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UV Photobiology of Marine Macroalgae

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Introduction

It is widely anticipated that increasing ultraviolet radiation (UVR) reaching the Earth's surface will continue in the forthcoming years as a result of significant depletion in the ozone column. Ozone accounts for only about 0.0001% of all gases in the Earth's atmosphere and the greatest concentrations exist in the stratosphere (a layer between 10 and 50 km above sea level). There is very little ozone in the atmosphere so that the layer of pure ozone would be less than half a centimeter thick if the whole amount were concentrated in a layer and compressed to one atmosphere pressure (Häder and Worrest 1991). Stratospheric ozone concentrations have been decreasing globally due to ozone destroying chemicals with life times of 10-120 years such as chlorofluorocarbons (CFCs), halons, methylchloroform, carbon tetrachloride. These chemicals catalytically break down hundreds of thousands of ozone molecules until they are removed from the atmosphere.

Ozone is known as an effective absorber of solar UV radiation, and reduction in the amount of ozone molecules may incur concomitant increase in UVR penetrating to the Earth's surface. The electromagnetic spectrum of solar energy reaching the Earth's surface contains a small portion of UVR which consists of wavelengths between 200 and 400 nm. The UV spectrum is conventionally divided into UV-A (320-400 nm), UV-B (280-320 nm), and UV-C (200-280 nm) (Caldwell 1981). Ozone depletions cause relatively large increases in the solar radiation of UVB range. While UVAR remains unaffected by changes in ozone concentrations since it is not absorbed by ozone molecules UVCR attenuation by ozone is so great that negligible UV in the wavelength of less than 290 nm reaches the ground levels. UVB quanta are highly energetic and effectively absorbed by and damaging important biological molecules such as DNA, proteins and lipids. UVBR directly alters the structure of DNA as well as harming nucleic acids indirectly (Mitchell and Karentz 1993). Proteins absorb UVBR due to their tryptophane, tryosine and phenylanine contents (Yu and Björn 1997). UVB irradiance produces large reductions in total lipid contents, thus affecting membrane systems (Kramer *et al.* 1991).

In the sea, UVBR decreases exponentially with increasing depth although the rate of reduction in UV irradiance depends upon the productivity of a given region (Kirk 1994). It has been observed in coastal waters that UVBR penetrates the upper few meters of the euphotic zone before being reduced to 1% of the surface irradiance (Jerlov 1976) whereas in clear oceanic water the same rate of reduction occurs at about 30 m. In line with the fact that the water column no longer serves as a UV shield for marine organisms in shallow waters extensive documentation of UV impact has been made primarily with microalgae in respect of population growth rates, carbon assimilation and nitrogen metabolism (Häberlain and Häder 1992; Behrenfeld *et al.* 1993; Davidson *et al.* 1994; Lesser *et al.* 1994; Worrest and Häder 1997). While motile caliber may confer many

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of microalgae protection by avoidance against harmful UVR benethic macroalgae fixed in position would have no choice but to be exposed to UVR reaching their habitats, thus being vulnerable to UV-induced damage. To date few macroalgae have been studied with reference to their responses to UVBR. The aim of this article is to examine photobiological effects of UVBR on various aspects of marine macroalgal physiology and then outline some of protection and recovery strategies that have been reported to be displayed possibly as an adaptation for survival to harsh UV environments.

Physiological Effects of UVBR

Most research to date on the effects of UVR on marine macroalgae dealt with measurements of photosynthesis, photosynthetic pigments, growth and survival. Physiological responses to UVBR to be described here are concerned mainly with the negative effects on those parameters. It should however be borne in mind that the UV chromophores, targets and mechanisms of UV damage are yet largely unknown.

