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Research Article

The Effects of UV Radiation on Chloroplast Clumping and Photosynthesis in the Seagrass *Halophila stipulacea* Grown under High-PAR Conditions

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Since potentially harmful ultraviolet radiation (UVR, 280–400 nm) and high photosynthetically active radiation (PAR, 400–700 nm) are present in the shallow waters of the Gulf of Aqaba where part of the seagrass *Halophila stipulacea's* population thrives, we examined the effects of high PAR with and without UVR on its photosynthesis and midday chloroplast "clumping phenomenon" (Sharon and Beer 2008). It was found that midday clumping occurred only under high PAR in the presence of UVR, which resulted in a 44% reduction in the absorption cross section (or absorption factor, AF) of the leaves and, accordingly, a parallel lowering of midday electron transport rates (ETR). In addition, UVR had a direct effect on the photosynthetic apparatus by lowering quantum yields and, thus, ETRs, while pigment relations remained unaltered. We conclude that the potentially harmful effects of UVR and high PAR on the photosynthetic apparatus of *Halophila stipulacea* are mitigated by their activation of chloroplast clumping, which functions as a means of protecting most chloroplasts from high irradiances, including UVR.

1. Introduction

While the mechanisms underlying chloroplast movements in plants have been studied on the intracellular and molecular levels [1, 2] their ecophysiological role(s) is less understood. These movements are in many plants induced by blue light [3–8], but in a few studies it was suggested that also ultraviolet (UV), or "near to UV", wavelengths could trigger chloroplast movements [9, 10]. Interestingly, Kondo et al. [11] reported that in many cases the chloroplast clumps are formed near or around the nuclei so as to protect them from high irradiances.

The only seagrass so far for which chloroplast movements have been described is *Halophila stipulacea* [12, 13]. In the latter work, it was found that chloroplast clumping occurred during midday only in plants growing under high irradiances (>450 μmol photons m^{-2} s^{-1}), while lower-irradiance grown plants maintained their chloroplasts evenly dispersed during the day. It was then suggested that the chloroplast clumping during midday may have a protective role against high irradiances.

In addition to high photosynthetically active radiation (PAR, 400–700 nm), coastal waters, especially clear tropical waters, also feature high levels of ultraviolet radiation (UVR, 280–400 nm) in their upper layers ([14, 15] and this study). Various marine plants respond to such high UVR levels by producing mycosporine-like amino acids (MAA, [16, 17]) and other UV absorbing compounds (i.e., flavones and flavones glycosides in seagrasses, [18–20]), changing morphologies [21], changing pigment contents [17, 22], downregulation of photosystem II (PSII, [23]), or shading by carbonate layers [24]. Also epiphytes may decrease the UVR (as well as PAR) levels reaching the leaves [25, 26]. Since many seagrasses thrive in clear tropical shallow waters, it may be that the midday chloroplast clumping found in at least one of them (*Halophila stipulacea*) has a protective role against UVR (in addition to high PAR as suggested by Sharon and Beer [13]). In light of this possibility, we investigated the role

Table 1: Midday values of PAR and UVR and percentage transmittances (%) of the in situ downwelling (at 6 and 30 m) and 50%-shaded water-table (under the control- and UV-filters) PAR (400–700 nm) and UVR (300–400 nm). The water-table values were measured on April 10, 2007, and the in situ values were measured on April 1, 2008, offshore the IUI, with the PRR-800 profiling radiometer (BioSpherical Instruments).

	PAR		UVR	
	(μmol photons m^{-2} s^{-1})	(%)	(μW m^{-2})	(%)
In situ, 6 m	750	45	2116	50
In situ, 30 m	90	5	134	3.0
Water-table + control-filter	860	45	2132	41
Water-table + UV-filter	860	45	192	7.4

