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Influence of UV-B Radiation on Photosynthesis, Growth and Pigmentation of *Chondrus ocellatus* (Rhodophyta) from Shallow Water

Taejun Han,* Young-Seok Han, Man-Gee Cho[1],
Jin-Hee Park[1], Jae-Gun Goo[2] and Sung-Ho Kang[3]

Division of Biology and Chemistry, University of Incheon, Incheon 402-749, Korea
[1]Engineering Research Centre, Dongseo University, Busan 617-716, Korea
[2]College of Ocean Science and Technology, Kunsan University, Kunsan 573-701, Korea
[3]Polar Research Center, Korea Ocean Research and Development Institute, Ansan P. O. Box 29, 425-600, Korea

ABSTRACT - The UV-B sensitivity was tested for the intertidal species *Chondrus ocellatus* from Korea, by measuring photosynthesis estimated as effective quantum yield (Φ_{PSII}) of photosystem II (PS II), growth and content and composition of photosynthetic pigments and UV-absorbing pigments (UVAPs). The Φ_{PSII} of the alga decreased with increasing time of exposure to UV-B radiation, followed by fast and nearly full recovery indicating dynamic photoinhibiton. Fresh weight-based growth and pigment contents of *C. ocellatus* were not seriously affected by UV-B radiation. A single broad peak at 327 nm was obtained from methanol extracts of *C. ocellatus*, and the absorbance peak increased with increasing UV. The single peak was resolved into three peaks (311, 330 and 336 nm) by the fourth-derivative, and quantitative change in response to UV-B radiation occurred only at 330 nm. High performance liquid chromatography (HPLC) analysis of purified extracts indicated that three MAAs (mycosporine-like amino acids) are present, asterina 330, palythine and shinorine. Field observations during three growing months showed that *C. ocellatus* exhibit the highest amount of UVAPs in May followed by July and little trace in September, coinciding with the species' phenology. In an ecological context, dynamic photoinhibition as well as accumulation of UVAPs may enable the shallow water red alga *C. ocellatus* to be well adapted to high UV-B environments.

Key words : *Chondrus ocellatus*, growth, photosynthesis, pigments, UV-B

INTRODUCTION

Solar radiation includes biologically damaging ultraviolet (UV)-B radiation (λ = 280-315 nm). Stratospheric ozone attenuates much of this radiation reaching the earth's surface, but recent observations of reduction in the ozone shield due to man-made chlorofluorocarbons developed considerable interest in the ecological and physiological consequences of UV-B radiation in macroalgae (Franklin and Forster 1997; Häder 2001; Bischof *et al.* 2002). Ultraviolet-B quanta are readily absorbed by biomolecules such as nucleic acids (as DNA and RNA), proteins and lipids which play a key role in the structure and function of plant cells (Bischof 2000).

Previous research concerning UV-B effects on ma-

*Corresponding author: Taejun Han, Tel. +82 32 7708245
Fax. +82 32 7708248. E-mail. hanalgae@incheon.ac.kr

croalgae have shown that the radiation causes various phytotoxic effects such as growth inhibition, destruction of photosynthetic pigments and decline in 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). 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). In this hypothesis intertidal species that are potentially more exposed to high solar radiation should be more resistant to UV-B radiation.

There are adaptive mechanisms by which macroalgae can minimize UV-induced damage. Strategies to reduce the damaging impact of UV radiation in marine macroalgae include repair of UV-induced damage of DNA by photoreactivation and excision repair (Pakker *et al.* 2000), and synthesis of UV-absorbing or screening compounds, which are carotenoids, coumarins, phenolic compounds and mycosporine-like amino acids (MAAs) (Karsten *et al.* 1998a, b; Sinha *et al.* 1998). These latter are water soluble substances characterized by a cyclohexenone or cyclohexenimine chromophore ring conjugated with one of several different amino acids, 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 that could protect DNA, proteins and UV-sensitive molecules from damaging UV radiation (Karsten *et al.* 1998a, b). However, there is still no consensus on the exclusive role of MAAs as UV protectants (Franklin *et al.* 1999; Van de Poll *et al.* 2001; Yakovleva and Titlyanov 2001).