Effects on photosynthetic activity

In general, UVBR has been reported to cause significant depressions in photosynthesis of marine macroalgae. The rates of photosynthesis measured by oxygen evolution were reduced after exposure to a given duration of artificial or solar UVB irradiation (Larkum and Wood 1993; Clendennen *et al.* 1996; Figueroa *et al.* 1997; Hanelt *et al.* 1997). One of the sensitive sites for damage by UVBR has been recognized to be the reaction centre of photosystem II (PS II) which consists of a chlorophyll-binding complex composed of two polypeptides (D1 and D2). The D1 and D2 polypeptide of the PS II reaction centre are degraded at an exceeding rate in response to UV (Greenberg *et al.* 1989; Jansen *et al.* 1996). Both photolysis of the PS II reaction centre subunits and modification of the primary quinone acceptor, QA, occur as a result of UV-induced damage (Bornman *et al.* 1984; Greenberg *et al.* 1989). Solar UVR impairs photosynthesis of the giant kelp, *Macrocystis pyrifera* (Clendennen *et al.* 1996). In this alga, energy transfer efficiency from the major light harvesting complex (LHC) to PS II has been observed to decrease perhaps due to UV-mediated functional disconnection of the fucoxanthin-chlorophyll protein complex (FCPC). Larkum & Wood (1993) described much higher sensitivity to artificial UVR in sublittoral red alga than in intertidal counterparts. For instance, the sublittoral red alga, *Kallymenia cribrosa*, showed 55% reduction in photosynthetically active radiation (PAR; 400-700 nm) + UVBR whereas littoral red, *Porphyra* sp., seemed almost insensitive to the same irradiation (Clendennen *et al.* 1996; Larkum and Wood 1993). Dark respiration rates appeared to be hardly affected by UV irradiation (Clendennen *et al.* 1996). This insensitivity may be in part explained by structural resistance of mitochondria to UV as has been observed in higher plants (Brandle *et al.* 1977).

Chlorophyll fluorescence can function as a sensitive probe for photosynthetic processes such as light absorption, energy transfer and photochemical reactions in PS II (Krause and Weis 1991). Reductions in variable fluorescence yield has therefore been adopted as an indicator of UV stress in marine plants (Dring *et al.* 1996; Figueroa *et al.* 1997; Larkum and Wood 1993). PAR+UVB irradiation caused a significant decrease in the F_v:F_m ratio of several macroalgal species with the greatest effects seen in sublittoral algae (Larkum and Wood 1993). It is not clear whether the decline in the F_v:F_m ratio was due to an increase in F_o or a decrease in F_m as F_o had been normalized to a fixed value in no regard of some changes noticed. While increase in F_o is characteristics of destruction of the PS II reaction centres a decrease in F_m may indicate an increase in non-photochemical quenching (Krause and Weis 1991). Larkum & Wood (1993) have concluded that both the reaction centre of PS II and elements of the photosynthetic electron transport chain close to PS II may be the primary sites of UV-induced photoinhibition. The variable fluorescence of different stages of three species of the Laminariales was reduced by artificial UV irradiation with recovery of different

degrees depending on both stages and UV durations (Dring *et al.* 1996). Hanelt *et al.* (1997) have defined photoinhibition as a protective process of photosynthesis, and differentiated it into dynamic and chronic photoinhibition. Dynamic photoinhibition is a process through which excessive absorbed energy can be converted harmlessly into thermal radiation whereas chronic photoinhibition results in an exceeding rate of degradation of the D1 protein and loss of photosynthetic activity. Relatively fast recovery of the variable fluorescence found in UV-exposed laminarian species may indicate that the decrease in the photosynthetic parameter is likely to be related to dynamic photoinhibition rather than photodamage.