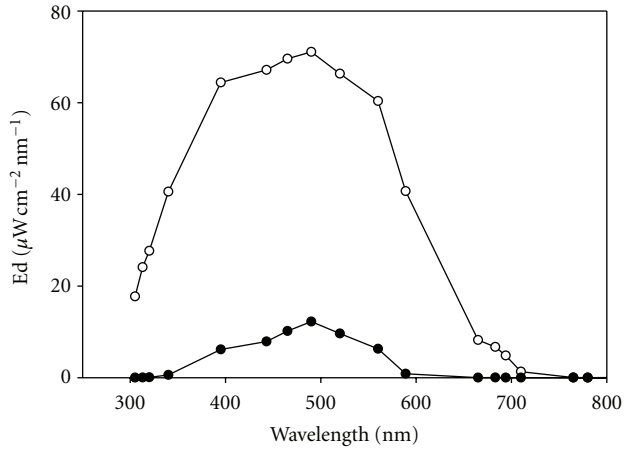


Figure 1: In situ transmitted downwelling irradiance (Ed) at 6 m (open circles) and 30 m (closed circles) measured with the PRR-800 (BioSpherical Instruments) on April 1, 2008, offshore the IUI.

of UVR in mediating chloroplast movements in this seagrass and the effects of UVR on some of its photosynthetic traits in plants acclimated to high irradiances.

2. Materials and Methods

Whole plants (including roots and rhizomes) of *Halophila stipulacea*, together with surrounding sediments, were collected at 20 m depth from the densest part of a monospecific meadow (extending from 7 to 33 m at the time of this study; the tidal range is <40 cm) located ca. 200 m south of the Inter-University Institute (IUI) in Eilat, Gulf of Aqaba, northern Red Sea (29°30′ N, 34°54′ E) during March and April, 2007. These plants were grown in cups containing their natural fine sandy sediment on an outdoor water table (a table with a 20 cm margin, forming a shallow container) through which natural seawater at 21°C was flowing. Thus, the leaves were submerged 5–10 cm under the water surface. The water table was shaded by a neutral-density net allowing 50% of the natural sunlight to reach the plants. Typical irradiances under the net were ~850 μmol photons m^{-2} s^{-1} during midday. The light under the shading net was further screened either through UV filters (supplied by the GKSS Forschungszentrum, Germany) placed just above the water surface over some of the plants or through control filters that transmitted UVR (from the same supplier). Both filters reduced PAR by ~20%, while the UV filter reduced wavelengths <400 nm by >80% (see Table 1 and Figure 2). The wavelength-dependent transmittance properties of the filters were verified using a miniature-fibre optical spectrometer (USB 2000, Ocean Optics, USA). All plant measurements were done after 14 days of acclimation to the water-table conditions. This time was found to be enough for the plants to feature diurnal chloroplast clumping under the control filters and was also found to be sufficient for the acclimation of several photosynthetic parameters to the chosen light regimes (see also [27]).

The solar irradiance (PAR and UVR) reaching the water surface was measured by a CM11B (Kipp & Zonen, The Netherlands) sensor at the IUI pier (displayed also at http://www.meteo-tech.co.il/eilat-yam/eilat_daily.asp). Spectral radiation measurements were done using a profile reflectance radiometer (PRR-800, BioSpherical Instruments Inc., USA) equipped with both spectral channel (300–875 nm, μW cm^{-2} nm^{-1}) and PAR (400–700 nm, μmol photons m^{-2} s^{-1}) sensors. Underwater spectral measurements of downwelling UVR, PAR, and infrared radiation were also done using the PRR-800, which was lowered from a boat offshore the IUI using a free-fall system (cf. [28]) in order to avoid boat shading and to keep the instrument in a vertical posture.

Chloroplast clumping was verified through microscopic observations on live leaves within 2 min of collection (using a Nikon YS100, Japan). The absorption cross sections (or absorption factor, AF) of the leaves (i.e., the fraction of incident irradiance absorbed by the photosynthetic pigments of the leaves) were estimated along the day by measuring the PAR above and below a submerged leaf with the Diving-PAM's quantum sensor (while subtracting the absorption of nonchlorophyllous pigments, see [13]). Chlorophyll contents of the leaves were determined after extraction in dimethyl formamide for 24 h in darkness. Absorbance was then measured spectrophotometrically according to Moran [29], and chlorophyll a and b contents were calculated on a leaf area basis. Total carotenoids were measured by their absorption maxima at 480 and 510 nm according to Gradinaru et al. [30]. Absorption spectra (300–400 nm) with special attention to absorption at 340 and 350 nm of the UV absorbing pigments (flavones and flavone-glycosides [20]) were measured after extraction in methanol using an Ultraspec 2100 Pro (Amersham Biosciences, UK) spectrophotometer.

