

Full Length Research Paper

Differential effects of UVA, UVB, and PAR on photosynthetic efficiency in red algae: *Gracilaria dentata*, *Hypnea musciformis* and *Centroceras clavulatum*

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The effects of distinct components of the solar spectrum (ultraviolet A, ultraviolet B, and photosynthetically active radiation) on *Gracilaria dentata*, *Hypnea musciformis*, and *Centroceras clavulatum* were investigated under laboratory conditions. Thalli of the samples were exposed to either unfiltered solar radiation or solar radiation filtered through WG 295, WG 320, and GG 400 cut-off filters. Photosynthetic pigments were quantified using spectrophotometry, and gas exchange was measured using a Clark electrode. Pigments were significantly ($P < 0.05$) bleached by all components of solar radiation used. Phycobilins were bleached even after short exposure, followed by carotenoids and then chlorophyll *a*, which was hardly affected. Photosynthetic oxygen production declined by 35-60% across species after 60 min of exposure, with ultraviolet B causing the highest inhibition. Respiration rates increased by 10-25%. *H. musciformis* exhibited greater resilience, maintaining a photosynthetic rate of $2.1 \pm 0.3 \mu\text{mol O}_2 \text{ g}^{-1} \text{ FW h}^{-1}$ compared to *G. dentata* or *C. clavulatum*. The ultraviolet B component, despite its lower intensity, had the most inhibitory effect on photosynthesis, likely due to oxidative stress and photobleaching of pigments. The findings highlight the differential susceptibility of red algae to solar radiation, emphasizing the need for further investigation into the mechanisms underlying ultraviolet-induced stress responses.

Key words: Absorption spectra, gas exchange, photobleaching, photoinhibition, photosynthetic pigments, solar radiation.

INTRODUCTION

Given their ability to perform oxygenic photosynthesis, solar radiation is one of the primary variables influencing

the growth of red algae in their habitat. The solar zenith angle, varying with time of day, latitude, and season, is

the primary factor influencing the Earth's surface UV radiation. These variations underpin the fluctuation of UV radiation and its trends, with additional contributions from elements such as particles, cloud cover, and ozone concentrations, which are especially prominent in Antarctica and high latitudes (Abbood and Al-Taai, 2018; Bais et al., 2019). Furthermore, dust plays a significant role, accounting for 30-50% of the total aerosol attenuation and acting as the primary factor governing the variability in overall aerosol impact (Fountoulakis et al., 2021). Despite the Montreal Protocol's efforts to restrict ozone-depleting substances like chlorofluorocarbons (CFCs), their continued use and persistence, coupled with biologically produced halogenated compounds, persistently erode the ozone layer in the stratosphere (Fang et al., 2019). The Montreal Protocol, in slowing the thinning of the ozone layer, has played a crucial role in balancing the combined effect in the stratosphere accompanying global warming that previously contributed to the depletion of ozone, creating a complex interplay of environmental factors impacting marine ecosystems (Bais et al., 2019; Williamson et al., 2019).

UV radiation penetration into the aquatic surface layer may vary depending on the time and space. For instance, in the purest ocean waters, the distance downwards with which UV-B radiation is lessened to 1% of its incident value is tens of metres; and in inland waters with large quantities of dissolved organic matter, it is tens of centimetres (Overmans and Agustí, 2020). Thus, the overall exposure of organisms and materials present throughout the entire depth of the top mixed layer is determined by how often they move (or are displaced) into this higher zone of high light exposure (Neale et al., 2023).

Inhibition of photosynthesis and DNA damage are two of UVB radiation's main effects on the algae community; prolonged exposure lowers growth rates (Williamson et al., 2019; El-Sheekh et al., 2021; Neale et al., 2023). Even though UVA radiation plays a positive role in photosynthesis in some algae, its presence in excessive quantities has some detrimental effects on algae (Neale et al., 2023).

In addition to contributing to the primary productivity along the coast and serving important functions in coastal fisheries, marine macroalgae are essential to the coastal carbon cycle (Paine et al., 2021). Red algae are mostly marine organisms living in coastal waters in intertidal and subtidal zones. With a few exceptions, they are non-motile organisms. Red algae can be found in sub-tidal

zones down to 40 m below the surface. Generally, red algae are the deepest seaweeds that can be found anywhere.

Hence, at a significant distance below the sea's surface, the thalli of deep-dwelling red algae are completely submerged. In red algae, phycobilins, carotenoids, and chlorophylls are the primary photosynthetic pigments used for light absorption. While chlorophyll *d* is found in certain species that heavily absorb blue and red light, chlorophyll *a* is found in all red algae (Murakami et al., 2004). Both blue and green light are absorbed by carotenoids, which are classified as xanthophylls (lutein and taraxanthin) and carotenoids (α - and β -carotenes). The primary pigments in red algae that absorb light are the phycobilins. Two photosynthesis reaction centres, Photosystem I (P700) and Photosystem II (P680), containing chlorophyll, absorb light energy (Barber and Archer, 2001).

