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Photosynthesis and Photoinhibition of Two Green Macroalgae with Contrasting Habitats

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We evaluated light-related traits of *Ulva pertusa* Kjellman from the intertidal and upper subtidal zones, and of *Umbraulva japonica* (Holmes) Bae & Lee (formerly *Ulva japonica*) within its upper growth limit of 10 m, in Korean coastal regions. *U. pertusa* showed significantly higher maximum photosynthetic rates, photosynthetic efficiency, saturating irradiances, and total pigment contents. However, green light-use efficiency at limiting irradiances was notably higher in *U. japonica*, possibly due to the presence of green light absorbing pigments like siphonaxanthin and siphonein. Non-enzymatic antioxidation capacity as determined by DPPH (α,α-diphenyl-β-picrylhydrazyl) radical scavenging rate was markedly higher in *U. pertusa* (50.49%) than in *U. japonica* (8.85%). Both species showed a substantial decrease in optimal photosystem (PS) II efficiency (F_v/F_m) with increasing PAR doses despite the degree of photoinhibition being more marked in *U. japonica*. After 24 h in dim light, *U. pertusa* rapidly and almost fully recovered F_v/F_m within an hour while *U. japonica* exhibited slow and incomplete PSII recovery over the full recovery period. A significant depression in photosynthetic activity with monochromatic UV-B radiation was observed in *U. japonica* only, followed by slight recovery in dim light. Light use efficiency and high irradiance tolerance may be important ecological axes along which the niche separation of green foliose algae occurs in Korean coastal waters.

Keywords: green light, PAR, photoinhibition, *Ulva pertusa*, *Umbraulva japonica*, UV-B

In coastal areas of Korea, there are two green macroalgal species of the Ulvales that grow in contrasting habitats. *Ulva pertusa* is a shallow-water species growing from the intertidal to the upper subtidal zones, whereas *Umbraulva japonica* (formerly *Ulva japonica*) is a deep-water species exclusively restricted to a depth range of 10 to 24 m, forming small monostand patches on the sea floor (Yokohama, 1989).

In aquatic environments, the light which penetrates a water column is highly variable in both irradiance and spectral quality (Kirk, 1983). The availability and spectral distribution of light may therefore be major environmental axes along which aquatic macroalgae could be segregated (Lüning, 1990).

Irradiance is an important ecological factor on which photoautotrophs depend. Certain species have been observed to occupy sunny or well lit sites, while others are found in shaded or poorly lit habitats. With respect to photosynthesis, species adapted to high-light sites have relatively higher light-saturated photosynthetic rates and light saturation points than species growing in low-light sites, although photosynthetic quantum yield is found to be higher in the latter species (Boardman, 1977).

Low light levels can pose a stress to macroalgae because irradiance limits photosynthesis, and therefore, net carbon gain and growth. The ability to increase net carbon gain under light-limited conditions can thus be a determining factor for the lower limit of macroalgal vertical distribution. In this regard, it is notable that the general trends reported for deep-water algae are higher light-use efficiencies and lower saturation irradiances for photosynthesis as compared to those of shallow-water inhabitants (Lüning, 1990). These attributes could increase the capacity of deep-water algae to establish and grow in sites with limited resources such as light. Optimal photosynthetic performance as a prerequisite for light adaptation is observed at 60 to 70 μmol photons m^{-2} s^{-1} for deep-water species, while it is found at 400 to 500 μmol photons m^{-2} s^{-1} for shallow-water species (Lüning, 1990).

On the other hand, high light levels may also stress macroalgae by causing severe damage to the photosynthetic apparatus. Shallow-water algae can tolerate high photon irradiances up to full sunlight with no apparent inhibition of photosynthesis or growth, whereas deep-water species are significantly affected by exposure to intense light. The degree of tolerance for intense irradiation appears to be related to the organism's protective functions and the efficacy of repair mechanisms after exposures (Franklin and Forster, 1997; Häder, 2001; Bischof et al., 2002). While photosynthetically active radiation (PAR) has previously been found to cause photoinhibition, recent studies indicate an equally strong impact of solar UV radiation outweighing its relatively low abundance compared with PAR (Franklin and Forster, 1997; Häder, 2001; Bischof et al., 2002). Potential physiological tolerance of excessive PAR in general and UV radiation in particular has been suggested to be an important factor regulating the upper depth limit of various macroalgal species (Graham, 1996; Häder et al., 1996; Hanelt et al., 1996; Bischof et al., 1998; Hanelt, 1998; Karsten et al., 1999).