Chlorophyll fluorescence was measured by pulse-amplitude-modulated (PAM) fluorometry using a Diving-PAM (Walz, Germany). Effective quantum yield ($\Delta F/Fm'$) measurements were carried out throughout the day using a leaf-distance clip (Walz, Germany), and photosynthetic electron transport rates (ETR) were calculated as $\Delta F/Fm' \times \text{PAR} \times \text{AF} \times 0.5$; PAR was measured with the Diving-PAM's quantum

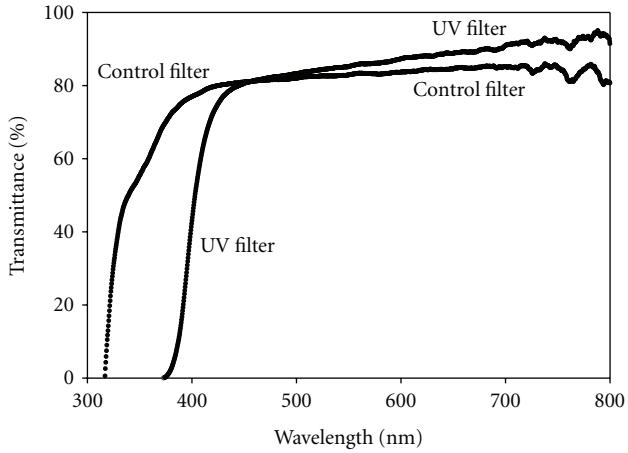


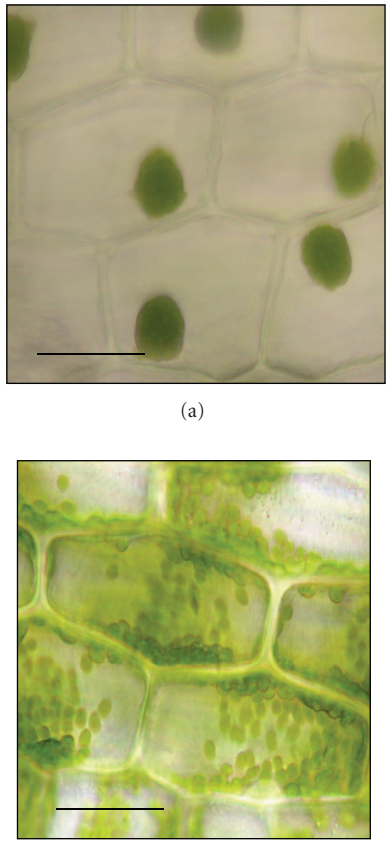
Figure 2: Transmission spectra of the control and UV filters (lines marked in graph) as measured using the USB-2000 (Ocean Optics).

sensor calibrated against a quantum-sensor-equipped Li-250A light meter (LiCor, USA).

3. Results

The midday underwater spectra (300–800 nm) from two depths and the integrated total PAR (400–700 nm) and UVR (300–400 nm) at those depths, as well as on the water table under the control or UV filters, are shown in Figure 1 and Table 1, respectively. The spectra (Figure 1) reveal high UVR values at 6 m depth that could hardly be detected at 30 m. Similarly, there were measurable amounts of red light (650–750 nm) available at 6 m but not at 30 m. In all, approximately 45% and 5% of surface PAR were present at 6 and 30 m depths, respectively, while the corresponding percentages for UVR were 50% and 3% (Table 1). The PAR measured under the filters on the water table was 45% of that of full sunlight while UVR was 41% and 7.4% under the control and UV filters, respectively (see Figure 2 for the spectral transmission of these filters). Unlike UVR, there was no reduction in red wavelengths by the UV filter (Figure 2).

