2018-11-16

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CRC press

CHAPTER 11

UV-B Radiation and the Green Tide-forming Macroalga *Ulva*

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Introduction

For plants, sunlight not only provides a source of energy to drive primary production, but also information to guide photo-morphogenesis and reproduction (Kendrick and Kronenberg 1994). Also light in the 400–700 nm waveband range (photosynthetic active radiation, PAR) solar radiation reaching the earth's surface contains a small fraction of ultraviolet-B radiation (UV-B; 280–320 nm), which is harmful to plants. UV-B quanta have high levels of energy and are effectively absorbed by important biological molecules, such as DNA, proteins, and lipids, which subsequently get destroyed. UV-B radiation directly alters the structure of DNA and indirectly damages nucleic acids (Mitchell and Karentz 1993). Proteins absorb UV-B because of their tryptophan, tyrosine, and phenylalanine contents (Yu and Bjorn 1997) and UV-B radiation affects membranes by causing large reductions in the total lipid content (Kramer et al. 1991).

There is variability in the responses to UV-B radiation between different species or isolates of individual species, and even within the life cycle of a single species (Dring et al. 1996, Häder et al. 1996, Han 1996, Bischof et al. 1998, Hanelt 1998, Wiencke et al. 2000). The degree of UV-B sensitivity depends largely on the efficiency of constitutive and UV-induced protection and repair mechanisms, such as the light-driven repair of spore germination and reproduction (Pakker et al. 2000a,b, Han et al. 2003b, 2004), structural attenuation (Dring et al. 1996), UV absorption, and the synthesis of screening compounds (Karsten et al. 1998a,b, Sinha et al. 1998).

In seawater, UV-B radiation decreases exponentially with depth, although the rate of reduction depends on the productivity of a given area (Kirk 1994). In turbid coastal waters, UV-B radiation only penetrates to a few meters, while in clearer oceanic waters, this same reduction occurs at depths of greater than 30 m (Jerlov 1976). Since the water

column does not screen UV radiation for marine organisms inhabiting shallow seas, the impacts of UV radiation on these ecosystems have been extensively studied, primarily focusing on the population growth rates, C assimilation, and nitrogen metabolism of microalgae (Häberlein and Häder 1992, Behrenfeld et al. 1993, Davidson et al. 1994, Lesser et al. 1994, Häder and Worrest 1997). While motility may provide protection for many microalgae by enabling them to avoid harmful UV radiation, exposure is unavoidable for sessile benthic macroalgae and they are, therefore, vulnerable to subsequent damage. Previous studies on the effects of UV-B on macroalgae have shown that radiation severely damages DNA, RNA, proteins, pigmentation, Rubisco, photosynthesis, growth, and reproduction (Franklin and Forster 1997, Häder 2001, Dring et al. 2001, Pang et al. 2001, Bischof et al. 2002b,c,d, Michler et al. 2002, Han et al. 2003b, 2004).

'Green tides' are a global phenomenon that occurs in coastal waters and estuaries as a result of anthropogenically-derived inputs of macronutrients, during which large blooms and accumulations of opportunistic green algae form. Amongst the most commonly occurring green algae species are those belonging to the macroalgal genus *Ulva*. (Valiela et al. 1997, Morand and Merceron 2005). *Ulva* spp. are cosmopolitan green algae found in fresh-, brackish-, and sea-water. Presently, about 594 species of *Ulva* have been recorded, of which only 129 have been classified and of which 16 have a global distribution. Green tides are reported in many coastal waters around the world including China, Finland, France, Japan, New Zealand, South Korea, and the United States, and several species of *Ulva* have been identified as the causative organisms, including *U. linza*, *U. pertusa*, *U. procera*, and *U. prolifera*. Macroalgal blooms not only impact recreational activities and threaten commercial fisheries, but they also alter natural biological communities and ecosystem functions of the affected environments. One such large-scale algal bloom, which received worldwide media coverage, occurred off the coast of the 600 km^2 island of Qingdao in late June 2008, just prior to the start of the Beijing Olympics and threatened the sailing competition. This green tide lasted for two weeks and more than one million tons of filamentous *Ulva* were removed with the efforts of more than 10,000 people. The cost of managing the bloom in Qingdao was estimated to have exceeded US$100 million. The high costs of managing green tides and the devastating impacts they have on natural ecosystems, have provided the impetus for research efforts to monitor *Ulva* growth and develop effective methods to prevent formations of large-scale blooms.

The main driver of blooms is eutrophication that is mainly based on marine-level nitrogen discharge. Eutrophication is particularly important to address, as it is likely to continue and increase in the future; potentially becoming one of the greatest threats to our coastal and estuarine systems.

It is generally believed that the amount of UV radiation reaching the earth's surface will continue to increase over the coming years due to a significant depletion of the ozone layer, and that this will likely lead to a relatively large increase in solar radiation in the UV-B range. Since marine macroalgae play key roles in coastal ecosystems, i.e., by providing food and shelter for a variety of consumers, it is important to understand the effects of UV-B on species, such as the intertidal *Ulva* spp. that cause green tides. This information is also necessary to predict future changes in coastal ecosystems due to enhanced UV-B radiation.

Hence, the purpose of this review is to present the current, collective understanding of the photobiological effects of UV-B radiation on the physiology of green tide-forming *Ulva* spp. and of the protection and recovery strategies that facilitate the successful survival of these species. This includes discussion on the effects on photosynthesis, morphology, growth, reproduction, spore liberation/spore germination, chloroplast, and cell movement, pigmentation, oxidative stress, antioxidant activity, UV-absorbing compounds and photoreactivation.

Effects of UV-B on Photosynthesis

Although UV-B accounts for only a small fraction of solar radiation, it has a considerable effect on photosynthesis. UV-B radiation reportedly causes significant photoinhibition, which is characterized by a decrease in quantum yield, reduced ability for photosynthetic O_2 evolution and fixation of photosynthetic CO_2. Excessive UV-B radiation causes significant thylakoid structural disruption and the inactivation of enzymes involved in CO_2 fixation and sugar production, as well as a decrease in primary and accessory photosynthetic pigment concentrations (Franklin and Forster 1997, Häder 2001, Sinha et al. 2001). Compared with the activities of internally bound photosynthesis components, thylakoid membranes of chloroplasts are more sensitive to UV-B. The expansion of the thylakoid membrane and the rupturing of the chloroplast double membrane can lead to changes in membrane permeability.