Spectral fields of PAR are selectively attenuated with depth depending on the optical characteristics of the water types (Kirk, 1983). This phenomenon creates the depth variation in light quality for macroalgal photosynthesis in the euphotic zone. Therefore, an algal type adapted to the predominant wavelength of available light for photosynthesis

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may have a competitive advantage over others.

In the present study, we evaluated the photosynthetic response of two foliose green algae to variations in the light environment in terms of both irradiance and spectral quality. We hypothesized that a species-specific difference in light requirements, light use efficiency and light tolerance required for photosynthesis would be evident, corresponding with the contrasting light conditions in their native habitats.

MATERIALS AND METHODS

Culture of Plants

Samples were collected at sites near Ahnin on the eastern coast of Korea (37.4°N, 129.1°E). *U. pertusa* was collected from rocks within the intertidal zone while *U. japonica* was collected by scuba diving in zone of 10 to 20 m depth. Immediately after transport to the laboratory, each species was placed in separate plastic tanks with aerated artificial seawater medium (Ott, 1965) and the stock cultures were maintained at 15°C under 20 to 30 μmol photons m^{-2} s^{-1} of white fluorescent light (FL400; Kumho, Korea) with a 12-h light-dark (LD) period for at least 24 h prior to experimental use.

Oxygen Evolution Measurements

Photosynthetic oxygen evolution of the thallus disks was measured with a Clark-type oxygen electrode (Rank Bros, UK) in a glass chamber (10 mL) maintained at 15°C. In each experiment $NaHCO_3$ (2.4 mM) was added to ensure saturation of inorganic carbon in the media. Maximum photosynthetic capacity (P_{max}) and photosynthetic efficiency (α) were derived from the hyperbolic tangent formulation, $P = P_{max} \tanh (\alpha I / P_{max})$, given by Jassby and Platt (1976). Values of I_k (light saturation point) were estimated from the equation, $I_k = P_{max} / \alpha$. The full spectrum ('white') light source for photosynthetic measurements was a slide projector fitted with a 240 W halogen lamp (Osram, Germany). The UV portion of the output was removed by a 395-nm cut-off foil (Ultraphan, Digefra, Germany). In order to generate green light the chamber was covered with green (#439) gelatin filters (Lee Lighting, UK) (Fig. 1). A gradient of photon irradiances between 2 and 300 μmol photons m^{-2} s^{-1} was produced by different distances or black nylon nets of various thickness interposed between the chamber and the projector. Photon irradiance measurements were made using a Li-Cor LI-1000 Datalogger with a cosine receptor (Lincoln, USA).

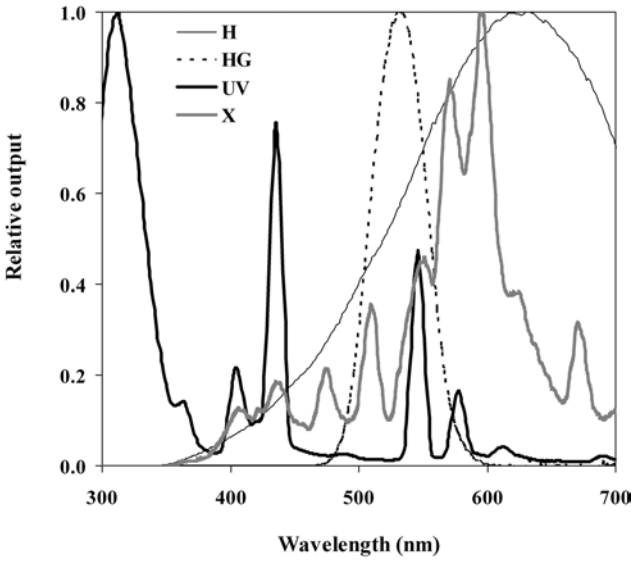

Figure 1. Spectral distribution of relative output emitted from various light sources, including halogen lamps (H), halogen lamps combined with green filters (HG) for photosynthesis study, and xenon lamps (X) and UV-B transilluminator (UV) for photoinhibition study.