The epidermal leaf cells of plants grown on the water table under control-filtered conditions featured midday clumping of chloroplasts, followed by their dispersal during the evening, while no such chloroplast movements could be detected in the UV-filtered plants (Figure 3). While peaking at midday, chloroplast aggregation and dispersal were observed between 09:00 and 15:00 and were paralleled by decreasing and increasing AF values, respectively. Because the only difference between the treatments was the presence and virtual absence of UVR, it is concluded that the UVR present for the control-filtered plants caused the chloroplast movements at the given PAR that resulted in their midday clumping. More precisely, it is likely that the wavelengths between 280 and 380 nm caused the clumping since these wavelengths were the absolute cut-off points for the control and UV filters, respectively. In comparison, also leaves of plants growing at 6 m depth clumped their chloroplasts during midday while those at 30 m did not ([31] and personal observations). These chloroplast movements resulted in a significant change (44%, $P < 0.0001$, t-test, $n = 10$) in the AF of the control-filter-grown plant leaves from early morning to midday while the UV-filtered plants did not show any significant differences in AF during the day (Figure 4, $P > 0.05$, t-test, $n = 10$); the AF values of the plants growing under the control filters were significantly lower ($P < 0.01$, repeated measure ANOVA, $n = 10$) than those of the UV-filtered plants between 10:00–14:00.



(a)

(b)

Figure 3: Light-microscopic photographs of epidermal cells of *Halophila stipulacea* during midday (at 850 μmol photons m^{-2} s^{-1}) grown for 14 days under a control filter (a) and under a UV filter (b). Black bars represent 10 μm.

Chlorophyll a + b contents showed no significant differences ($P > 0.05$, t-test, $n = 8$) between the UV- and control-filtered water-table plants after 14 days: Chlorophyll a contents were 2.3 ± 0.17 and 2.6 ± 0.27 mg cm^{-2} for the control- and UV-filtered plants, respectively, while chlorophyll b contents were 0.3 ± 0.1 mg cm^{-2} in both control- and UV-screened plants. Also carotenoid-absorption spectral peaks (at 480 and 510 nm) showed no significant difference ($P > 0.05$, t-test, $n = 8$) between the two types of water-table grown plants after 14 days of acclimation. Similarly, neither the absorption spectra in the region where flavones and flavones glycosides absorb (340–350 nm), nor the peak maxima of anthocyanin (290 nm), showed significant differences ($P > 0.05$, t-test, $n = 8$) between treatments with or without UVR.

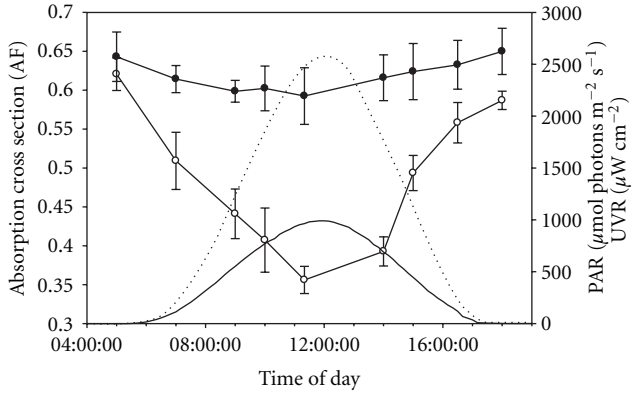


Figure 4: Daily changes in the absorption cross section (or absorption factor, AF) of plants grown on the water table for 14 days under control filters (open circles) or UV filters (closed circles), and PAR (400–700 nm) measured above the plants on the water table (full line) and UVR (300–400 nm) under the control filter (dotted line; there was no measurable UVR under the UV filter). Data points of AF are means of 10 replicates ± SE.

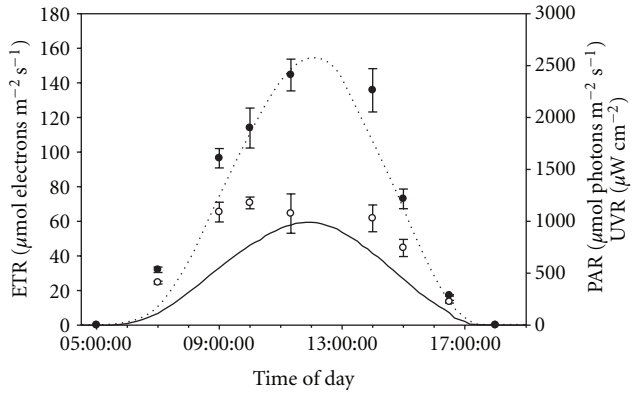


Figure 5: Daily changes in electron transport rates (ETR) of plants grown on the water table for 14 days under control filters (open circles) or UV filters (closed circles), and PAR (400–700 nm) measured above the plants on the water table (full line) and UVR (300–400 nm) under the control filter (dotted line; there was no measurable UVR under the UV filter). Data points are means of 8 replicates ± SD.