The present study was initiated to assess the influence of UV-B on photosynthesis, growth and pigmentation of the shallow water macroalga, *Chondrus ocellatus* (rhodophyte), occurring mainly from March to August on most coasts of Korea (Lee and Lee 1981). Additionally, the quantity and quality of UVAPs (UV-absorbing pigments) were measured to conjecture whether these substances could provide the alga with protection against UV radiation.

MATERIALS AND METHODS

1. Plant material and pre-treatment

Chondrus ocellatus Holmes was collected during May-Spetember 2000 at sites near Ahnin, Kangwondo, Korea (37.7° N, 129.1° E). Immediately after transport to the laboratory, the plants were maintained in plastic tanks with aerated artificial seawater medium (modified BG) (Han and Kain 1993) at 15°C under 5-10 μmol m^{-2} s^{-1} of continuous light (FL400, Kum-Ho, Korea).

2. Visible and UV-B radiation sources

The sources of visible illumination were white fluorescent tubes (FLR 40D/A, Osram, Germany). Three artificial UV-B lamps (TL20W/12, Philips, Netherlands) were used to produce UV radiation with an output peak at 312 nm. Radiation measurements were made using a LI-1000 quantum meter (Li-Cor, USA) for PAR and a Li-Cor LI-1800 underwater spectroradiometer with a cosine sensor for UV-B irradiance.

3. Experimental treatment and culture condition

Pieces of equal fresh weight (0.206 ± 0.002 g) were cut from healthy thalli and placed in unlidded Petri-dishes (100 × 10 mm) filled with medium 8 mm deep. For UV-B irradiation experiments the samples were irradiated with 1.0 W m^{-2} of UV-B for 1 and 5 h. The UV irradiance used in this study was similar to that measured on natural sites of the algal collection. Biological spectral weighting function (BSWF) was employed for comparing UV-B treatments with those used in other works. The weighted spectral irradiance defined as the product of the UV irradiance times the action spectrum of plant DNA damage normalised to 1 at 300 nm (Caldwell 1971) was calculated to produce the biologically effective irradiance for the UV-B lamps (Fig. 1).

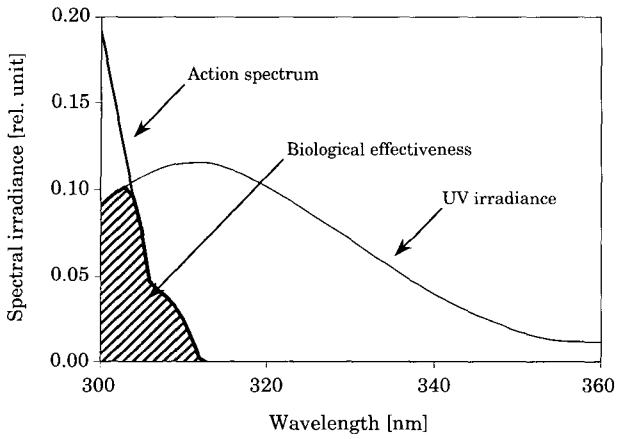

Fig. 1. UV-B lamp spectral irradiance and a biological action spectrum plotted as a function of wavelength. The area under the curve (shaded) is the biologically effective irradiance.

Table 1. Unweighted and weighted doses of UV-B radiation (kJ m^{-2}) used in the present study. The biological spectral weighting function is the generalized action spectrum for plant damage normalized at 300 nm (Caldwell 1971)

	Time of exposure [h]			
	1	2	3	5
Unweighted	1.8	3.6	5.4	9.0
$BED_{DNA\ damage}$	0.08	0.16	0.24	0.40

Time integration of the resulting irradiance gives biologically effective dose (BED) which is presented in Table 1.

