin and Forster 1997). Higher sensitivity to solar radiation of thicker *K. antarcitca* than *P. decipiens* may however suggest that a relationship between thallus morphology and high light sensitivity is not a universal application.

UV-absorbing pigments (UVAPs) are found in various species of macroalgae, and their physiocochemical characteristics have been identified in carotenoids, coumarins, phenolic compounds and mycosporine-like amino acids (MAAs) (Karsten *et al.* 1998a, b; Sinha *et al.* 1998). The UVAPs are generally known to act as a sunscreen that could prevent damaging UV radiation from reaching DNA, proteins and UV-sensitive molecules (Karentz 1994; Franklin and Forster 1997; Häder and Figueroa 1997; Han *et al.* 1998; Häder 2001). In this sense, higher concentrations of UVAPs in *P. decipiens* might be correlated with higher resistance to solar PAR and UV in comparison with *K. antarctica* containing lower concentrations of UVAPs. There was a significant reduction of UVAPs in *K. antarctica* grown under solar radiation. The synthesis of UVAPs is made at the expense of the build-up of a carbon skeleton, and the substantial energy required is supplied by photosynthesis (Hernando *et al.* 2002). The lowered concentrations of UVAPs in *K. antarctica* might therefore be ascribed to the inhibition of photosynthesis by high irradiances. Another explanation for the reduction in UVAPs of this species might be due to the release of substances from the cells resulting in a lowering of absorption. When cells are in shock, they do not grow actively and release MAAs as a consequence of cell lysis (Vernet and Whitehead 1996). No changes in the concentrations of UVAPs of *P. decipiens* exposed to high levels of solar irradiance as compared to initially measured levels may suggest that this species exhibited UVAPs at saturation levels. There may be physiological limitations to the accumulation of the osmotically active MAAs in the cells, since the maximal content is under the influence of osmotic regulation (Oren 1997). *P. decipiens* revealed a significant decrease in the amount of UVAPs when grown at 0.05 I_0. In the Antarctic diatom, *Thalassiosira* sp., transfer from high to low irradiance resulted in a decrease of MAA content (Helbling *et al.* 1996). It may be of great advantage to reduce the UVAP concentrations requiring substantial metabolic investment in situations when the existence of those substances is not essential for the fitness of the organism (Franklin and Forster 1997).

In both Antarctic red algae, resolution of one absorption peak into 3 or 4 bands in the 4th derivative curve indicates the presence of several different pigments. The presence of various UVAPs within a thallus could broaden the UV-filtering capacity, thus enhancing protection across a large range of wavelengths (Lesser 1996). *K. antarctica* had three MAAs, while *P. decipiens* contained four out of seven MAAs that had been identified in Antarctic macroalgae (Karentz *et al.* 1991). MAAs are water-soluble substances characterized by a cyclohexenone or cyclohexenimine chromophore ring conjugated with one of several different amino acids, and typically absorb in the wave range between 310 and 360 nm (Dunlap and Shick 1998). In macroalgae, the MAAs are known to occur predominantly in rhodophytes from polar to tropical regions and the occurrence of high MAA content in algae growing at high light exposed locations has been thought to act as a natural sunscreen (Karsten *et al.* 1998a, b). It is interesting to note that porphyra-334 and shinorine are oxidatively inert, representing a true sunscreen (Ehling-Schulz *et al.* 1997). The cumulative effect of the two MAAs may have increased protection in *P. decipiens* relative to *K. antarctica* containing only shinorine.

K. antarctica can be described as a subtidal species based on the evidence that it is at times found to occur in shallow water (Skottsberg 1923), but it usually persists at depths of >7 m (Chung *et al.* 1994). Significantly lower resistance of *K. antarctica* to direct sunlight compared to that of *P. decipiens* may be connected with the fact that the former species is often absent from the eulittoral. The active growth of *P. decipiens* over a wide range of solar irradiance levels, as found in the present study, seems to agree well with the wide vertical distribution ranging from the intertidal down to 25-30 m (Chung *et al.* 1994). Fast growth would also be of great advantage with regard to the rapid occupation of space in situations of competition for limited resources, and high rates of growth may maximize the reproductive output, thereby ensuring more likely success in later recruitments (Lambers *et al.* 1998). Many studies have so far shown that growth of seaweed species is enhanced in the absence of UV-B (Franklin and Forster 1997; Häder and Figueroa 1997; Han *et al.* 1998; Häder 2001). The present study, however, revealed that there

was no additional negative effect of the UV-B component of natural sunlight on growth of the two Antarctic algae except for the Chl *a* contents of the subtidal *K. Antarctica*, suggesting that UV-B sensitivity may be species-specific (Grobe and Murphy 1998; Dring *et al.* 2001; Michler *et al.* 2002).

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