Photosynthetic ETRs of the plants grown on the water table with or without UV screening are presented in Figure 5. Since these ETRs were calculated according to their respective AF values during the various times of the day (see Figure 4, cf. [13]), it follows that the differences in ETRs between control- and UV-filtered plants are partly due to the differences in AFs (here termed an "indirect" UVR effect). The maximum ETR reached at around midday by the UVR-protected plants coincided with the highest PAR reaching the water table while the ETRs for the control plants levelled off in the morning after ca. 9 o'clock. This, as well as the fact that the midday decrease in ETR in the control-filtered plants was more than the 44% that could be accounted for by the decrease in AF, indicates an excessive decrease of effective photosynthetic quantum yields by UVR under high PAR

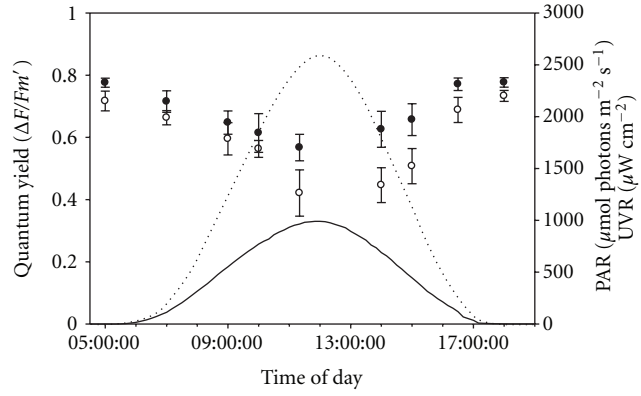


Figure 6: Daily changes in effective quantum yield ($\Delta F/Fm'$) of plants grown on the water table for 14 days under control filters (open circles) or UV filters (closed circles) and PAR (400–700 nm) measured above the plants on the water table (full line) and UVR (300–400 nm) under the control filter (dotted line; there was no measurable UVR under the UV filter). Data points are means of 8 replicates ± SD.

during the high-irradiance hours of the day. Indeed, $\Delta F/Fm'$ values were significantly lower ($P < 0.05$, t-test, $n = 8$) in the control-filtered than the UV-filtered plants from around 11:30 and throughout the afternoon (Figure 6), confirming a higher downregulation of PSII in the former as caused by UVR with high PAR (here termed a "direct" UVR effect).

4. Discussion

In a previous study, we suggested that the midday chloroplast clumping observed in *Halophila stipulacea* had a photoprotective role against high PAR during midday [13]. Here, we found that it is UVR that triggers the diurnal chloroplast movements that cause their midday clumping under high-PAR conditions. This was realised at midday UVR values of ca. 2000 μW m^{-2} on the water table (while filtering out UV prevented clumping). In nature, at depths where clumping does not occur (below ca. 10 m, at PARs <400 μmol photons m^{-2} s^{-1}), reduced UVR is usually accompanied with low PAR, but the UVR/PAR ratio may also change (here it was reduced by 46% from 6 to 30 m). Thus, it is possible that also the UVR/PAR ratio has an effect on the clumping phenomenon in shallow waters, but this was not quantified here. While the surface irradiance characteristics of the region where this study was conducted (northern Red Sea) are among the highest in the world [32], we were intrigued by finding high UVR doses similar to those on the shaded water table also in situ at 6 m depth. Indeed, midday chloroplast clumping was observed at that depth [31]. Thus, apparently, the successful adaptation of this plant to shallow waters (~6 m at the site studied) is partly based on its ability to reduce the absorption cross section (or AF) via chloroplasts movements, apparently resulting in protection from high irradiances, including UVR. In addition to shading one another, the clumped chloroplasts could protect the nucleus and its genetic material from excess UV (such as suggested by Kondo et al. [11]).