Measurements of Chlorophyll Fluorescence

In order to determine sensitivity to high PAR and UV, disks cut from the middle thallus part of each species were placed in Petri dishes (100 mm in diameter, 20 mm high), and exposed to high PAR irradiances (400, 800, and 1600 μmol photons m^{-2} s^{-1}) for 2 h, or to UV-B radiation of 1.0 W m^{-1} for 1-2 h. The irradiation sources were a xenon lamp (MS-SB200; MS Electronics, Korea) combined with a 395-nm cut-off foil (Ultraphan, Digefra, Germany) for PAR and a transilluminator (Bachofer, Germany) with a main output at 312 nm for UV-B. The UV-C portion (<295 nm) of the output of the UV-B source was removed by a 295-nm cut-off foil (Ultraphan, Digefra, Germany). Irradiance was measured using a Li-Cor LI-1000 quantum meter for PAR, and a UV radiometer with a UV-B sensor (DM-series; Spectronics, USA) for UV-B. After exposure to the different irradiation treatments, samples were withdrawn for measurement of optimal photosynthetic quantum yield, and then immediately transferred to dim light conditions for measurement of recovery from photoinhibition after 1 and 24 h. After experimental treatments, the thallus disks were kept in the dark in leaf clips (DCL-8; Walz, Germany) at room temperature (20°C) for 10 min before their photosynthetic quantum yields (F_v / F_m) were measured using a PAM-2000 (Walz, Germany) where F_o is the initial fluorescence and F_m is the maximum fluorescence and $F_v = F_m - F_o$ (Schreiber et al., 1996).

Biochemical Measurements

Immediately after transporting fresh samples from the field to the laboratory, disks (9-mm diameter) were excised from healthy middle thallus parts of the algae and weighed after removing surface water with paper tissue. Photosynthetic pigment contents were also determined, using a Specord spectrophotometer (S10; Zeiss, Germany) after extraction of thallus disks in 100% methanol for at least 24 h in the dark at 4°C. For chlorophyll and carotenoid contents, the methanolic extracts were measured at 666 nm (chlorophyll *a*: Chl *a*), 653 nm (chlorophyll *b*: Chl *b*) and 470 nm (carotenoids) (Lichtenthaler and Wellburn, 1983). To clarify the peak positions of specific pigments, fourth-derivative spectra involving five point intervals were generated for *in vivo* thallus and *in vitro* thallus extracts in absolute ethanol using algorithms after Savitzky and Golay provided by the manufacturer (Zeiss, Germany). Fourth derivative spectrometry is a spectral technique in which the rate of change of absorbance

with wavelength is measured as a function of wavelength (Butler and Hopkins, 1970a, b). In the derivative spectrum, the ability to detect and measure minor spectral features is enhanced. Non-enzymatic antioxidant activity of thalli was measured by DPPH (α,α-diphenyl-β-picrylhydrazyl) scavenging activity. Thallus disks were homogenized in 2 mL of absolute ethanol with a mortar and pestle, and the extracts then centrifuged at 7500*g* for 15 min. A 0.5-mL aliquot of the supernatant was mixed with a 0.5-mM DPPH ethanol solution (0.25 mL) and 100 mM of acetate buffer (pH 5.5, 0.5 mL). After incubating in the dark for 30 min, the absorbance of the mixture was measured at 517 nm to determine DPPH scavenging activity (Abe et al., 1998).

PAR Measurements

Underwater radiation (400-700 nm) at Ahnin on the eastern coast of Korea (37.4°N, 129.1°E) were measured with a Li-Cor LI-1800 underwater spectroradiometer at various depths on a cloudless day as previously described by Han et al. (2003b). The photon irradiance was measured at 1 nm interval and total quanta were integrated for PAR (400-700 nm) and green light (500-600 nm). The vertical attenuation coefficient of the two wavelength ranges of radiation was obtained using the regression analysis and used to determine the depth of the 1% surface irradiance.

RESULTS

Underwater Irradiance Profiles

Figure 2 shows the depth profiles of *in situ* irradiance at midday on a cloudless day. The depth of the 1% surface irradiance (I_o) as calculated from regression lines fitted on irradiance data at various depths was 19 m for PAR and 24 m for green light.

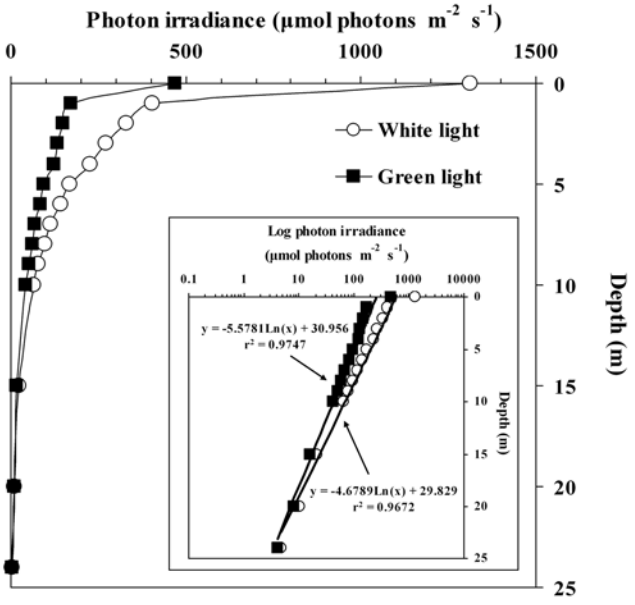

Figure 2. Depth profiles of integrated irradiances measured at Ahnin on eastern coast of Korea. Inset; vertical light expressed on log scale.