The inhibition of photosynthesis by UV-B exposure may be related to the direct effects on photosynthetic proteins and pigments, i.e., the degradation of D1 proteins in the reaction centre or Photosystem II (PSII; Vass 1997), or may be indirectly related to the reduction in the catalytic activity of enzymes, such as Rubisco and the decrease in the expression of genes involved in photosynthesis (Jordan et al. 1992, Mackerness et al. 1999). The formation of reactive oxygen species (ROS) in chloroplasts may primarily destroy PSII by oxidative D1 degradation (Lesser 2006). The reaction centre of PSII, one of the UV-B lesion sensitive sites, consists of a chlorophyll binding complex with two polypeptides: D1 and D2. These polypeptides degrade at high rates in response to UV radiation (Greenberg et al. 1989, Jansen et al. 1996). UV causes both photolysis of the PSII reaction centre subunits and the modification of the main steroid receptor QA.

Rubisco is one of the main targets of UV-B radiation in the photosynthesis of higher plants, phytoplankton, and benthic macroalgae (Strid et al. 1990, Jordan et al. 1992, Nogués and Baker 1995, Lesser et al. 1996, Allen et al. 1997, Bischof et al. 2000). The concomitant decrease in CO_2 assimilation may be the result of decreased activity and reduced enzyme levels. It has been reported that the reduction of RNA transcripts encoding Rubisco starts at a very early stage during UV exposure, even before further UV effects become apparent at a physiological level (Jordan et al. 1992, Mackerness et al. 1999).

There are significant differences in the degree of inhibition in different *Ulva* species. Measurements of chlorophyll a (Chl a) fluorescence can be used to investigate these degrees of inhibition on photosynthetic processes, such as light absorption, energy transfer, and photochemical reactions in PSII (Krause and Weis 1991) under

different combinations of PAR and UVR (PAR, PAR + UV-A, and PAR + UV-A + UV-B), and which indicate that the UV-B component of radiation has an additive inhibitory effect on photosynthesis of *Ulva* spp. (Figueroa et al. 1997, Bischof et al. 2002a,b, Han et al. 2004).

UV-B directly destroys PSII in *Ulva*, and indirectly reduces photosynthetic pigments, which in turn hinders photosynthetic efficiency. After irradiation with different UV radiations, the decrease in maximum quantum yield, as measured by Fv/Fm, was accompanied by a gradual decrease in pigment content (Nogués and Baker 1995). UV-induced suppression of photosynthetic yield can lead to reductions in carbohydrate synthesis and growth. However, it has been shown that reducing CO_2 assimilation under UV-B exposure is not necessarily accompanied by a reduction in the maximum quantum efficiency of photosynthesis (Nogués and Baker 1995).

In contrast, dark respiration rates seem to be almost unaffected by UV exposure (Clendennen et al. 1996). This insensitivity may be explained in part by the structural resistance of mitochondria to UV, as observed in higher plants (Brandle et al. 1977).

Photoinhibition has been observed in macroalgae that were exposed to UV-B and subsequently recovered under dim light. Dynamic photoinhibition is a protective mechanism that is caused by an active down-regulation of photosynthesis and has often been described in the genus *Ulva* (Osmond 1994, Hanelt 1998).

Some differences have been found in the results when photosynthetic performance was measured by O_2 evolution or Chl a fluorescence. For example, in *U. rotundata*, the photoinhibition rate of P_{max} is always lower than that of Fv/Fm, which indicates that when the photochemical process is down-regulated, the production of net saturated O_2 begins to decrease (Figueroa et al. 2003). In contrast, net Pmax is a parameter that is linked more to C assimilation and the Calvin cycle than to the processes related to photosynthetic efficiency or quantum yield at limited irradiances.

Flameling and Kromkamp (1998) proposed two possible explanations for the observed differences between O_2 evolution and Chl a fluorescence: (i) The production of net O_2 is affected by the consumption of O_2 or by the processes that affect linear electron transport, for example, cyclic electron transport around PSII, pseudocyclic electron transport in the Mehler reaction, Rubisco oxygenase activity, and light-dependent mitochondrial respiration. (ii) At saturating irradiances, photosynthesis turnover time may change, resulting in the effective quantum yield not matching the steady state O_2 yield. In addition to changes in the process of C assimilation, nitrate assimilation processes or nutrient restrictions can also affect the relationship between O_2 and fluorescence.

Exposure to solar UV-B can have many biological effects at the molecular, cellular, individual, and community levels. Species-specific adaptations to UV-B radiation have been reported, and even closely related species of the same genus, occupying different habitats, may have significantly different UV sensitivities. UV-resistant species are found in the intertidal zone, while more sensitive species are found in deeper waters. Seasonal variations in UV radiation also result in significant responses within and between species of marine macrobenthic communities throughout the year. Macroalgae can be classified by their ability to withstand solar UV radiation, and their extent of resistance is genetically determined, resulting in significant vertical stratification.

Possible differences in the adaptability of photosynthesis to UV radiation were tested in both the laboratory and in the field, in two *Ulva* spp.: *U. olivascens* from the intertidal zone and *U. rotundata* from the subtidal zone (Figueroa et al. 1997). *In situ*, UV-B radiation negatively affected photosynthesis and Rubisco in *U. rotundata*, while the UV doses required for 50% photoinhibition were lower in the subtidal species than in the intertidal species (Figueroa et al. 1997).

Although it has not been well studied in *Ulva* spp., some previous studies have examined UV adaptation at different life cycle stages. Typically, the early developmental stages of intertidal species have been found to be more sensitive to UV radiation than the adult stages (Major and Davison 1998, Coelho et al. 2000, Hoffman et al. 2003, Véliz et al. 2006). PSII activity in the filamentous stage of *Porphyra haitanesis* was impaired, unlike that in the adult blade stage, even when the solar radiation level decreased (Jiang and Gao 2008). It was reported that the higher UV sensitivity may be ascribed to a smaller amount of UV screening compounds.

A comparison of spore production, spore germination, and cell growth of *U. pertusa* after exposure to 1 Wm^{-2} UV-B radiation for 40 min showed that sporulation rate was not affected whereas germination rate was reduced to about 92% of the control, and cell size increased by 21% (Han et al. 2003a, 2004).

A comparative study of UV tolerance between different thallus regions of *U. pertusa* showed UV-sensitive gradients (Han et al. 2003a). *Ulva* spp. have long been considered as simple and uniform algae with little functional differentiation within the thalli. When comparing sensitivities between different thallus regions, a seven-day treatment with PAR and PAR+UV-A resulted in a significant reduction in the effective quantum yield of the whole thallus with subsequent recovery towards the initial values, while PAR + UV-A + UV-B radiation resulted in greater photoinhibition and less recovery. Significant differences in UV-B susceptibility were observed, with the marginal region of the thallus being more sensitive and the basal portion being the most resistant (Han et al. 2003a). Different responses may be attributable to differences in the cell types that make up the different thallus parts, and this may eventually translate into functional differences, such as high productivity (i.e., photosynthesis and growth) and reproduction of the marginal parts and the regeneration of new cells in the basal parts (Burrows 1959, Moss and Marsland 1976). The division of tasks among different cell types within a thallus may have adaptive value for the success of opportunistic algae, such as pioneer species. One of the benefits of the opportunity-based survival strategy is high productivity and rapid growth, which perfectly matches the characteristics of the marginal thallus region of *U. pertusa*, allowing for rapid invasion into the primary substrata (Littler and Littler 1980). In addition, the UV resistance of the basal region and the possibility of regeneration of new cells may increase the chances of green alga surviving under adverse conditions (Fletcher 1976).