While it was found in an earlier work that PAR correlated negatively with chlorophyll concentrations [13], manipulating UVR under constant PAR did not cause any changes in chlorophyll nor carotenoid contents in *Halophila stipulacea*. Supportively, also another *Halophila* species (*Halophila johnsonii*) did not show differences in absorption peak maxima for any photosynthetic and UV-protecting pigments when acclimated to various PAR and UV treatments [19] (but did increase its flavone and flavone-glycoside contents as a response to increased salinity, [33]). The apparent failure of *Halophila stipulacea* to induce the formation of UV-protecting substances stands in contrast to other tropical shallow-growing seagrasses [20, 22], corals [34], microalgae [17], and macroalgae [35], many of which do protect their tissues from UVR by the formation of UV-absorbing pigments. As based on our findings, apparently *Halophila stipulacea* utilizes chloroplast clumping instead of generating UV-blocking compounds in order to protect itself from high UVR and PAR. This mechanism may also be present in *Halophila ovalis*, which was found to produce less UV-blocking pigments than other genera [22], but this still needs to be proven.

While the reduction in midday ETRs was largely an indirect effect of UVR via the decreased AF values caused by the clumping of chloroplasts, UVR also affected photosynthesis directly by reducing quantum yields. The daily reduction in effective quantum yield can be seen as a dynamic form of photoinhibition (or downregulation of PSII) since values in the evening returned to morning values. One mechanism that could explain this midday reduction in effective quantum yields is the operation of the xanthophyll cycle, in which excess light energy is dissipated as heat [36]. Also, reaction centre repair via gene activation (e.g., D1-repair genes, [37]) can reduce photodamage and can be measured as a reversible diurnal damage. In addition, but to a lesser degree than the effective quantum yield, the maximal quantum yield (*Fv/Fm*) was also reduced by UVR with the acclimation time to the water-table conditions (data not shown). Since *Fv/Fm* is measured in predawn darkness, this decrease reflects an incomplete recovery from high irradiances that might indicate some chronic damage in the PSII repair mechanism. Thus, as part of the more general negative effects of UVR on phytoplankton [15] and other marine photosynthetic organisms [38], the chloroplast-based photosynthetic apparatus of some seagrasses is also influenced by UVR or high PAR with UVR. Perhaps logically, this radiation also activates mechanisms such as chloroplast clumping and a dynamic downregulation of photosystem II that protect at least *Halophila stipulacea* against it.

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References

[1] N. Suetsugu and M. Wada, "Chloroplast photorelocation movement mediated by phototropin family proteins in green plants," *Biological Chemistry*, vol. 388, no. 9, pp. 927–935, 2007.

[2] W. Yamashita, T. Kanegae, and A. Kadota, "Analyses on the actin dynamics during chloroplasts photorelocation movement in the moss Physcomitrella patens by use of tdTomato-talin," *Plant and Cell Physiology*, vol. 48, article 55, 2007.

[3] H. Gabryś, "Blue light-induced orientation movements of chloroplasts in higher plants: recent progress in the study of their mechanisms," *Acta Physiologiae Plantarum*, vol. 26, no. 4, pp. 473–478, 2004.

[4] S. L. DeBlasio, J. L. Mullen, D. R. Luesse, and R. P. Hangarter, "Phytochrome modulation of blue light-induced chloroplast movements in arabidopsis," *Plant Physiology*, vol. 133, no. 4, pp. 1471–1479, 2003.

[5] N. Sakuri, K. Domoto, and S. Takagi, "Blue light-induced reorganization of the actin filaments and the avoidence response of chloroplasts in epidermal cells of *Vallisneria gigatea*," *Planta*, vol. 221, pp. 66–74, 2005.

[6] D. R. Luesse, S. L. DeBlasio, and R. P. Hangarter, "Plastid movement impaired 2, a new gene involved in normal blue-light-induced chloroplast movements in *Arabidopsis*," *Plant Physiology*, vol. 141, no. 4, pp. 1328–1337, 2006.