Effects on photosynthetic pigments

Field studies on tropical macrophytes revealed that photopigments are adversely affected by solar UVR (Wood 1987, 1989). Destruction of chlorophyll has been recognized as another indicator of UV damage as well documented for higher plants (Caldwell 1983). The total chlorophyll content of the green alga, *Ulva pertusa*, declined with increasing durations of UVBR with the result that plants lost more than 50% of the total chlorophyll in 3 days after exposure to only 2 h UV at the irradiance (2.0 W m^{-2}) that simulated ambient levels (Han 1996). Reduction in chlorophyll concentrations after UV exposure may reflect either disturbances in chlorophyll biosynthesis pathways or the increased degradation of these pigments or their precursors due to absorption of high energy quanta. It has recently been suggested in higher plants that UVBR influences down-regulation of the expression of genes crucial for chlorophyll-binding proteins, thus causing chlorophyll degradations (Mackerness *et al.* 1996). Elevated UVB is also known to be involved in photooxidation of newly synthesized pigments. It is interesting to note that the degree of chlorophyll destruction in *Ulva pertusa* appears to be a function of UV dose at a specific UV irradiance. If the reciprocity is satisfied for this intertidal alga in a natural setting where radiation conditions are expected to vary, chlorophyll would be destroyed in response to the cumulative UV-dose regardless of fluctuations in UV irradiance (Han 1996).

In contrast to lowered photosynthetic performance under UV the photosynthetic pigments of UV-irradiated tissue of *Macrocystis pyrifera* were not significantly different from those of control tissue, suggesting that UV-incurred decrease in photosynthetic activity may not be paralleled by photodestruction of pigments (Clendennen *et al.* 1996). Meanwhile, depression of photosynthesis in the red alga, *Porphyra leucosticta*, exposed to solar UVR was consistent with reduced amount of pigment (Figueroa *et al.* 1997).

Effects on growth and survival

Reductions in growth and survival rate can be manifestations of UV stress. In those studies to be described following, growth was measured by length, surface area, or fresh weight of a whole or portion of plant with the survival rate by visual inspection of pigment loss. It is noteworthy that many of the studies have focused on the establishment stage of algae, highlighting that those early stages are of paramount importance affecting the performance of adult population in a given area.

Growth rates on fresh weight basis do not seem to be congruent between experiments conducted by different researchers. No significant differences in fresh weight-based growth rate were detected for the red alga, *Eucheuma striatum*, and the green alga, *Ulva pertusa*, between thalli treated with and without UV (Wood 1989; Han 1996) while fresh weight of *Gracilaria conferta* and *Ulva expansa* increased in UV-screened conditions relative to full solar radiation ones (Friedlander and Ben-Amotz 1991; Grobe and Murphy 1994). Grobe & Murphy (1994) maintained that smaller segments of thalli under UVBR was due to inhibition of cell division rather than cell enlargement. It is known that UVBR causes delay in progression through the cell cycle with G1 and G2 phases being arrested (Van't Hoff 1974). There are large species-specific differences in the sensitivity to UV, and a variety of spectrum of responses even within a species in coping with UV. Exposure to PAR+UV irradiation caused a significant growth

retardation in sublittoral but not in eulittoral algae (Kain 1987; Kain and Norton 1990; Leukart and Lüning 1994). When early germlings of intertidal alga, *Ulva lactuca*, were obtained in laboratory culture from fertile thalli growing at Helgoland and were then exposed to ambient and elevated levels of UVBR for several weeks in outdoor tanks in September, there was no inhibition of growth in terms of length and fresh weight compared with controls (Kuhlenkamp and Lüning 1998). The UV irradiances employed albeit not mentioned would have been less than 1.7-2.2 W m^{-2} which is known to be the typical values in midday summer sunlight in Helgoland (Dring *et al.* 1996). Recently, Lee & Han (1998) reported that exposure to UVBR at 4.0 W m^{-2} for 1-2 h resulted in substantial reductions in the surface area and number of cells of 8 day-old *Ulva pertusa* germlings. It is not feasible to directly compare the results of two different studies for so many practical difficulties, but it looks likely that a change in the ability to withstand UV could occur in *Ulva* between the age of 8 days and several weeks. The shift in UV sensitivity has been partially confirmed by direct comparison of UV responses in 8 day-old germlings with those in adult thalli of *Ulva pertusa* (Lee and Han 1998). The surface area and number of cells in germlings were reduced by 65-75% after exposure to artificial UVB at 4.0 W m^{-2} for 2 h whereas of the two parameters only the number of cells in adult thalli decreased to 65% of controls by UVBR of the same irradiance for 2.5 h. Dring *et al.* (1996) found that gametophytes and young sporophyte of three laminarian species differed in their UV sensitivities with being greater in gametophyte than in sporophyte stage. A switch in the sensitivity to strong light has already been observed between gametophytes and 1-2 celled sporophytes of *Laminaria japonica* (Fei *et al.* 1989) although the underlying mechanisms are still unclear.