The pH difference across the thylakoid membrane of the plastid triggers physiological responses, such as ATP synthesis and energy dissipation control. These processes have implications for plant productivity and potential applications in artificial photosynthesis and crop improvement (Quintano et al., 2019). Some studies have shown that elevated irradiance levels induce heightened stress responses in red algae, including reductions in key photosynthetic parameters and increases in the normal C: N ratios, mycosporine-like amino acids, and bleaching coverage; these effects are more pronounced in the apical parts of the thallus compared to the middle portions (Cruces et al., 2018; Quintano et al., 2019). It was hypothesized that different components of solar radiation [ultraviolet A (UVA), ultraviolet B (UVB), and photosynthetically active radiation (PAR)], will exhibit varying degrees of detrimental effects on photosynthetic pigments and photosynthesis rates in marine algal species (e.g., *Gracilaria dentata*, *Hypnea musciformis*, and *Centroceras clavulatum*). Specifically, UVB radiation will have the most pronounced negative impact on photosynthetic activity despite its lower light intensity compared to other components of the solar spectrum.

However, limited research has been conducted in tropical regions regarding the impact of solar radiation on red algae, particularly near the equator, where ozone depletion is most prevalent and, therefore, has the greatest impact (Wong et al., 2015). Consequently, this study aimed to evaluate the effects of distinct elements of solar radiation (200-500 nm), namely UVA, UVB, and PAR, on the pigmentation, photosynthesis, and survival of *C. clavulatum*, *H. musciformis*, and *G. dentata* to

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determine their sensitivity to UV radiation. Such investigations can enhance understanding of the consequences of heightened solar radiation incidence on the viability of these algae in their natural habitat as a result of ozone layer depletion.

MATERIALS AND METHODS

Sample collection

C. clavulatum [C. Agardh] (Montagne, 1846), *H. musciformis* [Wulfen] (Lamouroux, 1813), and *G. dentata* (Guiry and Guiry, 1852), were collected from Biriwa (50° 9' 27" N, 10° 8' 36" W), which is located in Ghana's Central Region approximately 10 km east of Cape Coast. Samples were collected three times over the course of one year, specifically in February, May, and September, to account for seasonal variations in environmental conditions.

The samples collected from their natural habitat in the intertidal zone during low tides were thoroughly cleaned with seawater to remove any unnecessary materials and placed in polythene bags filled with seawater. To lessen microbial or bacterial activity, seawater brought into the laboratory was autoclaved at 121°C for 20 min at 15 psi. The autoclaving process was conducted immediately before the experiment to ensure sterility. A portion of the autoclaved seawater was first passed through an aerating bubbler to increase humidity and then passed into the samples to maintain appropriate oxygen levels during incubation. This step was crucial, as bacteria can inhibit red algal growth by secreting toxic factors and disrupting algal metabolism.

Exposure of samples to solar radiation

Using an electronic balance (Sartorius BP610, Gottingen, Niedersachsen, Germany), a mass of 1 g of cleaned and washed samples was put into eight Petri dishes covered in carbon paper to control ambient light radiation exposure before the experimental treatment. The organisms were spread out in each of the labelled Petri dishes and exposed to sunlight. To keep the organisms from overheating and to maintain them as close as possible to the temperature of their natural environment, ice chips were placed on top of each Petri dish at a temperature of 15-20°C as suggested by Eggert and Wiencke (2000). To ensure accurate temperature control, an electronic thermometer (Model T14SL, Guangdong Genial Technology Co., Ltd, China) was used to monitor temperatures at regular intervals (every 10 min). If temperatures exceeded 20°C, additional ice chips were added to maintain the desired range. The Petri dishes were also positioned on an insulated surface to minimize heat absorption from the rooftop. The samples were exposed to solar radiation on the roof of the University of Cape Coast's College of Agriculture and Natural Science building between 10:00 and 14:00 h. The samples were kept moist by sprinkling small amounts of seawater on them every 15 min.

The organisms were subjected to different solar radiation wavelength components using optical cut-off filters (GG400, WG320, and WG 295 filters). These filters selectively blocked specific portions of the solar spectrum, allowing for an assessment of the effects of different wavelengths on photosynthetic performance:

1) GG 400 filter: Blocks all ultraviolet radiation (UV), allowing only

photosynthetically active radiation (PAR, wavelengths >400 nm) to pass through. This setup isolates the effect of visible light on algal physiology.

2) WG 320 filter: Eliminates UVB (280-320 nm) but allows UVA (320-400 nm) and PAR to pass through. This helps to distinguish the effects of UVA from UVB on photosynthesis.