[7] W. Krzeszowiec, B. Rajwa, J. Dobrucki, and H. Gabryś, "Actin cytoskeleton in Arabidopsis thaliana under blue and red light," *Biology of the Cell*, vol. 99, no. 5, pp. 251–260, 2007.

[8] I. Shihira-Ishikawa, T. Nakamura, S. I. Higashi, and M. Watanabe, "Distinct responses of chloroplasts to blue and green laser microbeam irradiations in the centric diatom *Pleurosira laevis*," *Photochemistry and Photobiology*, vol. 83, no. 5, pp. 1101–1109, 2007.

[9] H. Yatsuhashi, "Photoregulation systems for light-oriented chloroplast movement," *Journal of Plant Research*, vol. 109, no. 1094, pp. 139–146, 1996.

[10] V. Rodrigues, R. Bhandari, J. P. Khurana, and P. K. Sharma, "Movement of chloroplasts in mesophyll cells of Garcinia indica in response to UV-B radiation," *Current Science*, vol. 92, no. 11, pp. 1610–1613, 2007.

[11] A. Kondo, J. Kaikawa, T. Funaguma, and O. Ueno, "Clumping and dispersal of chloroplasts in succulent plants," *Planta*, vol. 219, pp. 500–506, 2004.

[12] E. A. Drew, "Physiological aspects of primary production in seagrasses," *Aquatic Botany*, vol. 7, pp. 139–150, 1979.

[13] Y. Sharon and S. Beer, "Diurnal movements of chloroplasts in *Halophila stipulacea* and their effect on PAM fluorometric measurements of photosynthetic rates," *Aquatic Botany*, vol. 88, no. 4, pp. 273–276, 2008.

[14] R. P. Dunne and B. E. Brown, "Penetration of solar UVB radiation in shallow tropical waters and its potential biological effects on coral reefs; results from the central Indian Ocean and Andaman Sea," *Marine Ecology Progress Series*, vol. 144, no. 1—3, pp. 109–118, 1996.

[15] S. Agustí and M. Llabrés, "Solar radiation-induced mortality of marine pico-phytoplankton in the oligotrophic ocean," *Photochemistry and Photobiology*, vol. 83, no. 4, pp. 793–801, 2007.

[16] K. Whitehead and M. Vernet, "Influence of mycrosporine-like amino acids (MAAs) on UV absorption by particulate and dissolved organic matter," *Limnology and Oceanography*, vol. 45, pp. 1788–1796, 2000.

[17] K. Gao, Y. Wu, G. Li, H. Wu, V. E. Villafañe, and E. W. Helbling, "Solar UV radiation drives CO_2 fixation in marine phytoplankton: a double-edged sword," *Plant Physiology*, vol. 144, no. 1, pp. 54–59, 2007.

[18] M. J. Durako, J. I. Kunzelman, W. J. Kenworthy, and K. K. Hammerstrom, "Depth-related variability in the photobiology of two populations of Halophila johnsonii and Halophila decipiens," *Marine Biology*, vol. 142, pp. 1219–1228, 2003.

[19] J. I. Kunzelman, M. J. Durako, W. J. Kenworthy, A. Stapleton, and J. L. C. Wright, "Irradiance-induced changes in the photobiology of *Halophila johnsonii*," *Marine Biology*, vol. 148, no. 2, pp. 241–250, 2005.

[20] Y. Meng, A. J. Krzysiak, M. J. Durako, J. I. Kunzelman, and J. L. C. Wright, "Flavones and flavone glycosides from *Halophila johnsonii*," *Phytochemistry*, vol. 69, no. 14, pp. 2603–2608, 2008.

[21] K. Monro and A. G. B. Poore, "Light quantity and quality induce shade-avoiding plasticity in a marine macroalga," *Journal of Evolutionary Biology*, vol. 18, no. 2, pp. 426–435, 2005.

[22] S. P. Dawson and W. C. Dennison, "Effects of ultraviolet and photosynthetically active radiation on five seagrass species," *Marine Biology*, vol. 125, no. 4, pp. 629–638, 1996.

