Provided for non-commercial research and education use. Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

http://www.elsevier.com/copyright

Aquatic Botany 91 (2009) 245-249

Contents lists available at ScienceDirect



Aquatic Botany



journal homepage: www.elsevier.com/locate/aquabot

## Short communication

# Wavelength-specific photosynthetic responses of *Halophila johnsonii* from marine-influenced versus river-influenced habitats

# Amanda E. Kahn, Michael J. Durako\*

Department of Biology and Marine Biology, University of North Carolina Wilmington Center for Marine Science, 5600 Marvin Moss Lane, Wilmington, NC 28409, United States

#### ARTICLE INFO

Article history: Received 30 September 2008 Received in revised form 16 June 2009 Accepted 22 June 2009 Available online 30 June 2009

Keywords: Halophila johnsonii Seagrass Action spectra Photophysiology UV pigments

#### ABSTRACT

The seagrass Halophila johnsonii Eiseman grows from the upper intertidal to 3 m depths in habitats ranging from near-marine inlets to tidal riverine. These habitats have distinct optical characteristics, primarily due to variable concentrations of watershed-derived chromophoric dissolved organic matter (CDOM), which increases the attenuation of short-wavelength (blue and UV) light. H. johnsonii contains a suite of flavonoids that are thought to serve as UV-protective pigments (UVP). In this study, photosynthetic responses at specific wavelengths were compared between plants from a riverinfluenced high-CDOM habitat (Oleta River) and those from an adjacent marine, low-CDOM environment (Haulover Inlet) in Florida. Oxygen flux was used to measure dark respiration and photosynthesis under near-constant radiant energy at nine specific wavelengths from 340 to 730 nm. Riverine plants had higher gross photosynthetic rates and quantum efficiencies than inlet plants at the shortest wavelengths (350, 400 and 450 nm), while inlet plant photosynthetic rates and quantum efficiencies were higher at the two longest wavelengths measured (694 and 730 nm). Riverine plants also exhibited greater variation in photosynthetic responses across the spectrum and more variable pigment levels among replicates. Chlorophyll a and b concentrations were significantly greater in riverine plants suggesting that they were more shade-acclimated compared to the marine populations. Differences in wavelength-specific photosynthetic responses and chlorophyll levels indicate that the riverine plants were blue-shade acclimated. The higher and more variable UVP levels in the riverine population were not consistent with shade acclimation; however, these flavonoid pigments may protect chloroplasts from photodamage during short-term, high intensity irradiance conditions that occur over the course of tidal cycles at this highly fluctuating riverine site.

© 2009 Elsevier B.V. All rights reserved.

### 1. Introduction

Photosynthetic responses to variations in light quality have been examined in corals, macro- and microalgae and land plants (Lüning and Dring, 1985; Bukhov et al., 1995; Lesser and Lewis, 1996; Mouget et al., 2004). In addition, light quality has been shown to affect plant growth (Tattini et al., 2004; You and Barnett, 2004; Godínez-Ortega et al., 2008) pigment composition (Franklin et al., 2001; Mercado et al., 2004; Mouget et al., 2004), and spectral quantum yields (Lüning and Dring, 1985). The light quality and quantity to which *Halophila johnsonii* is exposed, is highly variable among habitat types as this seagrass grows from the intertidal zone to 3 m depths in both marine- and river-influenced environments in southeastern Florida (Virnstein and Morris, 1996). Variation in light quality, especially in river-influenced habitats, is high and mainly due to variable but relatively high concentrations of chromophoric dissolved organic matter (CDOM). CDOM exponentially absorbs short-wavelength light (UV-blue, Kirk, 1994). Compared to plants from low-CDOM environments, differences in light quantity and quality in a river-influenced environment, particularly at shorter wavelengths, may affect photosynthetic responses of riverine *H. johnsonii* populations.

UV-absorbing compounds, such as mycosporine-like amino acids (MAAs), in other marine photosynthetic organisms, such as dinoflagellates and red algae, increase under increased shortwavelength irradiance (Klisch and Häder, 2002; Korbee et al., 2005). The green alga *Dasycladus* increases UV-screening compounds in response to increased UV radiation, as does the seagrass *Thalassia testudinum*; though the compounds in these two plants are different from MAAs (Gómez et al., 1998; Detrés et al., 2001). *H. johnsonii* contains UV-absorbing accessory pigments that are thought to function as UV-protecting pigments (UVPs, Durako et al., 2003; Kunzelman et al., 2005; Krzysiak, 2006). *H. johnsonii* contains a suite of 15 flavonoid compounds, 7 of which were

<sup>\*</sup> Corresponding author. Tel.: +1 910 962 2373; fax: +1 910 962 2410. *E-mail address:* durakom@uncw.edu (M.J. Durako).