Table 1. Comparisons of *P* vs *I* curve parameters for *U. pertusa* and *U. japonica*. Values are means and 95% confidence intervals of 7-8 measurements. Units: P_{max}, mg O_2 (g Chl *a*)$^{-1}$ h^{-1}; α, mg O_2 g^{-1} Chl *a* h^{-1} (μmol m^{-2} s^{-1})$^{-1}$; I_k, μmol m^{-2} s^{-1}. Values with different superscript letters are significantly different at $P < 0.05$ with small letters used for light quality and capital letters for species.

		Species	
		U. pertusa	*U. japonica*
P_{max}	White	123.10 ± 18.55 ^{aA}	71.54 ± 8.05 ^{aB}
	Green	77.90 ± 9.17 ^{bA}	73.13 ± 9.41 ^{aA}
α	White	1.55 ± 0.22 ^{aA}	1.36 ± 0.37 ^{aA}
	Green	0.62 ± 0.07 ^{bA}	1.44 ± 0.19 ^{aB}
I_k	White	79.30 ± 2.17 ^{aA}	54.19 ± 8.51 ^{aB}
	Green	125.78 ± 8.65 ^{bA}	51.06 ± 5.06 ^{aB}

Photosynthesis

P_{max} and α of the shallow-water species *U. pertusa* in green light were respectively 71 and 30% of those under white light, while similar values of P_{max} and α were recorded for the deep water *U. japonica* in response to white and green light (Table 1). Inter-specific differences in P_{max} and α were noted between the studied algae. In white light, P_{max} of *U. pertusa* was 23% higher than *U. japonica*, whereas P_{max} did not differ between the species in green light. There was no significant difference in photosynthetic efficiency between the species when exposed to white light, but values of α were 2.3-fold higher in *U. japonica* under green illumination.

The saturation irradiance of photosynthesis (I_k) in white and green light was higher in *U. pertusa* than in *U. japonica* (Table 1).

Photoinhibition

When exposed to high PAR for 2 h, F_v / F_m of *U. pertusa* decreased substantially and the degree of photoinhibition increased with the dose of PAR (Fig. 3). F_v / F_m of *U. japonica* showed similar responses to those of *U. pertusa*, but photoinhibition was more intense. F_v / F_m was recovered in both species when the irradiated samples were transferred back to dim light conditions. *Ulva pertusa* showed rapid and almost full recovery within 1 h, but recovery in *U. japonica* was slower and reached only 30 to 80% of initial F_v / F_m values after 24 h. The degree of recovery was greater in samples subjected to lower irradiances during the exposure period.

When exposed to UV-B radiation (1.0 W m^{-2}) from a transilluminator for 1 or 2 h, there was no significant change in F_v / F_m in *U. pertusa*, but F_v / F_m decreased to 49% (1 h) and 26% (2 h) of the initial in *U. japonica* (Fig. 4). Following 24 h in dim light, F_v / F_m of *U. japonica* irradiated with UV-B for 1 or 2 h recovered to 64 and 35% of the initial value, respectively.

Biochemical Characteristics

Concentrations of all photosynthetic pigments were greater in *U. pertusa* than in *U. japonica* (Table 2), but the ratio of Chl *b* to Chl *a* was higher in *U. japonica* than in *U.*