Effects of UV-B on Growth

In macroalgae, a decline in growth rate can be a result of UV stress. Relatively inconsistent changes in surface area and fresh weight have been recorded for *Ulva* spp., and it is, therefore, difficult to ascertain the effect of UV-B on these growth parameters.

The effects on growth rate based on fresh weight do not show much consistency between experiments performed by different researchers. No significant differences in fresh weight-based growth rate were detected for *U. pertusa*, between thalli treated with and without UV radiation (Han 1996), while the fresh weight of *U. expansa* increased more in UV-screened conditions than when exposed to full solar radiation conditions (Grobe and Murphy 1994). In the laboratory, artificial UV-B radiation of 2 Wm^{-2} for various periods did not affect the fresh weight of *U. pertusa*. Furthermore, cell size was not affected by UV-B. Grobe and Murphy (1994) argued that the smaller-sized thalli grown under UV-B radiation were the result of an inhibition of cell division rather than of cell expansion. It is known that UV-B causes a delay in progression through the cell cycle, and an arrestment in the G1 phase and G2 phase by interfering with protein synthesis (Van't Hoff 1974).

Investigations into the possible mechanisms behind UV-B induced growth reduction in *U. expansa* were made with two hypotheses: (i) the formation of cross-linking between cell wall components via the catalytic action of the peroxidase enzyme using hydrogen peroxide (H_2O_2) and (ii) a reduction in turgor pressure (Grobe and Murphy 1997). However, peroxidase enzymes and extracellular H_2O_2 did not appear to be involved in the reduction of the growth rate of *U. expansa* under UV-B exposure which did not affect cell turgor either. Thus, UV-B appears to inhibit the growth of *U. expansa* through several processes other than viscoelastic expansion (Grobe and Murphy 1997).

There are large species-specific differences in sensitivity to UV, and a spectrum of responses for coping with UV, even within a single species. It is noteworthy that many of the studies have focused on the establishment stage of algae, highlighting that those early stages are the most sensitive and are of paramount importance in determining the performance of the adult population in a given area.

When early germlings of the intertidal alga *U. lactuca* were exposed to ambient and elevated levels of UV-B for several weeks in outdoor tanks, no inhibition of growth was observed in terms of length and fresh weight compared with those of the controls (Kuhlenkamp and Lüning 1998). In contrast, Lee and Han (1998) reported that the surface area and cell number of eight-day-old *U. pertusa* germlings decreased significantly when exposed to UV-B at 4 Wm^{-2} for 1 to 2 hr. Although it is not possible to directly compare the results of the two different studies, there appears to be an age-related change in the ability of *Ulva* to withstand UV radiation. Changes in UV sensitivity in *U. pertusa* were partially confirmed by a direct comparison between UV-B responses in eight-day-old germlings and those in adult thalli (Lee and Han 1998). The cell surface area and cell number of the germlings decreased by 65–75% after 2 hr of exposure to artificial UV-B at 4 Wm^{-2}; however, only the number of cells of adult thalli decreased to 65% of that of controls after the same treatment for 2.5 hr. Changes in susceptibility to strong light have already been observed between gametophytes and the 1–2-celled sporophytes of *Laminaria japonica* (Fei et al. 1989), although the underlying mechanisms are still unclear.

Further quantitative assessments are required to fully understand the impact of UV-B induced growth inhibition on *Ulva* spp.

Effects of UV-B on Reproduction, Spore liberation, and Spore Germination

Ulva spp. are common, fast-growing macrophytes in the intertidal zone, and are considered to be the first colonizers of open substrate (Littler and Littler 1980, Beach et al. 1995). The worldwide presence of these green algae is attributed to their tolerance of a wide range of environmental conditions and their superior reproductive capacity (Smith 1947). *Ulva* sporulation involves the direct conversion of vegetative cells into reproductive divisions, resulting in zoospores or gametes (Føyn 1959). The environmental conditions required to initiate sporulation have previously been documented, and sporulation is known to be affected by light, temperature, nutrients, desiccation, water movement, tidal conditions, and the presence or absence of external symbiotic bacteria (Smith 1947, Christie and Evans 1962, Nørdby 1977, Provasoli and Pintner 1980, Stratmann et al. 1996). Since UV-B radiation is known to have various negative effects on macroalgae, it was surprising when the growth of *U. pertusa* was observed to be stimulated, rather than negatively affected, by UV-B exposure (Franklin and Forster 1997, Häder and Figueroa 1997, Han et al. 1998, Häder 2001). Considering that vegetative growth and reproduction represent antagonistic pathways (Lüning and Neushul 1978), and that the same genes are associated with the control of these two phenomena in *Ulva* (Løvlie and Bråten 1968), the enhanced growth and reduced reproduction after UV-B exposure may indicate that an appropriate level of UV-B quanta acts as a signal to switch the mechanism from growth to reproduction. It is, therefore, hypothesised that the UV-stimulated growth of *U. pertusa* was the result of a UV-induced delay in sporulation. In higher plants, it has been found that UV-B radiation can affect the timing and extent of reproduction by altering, rather than disrupting, regulatory mechanisms (Saile-Mark and Tevini 1997). The role of UV-B as a signal that affects the transcription rate of particular genes has been recognized in higher plants (Jenkins 2017).

Algal reproductive organs are poorly protected and are susceptible to the damaging effects of UV-B. Reductions in reproduction are expected to occur in *U. pertusa* inhabiting the intertidal zone when the algae are exposed to higher doses of UV-B radiation due to ebb tides, and this could cause potentially harmful consequences for population dynamics (Han et al. 2003b). In the laboratory, the incidence of sporulation in plants irradiated with UV-B was significantly lower, and the extent of reduction was greater in plants exposed to higher UV doses. When the results are extrapolated to events that may occur in nature, there are many difficulties owing to the differences in the energy distribution within the UV-B range emitted by the lamp and sunlight. However, expressing irradiance as biologically effective irradiance (BEI) allows treatments applied under laboratory conditions to be compared with the radiation experienced under natural conditions.