<sup>0304-3770/\$ –</sup> see front matter  $\circledcirc$  2009 Elsevier B.V. All rights reserved. doi:10.1016/j.aquabot.2009.06.004

A.E. Kahn, M.J. Durako/Aquatic Botany 91 (2009) 245-249

previously undescribed (Meng et al., 2008). Flavonoid compounds are widely distributed in plants and are known to serve as UVPs, as well as having a variety of other functions (Harborne and Williams, 2000). Durako et al. (2003) observed a decrease in UV-absorbing pigments when intertidal plants were transplanted into a deeper habitat and they suggested that in H. johnsonii, the compounds may play a role in the ability of this species to colonize the upper edge of intertidal habitats to the exclusion of the co-occurring subtidal congeneric, Halophila decipiens, which lacks UVPs. Other studies have suggested that the UVP production in H. johnsonii is a response to increased photosynthetically active irradiance (PAR) or that they serve a secondary physiological function and respond to general stress (Kunzelman et al., 2005; Kahn and Durako, 2008). However, it is unknown how the presence and variation in concentration of the UVPs affects photosynthetic responses of H. *johnsonii* in habitats of different light quality conditions.

The purpose of this study was to examine wavelength-specific photosynthetic responses in *H. johnsonii* from marine-influenced (low-CDOM) vs. river-influenced (high-CDOM) habitats. Photosynthetic pigments and UVP absorbance were also compared between plants from each site. We hypothesized that decreased UV stress in plants from high CDOM environments may allow for more efficient photosynthesis, particularly at shorter wavelengths, because of the reduced need for UVPs in these plants.

#### 2. Materials and methods

*H. johnsonii* plants were collected in July 2008 at approximately 1 m depths from a site near Haulover Inlet (25°54′N, 80°07′W) and a site by the mouth of the Oleta River (25°55′N, 80°07′W) in northern Biscayne Bay, Florida. Water depth was measured using a graduated pole ( $\pm$ 5 cm) at the initiation of sampling. Apparent optical properties at these two sites were previously determined during seasonal sampling (Kahn, 2008). Water column irradiance profiles (10 cm increments) were recorded with a SATLANTIC<sup>®</sup> spectral radiometer at seven specific wavelengths: 412, 443, 490, 510, 554 and 665 nm. The spectral light attenuation coefficient [ $K_d(\lambda)$ ] at 412 nm was calculated as an estimate for CDOM using the following equation (Kirk, 1994):

$$K_d(\lambda) = \frac{\ln(E_z(\lambda)/E_o(\lambda))}{z}$$

where  $E_o(\lambda)$  is the irradiance of a specific wavelength measured at subsurface and  $E_z(\lambda)$  is the irradiance at that wavelength at each given depth, *z*, with increments of 10 cm. Over a yearlong period, the two sites consistently exhibited optical conditions characteristic of river- and marine-influenced environments (Fig. 1; Kahn, 2008).

Rhizome segments of *H. johnsonii*, containing at least four leaf pairs, were planted in plastic pots containing sediment from the site and transported in ambient water to the University of North Carolina Wilmington Center for Marine Science (Wilmington, NC) in coolers. Within 24 h after collection, the plants were placed in tanks of filtered seawater maintained at a salinity of 34 (UNESCO, 1985) in a temperature-controlled greenhouse for 1 week until used for photosynthetic measurements, which were completed over a 3-day period.