There are another evidence of discrepancy in the sensitivity to sunlight between gametophytes and early sporophytes of laminarian species or between species. Under December sunlight at Helgoland (340-400 μmol m^{-2} s^{-1}), over 90% of the gametophytes of *Laminaria hyperborea* and *L. digitata* were killed after 30 min exposure (Lüning 1980), but some early sporophytes (10 day-old) of both species showed more than 90% survival percentage when exposed to 512 μmol m^{-2} s^{-1} for the same duration at Port Erin, Isle of Man (Han 1992). Laminarian gametophytes of Californian species growing in the deeper sublittoral were killed after having received about half the quantum dose of solar radiation that caused the corresponding value of mortality in the species from the upper sublittoral (Lüning and Neushul 1978). Additionally, 60 min exposure to October sunlight at Port Erin, Isle of Man was lethal to *Laminaria hyperborea* (3% survival percentage) whereas *L. digitata* survived about 50% in the same treatment, confirming its higher resistance to high solar radiation than the former species (Han and Kain 1996).

Effects on cell and chloroplast movement

Many marine algae exhibit cellular movement phenomena ranging from ephemeral motility of reproductive cells to chloroplast movements. Cellular movement systems are mainly used to orient algae and their photosynthetic organelles in optimal light conditions for the algal growth and reproduction (Melkonian 1992).

The movement of macroalgal unicells has been recognized to show phototactic and/or chemotactic responses (Jones and Babb 1968; Amsler and Neushul 1989). Maintenance of the swimming behaviours of reproductive cells could be an influential determinant of dispersal and reproductive strategies of macroalgae (Amsler and Neushul 1991). To date we have not seen any study done on UVBR effects on macroalgal cell motility although it has been well documented that microalgae are impaired in their movement and orientation responses by UVBR (see reviews by Häder and Worrest 1991; Worrest and Häder 1997). Park & Han (1998) have recently observed in the green alga, *Ulva pertusa*, that motility of the biflagellate cells is significantly depressed by short durations of UVBR (at 2.4 W m^{-2}) with severe disintegration of the cells exposed to UVB for longer than 30 min.

Chloroplast arrangements have been documented to represent two contrasting patterns in relation to