To generate a BEI of UV-B lamps and solar energy, the weighted spectral irradiance is defined as the product of the UV irradiance multiplied by the spectrum of plant DNA damage, normalized to 1 at 300 nm (Caldwell 1971). Considering that the vertical attenuation coefficient of UV-B (k = 300–320 nm) of KUV-B on the east coast of South Korea is 0.54 m^{-1} (Han et al. 2003b) and the total biologically effective UV-B dose of 50% inhibition of sporulation is 0.085 $Dose_{eff}$ kJ m^{-2}, the time required to

achieve 50% inhibition below 1 m in Ahnin eastern coastal waters will be longer than 13 hr. This analysis shows that the time required for 50% inhibition of sporulation in *U. pertusa* close to the surface of the water is 2.5 hr and extends to > 13 hr at depths below 1 m, which is too long to cause damage to the sporulation process. Therefore, it is expected that the inhibition of *Ulva* sporulation by UV-B radiation will not occur even in shallow water.

The spore liberation period of the UVR-treated alga *U. fasciata* was prolonged for 4 d. Spore liberation is an important event in the life cycle of macroalgae and the viability and development of spores are controlled by many environmental factors, such as temperature, light, photoperiod, and salinity, which may stimulate or inhibit these processes (Krupnova 1984, Makarov 1987, Voskoboinikov and Kamnev 1991). Any effects on spore liberation will eventually lead to the decline of the seaweed population.

The germination success of UV-B-irradiated *U. pertusa* spores was significantly lower than that of the unexposed controls, and the degree of reduction was related to the UV dose (Han et al. 2004). When exposed to December sunlight, the germination percentage of *U. pertusa* spores exposed to solar radiation for 1 hr reached 100%, irrespective of irradiation treatment conditions. However, after 2 hr of exposure to sunlight, complete inhibition of germination was observed in the PAR + UV-A + UV-B treatment compared with the 100% germination rate observed in the PAR and PAR + UV-A treatments (Han et al. 2004).

The establishment stage of macroalgae is obviously important and affects the performance of the adult population; however, most studies have evaluated the effect of UV-B radiation on the macroscopic stages of algae (Bañares et al. 2002).

Chloroplast and Cell Movement

Many marine algae show cell movement phenomena ranging from the transient motility of reproductive cells to chloroplast movement. The movement of macroalgal unicells has been shown to exhibit phototactic, and/or chemotactic responses (Jones and Babb 1968, Amsler and Neushul 1989).

Maintenance of the swimming behaviour of reproductive cells can be an important determinant of algal dispersion and the reproductive strategies of macroalgae (Amsler and Neushul 1991). To date, few studies have assessed the effects of UV-B on macroalgal cell motility, despite it having been well documented that movement and orientation responses in microalgae are impaired by UV-B radiation (Häder and Worrest 1991, 1997).

Park and Han (1998) noted that in *U. pertusa*, the motility of biflagellate cells was markedly reduced after short durations of UV-B exposure. After the addition of 10^{-4}–10^{-5} M DCMU, an inhibitor of electron transport and a specific and sensitive inhibitor of photosynthesis, the motility of *U. pertusa* gametes decreased to 50% of that of the control. When *U. pertusa* gametes were treated simultaneously with UV-B and DCMU, their motility was reduced by 90%, implying that the two agents attack the same photosynthetic site, and that the decrease in motility was due to the collapse of photosynthesis.

In some macroalgae, the chloroplasts move between a facial position with a low photon fluence rate (a high absorption area) and a profile position with a high photon fluence rate (a low absorption area). The facial position guarantees maximum energy reward because the highest percentage of chloroplasts within cells will be struck by light. Therefore, such chloroplast movement has been considered as an adaptive mechanism to ensure maximum light absorption by the chloroplast, as well as protecting the photosynthetic pigments from photo-degradation. For example, in the brown alga *Dictyota dichotoma* it has been suggested that movement of chloroplasts from facial to profile positions is a photoprotective mechanism synchronised with a gradual increase in the photon fluence rate according to changes in tidal levels (Hanelt and Nultsch 1990).

However, a study on the green alga *U. pertusa* found no significant difference in UV sensitivity with respect to the total chlorophyll content between different chloroplast configuration arrangements (Kong et al. 2002).

It has been reported that *U. pertusa* lost the rhythmical changes in chloroplasts after UV-B exposure, while the chloroplasts of control cells sustained such rhythmicity, with minimal and maximal changes occurring in the middle of the dark and light period, respectively (Kong et al. 2002). Previous studies have illustrated the mechanism of cell motility involving microtubules (MTs) and possibly actin filaments. The interaction between MTs and actin plays an important role in organizing the cytoskeleton and maintaining chloroplast movement (Melkonian et al. 1992). It is noteworthy that UV-B changes the MT structure as tubulin absorbs maximally at 280 nm because of its high content of amino acids with aromatic side chains (Zamansky et al. 1991). Thus, damage to MTs causes a cascade of effects on cell motility.

Plant movement is generally known to occur following a single reaction chain, starting with the recognition of the stimulus, continuing with a single transduction, resulting in the observed response. Photoreceptors participate in the first step of the reaction chain, and the driving force of the transduction process may be a change in ion transport across the cell membrane owing to the activation or inactivation of ion pumps, or a change in membrane permeability. UV-B has been observed to affect cell movement by damaging photoreceptor organelles and several components of the membrane channel (Hada et al. 1993, Sgarbossa et al. 1995).

Pigmentation

Photosynthetic pigments are important targets of UV-B radiation. The ambient level of UV-B radiation reduces the concentration of major photosynthetic pigments in phytoplankton and macroalgae with Chl a being more strongly affected than chlorophyll b (Chl b) (Teramura 1983, Strid et al. 1990).

The UV-induced decrease in the total chlorophyll concentration may reflect either a decrease in pigment synthesis through physical disturbances in chloroplast thylakoids or an increase in pigment destruction due to the absorption of high energy content. Considering that the amount of chlorophyll is related to the number of thylakoids in the chloroplast, it is noteworthy that *Chlorella* exposed to UV radiation showed swelling of the thylakoid membranes and destruction of the outer membranes

(Ford et al. 1995). Regardless, it is known that UV quanta are absorbed by chlorophyll, indicating a direct impact of UV radiation on chlorophyll (Halldal 1967).

The destruction of carotenoids may also account for the loss of chlorophyll, as carotenoids protect photosynthetic components from photo-disruption. There is evidence that the xanthophyll cycle is also a target for UV-B radiation. Under field conditions, the de-epoxidation of violaxanthin to zeaxanthin in *U. lactuca* was inhibited following exposure to UV-B (Bischof et al. 2002a,b) and, as a consequence, the ability of the alga to efficiently respond to high radiation stress via thermal energy dissipation is diminished (Demmig-Adams 1990, Young and Frank 1996). This can increase the formation of reactive oxygen species (ROS) during photosynthesis, potentially leading to photooxidation of the photosynthetic system (Asada and Takahashi 1987).