3) WG 295 filter: Blocks UVC (<295 nm) but allows UVB, UVA, and PAR to pass through. Since UVC is largely filtered out by the Earth's atmosphere, this treatment simulates natural solar exposure conditions more accurately.

4) Unfiltered exposure: Samples were directly exposed to full sunlight, receiving all components of solar radiation, including UVA, UVB, and PAR. The organisms were exposed to both unfiltered solar radiation and photosynthetically active radiation (PAR). All UV radiations are eliminated by the GG 400 filter, which only permits light with wavelengths longer than 400 nm to pass through. The WG 320 filter effectively eliminates any UVB light by allowing only light with wavelengths longer than 320 nm to pass through. In a similar vein, UVC is effectively eliminated by the WG 295 filter, which only permits light with wavelengths longer than 295 nm to pass through.

The absorbance at peak wavelengths for different time intervals was measured after exposure to different solar radiation components, namely, unfiltered solar radiations, PAR+UVA+UVB, PAR+UVA, and PAR only (Table 1). The experimental design included four replicates of each sample organism per solar radiation combination type. This approach allowed for the determination of the differential impact of UVA, UVB, and PAR on pigment integrity and photosynthetic efficiency, addressing the study's objective of understanding the effects of solar radiation on red algae.

Measurement of solar radiation

The amount of solar radiation reaching the organisms during the experimental period was determined with a radiometer RM-12 (Opsytec Dr.Grobel, Ettlingen, Germany). The fluence rates for the components of solar radiation were measured for the wavelength bands of UVA (315-400 nm), UVB (280-315 nm), and visible radiation (400-700 nm). Fluence rate is used to calculate dose rates from radiation sources. It is a volume quantity that indicates potential radiation exposure. The fluence rates (intensity) of the solar irradiance was measured in watts per square meter ($W m^{-2}$) using a Gossen Mavolux digital luxmeter (Nurnberg, Germany) at 30-min intervals on each sampling date to determine the power of light hitting a specific surface in a single direction. The luxmeter was positioned at a consistent height above the samples to minimize variations due to shading or reflection. To ensure accuracy, the device was calibrated before each measurement session, and multiple readings were taken and averaged for each time point. The recorded intensity values were then compared across different treatments to evaluate the effects of varying radiation exposure.

Gas exchange measurement

The gas exchange was measured using a Clark electrode (Dubinsky et al., 1987). The sample was washed thoroughly with autoclaved seawater to prevent any bacterial contamination. A mass of 2 g of each organism was weighed and placed in a separate conical flask, and 100 ml of sterilized seawater was added. A magnetic stir bar was also placed in the flask, and the flask was stirred on a magnetic stirrer. Meanwhile, the

Table 1. Components of solar radiation received at various durations by the organisms.

Time of day (h)	Light Intensity (W m ⁻²)				Gb(i) (W m ⁻²)	T2m (°C)
	UVA	UVB	Visible light	Total sunlight		
10.0	60	15	787	1030	572.99	29.79
10.5	75	17	1060	1240	-	-
11.0	60	18	825	1170	680.99	29.52
11.5	65	20	829	1190	-	-
12.0	61	20	1020	1030	680.99	29.74
12.5	65	19	980	1020	-	-
13.0	60	18	1098	1169	659.99	29.46
13.5	60	20	982	982	-	-
14.0	61	19	920	983	524.99	30.07

Gbi: Beam (direct) irradiance on the inclined plane (plane of the array); T2m: 2-m air temperature.

Source: JRC Photovoltaic Geographical Information System (PVGIS) - European Commission

microprocessor oximeter (Oxi 196, Berlin-Germany) was switched on for 15 min (to polarize the electrode) and adjusted to the salinity of seawater that was measured to be 34‰ using conductivity measurement. A slide projector, serving as a light source, and a magnetic stirrer were assembled in a straight line such that the light was directed at the organism. The setup was prevented from exposure to external sources of light with a black cloth, and the distance between the light source and the magnetic stirrer was maintained at 70.0 cm to prevent overheating. The electrode of the oximeter was introduced into the conical flask as the slide projector was switched on to provide a constant source of light. The light and the magnetic stirrer were switched on simultaneously and, with the aid of the microprocessor oximeter, the amount of oxygen evolution in mg per unit mass of algae per second was measured at 30-s intervals for four minutes. The dark respiration was also recorded, during which time the light source was switched off for the same duration and at the same time intervals.

The effects of irradiation on gas exchange measurement

By employing cut-off filters to expose the organisms to solar radiation as detailed in the exposure of samples to solar radiations, the effects of irradiation on gas exchange were ascertained. Equal samples of organisms filtered through the WG295, WG320, or GG400 filters and exposed to direct sunlight or solar radiations were collected at 15-min intervals, and the amount of oxygen gas evolved was measured.