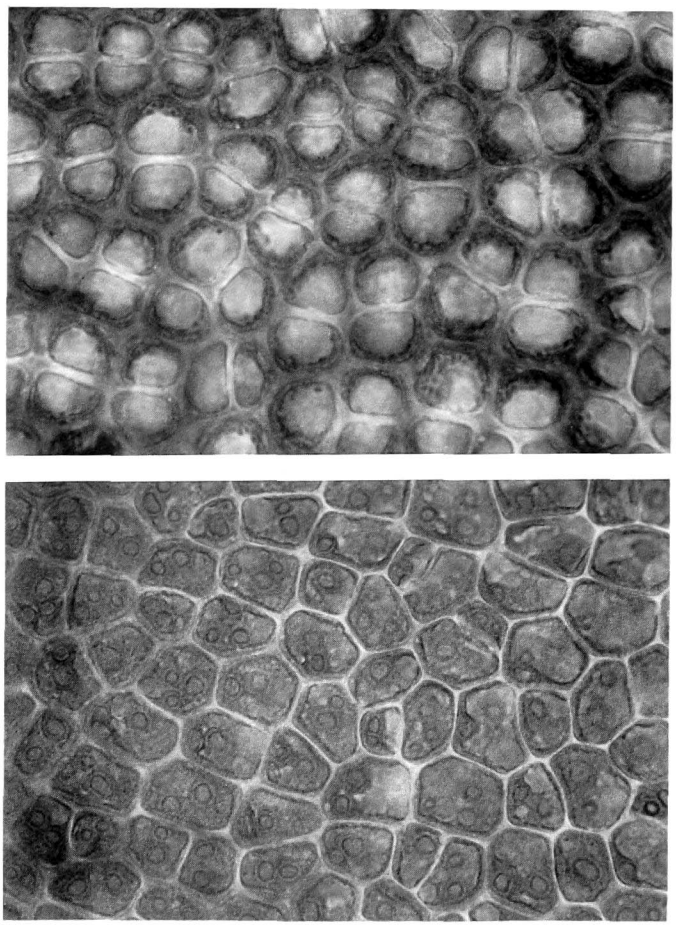

Fig. 1. *Ulva pertusa*. Photomicrograph of chloroplasts taken at different times of the same day (magnification x 400). Above, chloroplasts in profile position at 0600 h; below, chloroplasts in face position at 1200 h (T. Han and J.-A. Kong, unpublished data).

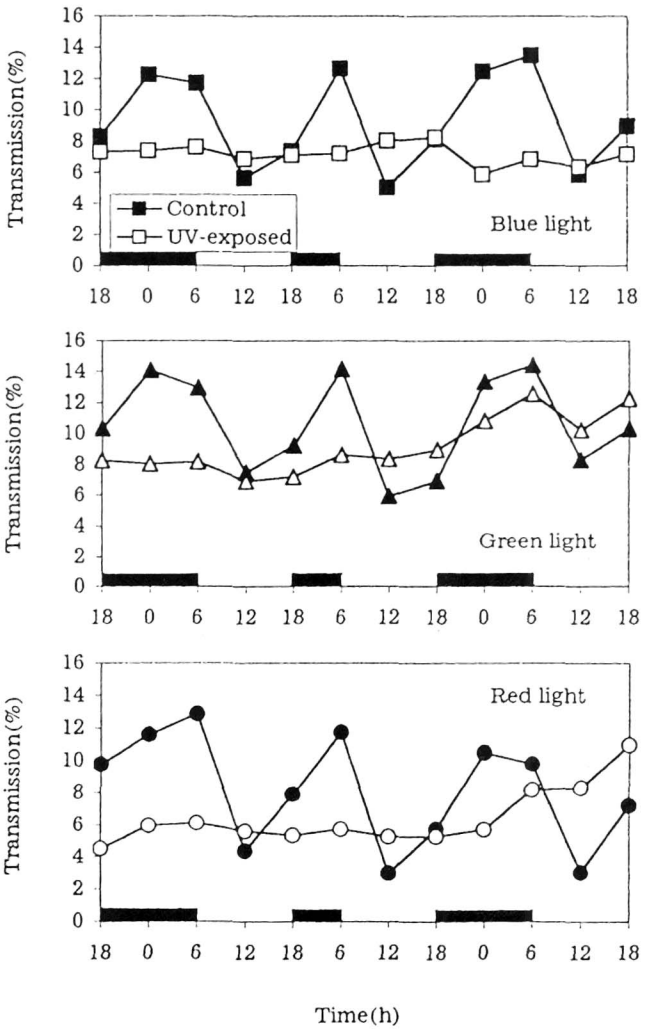

Fig. 2. *Ulva pertusa*. Transmittance changes measured at every 6 h during 72 h. The algal discs were incubated under different light qualities of 10 μmol m^{-2} s^{-1} after exposure to UVBR at 2.0 W m^{-2} for 2 h (T. Han and J.-A. Kong, unpublished data).