In *U. pertusa* there is a significant correlation between total chlorophyll content and UV dosage and it seems that an overall change in chlorophyll concentration is a response to cumulative UV doses, even at a fixed UV-B irradiance (Han 1996). Intertidal macroalgae expectedly experience a wide variety of radiation conditions due to changes in tidal conditions, water clarity, and atmospheric transparency. If the total chlorophyll content and UV dosage is effectively correlated in *U. pertusa* in the natural environment, the destruction of chlorophyll by UV-B radiation would still occur, despite variations in UV radiation.

However adaptations, such as increased protection via carotenoids have been shown to increase in *Ulva* spp. under exposure to UV-B (Beauchamp 2012). *Ulva* spp. in upper coastal areas showed a higher amount of chlorophyll than their lower coastal counterparts, suggesting an adaptability to protect themselves from the degradation of chlorophyll under high solar irradiance.

Oxidative Stress and Antioxidant Activity

Increased UV-B radiation (280–315 nm) can cause damage to aquatic plants, and lead to a reduction in growth and pigmentation, the inhibition of photosynthesis, and changes in morphology. One of the major causes of the biological effects of UV-B is the production of ROS via intracellular photo-sensitising chromophores, such as tryptophan, nicotinamide adenine dinucleotide, riboflavin, and porphyrin.

ROS are generated as by-products of the electron transport system during photosynthesis and mitochondrial respiration. ROS-mediated modifications of cellular components and associated cellular damage play important roles in metabolic disorders and cell death. Oxidative stress caused by increased ROS affects important biomolecules and causes changes in many biological processes. For example, excessive ROS can directly attack the polyunsaturated fatty acids in cell membranes, causing complicated processes of lipid peroxidation, and can oxidatively damage DNA and proteins. In plants, ROS cause the inactivation and degradation of Rubisco and other components of the Calvin cycle and interfere with photosynthesis.

However, seaweed contains various antioxidant molecules and secondary metabolites that protect against oxidative damage (Choi et al. 2011, Park et al. 2016). Glutathione (GSH, L-γ-glutamyl-L-cysteinylglycine) is the main antioxidant compound in cells and is a reducing agent for many biochemical processes. Either directly or

via glutathione peroxidase (GPX)-catalysed reactions, GSH is oxidised to glutathione disulfide (GSSG) and is secreted from cells, reducing the cellular glutathione content. The ratio of GSH/GSSG also decreases under oxidative stress conditions, unless GSSG is either reduced to regenerate GSH through a glutathione reductase (GR) system or secreted out of the cells. Therefore, the content of glutathione and the redox state are highly sensitive indicators for both the antioxidant capacity of and oxidative stress in cells (Choi et al. 2011). GSH is also involved in the ascorbic acid-glutathione pathway (Halliwell-Asada pathway), which plays an important role in protecting plant cells from ROS and requires GSH for the reduction of dehydroascorbic acid to ascorbic acid or H_2O_2 through an ascorbic acid peroxidase-catalysed reaction. In addition to its role as an antioxidant, GSH plays an important role in various processes, such as enzymatic reactions, transport, and protein and DNA synthesis. Plants also contain a variety of other antioxidant molecules, such as carotenoids and polyphenols, and several antioxidant enzymes, such as its various forms of superoxide dismutase (SOD) and catalase (CAT).

A comparative study of the oxidative stress and antioxidant effects of three types of marine algae exposed to UV-B was conducted using *U. pertusa* (a chlorophyte), *L. japonica* (a phaeophyte), and *Grateloupia lanceolata* (a rhodophyte) collected from the intertidal zone in Korea (Park et al. 2016). *Ulva pertusa* showed a strong adaptive antioxidant response to UV radiation, as indicated by a decrease in lipid peroxidation, a reduction in cell glutathione, and an increase in the ratio of reduced to oxidised glutathione, in line with a decrease in glutathione metabolism and ROS enzyme activity. This contrasted with the responses of two other seaweed species (*L. japonica* and *G. lanceolata*) that were significantly more sensitive to UV radiation, i.e., their exposure was correlated with a decrease in antioxidant enzyme activity, as indicated by an increase in lipid peroxidation and a decrease in glutathione content.

Depending on the degree of oxidative stress, antioxidant activity can be adjusted as an adaptive response. There were temporal changes in oxidative stress and antioxidant activity in *U. pertusa* when collected in July, September, and November (Choi et al. 2011). The level of lipid peroxidation, an oxidative stress marker, was lower in September and higher in November than in July. Glutathione content and redox state correlated well with lipid peroxidation, and the glutathione pool was in a more reduced state in September. The glutathione content was lower and more oxidised in November. The low lipid peroxidation in September was due to increased glutathione pools and increased ROS scavenging capacity supported by reduced GCL, GPx, and SOD activities. The increased lipid peroxidation and oxidation and the depletion of glutathione in November suggested that ROS production was very high and overwhelmed the increased SOD and GR activity that occurred as an adaptive response to the increased oxidative stress. However, the decrease in catalase activity in September and November may be related to the control of the intrinsic temporal changes of the algal metabolism rather than antioxidant protection. It has also been observed that the antioxidant itself becomes a target for oxidative damage, resulting in activity loss. Thus, if the oxidative stress is too high, the cells suffer from oxidative damage, and if the level of stress is moderate, the cells will adapt to stress by an inducible increase in antioxidant function.

The strong UV-adaptive response via the changes in antioxidants in *U. pertusa* allows this species to efficiently recover from UV-induced oxidative stress, enabling it to occupy the shallow intertidal zone.

UV-absorbing Compounds

Several adaptive mechanisms to minimise UV-induced damage have been reported in macroalgae, including avoidance by the movement of cells and/or cell organelles, epidermal attenuation of UV radiation transmission, synthesis of screening pigments, and repair damage by photo-enzymatic activity.

UV-absorbing compounds act as sunscreens, preventing damaging UV radiation from reaching the DNA, proteins, and other sensitive molecules in cells (Franklin and Forster 1997, Häder 2001).