Extraction and determination of photosynthetic pigments

To determine the pigment contents of the samples, the Beer-Lambert law was used, which relates the absorbance of light to the concentration of pigments in the solution. The pigments were extracted using a pH 7 buffer solution consisting of 0.5 M KH₂PO₄ and 0.5 M K₂HPO₄. Fresh samples were cleaned with seawater, ground using a mortar and pestle, and mixed with 10 ml of the buffer. Triton X-100 (20 µl) and 20 µl of phenylmethylsulfonyl fluoride (PMSF) were added to solubilize the membranes. The mixture was allowed to stand for 20 min and then centrifuged at 6000 rpm for 10 min to remove cell debris. The supernatant was collected, and the pigment levels were determined using a

spectrophotometer at specific wavelengths (that is 415, 495, 565, 615 and, 665 nm), corresponding to chlorophyll a, carotenoids, phycoerythrin, phycocyanin, and chlorophyll a, respectively.

For each pigment, the Beer-Lambert law ($A = \epsilon lc$) was used to calculate the concentration, where A is the absorbance at the $\lambda_{\max}$ of the pigment, ϵ is the molar absorptivity coefficient (extinction coefficient) specific to that pigment at the given wavelength, l is the path length of the cuvette or sample cell (1 cm), and c is the concentration of the pigment in solution.

The molar absorptivity coefficient used for chlorophyll a at 665 nm was 86,300 L·mol⁻¹·cm⁻¹ (Porra et al., 1989). For the additional pigments, chlorophyll a at 415 nm has an estimated molar absorptivity of approximately 111,700 L·mol⁻¹·cm⁻¹ in diethyl ether (Porra et al., 1989). Carotenoids, specifically β -carotene, exhibit a molar absorptivity coefficient of approximately 139,500 L·mol⁻¹·cm⁻¹ at 451 nm in hexane, though values at 495 nm are generally lower and solvent-dependent (Lichtenthaler and Buschmann, 2001). The molar absorptivity coefficient for R-phycoerythrin at 565 nm has been reported as approximately 1,200,000 L·mol⁻¹·cm⁻¹ (Scanlan, 2003), while C-phycocyanin at 615 nm has a molar absorptivity of approximately 1,540,000 L·mol⁻¹·cm⁻¹, closely aligned with its peak absorption at 620 nm (Zechmeister, 2012). The concentration in mol L⁻¹ was converted to µg ml⁻¹ using the molecular weights of the respective pigments.

The mixture was then carefully poured into a test tube, making sure there were no bubbles. The absorption spectra were determined at regular wavelength intervals of solar radiation for each organism. The absorbance was measured from 350 nm, increasing at 5 nm intervals up to 700 nm using a spectrophotometer (Jenway 6105 UV/Vis-Burladingen, Germany) to determine the wavelength of maximum (peak) absorption. The initial absorbance of the unirradiated (control) sample was subtracted from each absorbance of the irradiated samples for each peak. The rate of bleaching was found by calculating the absorbance changes during exposure at prominent absorption maxima, showing the involvement of the major photosynthetic pigments for the different treatments.

Data analysis

Analysis of variance (ANOVA) was used to test the effects of the three different irradiation filters and the control on the red algae.