Immediately after exposures to UV-B radiation, measurements of chlorophyll *a* fluorescence of PS II were done to detect changes in photosynthetic activity. The effective photosynthetic quantum yield of PS II (Φ_{PSII}) of the samples, defined as $(F_m'-F_t)/F_m'$, was measured using a pulse-amplitude-modulated fluorometer (Diving PAM, Walz, Germany), where F_m' is the maximum fluorescence of the light-adapted samples, and F_t is the current steady state fluorescence (Krause and Weis 1991; Schreiber *et al.* 1996).

The samples irradiated with UV-B for 1 h or 5 h were then transferred to Petri-dishes containing newly prepared medium and kept in 50 μmol m^{-2} s^{-1} PAR at 15°C and the Φ_{PSII} was recorded at regular intervals.

In another experiment thallus pieces of the alga were irradiated with UV-B for 1-3 h and subsequently placed at 50 μmol m^{-2} s^{-1} of PAR under a 12 : 12 h LD for 6 day-culture before the specific growth rate (SGR) in terms of fresh weight was determined. The fresh weight of samples was measured by weighing after removing surface water with dry tissue and SGR was calculated as follows:

$SGR\,(\%\ day^{-1}) = 100\ Ln\,(W_t - W_o)\ t^{-1}$

(ln: natural logarithm, W_t: final fresh weight, W_o: initial fresh weight, t: length of incubation in days).

4. Pigment extraction and quantification

For photosynthetic pigment and UVAP extraction, the weighed thalli were immersed in 99.9% methanol for at least 24 h in the dark at 5°C and the absorption spectra of thallus extracts were determined using a spectrophotometer (Specord S10, Zeiss, Germany). Photosynthetic pigments, chlorophyll *a* (Chl *a*) and carotenoids, were estimated following the equation given by Lichtenthaler and Wellburn (1983). Total amount of UVAP was expressed as a ratio of the absorbance maximum in the UV range (280-400 nm) with the chlorophyll absorbance maximum at 665 nm (Post and Larkum 1993). To clarify sample-specific absorption by suppressing a background overlaying a sample scan, the fourth-derivative spectra involving 13 point intervals were also generated with algorithms after Savitzky and Golay provided by the manufacturer (Zeiss, Germany) (Butler and Hopkins 1970). In order to find out the UV-absorbing substances likely to contribute to increase in the overall amount of UVAPs, comparisons of absorbance values at the three peaks resolved by fourth derivative were made on the samples treated differently.

5. High performance liquid chromatography (HPLC) analysis

Field-collected samples were dried with silica gel, pulverized and extracted in 20 vol. (w/v) 80% methanol at 45°C for 2 h. The methanol solution was then evaporated to dryness *in vacuo*. The dried extracts were redissolved in 10 vol. (w/v) distilled water and the supernatant was filtered through 0.45 μm membrane filters (Gelman, USA). UV-absorbing pigments were separated and identified by HPLC 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 1.0 ml/min. Separation was carried out at 40°C maintained by 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 prepared from *Porphyra yezoensis* Ueda collected in Korea.

6. Variations of the UVAPs in the field

C. ocellatus samples were collected in May, July and September 2000, and washed with filtered seawater in the laboratory. The UVAPs were extracted by homogenizing the thalli with 99.9% methanol in a mortar. The homogenates were filtered through a filter paper (0.45 µm pore size, Whatman, UK), and the filtrates were subjected to spectrophotometric scanning between 280 and 400 nm.

7. 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).

RESULTS

Ultraviolet-B radiation provoked different degrees of inhibition in the Φ_{PSII} depending on length of exposures (Fig. 2). The Φ_{PSII} declined with increasing length of exposure, reaching minimal values of 53% of control after receiving 0.4 kJ $m^{-2}{}_{BED}$. However, there was almost complete recovery of the Φ_{PSII} when placed in PAR after 0.08 kJ $m^{-2}{}_{BED}$ of UV-B exposure.