Various compounds have been identified from marine macroalgae, and some have been extensively studied, including such characteristic compounds as carotenoids, coumarins, phenolics and, in particular, mycosporine-like amino acids (MAAs) (Karsten et al. 1998a,b, Pérez-Rodríguez et al. 2001, 2003). From a survey of macroalgae from polar and temperate to tropical regions, the widespread presence of MAAs, especially in red algae (Karsten et al. 1998a,b, Hoyer et al. 2001, Shick and Dunlap 2002, Huovinen et al. 2004), has been noted. A MAA consists of a cyclohexenone ring linked to amino acid side groups. These compounds absorb wavelengths in the range of 310 to 365 nm across the UV-B and UV-A (320–400 nm) portions of the solar spectrum but transmit PAR (400–700 nm). Brown and green algae are reportedly deficient in MAAs and probably depend on other UV-protection compounds and mechanisms for UV defence (Shick and Dunlap 2002, Huovinen et al. 2004).

Seven MAAs have been isolated from marine macroalgae and have been identified as mycosporine-glycine, shinorine, porphyra-334, palythine, asterina-330, palythinol, usujirene, and palythene. The role of MAAs as UV protectants is inferred from the observation that their concentration correlates with the environmental UV fluence that an organism can experience. However, the association between the levels of UV-absorbing compounds and UV-B sensitivity is not always simple. For instance, since the main absorption band of MAAs is consistent with the UV-A spectrum, it is difficult to hypothesise that the compounds play a protective role in minimising UV-B damage. For example, methanol extracts of *U. pertusa* and *Kjellmaniella crassifolia* (Phaeophyta) showed strong absorption characteristics at 300 nm and 340 nm, respectively, however, UV-B sensitivity was significantly different between the species, with the green alga being far less sensitive than the brown alga.

The biochemical detection and characterization of MAAs is well established in various macroalgae, but the physiological and ecological functions of the compounds are still relatively unknown. The possibility of MAAs as UV-protecting agents remains to be determined by continued and comprehensive studies of these compounds.

Ulva pertusa synthesizes a UV-B absorbing compound with a pronounced absorption peak at 294 nm in response to UV-B and the amount induced is proportional to the UV-B dose (Han and Han 2005). This is interesting as the induction of UV-absorbing compounds as a defence system has been reported in few green

macroalgae (Hoyer et al. 2001) although they are present in some green microalgae, such as *Chlorella* and *Scenedesmus* (Xiong et al. 1999). In *Scenedesmus* spp. two UV-absorbing compounds with maximum absorptions at 292 nm and 302 nm were noted, but their chemical nature has not yet been elucidated.

The polychromatic spectrum for the induction of UV-B absorbing compounds in *U. pertusa* showed a prominent peak at 292 nm and a smaller peak at 311.5 nm (Han and Han 2005). *Ulva pertusa* appears to have UV-B absorbing chromophores similar to those reported in higher plants, which reportedly have a maximum number of these chromophores between 290 and 310 nm (Herrlich et al. 1997). In higher plants, it has been suggested that the chemical entity of the chromophore is either a flavin or pterin (Ensminger and Schafer 1992), or possibly an aromatic residue of a protein (Kim et al. 1992).

The presence of UV-B photoreceptors has been suggested in several other green macroalgae. The action spectrum of the photoresponse in the rhizome of *Bryopsis plumosa*, a symbiotic alga, showed a maximum peak at 260 nm but another peak at 310 nm (Iseki and Wada 1995). The green macroalga *Prasiola stipitata* produces UV absorbing substances, and the action spectrum showed the maximum effectiveness at 300 nm (Gröniger and Häder 2002). Further studies are required to identify UV-B-absorbing chromophores in *U. pertusa*, because the response to UV-B may be a consequence of cellular effects, such as DNA damage and photooxidation products rather than UV-B itself (Portwich and Garcia-Pichel 2000).

Ulva pertusa shows a rhythmic induction of UV-B-absorbing compounds, even after 12 hr of PAR + UV-A + UV-B followed by 12 hr in the dark, with accumulation being confined to the light period (Han and Han 2005). The alga studied also appeared to accumulate UV-B exposure despite intermittent exposure to white light-dark periods, indicating the presence of a UV-B quantum counting system for at least 5 d. A similar pattern for MAA synthesis has been observed in some N_2-immobilised cyanobacteria (Sinha et al. 2001). In *Anabaena* spp., *Nostoc commune*, and *Scytonema* spp. an induction of shinorine was observed to occur during the light period. In an ecological context, the dependency of the accumulation of protection compounds on UV-B exposure makes it possible for *U. pertusa* to adapt to the continuous fluctuation of solar UV-B radiation reaching its natural habitat.

Under artificial UV-B irradiation, the accumulation of UV-B absorbing compounds in *U. pertusa* was accompanied by reduced growth (Han and Han 2005). Secondary product formation and vegetative growth are known to be antagonistic processes (Zenk et al. 1977). Additionally, it has been demonstrated that secondary metabolites that are not formed under optimal growth conditions begin to accumulate after a reduction in cell growth (Zenk et al. 1977). In *U. pertusa*, it appears that UV-B radiation causes a growth decline, thereby switching from primary metabolism to secondary metabolism, and inducing UV-B absorbing compounds (Han and Han 2005). In the same species, it is suggested that low levels of UV-B act as a signal for the transition from somatic growth to reproduction (Han et al. 2003).

However, UV-B-induced growth reduction can also be a by-product of the accelerated production of UV-B-absorbing compounds. To produce UV-absorbing compounds, considerable metabolic investment is required in terms of photon and nitrogen costs (Raven 1991). The accumulation of UV-B absorbing compounds by

U. pertusa after UV-B exposure may also represent a mechanism for reducing growth, in order to reduce UV-B exposure, as a trade-off between growth and defence (Han and Han 2005).

Few studies have addressed the relationship between the concentration of UV-absorbing compounds and antioxidant activity in macroalgae. Therefore, the significant correlation between the concentration of UV-B-absorbing compounds and non-enzymatic antioxidant activity in *U. pertusa*, is notable (Han and Han 2005). This finding lends support to the hypothesis that these compounds serve as antioxidants for protection against UV-B-induced photo-oxidative stress. A similar concentration-dependent relationship between mycosporine-glycine and antioxidants has been reported for the ascidian *Lissoclinum patella* and the zoanthid *Palythoa tuberculosa* (Dunlap and Yamamoto 1995, Suh et al. 2003). Producing UV-B-absorbing compounds with dual functions (screening and antioxidant) may be a cost-saving strategy for *U. pertusa*. Since there is a spectral discrepancy between the absorption properties of UV-absorbing compounds and UV-B radiation, it is questionable whether these compounds offer complete protection against UV-B radiation. Also, the protective function of UV-absorbing compounds in many algae has been inferred from observations that the compounds accumulate in proportion to the degree of exposure to UV-B; however, the mere presence of UV-absorbing compounds does not guarantee protection against the harmful effects of UV radiation (Shick and Dunlap 2002). For example, in the dinoflagellate, *Prorocentrum micans*, the MAAs produced after UV exposure did not protect the photosynthetic mechanism, as cellular chlorophyll concentrations and Rubisco activity were significantly reduced despite their presence, whereas in *Gymnodinium sanguineum* the cells with higher concentrations of MAA were less sensitive to UV-B radiation (Lesser 1996, Neale et al. 1998). The results from a study on *U. pertusa*, which showed that the sensitivity of photosynthetic performance as measured by dark-adapted Chl a fluorescence, correlated inversely with the concentrations of UV-B-absorbing compound in the thallus imply that induction of UV-B-absorbing compounds under UV-B seemingly play an important role in protection UV-B radiation (Han and Han 2005). The induction of UV-B-absorbing compounds by UV-B radiation is a selective advantage of *U. pertusa*, which may initiate the defence mechanism in response to the harmful effects of the radiation. Further research is required to better understand the efficiency and mode of protection of these UV-B absorbing compounds (Lesser 1996, Neale et al. 1998).