Leaf pairs from the second node back from the rhizome apical were haphazardly chosen from separate plants and used as sample material. Two leaf pairs per site (four blades) were used for each photosynthesis versus wavelength measurement and a total of six replicates from each site were performed. Wavelength-specific leaf photosynthetic responses were determined using oxygen flux measurements in a Hansatech<sup>®</sup> oxygen electrode system. Leaves were placed in the electrode cuvette chamber in 2 ml of seawater made from Instant Ocean<sup>®</sup> salts and deionized (DI) water to



**Fig. 1.** Annual average spectral diffuse attenuation coefficients  $[K_d(\lambda)]$  (+standard error) from quarterly sampling at the Haulover Inlet (grey) and Oleta River (black) measured at (a) high tide and (b) low tide with a tidal amplitude of ~1 m (from Kahn, 2008). Note *x*-axis scale is categorical.

salinity 34 at 25 °C. The seawater was N<sub>2</sub>-sparged for 10–15 min to reduce initial oxygen concentration in the chamber to about 25% saturation (Beer et al., 2001). A circulating temperature-controlled water bath was used to maintain temperature and the media within the cuvette was stirred to maintain an even distribution of gases. The oxygen electrode control box was connected to a computer, and oxygen concentration measurements were recorded every 4 s using the WINDAQ<sup>®</sup> program from DATAQ Instruments Inc.

Photosynthetic responses to spectrally varying radiant energy were measured at the following nine wavelengths: 340, 400, 450, 500, 550, 600, 650, 694 and 730 nm. Illumination was provided by a 1000W Hg(Xe) bulb (Newport, Oriel Instruments U.S.A.) with a broad spectral output, housed in a Spectral Energy GM252 high intensity quarter meter grating monochromator (Spectral Energy Corporation, Westwood, New Jersey). For all but the 340 nm wavelength measurements, the monochromator aperture was fully opened. The full-spectrum light passed through 10 nm full width-half maximum (FWHM) narrow-bandpass filters (Edmund Optics<sup>©</sup>) at each of the eight wavelengths and then through a variable neutral density filter (Edmund Optics<sup>©</sup>), which was used to maintain near-constant radiant energy (60  $\mu$ W cm<sup>-2</sup>) at each wavelength. The 340 nm wavelength irradiance was achieved by setting the monochromator to 340 nm (10 nm bandwidth) and adjusting the intensity with the neutral density filter. Radiant energy levels for each treatment were measured prior to initiating oxygen measurements using a cosine collector on a 200 µm diameter fiber optic cable connected to an OceanOptics<sup>©</sup> USB 2000 spectrophotometer. The spectrometer was calibrated using SpectraSuite and a calibrated halogen light source (LS-1CAL, OceanOptics<sup>©</sup>).

A.E. Kahn, M.J. Durako/Aquatic Botany 91 (2009) 245-249

Preliminary experimental trials and linear regression analyses were done to examine changes in oxygen-flux rates over time in the varying wavelength treatments to determine times required to reach steady-state dark respiration and photosynthetic rates (data not shown). We also verified that respiration rates did not change between light treatments (data not shown), so initial respiration rates were used for all gross photosynthesis calculations. For each sample, leaves were placed in the oxygen electrode cuvette and maintained in the dark for 5 min after which time respiratory oxygen consumption was measured for an additional 5 min. The leaves were then exposed for 3 min to each of the nine light treatments from 340 to 730 nm. Linear regression analyses of the rate of change in oxygen over time were performed in Sigma-Plot<sup>©</sup>10.0. For the light treatments, oxygen flux was measured during the last 2 min at each treatment wavelength; the initial 1 min was necessary to establish steady-state oxygen fluxes in the chamber at each new treatment. Gross photosynthesis was calculated by adding respiratory oxygen consumption to the net rate of photosynthesis at each light treatment ( $\mu$ mol O<sub>2</sub> h<sup>-1</sup>). Following photosynthetic measurements, each leaf blade width and length were measured to calculate total leaf area using the equation of an ellipse. Leaves were then ground in cold 95% acetone using a mortar and pestle for pigment extraction. After 4 h on ice in the dark, the supernatant was transferred to a 1 cm quartz cuvette and the absorbance of the extract from 300 to 800 nm was measured using an Ocean Optics<sup>©</sup> spectrometer and SpectraSuite software (Durako et al., 2003). The UVP absorbance was measured from 341 to 345 nm (Durako et al., 2003; Kunzelman et al., 2005). The concentrations of chlorophyll a and b were calculated using the following dichromatic equations (Jeffrey and Humphrey, 1975) and normalized to total leaf area used in each replicate:

 $\mu g \, chl \, a = 11.93 (A_{664}) - 1.93 (A_{647})$ 

 $\mu g \, chl \, b = 20.36 (A_{647}) - 5.50 (A_{664})$ 

Gross photosynthesis for each replicate was normalized to the total chlorophyll *a* concentration ( $\mu$ g) in the leaf tissue (four leaves) in the oxygen chamber. To compare quantum efficiencies of photosynthesis for each population among wavelengths, radiant energy values (60  $\mu$ W cm<sup>-2</sup>) were converted to quantum fluxes (photons cm<sup>-2</sup> s<sup>-1</sup>) at each wavelength in SpectraSuite using an area integration for the 10 nm FWHM peak width, an integration time of 3000 ms and the average of 5 scans per measurement.