The growth of *C. ocellatus* was not significantly affected by the different UV-B exposures, exhibiting positive growth rates over all treatments ranging from 1.5-1.7% d^{-1} in UV-irradiated samples to 2.5% d^{-1} in control (Fig. 3).

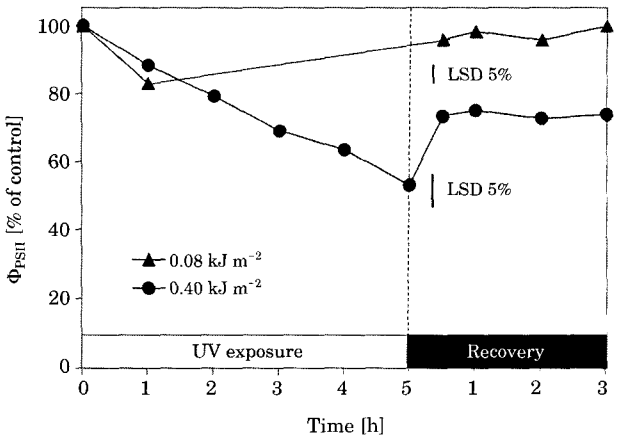

Fig. 2. Effective quantum yield of PS II (Φ_{PSII}) (% of control) in *C. ocellatus* during exposure to 0.08 and 0.40 kJ $m^{-2}{}_{BED}$ of UV-B radiation and subsequent recovery in PAR for 0.5, 1, 2, 3 h. Data are expressed as mean value (n = 5) and the bar represents the least significant difference (LSD) at p = 0.05.

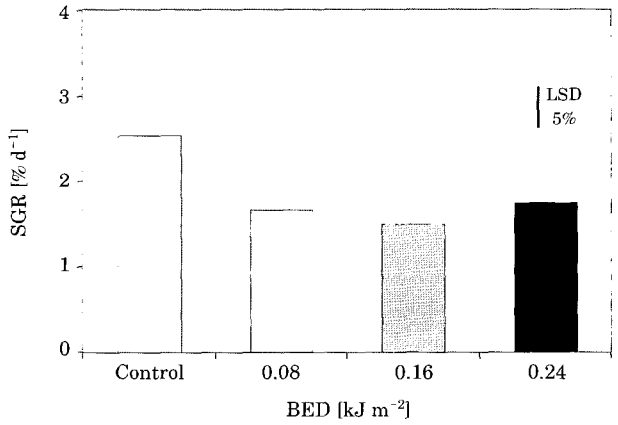

Fig. 3. Specific growth rates (% d^{-1}) of *C. ocellatus* exposed to 0.08. 0.16, 0.24 kJ $m^{-2}{}_{BED}$ of UV-B radiation, measured after 6 d in only PAR. Data are expressed as mean value (n = 5) and the bar on the right represents the least significant difference (LSD) at p = 0.05.

As shown in Table 2, no statistically significant differences in the photosynthetic pigment concentrations were found between control and UV-B irradiated plants of *C. ocellatus*.

Methanol extracts of *C. ocellatus* showed a single broad peak at 327 nm, but significant statistical differences were noted in the absorption spectra of extracts from control and UV-B treated samples; the absorption peak values increased when exposed to 0.16-0.24 kJ $m^{-2}{}_{BED}$

Table 2. Chlorophyll *a* and carotenoid concentration (mg g^{-1} FW) in samples of *C. ocellatus* after control and UV-B treatments. Data are expressed as mean ± 95% confidence intervals (n = 10)

UV-B_{BED} [kJ m^{-2}]	Chlorophyll *a*	Carotenoids
Control	356.3±43.1	23.5±3.7
0.08	309.9±63.1	18.9±6.5
0.16	256.7±107.5	13.6±7.9
0.24	243.0±51.7	11.1±9.1