Photo-reactivation

UV-B quanta are easily absorbed by biomolecules, such as nucleic acids (DNA, RNA, etc.), proteins, lipids, etc., which play important roles in the structure and function in cells of chloroxygenic organisms (Bischof et al. 2002a). UV damage to DNA involves structural changes, such as the formation of thymine dimer and 6–4 photoproducts (Pakker et al. 2000a, van De Poll et al. 2001).

On the contrary, the reversal of the harmful effects of UV radiation by subsequent illumination with longer wavelengths is almost universally observed in organisms (Jagger et al. 1964, Caldwell 1971). This phenomenon, known as photoreactivation,

has been observed in some macroalgae with recovery from interference with DNA synthesis, nuclear division, and translocation, and from dimerization of DNA, loss of viability, delay in germination, and inhibition of spore production (Han and Kain 1992, 1993, Huovinen et al. 2000, Pakker et al. 2000a,b, Han et al. 2003b, 2004).

The mechanism of photoreactivation is relatively well described for DNA, one of the most common UV lesions, and involves the restoration of UV-incurred damage in DNA by the photoreactivation (i.e., the absorption of light energy) of enzymes that monomerise dimers formed in UV-irradiated DNA (Karentz 1994). In general, DNA photoreactivating enzymes have UV and blue light requirements for optimum catalytic functions (Saito and Werbin 1970, O'Brien and Houghton 1982, Eker et al. 1990).

In contrast, Han and Kain (1992, 1993) reported that exposure to visible light enhanced the survival of UV-irradiated young laminarian sporophytes, but little is known about the functional role of photoreactivation. The blue light requirements for effective reactivation from UV-damage in young laminarian sporophytes corresponded to the report that the most effective reversal of UV damage is known to occur under near-UV and blue radiation (Jagger 1964, Caldwell 1971, Halldal and Taube 1972). It has also been reported that the degree of recovery increases with increasing photon irradiances (Han and Kain 1992, Han et al. 2003b, 2004).

DNA damage is known to result in decreased spore viability and to delay germination and the development of spores (Huovinen et al. 2000, Wiencke et al. 2000) at the initial stage of survival of macroalgae. The germination success of UV-B-irradiated spores of the intertidal green alga *U. pertusa* was significantly lower than that of the un-irradiated control spores, and the extent of the reduction was correlated with the UV dose (Han et al. 2004).

After exposure to moderate levels of UV-B radiation, subsequent exposure to visible light produced significantly higher rates of spore germination in *U. pertusa* under higher photon irradiances and blue light than it did under lower irradiances and red light (Han et al. 2004). The main targets of UV-B radiation in spores of *U. pertusa* are unknown, but it is noteworthy that the rate of spore germination has been shown to depend on photon irradiances during the post-illumination period.

Macroalgae living in the intertidal zone have a high degree of resistance to adverse environmental conditions (Davison and Pearson 1996). *Ulva* spp. with irradiance-dependent reactivation from UV-B damage may have a greater selective advantage than other species when competing for space in shallow water habitats that are frequently exposed to high intensity UV-B.

For UV-B irradiated *Ulva* spores, blue light was the most effective for reactivation of germination (Han et al. 2004). The lack of discernible germination in red light eliminates the involvement of photosynthetic pigments for the reactivation process. Similar reactivation by blue light has been reported for cyanobacteria (Saito and Werbin 1970, O'Brien and Houghton 1982, Eker et al. 1990). In *Ulva* spp., the phototaxis of zoospores is guided by blue light but not by green and red light (Callow and Callow 2000). The action spectrum of the photoreactivation of germination in *U. pertusa* spores irradiated with UV-B shows a large peak at 435 nm and a smaller but significant peak at 385 nm (Han et al. 2004). The improving effect of blue light on the germination of *U. pertusa* exposed to UV-B radiation seems to be related to the presence of a

photoreactivation system that is similar to that found in other organisms. The action spectrum is similar to the DNA photoreactivation of cyanobacteria (van Baalen and O'Donnell 1972, Eker et al. 1990), with a major peak at 436 nm, and that of the higher plant, *Zea mays*, with a broad single peak at 385 nm (Ikenaga et al. 1974). The similarity between the action spectra suggests that the mechanism of photoreactivation may require DNA repair, and that the UV-B target involved in the *Ulva* spore germination may be DNA.

A variety of plant responses induced by blue/UV-A radiation have been reported, and there is now convincing evidence for the existence of multiple blue light/UV-A photoreceptors absorbing principally UV-A (315–400 nm) and blue (400–500 nm) wavelengths. Blue photoreceptors involved in the reactivation of spore germination in UV-B-irradiated *U. pertusa* may be one of these groups.

In addition to the matting properties that act as a selective UV-B filter for spores under the parent canopy, germination repair by blue/UV-A light after UV-B exposure probably explains the success of germination of *U. pertusa* spores in a shallow water environment that is influenced by strong solar UV radiation (Bischof et al. 2002d, Han et al. 2003b). If the early life stages are decisively important for the recruitment of the next generation, the presence of a light-driven repair system in the settled spores is a viable option for the successful continuation of *U. pertusa* in areas receiving intense solar UV-B radiation.

Mat-forming and Morphology

Ulva spp. often cause green tides. Thalli occur in a dense multi-layered mat floating on the water surface (Hernández et al. 1997, Vergara et al. 1997, 1998). The top layer is periodically exposed to high solar radiation, but the shaded layer receives reduced irradiance (Vergara et al. 1997, 1998). These so-called *Ulva* mats are frequently observed in soft bottom habitats in shallow coastal areas. A study on the influence of solar UV radiation on the *Ulva* canopy proposed canopy formation as an ecological strategy to shield the sub-canopy layers from harmful UV-B radiation by significant absorption of UV-B in the bleached top layer of the mat (Bischof et al. 2002a).