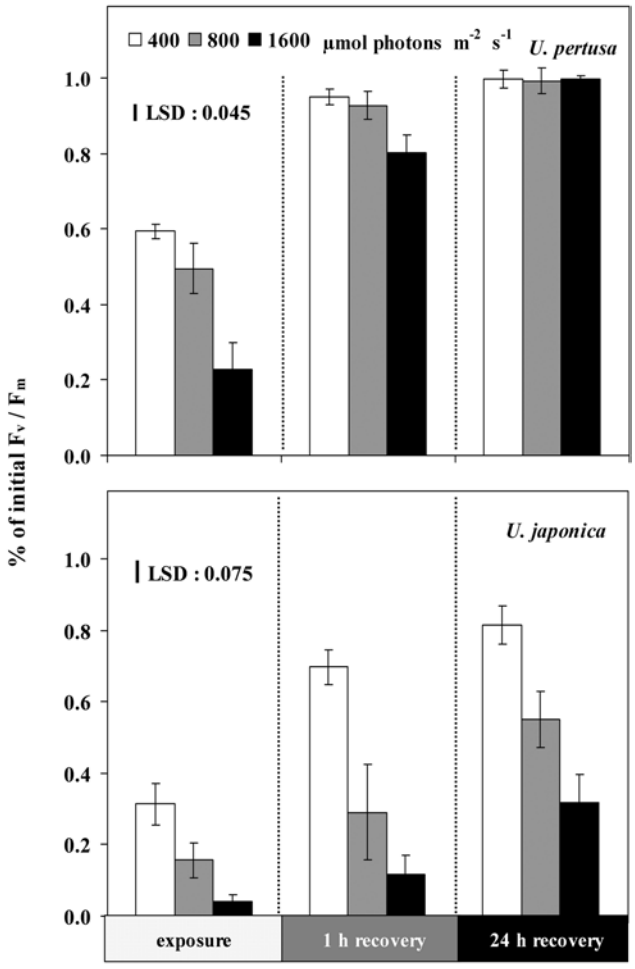

Figure 3. Chlorophyll fluorescence yield in *U. pertusa* and *U. japonica* after exposure to different irradiances of PAR for 2 h, and after 1 and 24 h in dim light. Initial intrinsic efficiencies of PS II, measured as F_v/F_m, in dark-adapted, intact samples, were 0.74 for *U. pertusa* and 0.72 for *U. japonica*. Means and 95% confidence intervals are shown (n=10). Bar with number denotes least significance difference (LSD) at 5% level.

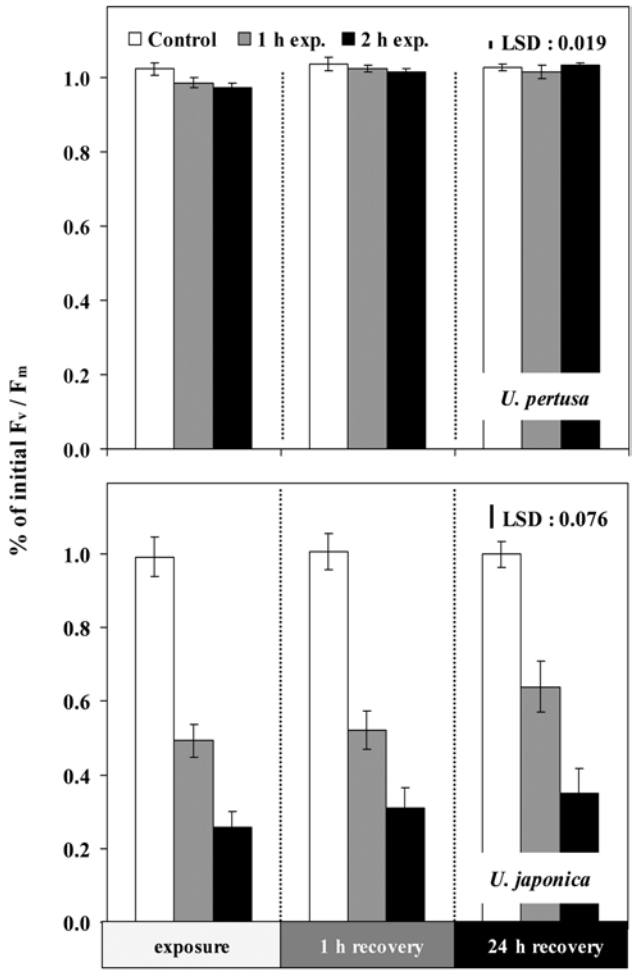

Figure 4. Chlorophyll fluorescence yield in *U. pertusa* and *U. japonica* after exposure to 1.0 W m^{-2} of UV-B for 1 or 2 h, and after 1 and 24 h in dim light. Initial intrinsic efficiencies of PS II, measured as F_v/F_m, in dark-adapted, intact samples, were 0.74 for *U. pertusa* and 0.72 for *U. japonica*. Means and 95% confidence intervals are shown (n=10). Bar with number denotes least significance difference (LSD) at 5% level.

pertusa. From fourth derivative analysis of *in vivo* thallus and organic solvent extracts, *U. japonica* showed the peak absorbances resolved at 476 and 488 nm for intact thalli, and 448 and 456 nm for ethanol extracts, respectively, while *U. pertusa* had no discernible peaks at these same wavelengths (Fig. 5). DPPH-radical scavenging activity as a measure of non-enzymatic antioxidation was found to be 50.5% for *U. pertusa* and 8.9% for *U. japonica* (Table 2).