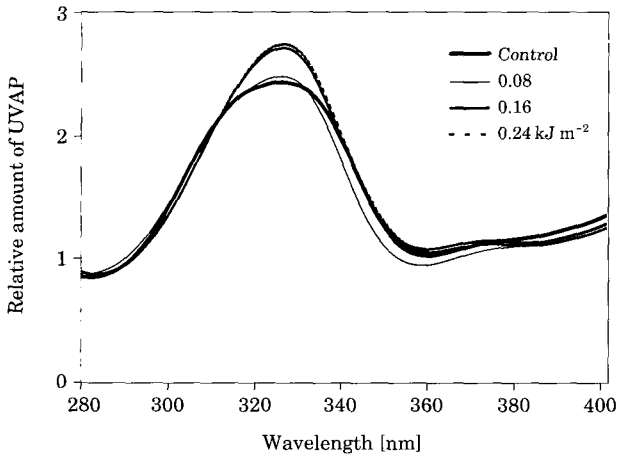

Fig. 4. UV absorption spectra normalized with the chlorophyll absorbance maxima of the methanol extracts from control and UV-irradiated samples of *C. ocellatus*.

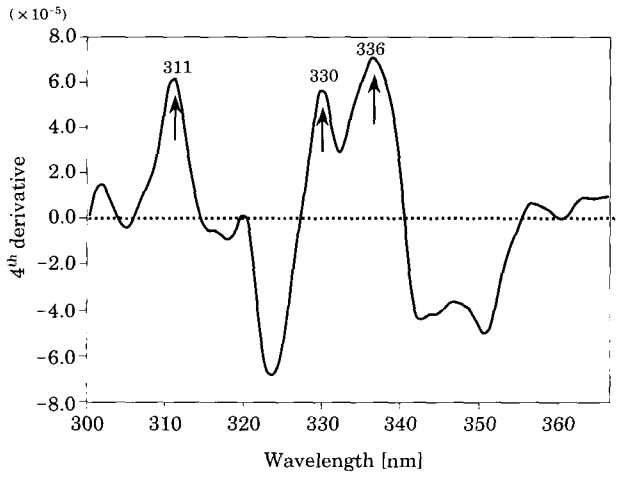

Fig. 5. Fourth-derivative spectra of the UV absorption spectrum of control samples of *C. ocellatus*.

UV-B (Fig. 4). The fourth derivative separated the single peak into three components resolved as absorbance maxima at 311, 330 and 336 nm indicating that

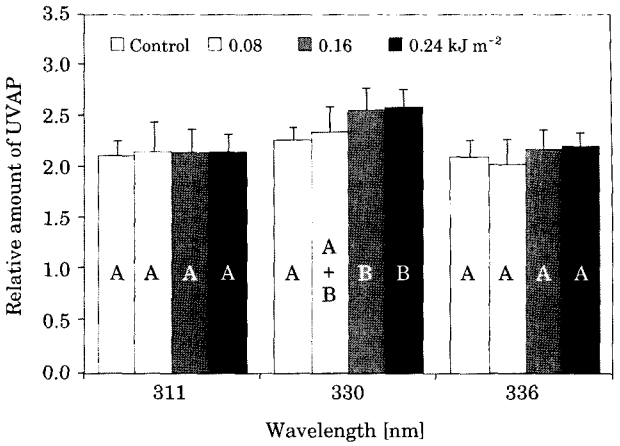

Fig. 6. Relative amount of different UV-absorbing pigments in *C. ocellatus* exposed to 0.08, 0.16, 0.24 kJ m^{-2}_{BED} of UV-B radiation, measured after 6 d in only PAR. Data are shown as mean for 10 replicates. Bars labeled with different letters are significantly different at p = 0.05.