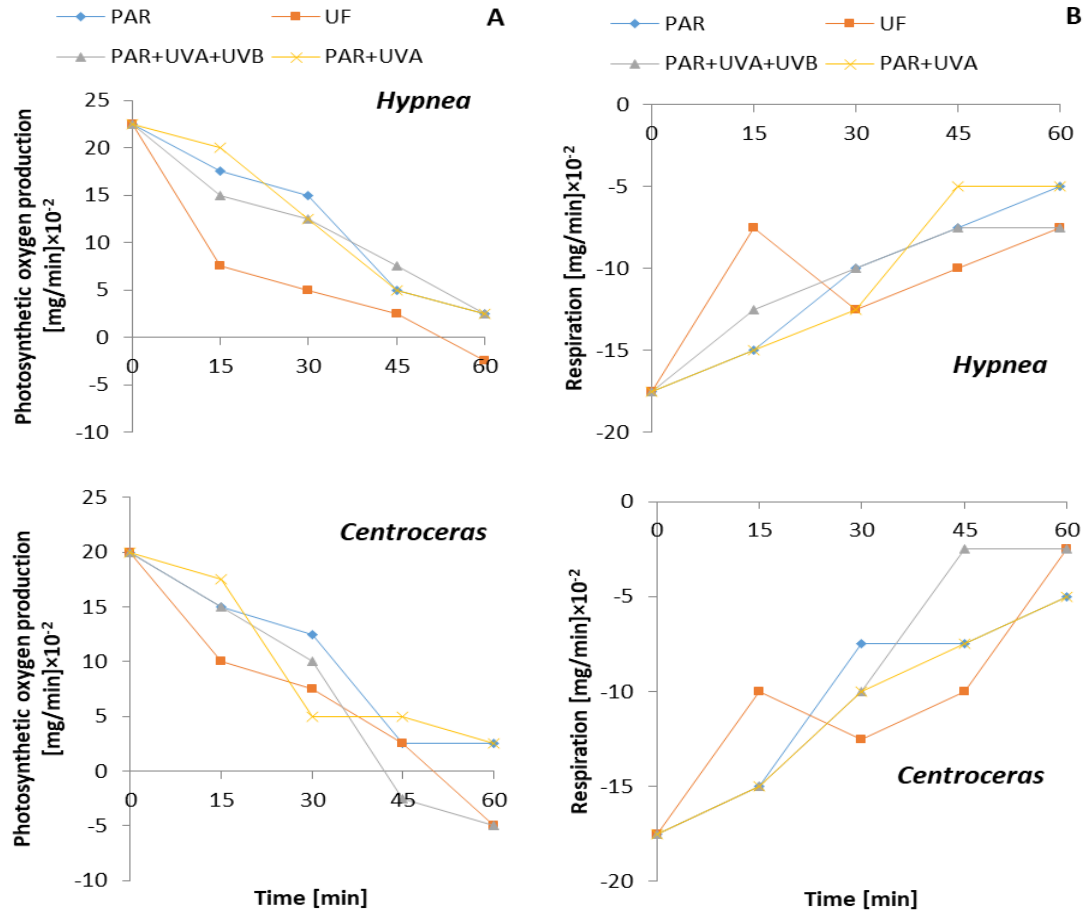


Figure 1. Photosynthetic oxygen production and respiration in *Centroceras clavulatum* (A) and *Hypnea musciformis* (B) after exposure to various combinations of solar irradiation wavelengths for 60 min. Values are means of 4 replicates.

ANOVA was chosen as it allows for the comparison of multiple treatment groups to assess whether there are statistically significant differences among them. To verify the assumptions of ANOVA, normality was assessed using the Shapiro-Wilk test, and homogeneity of variance was checked using Levene's test. If these assumptions were violated, data transformations or non-parametric alternatives were considered (Appendix 1 and 2).

To distinguish between meaningful variations in the means, a Duncan multiple range test (DMRT) was employed (Duncan, 1955; Ott and Longnecker, 2010). DMRT was chosen due to its ability to control Type I error while allowing for pairwise comparisons of multiple treatments. The statistical significance level (α) was established at $P < 0.05$.

RESULTS

Components of solar radiation

Table 1 shows the various components of solar radiation

received at different times of the day, from 10:00 to 14:00 h. The total incident sunlight was between ~ 1000 and 1240 W m^{-2} , with visible light following a similar pattern but at a slightly lower range of 800 to 1100 W m^{-2} . Both total sunlight and visible light intensities showed peaks and troughs throughout the observed time. In contrast, UVA and UVB maintained relatively constant and low intensities. UVA remained slightly below 50 W m^{-2} , while UVB was just above 0 W m^{-2} . The air temperature at 2 m above the study area hovered between 29 - 30°C .

Effects of solar radiation on photosynthetic oxygen production

On exposure to solar radiation, oxygen production decreased quickly, even following brief periods of exposure. For *H. musciformis*, the initial photosynthetic

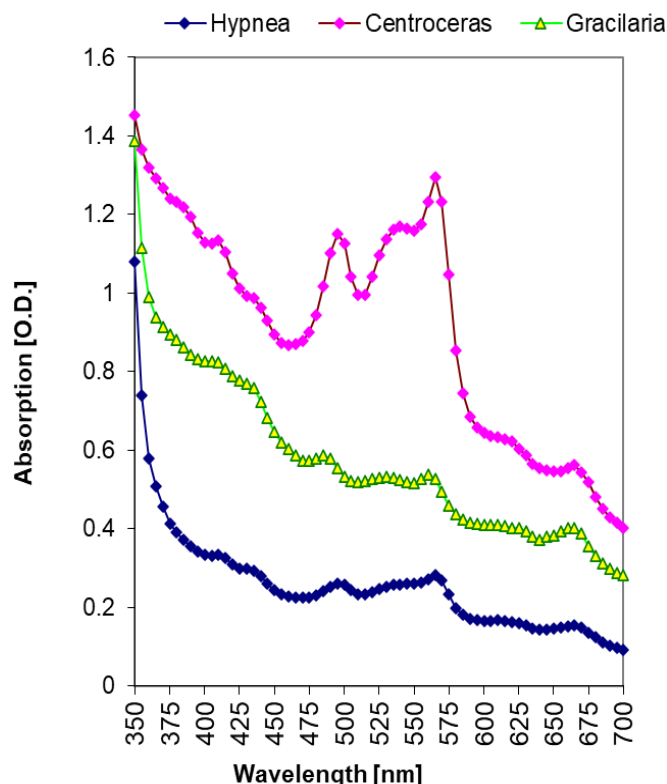


Figure 2. Absorption spectra of *Centroceras clavulatum*, *Gracilaria dentata* and *Hypnea musciformis*.