basic requirements to optimize light harvesting for photosynthesis; face and profile arrangements (Fig. 1). The face position ensures the greatest energy rewards because cells can have the greatest proportion of the chloroplasts in contact with light striking upon them. The profile position with chloroplast orientation parallel to the light direction may protect the chloroplasts against excessive irradiation. Recently, Kong & Han (1998) found in the green alga, *Ulva pertusa*, that UVB-irradiated cells lost rhythmicity of changes in chloroplast area due to different arrangements in the upper cell surface while chloroplast area of control cells displayed rhythmic changes with the maxima in the middle of light period and the minima in the mid-dark period (Fig. 2). Previous studies pointed to a mechanism of cell motility involving microtubules (MTs) and perhaps actin filaments. Interactions between MTs and actin may play an important role in the maintenance of cytoskeletal organization and chloroplast movements (Melkonian 1992). It is not surprising to note that UVBR alters microtubule organization, considering the fact that tubulin absorbs maximally at 280 nm due to its high content of amino acids with aromatic side chains (Zamansky *et al.* 1991). Damage of microtubules would cause many ramifications on cell motility. On the other hand, movements in plants are generally known to be run by a single reaction chains, starting with perception of a stimulus, continuing with single transduction and resulting in the observed response. Photoreceptor pigments must be involved in the first step of reaction

chains, and driving force for transduction processes appears to be a change in ion transport across the cell membrane due either to activation or inactivation of ion pumps or to alterations in membrane permeability. It has been observed that UVBR affects cellular movements by damaging some components of the photoreceptor organelles and membrane channels (Sgarbossa *et al.* 1995; Hada *et al.* 1993).

Adaptive mechanisms

There are adaptive mechanisms reported by which macroalgae can minimize UV-induced damage. Those include UV avoidance by movement of cell or cell oganelles, epidermal attenuation of UV transmittance, synthesis of UV-screening pigments, UV-damage repair by photoenzymatic activity.

It has already been pointed out that chloroplasts occupy the face position at low photon fluence rates (high absorptional area) and moves to the profile position at high photon fluence rates (low absorptional area). Such chloroplast movements have therefore been considered as an adaptive mechanism of ensuring maximum light absorption by the chloroplasts or protection of photosynthetic pigments againt photodestruction. In the brown alga, *Dictyota dichotoma*, chloroplast movements from the face to profile position have been suggested to be a light protective mechanism, in synchrony with the gradual increase of the photon fluence rates by decreased sea level during low tide (Hanelt and Nultsch 1990). However, a recent study on the green alga, *Ulva pertusa*, showed that there was no significant differences in the UV sensitivity in terms of the total chlorophyll content between the plants of different chloroplast arrangements (Fig. 3), which was inconsistent with what could be expected if chloroplasts movemens provided UV protection.

Morphological characteristics of macroalgae have been reported to affect their physiological responses to physical stress agents such as high irradiance, desiccation, wave action (Davison and Pearson 1996). In higher plants, attenuation of UV reaching the mesophyll by epidermis has been one of the important factors to determine the plant's sensitivity to UVR (Day *et al.* 1992). In general, algal species

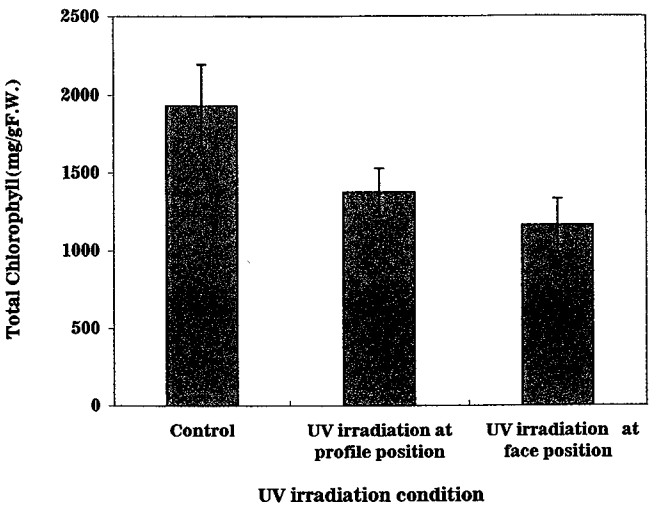

Fig. 3. *Ulva pertusa*. Comparisons of UV sensitivity in terms of the total chlorophyll contents between the algal discs with different chloroplast positions. UV irradiation was given either at 0600 h or at 1200 h (T. Han and J.-A. Kong, unpublished data).