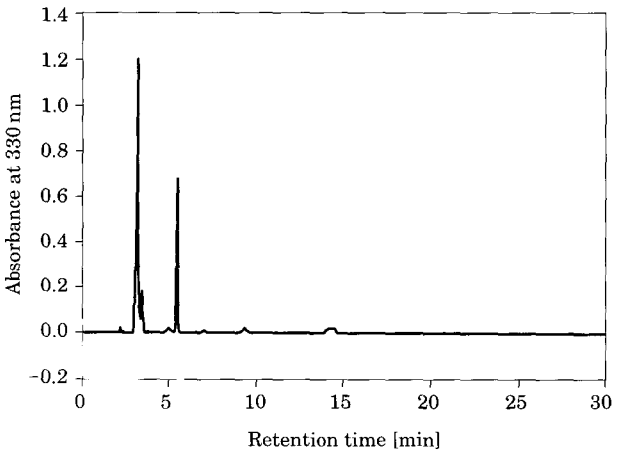

Fig. 7. High performance liquid chromatography separation of MAAs in *C. ocellatus* (first peak: palythine, second peak: asterina-330, third peak: shinorine).

there may be UVAPs of three different natures (Fig. 5). Only at 330 nm was change in the relative amount observed and increasing the length of exposure to UV-B resulted in increased UVAPs (Fig. 6). Further investigation into the UVAPs with a peak absorbance at 330 nm by HPLC analysis revealed that *C. ocellatus* contained three MAAs, namely, asterina 330, palythine and shinorine (Fig. 7).

When *C. ocellatus* thalli were collected in the field during the same spring to autumn period and the

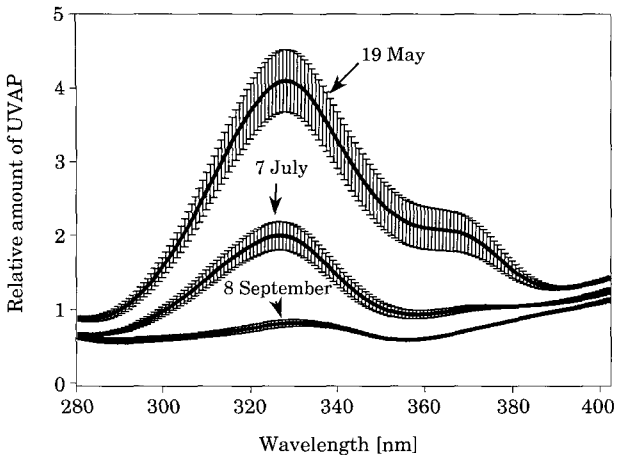

Fig. 8. Seasonal variations in the relative amount of UV-absorbing pigments of *C. ocellatus*. Data are expressed as mean ± 95% confidence intervals (n = 10).

amount of UVAPs was measured, it was highest in May, with a decline towards September (Fig. 8).

DISCUSSION

UV-B radiation has been reported to cause significant depression in photosynthesis of marine macroalgae (Franklin and Forster 1997; Häder and Figueroa 1997; Han *et al.* 1998; Häder 2001). In the present study, the UV-B treatments decreased the Φ_{PSII} of the red alga *C. ocellatus*. There is no consensus about the factors that are involved in the decrease of photosynthetic capability in phototrophs exposed to UV-B radiation, but many reports of changes in chlorophyll fluorescence kinetics in macroalgae have indicated that PS II may be one of the main targets of UV-B radiation (Franklin and Forster 1997; Häder and Figueroa 1997; Han *et al.* 1998; Häder 2001).

When the course of recovery was followed after UV-B irradiation the Φ_{PSII} in *C. ocellatus* exposed to UV-B radiation of 0.08 and 0.40 kJ m^{-2}_{BED} respectively recovered up to 96% and 73% of control within 30 min. Photoinhibition is classified into two types: dynamic photoinhibition which is a protective mechanism resulting from active down regulation of photosynthesis and chronic photoinhibition characterized by photodamage of PS II reaction centers (Osmond 1994). In this sense, *C. ocellatus* appears to show dynamic photoinhibition when exposed to UV-B.