One-way ANOVA was used to examine variation in chlorophyll concentrations and UVP absorbance between the two sites. When significant differences were obtained with a 95% confidence limit, Tukey tests for all pair-wise multiple comparisons were applied. A two-way ANOVA was applied to examine main effects and interactions between-sites and among-wavelengths on the variability of gross photosynthesis and quantum efficiencies. *t*-Tests were performed to examine differences in specific wavebands between the sites and between specific wavebands within a site. All statistical analyses were performed in SigmaStat<sup>®</sup> 3.5.

#### 3. Results

Total leaf areas used for the oxygen measurements were not significantly different between the two sites (P = 0.570). Two-way ANOVA indicated that wavelength (P = 0.01) and site × wavelength interactions (P = 0.02) were significant sources of variability in *H. johnsonii* quantum efficiencies, but that site was not a significant main effect (P = 0.06). Quantum efficiencies in plants from Oleta River were significantly greater (P = 0.02) at the three shortest wavelengths (340, 400 and 450 nm) compared to the longest wavelengths (694 and 730 nm) with the intermediate wavelength



**Fig. 2.** *Halophila johnsonii*: average (+standard error) photosynthetic response from the Haulover Inlet (grey) and Oleta River (black) populations at the nine wavelength treatments (n = 6) (a) quantum efficiency (normalized to irradiance as photons cm<sup>-2</sup> s<sup>-1</sup>) and (b) gross photosynthetic rate at a near-constant radiant energy of 60  $\mu$ W cm<sup>-2</sup>.

treatments having intermediate quantum efficiencies (Fig. 2(a)). In contrast, quantum efficiencies of Haulover plants exhibited no significant among-wavelength variability between 400 and 730 nm (Fig. 2(a)), despite the apparent peak at 340 nm. The main effects of wavelength and site did not significantly effect variability in gross photosynthetic rates (P = 0.06 and 0.1), but there was significant site  $\times$  wavelength interaction (P = 0.02). H. johnsonii from the Haulover site had significantly greater (P = 0.05) gross photosynthesis at 694 nm than the Oleta plants (Fig. 2(b)). At the shorter wavelengths of 340, 400 and 450 nm, H. johnsonii from Oleta River had consistently higher average rates of gross photosynthesis than the Haulover plants (Fig. 2(b)), though the differences were not significant (P = 0.3, 0.5 and 0.8, respectively). This was likely due to the greater variation in photosynthetic responses at the shorter wavelengths (Fig. 2) in the Oleta River plants compared to the Haulover Inlet replicates.

Chlorophyll a and *b* concentrations (Table 1) were significantly greater in Oleta River than Haulover Inlet leaves (P = 0.04 and 0.02,

#### Table 1

Halophila johnsonii: average concentrations (±standard deviation) of chlorophyll *a* and *b* (µg chl mm<sup>-2</sup> leaf area), ratio of chlorophyll *b*:*a*, and UVP absorbance (per mm<sup>2</sup> leaf area) of plants from each site used in experiments.

		-		
Site	chl a	chl b	chl b:a	UVP
Oleta River Haulover Inlet	$\begin{array}{c} 0.149 \pm 0.05 \\ 0.092 \pm 0.01 \end{array}$	$\begin{array}{c} 0.064 \pm 0.02 \\ 0.037 \pm 0.01 \end{array}$	$\begin{array}{c} 0.432 \pm 0.04 \\ 0.394 \pm 0.03 \end{array}$	$\begin{array}{c} 0.012 \pm 0.003 \\ 0.007 \pm 0.002 \end{array}$

respectively). Although on average it was slightly higher in Oleta River plants (Table 1), the ratio of chl *b*:chl *a* was not significantly different between sites (P = 0.08). UVP values were also significantly greater in the river plants compared to inlet plants (P = 0.01). UVP absorbance for *H. johnsonii* from Oleta River exhibited greater variation among replicates ranging from 0.016 to 0.009, whereas UVP absorbance values from Haulover Inlet samples were relatively constant, ranging only from 0.009 to 0.005 (Table 1).