with thin thalli are shown to be more susceptible to UV damage than those with thick thalli (Halldal 1964). Direct comparisons to see if macrophytes of different morphology exhibit different tolerances to UV have scarcely been made. When the two species, *Kjellmaniella crassifolia* and *Pachymeniopsis* sp., possessing thick thalli of several cell layers and another species, *Ulva pertusa*, with thin thalli of only two cell layers were tested for their sensitivity to artificial UVBR, fresh weight was reduced by 68.2% in the brown, *Kjellmaniella crassifolia*, by 21.4% in the green, Ulva pertusa, whereas it was enhanced by 11.1% in the red alga, *Pachymeniopsis* sp. (Fig. 4). Chlorophyll *a* content declined up to 95.3% of controls in the brown alga, to 58.0% in the green alga, and to 80.6% in the red alga after 1h exposure to 2.0 W m^{-2} of UVBR. These results may suggest that thallus morphology does not appear to influence the physiological responses to UV at least in the three species.

The UV absorbing substances are found in various species of marine algae (Sivalingam *et al.* 1974). Their physiochemical characteristics have been identified to be mycosporine-like amino acids (MAAs), which are water-soluble and strongly absorbing in the range 310 to 360 nm. The UV absorbing pigments are generally known to act as a natural sunscreen that could protect DNA, proteins and UV-

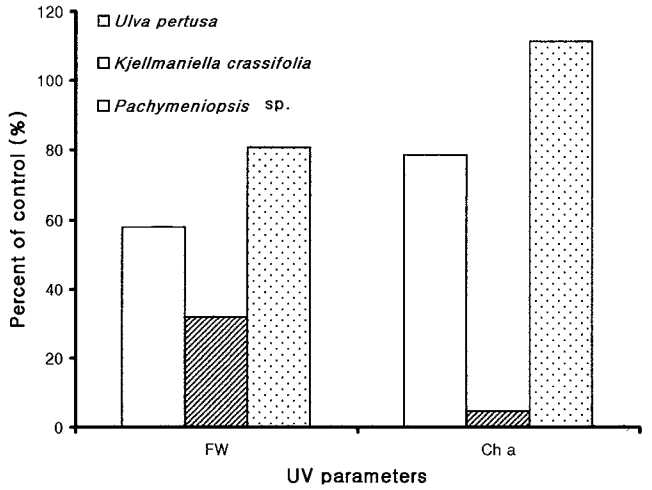

Fig. 4. Effects of UVBR on three species of Korean macrophytes with different morphology. UV irradiance was 2.0 W m^{-2} (T. Han, unpublished data).