Table 2. Pigment contents and antioxidant capacity of *U. pertusa* and *U. japonica*. Means and 95% confidence intervals are shown. Different superscripts denote significant differences at the indicated p-ranges.

	Species		p value
	U. pertusa	*U. japonica*	
Chl *a* (mg g FW^{-1})	0.95 ± 0.06 [a]	0.52 ± 0.03 [b]	$p < 0.001$
Chl *b* (mg g FW^{-1})	0.92 ± 0.10 [a]	0.58 ± 0.05 [b]	$p < 0.001$
Car (mg g FW^{-1})	0.15 ± 0.03 [a]	0.10 ± 0.01 [b]	$p < 0.05$
Chl *b* / Chl *a*	0.96 ± 0.06 [a]	1.10 ± 0.05 [b]	$p < 0.01$
Car / Chl *a*	0.16 ± 0.03	0.19 ± 0.04	$p > 0.05$
Antioxidant activity (%)	50.49 ± 5.52 [a]	8.85 ± 2.22 [b]	$p < 0.001$

DISCUSSION

Photosynthesis

In aquatic environments, both total irradiance and spectral quality changes with depth and geographic location (Jerlov, 1976). In coastal waters off Ahnin, measurements of the solar radiation depth profile have shown that green light predominates in the deep euphotic zone. This means that one algal species efficiently absorbing the predominant wavelength of available light may have a competitive advantage over another (Kirk, 1983).

In thin thalli, like *Ulva* and *Umbraulva*, the package effect is relatively small so that each light-harvesting pigment such chlorophyll *a* and *b* is expected to be efficiently involved in photon absorption (Ramus, 1983). The shallow water alga,

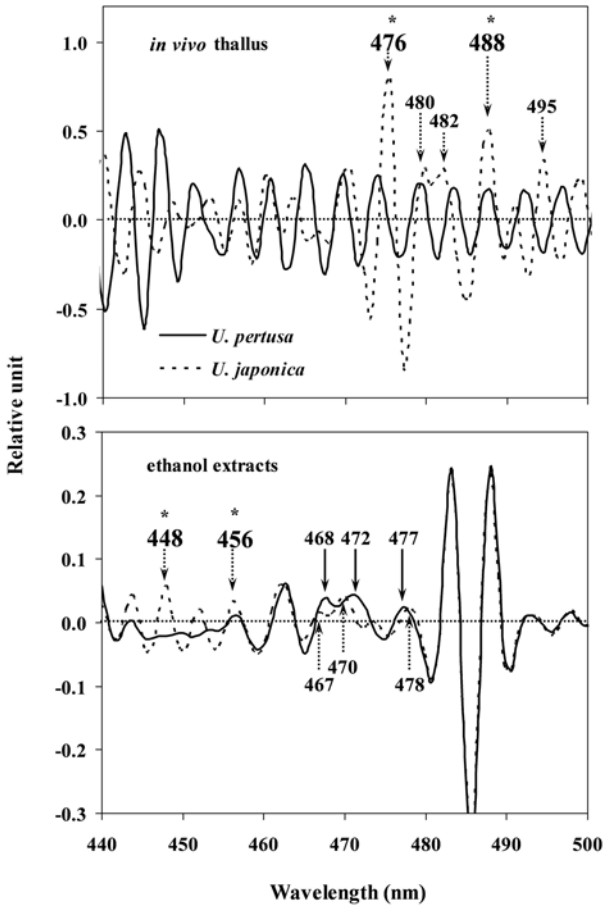

Figure 5. Fourth derivative spectra of mean absorption spectra of *in vivo* thallus and ethanol extracts of *U. pertusa* and *U. japonica*.