#### 4. Discussion

Wavelength-specific photosynthetic responses differed between the riverine and inlet populations of H. johnsonii examined in this study, with the greatest differences occurring at the three shortest wavelengths (340, 400 and 450 nm) and 694 nm. The differences in wavelength-specific photosynthesis, chlorophyll concentration and UVP absorbances are likely acclimatory responses of the two populations to the distinct optical environments in which they grow. The wavelength-specific photosynthetic responses mirror the comparatively greater increase in spectral diffuse attenuation coefficients  $[K_d(\lambda)]$  with decreasing wavelength at the riverine site (Fig. 1), reflecting higher CDOM levels at this site. These differences indicate that there is a spectral component in the light acclimation of H. johnsonii. The Oleta river plants are most photo-efficient (i.e., shade-acclimated) at the least available wavelengths in their CDOM-rich environment and thus, may be considered blue-shade acclimated.

The Oleta River plants also had higher, but more variable, chlorophyll and UVP levels than plants from Haulover Inlet. Higher chlorophyll levels are indicative of shade acclimation, whereas higher UVP levels are more characteristic of a sun-acclimated response. Figueroa et al. (2003) observed a significantly greater amount of UV-absorbing compounds in sun-adapted vs. shadeadapted Porphyra (a red alga) and increased photosynthesis of sun vs. shade plants at high light has been observed in terrestrial plants (Bukhov et al., 1995). The spectral attenuation coefficient  $[K_d(\lambda)]$  at 412 nm at the Oleta River site is about twice that of the Haulover Inlet site at both high and low tides (Fig. 1). This reflects differences in the quantity and quality of light between the two environments with a greater penetration of short-wave radiation at the Haulover site. Changes in light quantity and quality can lead to changes in accessory pigment composition in seagrasses and macroalgae, with increased synthesis of accessory pigments or UV-absorbing compounds under blue wavelength light or increased UV radiation (Gómez et al., 1998; Detrés et al., 2001; Godínez-Ortega et al., 2008). In our study, the differences in UVP levels between the two populations suggest that *H. johnsonii* from the riverine population was more high-light adapted than plants from the inlet population. However, the increased levels of chlorophyll in riverine plants and spectral attenuation of light at the riverine site suggest otherwise. Increased chlorophyll concentrations and greater leaf areas are characteristics of shade adaptations (Andrews et al., 1984; Goldsborough and Kemp, 1988; Czerny and Dunton, 1995). Although leaf pairs used in this study had similar leaf areas, a seasonal study of H. johnsonii reported both greater leaf area and higher chlorophyll concentrations in plants from the Oleta River compared to the Haulover Inlet site (Kahn, 2008). River-influenced populations of H. johnsonii may be shade adapted (high chlorophyll concentrations, larger leaf area) in terms of their long-term light history, but may additionally exhibit shorter term acclimatory responses (e.g., downregulation of quantum yields, Kahn, 2008) to daily extremes in the light environment driven by changes in tidal depth (Virnstein and Morris, 1996) and CDOM concentration. The high variability of chlorophyll and UVP levels in the riverine population may reflect the proportionally higher degrees of fluctuation in environmental characteristics, including the light field, at the Oleta River site (Kahn, 2008).

Although the study by Durako et al. (2003) suggested that decreased UV radiation resulted in a decrease in UVP production in H. johnsonii, a subsequent study by Kunzelman et al. (2005) observed no change in UVP accumulation between PAR only and PAR + UV treatments and suggested that UVP production in this species responded to overall changes in irradiance. Results from a mesocosm study by Kahn and Durako (2008) also support this as no decrease in UVP was observed in treatments with increased CDOM, but UVP absorbance was higher when day-lengths were longer. Gould et al. (1995) observed that flavonoids in understory plants may respond to short-term exposure to high-intensity sunflecks rather than to the average light field. They further suggested that these compounds protect chloroplasts, which are shade-adapted, during these high-intensity, short-term exposures to increased irradiance (Gould et al., 2000). Oleta River Halophila johnsonii plants have higher concentrations of chlorophyll that may increase photosynthetic efficiency under the chronic lower light levels that characterize river-influenced environments, but these plants may be exposed to high light (sunflecks) during midday low tides and periods of low river discharge (decreased CDOM). The flavonoids in H. johnsonii may protect shadeacclimated chloroplasts during the shorter term exposures to intense irradiance (i.e., acclimation to the variance rather than to the mean). Thus, the higher and more variable concentration of flavonoids in the Oleta River plants compared to the Haulover Inlet plants may be a response to the relatively greater variability of environmental factors such as light and salinity, which can undergo extreme changes on short-temporal scales in the riverinfluenced tidal lagoon environment.