It has been reported that the morphological features of macroalgae affect their physiological responses to physical stress agents, such as high irradiance, desiccation, and wave motion (Davison and Pearson 1996). In higher plants, attenuation of UV radiation that reaches the mesophyll via the epidermis is one of the important factors determining the susceptibility of plants to UV radiation (Day et al. 1992). In algae, it is presumed that macroalgae with thin thalli are more susceptible to UV damage than those with thick thalli (Halldal 1964). However, there have been few direct comparisons of whether different macrophyte morphologies show different tolerances to UV radiation. In response to tests regarding the effects of artificial UV-B radiation, the brown macroalga *K. crassifolia* and the red macroalgae *Pachymeniopsis* spp. were seen to both possess thick thalli with several cell layers, and the green macroalga *U. pertusa* was seen to possess thin thalli with only two cell layers (Han et al. 1998). After 1 hr of exposure to UV-B 2 Wm^{-2}, the chlorophyll content was compared with that of the control specimens and in the brown alga was found to have decreased to

95.3%, in the green alga to 58.0%, and in the red algae to 80.6% of that of the control specimens. In addition, the fresh weights were reduced by 68.2% in *K. crassifolia* and by 21.4% in *U. pertusa*, whereas it was enhanced by 11.1% in the red algae *Pachymeniopsis* spp. (Han et al. 1998). These results may suggest that thallus form does not greatly affect the physiological response to UV radiation, at least in these three species.

Conclusion

Global climate change can also alter the exposure of ecosystems to UV-B radiation by affecting geochemical processes that influence ozone depletion. In addition, UV-B radiation may affect the cycling of C and inorganic nutrients, such as nitrogen, through changes in macroalgal communities. This could occur due to the effects of UV-B radiation on photosynthetic performance and the chemical properties of damaged and dead algal substances falling to the bottom. It is well known that seaweeds and seagrasses are the main vehicles for C assimilation of ~ 1 Pg C yr^{-1} (Chung et al. 2011) and may become C sinks for anthropogenic CO_2 emissions. The C assimilation capacity of *U. pertusa* is estimated at 9.49 kg ton^{-1} hr^{-1}, i.e., an estimated 10.25 tons of C assimilation over 6 months, based on a daily photosynthetic period of 6 hr (Han et al. unpublished). The effect of UV radiation on the C cycle may affect the cycling of metals and mineral nutrients (Zepp et al. 2007). It is noteworthy that the EC_{50} values of *U. pertusa* for four metals is lower than those of the standard Microtox and five other standard test organisms, and that *U. pertusa* can even be used as a model test organism to detect metal toxicity (Han and Choi 2005). The combined effects of UV radiation and metal toxicity can, therefore, have serious impacts on *Ulva* spp.

UV radiation can affect the nitrogen cycle in several ways, including changes in the decomposition of nitrogenous organics and effects on nitrogen fixation (Zepp et al. 2007). In addition, in aquatic environments UV interactions with inorganic nitrogen species, such as nitrate and nitrite are an important source of ROS, including the highly reactive hydroxyl radical.

Alternatively, some adaptive mechanisms for UV-B radiation stress may depend on the nutritional status of seaweeds and the nutrient availability in seawater. For instance, nitrogen limitation can affect photosynthetic capacity and the content of protective compounds, thus increasing the sensitivity of seaweed to UV-B (Korbee et al. 2005). Increased levels of UV radiation and eutrophication can increase the energy investment needed for the synthesis of MAAs in macroalgae, thereby providing more protection under UV-B stress (Peinnado et al. 2004).

The release of ozone-depleting gases has presumably ceased since 1980, but a full recovery of the ozone layer is not expected until 2070 and, owing to its possible interaction with climate change, the effects of UV-B radiation are uncertain (Figueroa and Korbee 2010).

UV-B exists as a general abiotic factor, and the currently observed physiological patterns are the result of long-term adaptation and acclimation of individual species to various irradiations. Therefore, the adverse effects of UV-B exposure may consequently be offset to some extent, however, the permanent suppression of physiological

processes may result. There is a possibility that the increased UV-B exposure caused by the thinning of the stratospheric ozone layer may disturb this balance, leading to further damage. It is still to be determined if, or to what extent, the adaptive and protective responses of macroalgae will be sufficient to re-establish this balance.

However, the presence and antioxidant capacity of UV-B-absorbing compounds in *U. pertusa* as well as its mat-forming properties and light-driven photo-repair give this species superior selective advantages over other macroalgae and enabling it to thrive in the presence of intense UV-B radiation (Fig. 11.1). *Ulva* spp. are evidently the fittest macroalgae of the intertidal zone where the macroalgal community is often exposed to high levels of solar radiation.

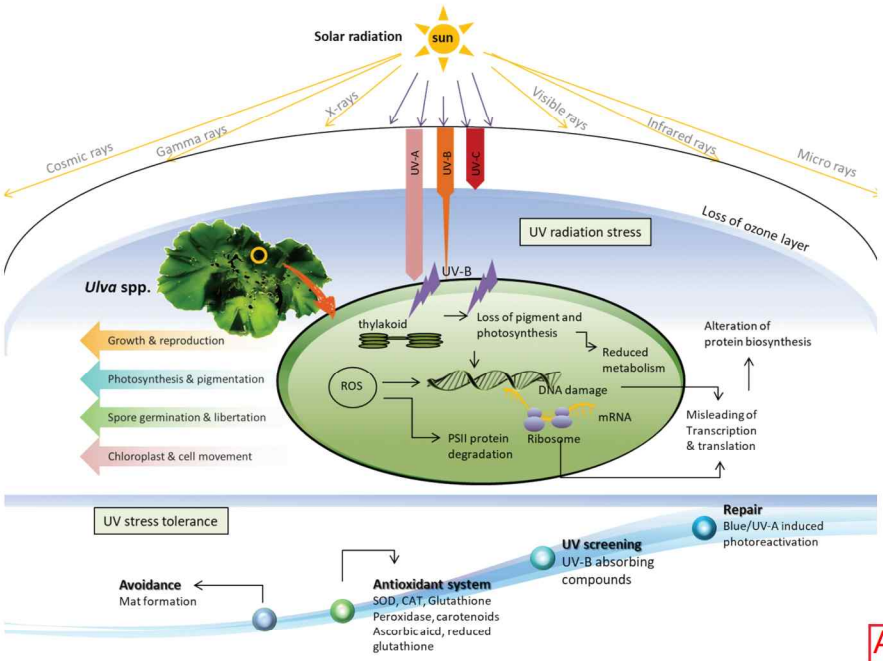

Fig. 11.1

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This work was supported by a Grant of Incheon National University Research (2012).

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