U. pertusa, appears to utilize 'white' (in fact, orange-red) quanta far more efficiently than green, complying well with the characteristics of its pigment composition mainly made of chlorophylls and carotenoids whereas the deep water *U. japonica* exhibited unexpectedly increased saturating rates of photosynthesis and quantum yields in green light. Considering that the photosynthetic efficiency is known to be regulated by accessory pigment contents, it is firstly notable that the fourth derivative spectrophotometric determination of *in vivo U. japonica* thallus and ethanol extracts revealed peak positions that fitted well with previously reported absorption maxima for siphonaxanthin and siphonein (Rowan, 1989). On the other hand, no such peaks were found in *U. pertusa*. In this regard, the presence of these green light-absorbing pigments in *U. japonica*, but not in *U. pertusa*, may partly explain the 2.3-fold more efficient photosynthetic use of green light by the former species. In fact, it has been reported that the functional role of siphonaxanthin is to capture light and transfer the energy to Chl *a* with great efficiency (Yokohama, 1989). The deep water species also had significantly higher Chl *b*/*a* ratio than the shallow water species. As the two pigments have absorption peaks in the blue (448 and 456 nm), however, the higher ratio may not account for the more efficient use of green light for photosynthesis. It has been suggested in green macroalgae that Chl *b*/*a* ratios are species-specific characteristics, but not adaptive values (Keast and Grant, 1976).

U. pertusa may not require high efficiency to capture light as it occupies ecological niches exposed to predictably high light whereas, in its native habitats that receive limited amounts of photons, *U. japonica* would need to make efficient use of the light available. The higher α indicates that *U. japonica* has a more efficient way of converting light into

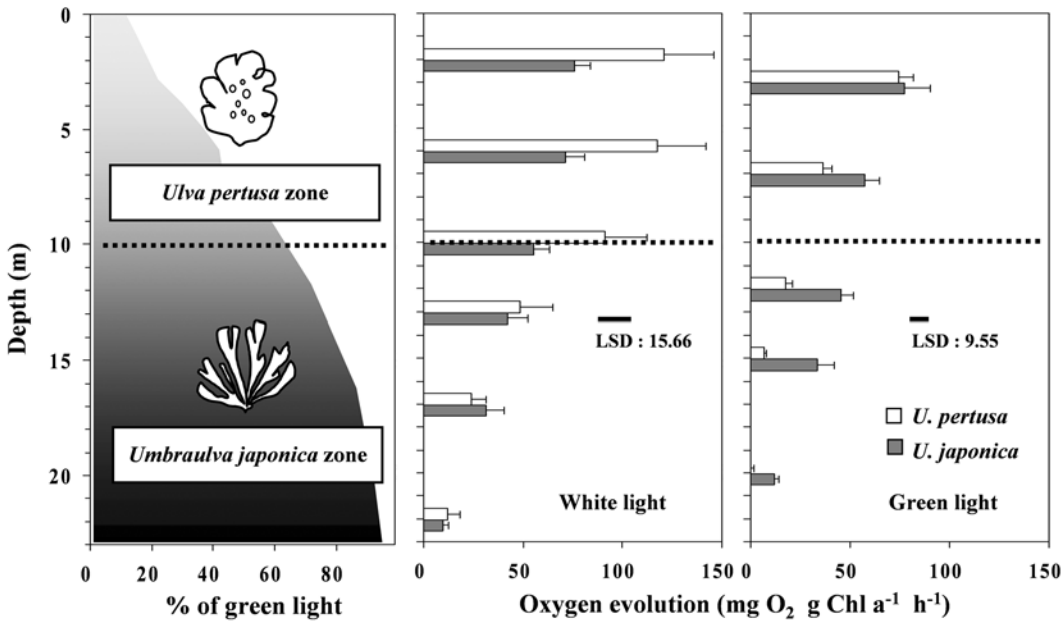

Figure 6. Estimated photosynthetic rates of *U. pertusa* and *U. japonica* at different depths in Ahnin coastal waters. Biologically effective irradiance (BEI) was calculated for artificial lamps used for photosynthetic rate measurements in the laboratory, as well as solar radiation reaching a given depth. A conversion factor was then determined to match measurements from the artificial lamps with those from solar radiation with corresponding BEIs. Each value of photosynthetic rates derived from white and green light was then plotted against the depth of the corresponding BEI.

fixed carbon at limiting irradiances and it would give *U. japonica* a competitive advantage over *U. pertusa* in shaded and greenish habitats.

Saturating irradiances for an alga tend to show some correlation with the species' habitat (Lobban and Harrison, 1994). The I_k value (79 μmol m^{-2} s^{-1}) for *U. pertusa* seems to be very low for this plant mainly occupying the intertidal zone (Yokohama, 1989), and even lower than those previously reported for the same species (Han et al., 2003a). It is characteristic of early colonizer species to show great physiological plasticity in terms of photosynthesis, growth and acclimation potential (Bazzaz and Picket, 1980). In diverse light climate conditions in shallow waters, elasticity of light requirements for photosynthesis may be a coping mechanism for the plant's survival (Han et al., 2003a). On the other hand, the I_k value (54 μmol m^{-2} s^{-1}) for *U. japonica* appears to be equivalent to that of deep subtidal algae (Lüning, 1990) confirming that this species is a shade alga.