#### Acknowledgements

The authors would like to thank J. Beal with the Florida Fish and Wildlife Conservation Commission for collection assistance and use of their research vessel and S. Dale at Oleta River State Park, Florida for lodging. We also thank R. Whitehead and R. Kieber at the UNCW MACRL Lab for the use of their monochromater. All plant material was collected under Special Activity License 06SR-972 issued by the Florida Fish and Wildlife Conservation Commission. This project was funded by NOAA grant WC133F05SE7321 and the University of North Carolina Wilmington Coastal Ocean Research and Monitoring Project student summer research grant.

#### References

- Andrews, M., Box, R., Mcinroy, S., Raven, J.A., 1984. Growth of *Chara hispida*. II. Shade adaptations. Ecology 72, 885–895.
- Beer, S., Björk, M., Gademann, R., Ralph, P., 2001. Measurements of photosynthetic rates in seagrasses. In: Short, F.T., Coles, R.G. (Eds.), Global Seagress Methods. Elsevier Science Amsterdam The Netherlands. pp. 183–198
- Elsevier Science, Amsterdam, The Netherlands, pp. 183–198. Bukhov, N.G., Drozdova, I.S., Bondar, V.V., 1995. Light response curves of photosynthesis in leaves of sun-type and shade-type plants grown in blue or red light. J. Photochem. Photobiol. B: Biol. 30, 39–41.
- Czerny, A.B., Dunton, K.H., 1995. The effects of in situ light reduction on the growth of two subtropical seagrasses, *Thalassia testudinum* and *Halodule wrightii*. Estuaries 18, 418–427.
- Detrés, Y., Armstrong, R.A., Connelly, X.M., 2001. Ultraviolet-induced responses in two species of climax tropical marine macrophytes. J. Photochem. Photobiol. B: Biol. 62, 55–66.
- Durako, M.J., Kunzelman, J.I., Kenworthy, W.J., Hammerstrom, K.K., 2003. Depthrelated variability in the photobiology of two populations of *Halophila johnsonii* and *Halophila decipiens*. Mar. Biol. 142, 1219–1228.
- Figueroa, F.L., Escassi, L., Pérez-Rodríguez, E., Korbee, N., Giles, A.D., Johnsen, G., 2003. Effects of short-term irradiation on photoinhibition and accumulation of mycosporine-like amino acids in sun and shade species of the red algal genus *Porphyra*. J. Photochem. Photobiol. B: Biol. 69, 21–30.
- Franklin, L.A., Kräbs, G., Kuhlenkamp, R., 2001. Blue light and UV-A radiation control of synthesis of mycosporine-like amino acids in *Chondrus crispus* (Flordeophyceae). J. Phycol. 37, 257–270.