[23] F. L. Figueroa, C. Jiménez, B. Viñegla et al., "Effects of solar UV radiation on photosynthesis of the marine angiosperm *Posidonia oceanica* from southern Spain," *Marine Ecology Progress Series*, vol. 230, pp. 59–70, 2002.

[24] K. S. Beach, H. B. Borgeas, and C. M. Smith, "Ecophysiological implications of the measurement of transmittance and reflectance of tropical macroalgae," *Phycologia*, vol. 45, no. 4, pp. 450–457, 2006.

[25] R. P. Trocine, J. D. Riceand, and G. N. Wells, "Inhibition of seagrass photosynthesis by Ultraviolet-B radiation," *Plant Physiology*, vol. 68, pp. 74–81, 1981.

[26] L. A. Brandt and E. W. Koch, "Periphyton as a UV-B filter on seagrass leaves: a result of different transmittance in the UV-B and PAR ranges," *Aquatic Botany*, vol. 76, no. 4, pp. 317–327, 2003.

[27] Y. Sharon, J. Silva, R. Santos, J. W. Runcie, M. Chernihovsky, and S. Beer, "Photosynthetic responses of *Halophila stipulacea* to a light gradient. II. Acclimations following transplantation," *Aquatic Biology*, vol. 7, no. 1-2, pp. 153–157, 2009.

[28] J. T. O. Kirk, *Light and Photosynthesis in Aquatic Systems*, Cambridge University Press, Cambridge, UK, 1994.

[29] R. Moran, "Formulae for determination of chlorophyllous pigments extracted with *N,N*-dimethylformamide," *Plant Physiology*, vol. 69, pp. 1376–1381, 1982.

[30] C. C. Gradinaru, I. H. M. van Stokkum, A. A. Pascal, R. Van Grondelle, and H. van Amerongen, "Identifying the pathways of energy transfer between carotenoids and chlorophylls in LHCII and CP29. A multicolor, femtosecond pump-probe study," *Journal of Physical Chemistry B*, vol. 104, no. 39, pp. 9330–9342, 2000.

[31] J. W. Runcie, D. Paulo, R. Santos, Y. Sharon, S. Beer, and J. Silva, "Photosynthetic responses of *Halophila stipulacea* to a light gradient. I. In situ energy partitioning of non-photochemical quenching," *Aquatic Biology*, vol. 7, no. 1-2, pp. 143–152, 2009.

[32] G. Winters, Y. Loya, R. Röttgers, and S. Beer, "Photoinhibition in shallow-water colonies of the coral *Stylophora pistillata* as measured *in situ*," *Limnology and Oceanography*, vol. 48, no. 4, pp. 1388–1393, 2003.

[33] A. E. Kahn and M. J. Durako, "Photophysiological responses of Halophila johnsonii to experimental hyposaline and hyper-CDOM conditions," *Journal of Experimental Marine Biology and Ecology*, vol. 367, pp. 230–235, 2008.

[34] W. C. Dunlap and J. M. Shick, "Ultraviolet radiation-absorbing mycosporine-like amino acids in coral reef organisms: a biochemical and environmental perspective," *Journal of Phycology*, vol. 34, no. 3, pp. 418–430, 1998.

[35] U. Karsten, T. Sawall, D. Hanelt et al., "An inventory of UV-absorbing mycosporine-like amino acids in macroalgae from polar to warm-temperate regions," *Botanica Marina*, vol. 41, no. 5, pp. 443–453, 1998.

[36] B. Demmig-Adams and W. W. Adams, "Photoprotection in an ecological context: the remarkable complexity of thermal energy dissipation," *New Phytologist*, vol. 172, no. 1, pp. 11–21, 2006.

[37] M. Kimura, Y. Y. Yamamoto, M. Seki et al., "Identification of *Arabidopsis* genes regulated by high light-stress using cDNA microarray," *Photochemistry and Photobiology*, vol. 77, no. 2, pp. 226–233, 2003.

[38] R. P. Sinha, M. Klisch, A. Groniger, and D. P. Hader, "Ultraviolet-absorbing/screening substances in cyanobacteria, phytoplankton and macroalgae," *Journal of Photochemistry and Photobiology B*, vol. 47, no. 2-3, pp. 83–94, 1998.