Photoinihibition

Changes in the F_v / F_m ratio in response to high PAR treatment seem to correspond with the plants' habitat-related sensitivity. After exposures to high PAR levels equivalent to those recorded between the surface and 2 m depth in Ahnin coastal waters, both species exhibited a significant decline in F_v / F_m, with the degree of reduction being more pronounced in *U. japonica*. The recovery kinetics were even more markedly different between the two species. While *U. pertusa* showed fast and almost complete recovery within an hour, *U. japonica* had a slow and limited recovery in maximal photosynthetic efficiency over a 24-h period.

The two species also showed contrasting photosynthetic activities in response to short-term (1-2 h) exposure to UV-B radiation at an irradiance that simulated ambient surface water levels (Han et al., 2003b). *U. pertusa* was insensitive to UV-B irradiation, whereas *U. japonica* experienced a significant photoinhibition with only slight subsequent recovery in dim light. Recent research has revealed that sensitivity to high PAR and UV-B radiation varies among different species, and that intertidal species potentially exposed to high solar radiation are more resistant to UV-B radiation than their subtidal counterparts (Franklin and Forster, 1997).

It is widely known that reactive oxygen species (ROS) such as O_2^{1-}, $^1O_2$, ·OH, and H_2O_2 produced upon exposure to high PAR and UV-B are involved in the mechanism of photoinhibition (Franklin and Forster, 1997). Algal resistance to such stress factors may be associated with the antioxidant capacity of algae, as the increased levels of antioxidant constituents may prevent stress damage (Richter et al., 2003). The present study revealed significantly higher non-enzymatic antioxidant activity in *U. pertusa* than in *U. japonica*, as determined by the DPPH scavenging rate, corresponding with the greater tolerance to high PAR or UV-B in the former species.

Ecological Significance

It is expected that each species will occur in the depth range at which sufficient light is available for photosynthesis and where excessive irradiances can be tolerated or compensated for by recovery. In order to correlate available light climate with the ecological significance for vertical distribution of the plants, laboratory measurements of P-I relations were used to estimate *in situ* photosynthetic performance. Extrapolating the results to possible events in nature presents many difficulties due to the difference in energy distribution within the PAR range between the lamps and sunlight. Expressing irradiance in terms of biologically effective irradiance (BEI) would, however, permit the comparison of treatments administered under laboratory conditions to radiation occurring under natural conditions. In this study, the BEI was calculated as the product of the spectral irradiance and the *in vivo* thallus absorption spectrum. Figure 6 shows photosynthetic rates of the studied algae at different depths, plotted based on BEIs transformed from *in situ* irradiances measured at midday on a sunny day in Ahnin coastal waters. The photosynthetic rates derived from white light were estimated to be significantly higher in *U. pertusa* than in *U. japonica* at depths down to 10 m, below which interspecific difference in the rates would not be expected. Estimates of photosynthetic performance based on green light measurements suggest that *U. japonica* could have significantly higher photosynthetic rates than *U. pertusa* for the whole water depth profile starting from 3 m below the surface. Considering that green wavelength light constitutes more than 50% of the total PAR at 10 m (Fig. 6, left panel), the latter scenario would be more reflective of what could happen in the field. Therefore, significantly higher photosynthetic activity at limiting irradiances of green light appears to provide *U. japonica*, but not *U. pertusa*, the physiological capacity to extend its vertical range of distribution into depths greater than 10 m.

Tolerance of high light stress may be one factor determining the competitive ability of macroalgae at the upper limits of their zones (Franklin and Forster, 1997). *U. pertusa* may achieve full protection against the adverse effects of high PAR and UV-B by exhibiting dynamic photoinhibition, possibly related to the xanthophyll cycle or to antioxidant activity, in addition to their known properties of forming multicellular mats, photorepair and synthesizing UV-B protective compounds (Han et al., 2004; Han and Han, 2005). In contrast, exposure to sunlight between the surface and 2 m depth could cause severe photodamage to the PS II of *U. japonica*. And, even if it initially survived the intense solar irradiances, subsequent incomplete photosynthetic competence due to its low capacity to restore PS II activity may prevent it from flourishing in the surface water environment. Vulnerability to high solar irradiance may therefore be a reason for the usual absence of *U. japonica* from shallow waters (Yokohama, 1989).

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