#### A.E. Kahn, M.J. Durako/Aquatic Botany 91 (2009) 245-249

- Godínez-Ortega, J.L., Snoeijs, P., Robledo, D., Freile-Pelegrín, Y., Pedersén, M., 2008. Growth and pigment composition in the red alga *Halymenia floresii* cultured under different light qualities. J. Appl. Phycol. 20, 253–260.
- Goldsborough, W.J., Kemp, W.M., 1988. Light responses of a submerged macrophyte: implications for survival in turbid tidal waters. Ecology 69, 1775–1786.
- Gómez, I., Pérez-Rodríguez, E., Viñegla, B., Figueroa, F.L., Karsten, U., 1998. Effects of solar radiation on photosynthesis, UV-absorbing compounds and enzymatic activities of the green alga *Dasycladus vermicularis* from southern Spain. J. Photochem. Photobiol. B: Biol. 47, 46–57.
- Gould, K.S., Kuhn, D.N., Lee, D.W., Oberbauer, S.F., 1995. Why leaves are sometimes red. Nature 378, 241–242.
- Gould, K.S., Markham, K.R., Smith, R.H., Goris, J.J., 2000. Functional role of anthocyanins in the leaves of *Quintinia serrata* A. Cunn. J. Exp. Bot. 51, 1107–1115.
- Harborne, J.B., Williams, C.A., 2000. Advances in flavonoid research since 1992. Phytochemistry 55, 481–504.
- Jeffrey, S.W., Humphrey, G.F., 1975. New spectrophotometric equations for determining chlorophylls a, b, c<sub>1</sub>, and c<sub>2</sub> in higher plants, algae and natural populations. Biochem. Physiol. Pflanz. 167, 191–194.
- Kahn A.E., 2008. Physiological ecology of the seagrass Halophila johnsonii in marine and riverine influenced environments. PhD Dissertation for the University of North Carolina Wilmington.
- Kahn, A.E., Durako, M.J., 2008. Photophysiological responses of *Halophila johnsonii* to experimental hyposaline and hyper-CDOM conditions. J. Exp. Mar. Biol. Ecol. 367, 230–235.
- Kirk, J.T., 1994. Light and Photosynthesis in Aquatic Ecosystems, 2nd ed. Cambridge University Press, Cambridge UK, 22 pp.
- Klisch, M., Håder, D.-P., 2002. Wavelength dependence of mycosporine-like amino acid synthesis in *Gyrodinium dorsum*. J. Photochem. Photobiol. B: Biol. 66, 60–66.
- Korbee, N., Figuroa, F.L., Aguilera, J., 2005. Effects of Light quality on the accumulation of photosynthetic pigments, proteins and mycosporine-like amino acids in the red alga *Porphyra leucosticte* (Bangiales, Rhodophyta). J. Photochem. Photobiol. B: Biol. 80, 71–78.

- Krzysiak, A.J., 2006. The isolation and characterization of natural products from marine plants and microorganisms. A Thesis for University of North Carolina Wilmington.
- Kunzelman, J.I., Durako, M.J., Kenworthy, W.J., Stapleton, A., Wright, J.L.C., 2005. Irradiance-induced changes in the photobiology of *Halophila johnsonii*. Mar. Biol. 148, 241–250.
- Lesser, M.P., Lewis, S., 1996. Action spectrum for the effects of UV radiation on photosynthesis in the hermatypic coral *Pocillopora damicornis*. Mar. Ecol. Prog. Ser. 134, 171–177.
- Lüning, K., Dring, M.J., 1985. Action spectra and spectral quantum yield of photosynthesis in marine macroalgae with thin and thick thalli. Mar. Biol. 87, 119– 129.
- Meng, Y., Krzysiak, A.J., Durako, M.J., Kunzelman, J.I., Wright, J.L.C., 2008. Flavones and flavone glycoosides from sea grass *Halophila johnsonii*. Phytochemistry 69, 2603–2608.
- Mercado, J.M., Sánchez-Saavedra, M.dP., Correa-Reyes, G., Lubián, L., Montero, O., Figueroa, F.L., 2004. Blue light effect on growth, light absorption characteristics and photosynthesis of five benthic diatom strains. Aquat. Bot. 78, 265–277.
- Mouget, J.-L., Rosa, P., Tremblin, G., 2004. Acclimation of *Halea ostrearia* to different spectral qualities—confirmation of 'chromatic adaptation' in diatoms. J. Photochem. Photobiol. B: Biol. 75, 1–11.
- Tattini, M., Galardi, C., Pinelli, P., Massai, R., Remorini, D., Agati, G., 2004. Differential accumulation of flavonoids and hydroxycinnamates in leaves of *Ligustrum vulgare* under excess light and drought stress. New Phytol. 163, 547–561.
- UNESCO, 1985. The international system of units (SI) in oceanography. UNESCO Technical Papers No. 45, IAPSO Publ. Sci. No. 32, Paris, France.
- Virnstein, R.W., Morris L.J., 1996. Seagrass preservation and restoration: a diagnostic plan for the Indian River Lagoon. Technical Memorandum #14. St. Johns River Water Management District, Palatka, FL, 43 pp. plus appendices.
- You, T., Barnett, S.M., 2004. Effect of light quality of production of extracellular polysaccharides and growth rate of *Porphyridinum cruentum*. Biochem. Eng. J. 19, 251–258.