oxygen production was $22.5 \times 10^{-2} \text{ mg L}^{-1} \text{ min}^{-1}$ (Figure 1A). However, the photosynthetic rate decreased with exposure to solar radiation. Photosynthesis was mostly adversely affected in the thalli of *H. musciformis* exposed to unfiltered solar irradiation. The photosynthetic oxygen production under UF decreased drastically to $7.5 \times 10^{-2} \text{ mg L}^{-1} \text{ min}^{-1}$ at 15 min of exposure and at 60 min to $-2.5 \times 10^{-2} \text{ mg L}^{-1} \text{ min}^{-1}$, resulting in a net oxygen uptake rather than oxygen yield. The thalli exposed to PAR+UVA were least affected at 15 min of exposure. For the thalli of *H. musciformis* exposed to PAR only, PAR+UVA, and PAR+UVA+UVB, photosynthetic oxygen production was reduced gradually to $2.5 \times 10^{-2} \text{ mg L}^{-1} \text{ min}^{-1}$ at 60 min of exposure. In *G. dentata*, a similar decline in the rate of photosynthesis occurred as in *H. musciformis*, even at 15 min and thereafter, as a result of exposure to solar irradiation (data not shown).

For *C. clavulatum*, the initial photosynthetic oxygen evolution was $20.0 \times 10^{-2} \text{ mg L}^{-1} \text{ min}^{-1}$. However, after 15 min of exposure to unfiltered sunlight (UF), oxygen production was reduced by half ($10.0 \times 10^{-2} \text{ mg L}^{-1} \text{ min}^{-1}$) and further reduced to $-5.0 \times 10^{-2} \text{ mg L}^{-1} \text{ min}^{-1}$ at 60 min. Similarly, photosynthetic oxygen production for the thalli exposed to PAR+UVA+UVB decreased rapidly to -2.5×10^{-2}

$\text{mg L}^{-1} \text{ min}^{-1}$ at 45 min and then to $-5.0 \times 10^{-2} \text{ mg L}^{-1} \text{ min}^{-1}$ at 60 min of exposure. With PAR only, the photosynthetic oxygen production of the thalli decreased to $5.0 \times 10^{-2} \text{ mg L}^{-1} \text{ min}^{-1}$ after 30 min and then gradually to $2.5 \times 10^{-2} \text{ mg L}^{-1} \text{ min}^{-1}$ at 60 min of exposure. The rate of photosynthesis was similar for PAR+UVA, with a gradual reduction after 30 min to $2.5 \times 10^{-2} \text{ mg L}^{-1} \text{ min}^{-1}$ at 60 min of exposure, exactly at the same rate as for PAR only. Therefore, unfiltered solar radiation and a combination of PAR+UVA+UVB were the most devastating treatments to photosynthesis rates in *C. clavulatum*.

Respiration

Overall, dark respiration in thalli of *H. musciformis* also decreased on exposure under the same conditions as for photosynthesis (Figure 1B). The respiration rate was lower in the *H. musciformis* thalli exposed to PAR+UVA at 15 min but increased after 30 min. It decreased sharply after 30 min and became relatively stable from 45 to 60 min of exposure.

Surprisingly, the thalli exposed to unfiltered solar irradiation were least affected after 45 min of exposure. With PAR+UVA+UVB and PAR only, the rate of respiration decreased gradually for 60 min of exposure. The effect of solar radiation on the rate of respiration in *G. dentata* was similar to that in *H. musciformis* (data not shown). Respiration was at its lowest in the *C. clavulatum* thalli exposed to unfiltered solar irradiation at 15 min, but it increased thereafter at 30 min and then decreased gradually between 45 and 60 min (Figure 1B). For the thalli exposed to PAR+UVA+UVB, respiration rates decreased up to 60 min of exposure. The rate of respiration was reduced in the thalli exposed to PAR only and PAR+UVA.

Absorption spectra

Absorption maxima occurred at the same wavelength for the three algae for each pigment. That is, 415, 495, 565, 615 and 665 nm, corresponding to chlorophyll *a*, carotenoids, phycoerythrin, phycocyanin and chlorophyll *a*, respectively (Figure 2). *C. clavulatum* had the highest absorption maxima, followed by *G. dentata*, and then *H. musciformis* with the lowest. Phycoerythrin had two smaller peaks at 520 and 545 nm in addition to the major peak at 565 nm, which correspond to monomer, trimer, and hexamer, respectively. The absorbance of *C. clavulatum* thalli exposed to unfiltered solar radiation, PAR+UVA+UVB, PAR+UVA, and PAR increased during the first hour but declined sharply at 2 h of exposure (Figure 3). It became relatively constant after 3 h of exposure. It was obvious that chlorophyll *a* (red and soot bands) had the highest absorbance followed by