Growth may be a good indicator of UV radiation effects since it represents an integration of many inherent variables (Altamirano *et al.* 2000). The present study seems to indicate that there is no serious UV-induced damage on physiological processes in *C. ocellatus*, and that the growth response might be closely related to the reduction and fast recovery of photosynthesis after UV exposures. In red algae, however, the effects of UV radiation on fresh weight do not seem to be congruent between studies and therefore could reflect species differences. For instance, fresh weight of *Gracilaria conferta* increased in UV-screened conditions relative to full solar radiation which indicates the inhibitive effect of UV-B on their growth (Friedlander and Ben Amotz 1991). On the other hand, fresh weight did not differ in the red alga, *Eucheuma striatum*, between thalli irradiated with and without UV (Wood 1989).

The photosynthetic pigments have been recognized to be one of the possible targets for UV-B radiation (Franklin and Forster 1997; Karsten *et al.* 1999). The reason for the UV-induced decrease in the pigment contents 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). The UV response found in the red alga is in agreement with the previous reports regarding UV-B effects on shallow water dwelling macroalgae in which chlorophyll contents remained unaffected by ambient levels of UV radiation (Grobe and Murphy 1998; Altamirano *et al.* 2000; Han *et al.* 2001).

The MAAs are generally known to act as a sunscreen, but direct experimental test for the functional role of UV-absorbing substances has scarcely been made. Recently, limited protection by UVAPs against UV-B damage has been reported in some red algal species (Karsten *et al.* 1998b; Franklin *et al.* 1999; Yakovleva and Titlyanov 2001). The presence of various MAAs with different absorption maxima within a *C. ocellatus* thallus could broaden the UV-filtering capacity, thus enhancing protection across a large range of wavelengths (Lesser 1996). This may in turn suggest a correlation between MAAs presence and UV-B resistance.

There was significant increment in the amount of UVAP with the absorbance maximum at 330 nm while the others remained unchanged. The red alga *C. crispus* produced MAAs in response to natural solar radiation and the MAA induction response was individual MAA-specific with shinorine showing the greatest change in its concentrations after UV-B exposures (Karsten *et al.* 1998b) In the Arctic red alga *Devaleraea ramentacea* the concentrations of mycosporine-glycine and palythine were strongly induced by UV-B (Karsten *et al.* 1999). In this respect, it is interesting to note that UV-B irradiated *C. ocellatus* changed the amount of UVAP with the maximum absorbance at 330 nm and that HPLC analysis of the UVAPs identified the existence of palythine and shinorine apart from asterina 330, implying a general UV protective role of MAAs confined to palythine or shinorine or both.

The seasonal fluctuation of UVAPs appears to coincide with phenological behaviours of *C. ocellatus* growing on Korean coasts which shows its first appearance in late March but disappears by late August (Lee and Lee 1981). This implies that UV protection provided by UVAPs may be an influential factor for the survival of this species in the field. Considering the UVAP accumulating capacity of the plants in response to UV-B, however, the seasonal variations in the amount of UVAPs do not seem to be commensurate with UV environment since more UVAPs should exist in the samples collected in July than in May, because it is nearer to the summer solstice. Antarctic red alga *Palmaria decipiens* showed higher content and greater variety of UVAPs in summer than in winter (Post and Larkum 1993). The physiological limitations to the accumulation of osmotically active molecules such as MAAs may be responsible for the drastic summer decrease of UVAPs in *C. ocellatus* (Oren 1997) since this species has been found to be susceptible to changes in salinity, indicating an inefficacy of osmoregulatory function (Park and Han 1998). This lowered content of UVAPs, in turn, may provide less protection against UV radiation with a result of diminishing the species from the littoral zone.

In an ecological context, *C. ocellatus* appears to be well adapted to high UV-B conditions by showing dynamic photoinhibition and accumulating MAAs, which may explain the typical occurrence of this species in the shallow waters from late spring to early autumn when they are likely to experience excessive UV-B irradiances.

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