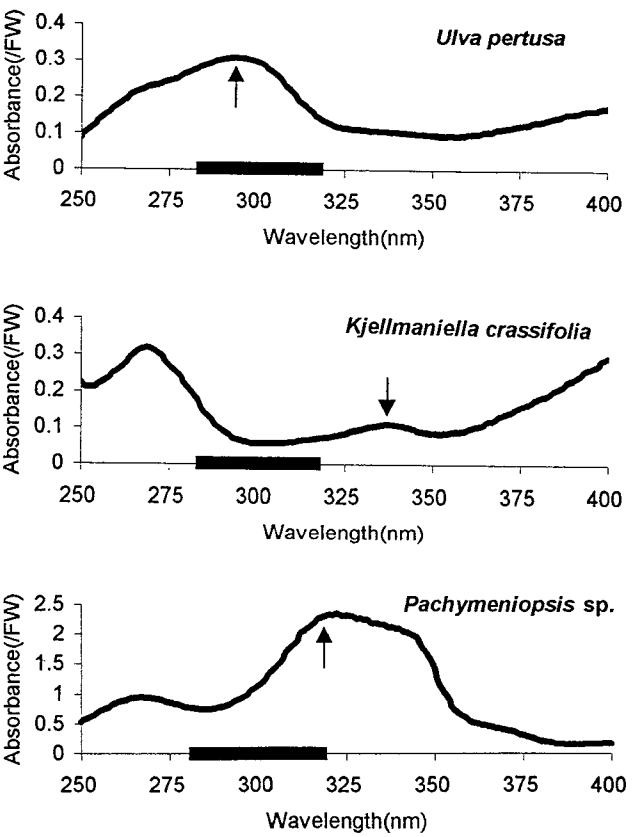

Fig. 5. Amounts of UV-absorbing substances estimated from spectrophotometric scan of methanol extracts (80%) in three species of Korean macrophytes (T. Han, unpublished data).

sensitive molecules from damaging UVR. The presence of UVBR absorbing substances in *Ulva pertusa* seemed to provide a meaningful protection against UVB damage to photosynthetic pigments while *Kjellmaniella crassifolia* was severely damaged by the same dose of UV although it has UV-absorbing substances with the absorption peak at 340 nm (Fig. 5). In the red alga, *Chondrus crispus*, the accumulation of MAAs with their absorption peak in the UVA range did not ensure higher growth or amelioration of chloroplast-encoded protein synthesis compared with the same plants lack of the compounds under UVB irradiation condition (Franklin *et al.* 1998). These results suggest that the protective function may be most obvious when the absorption band of the UV-absorbing substances corresponds with the waveband of incoming UVR.

In addition to rather passive ways of UV protection described above, macroalgae are known to recover from UV damage through photorepair. The major damage by UVR probably occurs due to molecular modifications, mostly of DNA. Photoproducts such as cyclobutane pyrimidine dimers (CPDs) have been found in some UV-irradiated higher plants and microalgae (Karentz *et al.* 1991; Cadet *et al.* 1992). When CPDs are formed from dimerization of adjacent pyrimidines on the same strand of DNA there will be changes in DNA replication, transcription and gene expression, which may then be followed by deleterious symptoms in physiological responses. Reversal of the injurious effects of UV radiations by subsequent illumination of longer wavelengths has been extensively observed in various taxonomic groups (Jagger 1958), and this photoreactivation is recognized as photolyase-catalyzed reversal of CPDs (Mitchell and Karentz 1993). To our knowledge, CPD repair has never been measured in macroalgae although comparable phenomena were observed in three species of the Laminariales by Han & Kain (1992, 1993) in which survival of young sporophytes exposed to UVCR was enhanced by blue light.

Conclusion

Studies of UVBR effects on macroalgae are still scanty, and further exploration is required.

Damaging effects of UVBR could cause a chain reaction, bringing about alterations in aquatic ecosystems where macroalgae play an integral role. For example, differential sensitivity among macroalgae to UVBR may lead to shifts in the floristic composition in the macroalgal community, thus changing the total primary productivity. This may then result in changes in the energy transfer between trophic levels. Little studies of UVBR have so far been performed at the ecosystem level.

There are biological and physico-chemical features of environments that may modify algal sensitivity to UVBR. The extent of exploitation of repair processes and protective mechanisms can alter potential biological effects of UVR on each species. UVBR may also act in concert with any of physico-chemical agents such as nutrients, salinity, desiccation and PAR to affect either synergistically or antagonistically physiological responses in macrophytes.

These aspects certainly await clarification by more experimental work both in laboratory and in the field before a satisfactory prediction of possible damage due to increasing UVR can be offered.

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