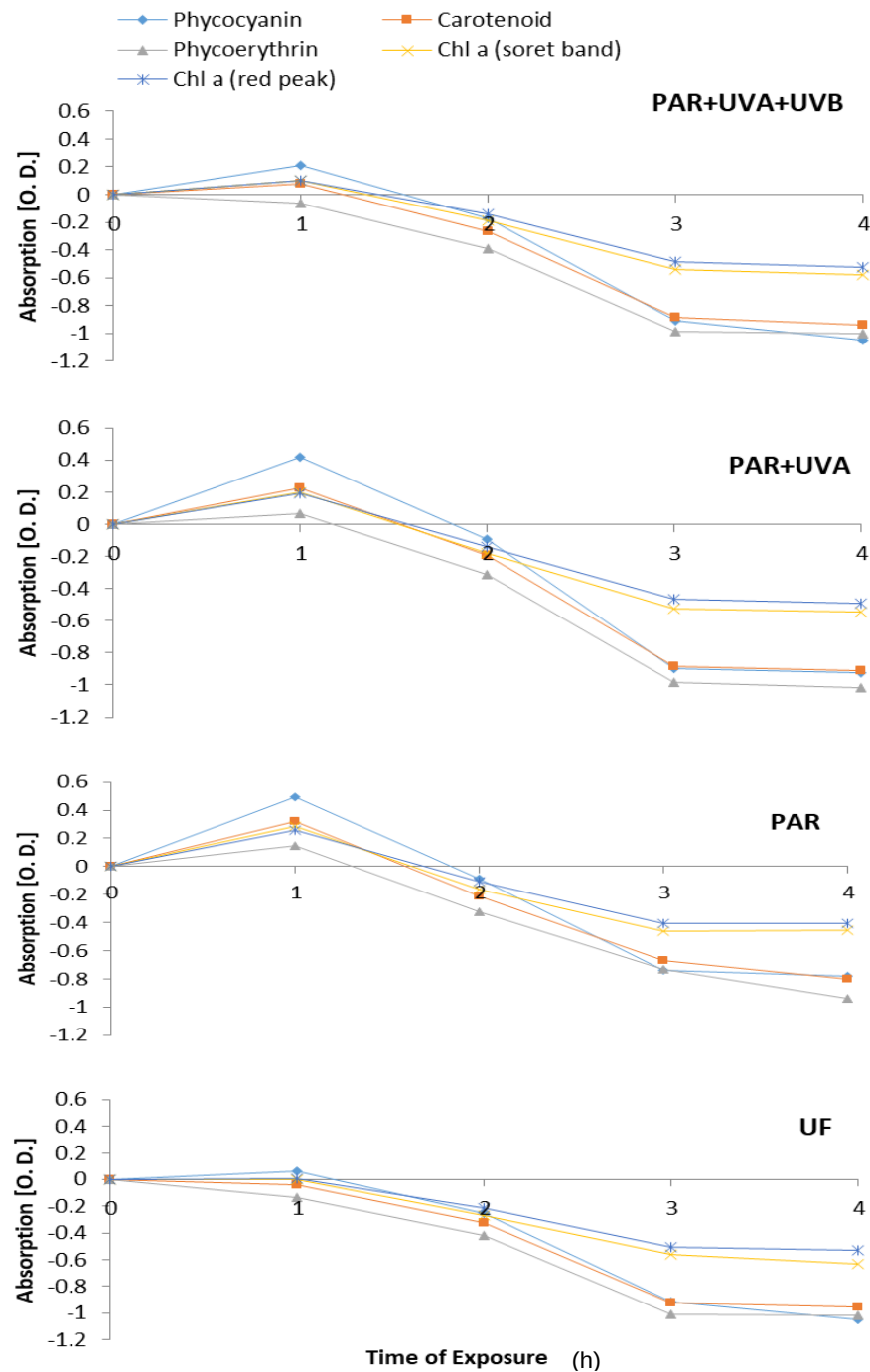


Figure 3. Kinetics of bleaching of photosynthetic pigments in thalli of *Centroceras clavulatum* after exposure to different durations of PAR+UVA+UVB, PAR+UVA, PAR only, and unfiltered solar irradiation (UF).

carotenoids and phycocyanin, and the least absorbance was for phycoerythrin. The rate of bleaching of photosynthetic pigments in *H. musciformis* thalli exposed to PAR+UVA+UVB and PAR+UVA is as shown in Figure

4. After 1 h of exposure, absorbance for chlorophyll *a* was increased, whereas that for phycoerythrin was reduced. At 4 h of exposure, the least absorbance was for phycoerythrin and phycocyanin, followed by

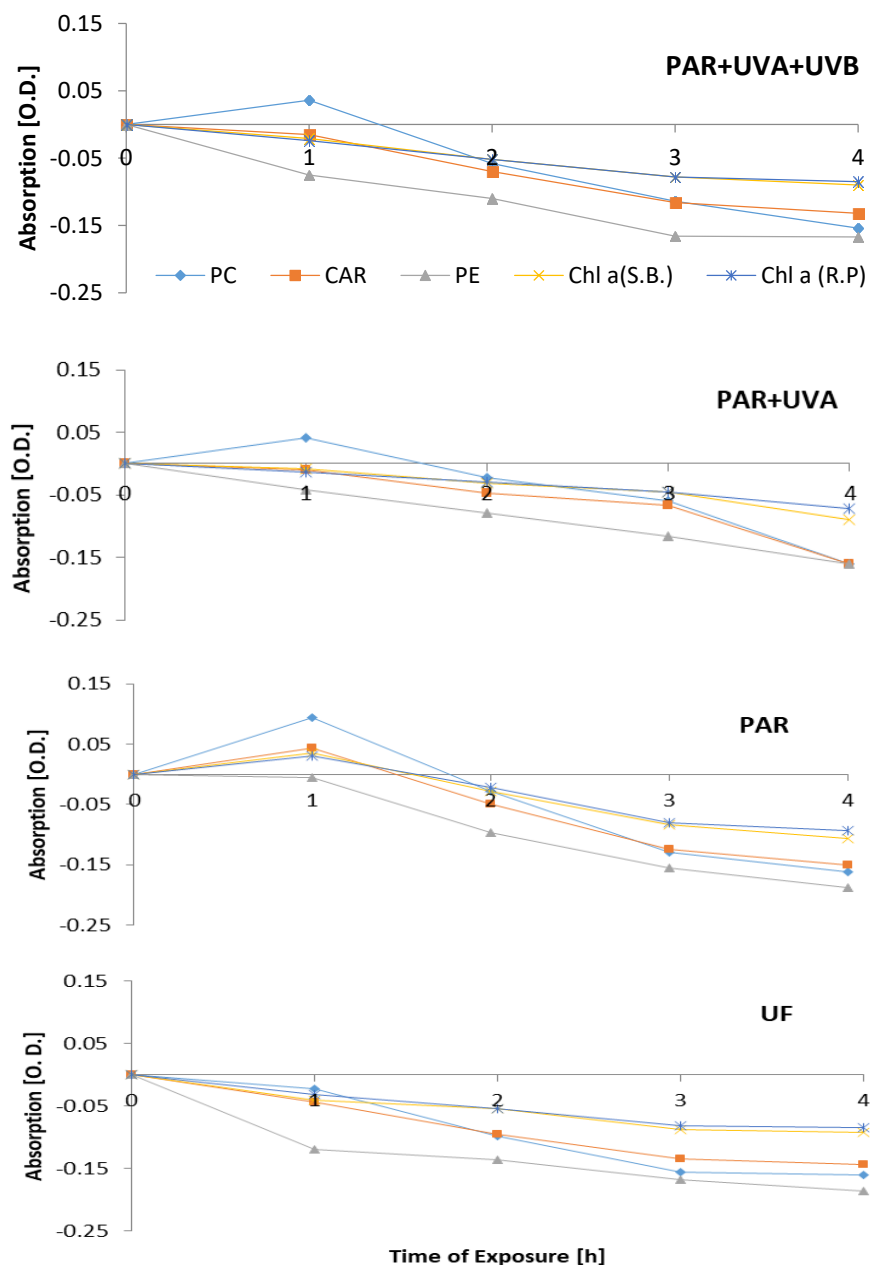


Figure 4. Kinetics of bleaching of photosynthetic pigments in thalli of *Hypnea musciformis* after exposure to different durations of PAR+UVA+UVB, PAR+UVA, PAR, and unfiltered solar irradiation (UF).

carotenoids and chlorophyll *a* (soret band and red peak), which had the highest absorbance. In the thalli exposed to PAR only, absorbance was increased at 1 h of exposure to solar radiation. Thereafter, there was a sharp decline of up to 3 h after exposure. Absorbance was lowest for phycoerythrin, and the highest was for chlorophyll *a* (red peak). At 4 h of exposure, chlorophyll *a*

(red peak) had the highest absorbance followed by carotenoids, phycocyanin, and phycoerythrin with the least.

For the thalli of *H. musciformis* exposed to unfiltered solar radiation, the absorbance of all the photosynthetic pigments decreased at 1 h of exposure. The absorbance was lowest for phycoerythrin, whereas the highest

absorbance was for chlorophyll *a*. At 4 h of exposure, the least bleached pigment was chlorophyll *a* (red peak and solet band), followed by carotenoids, phycocyanin, and phycoerythrin being the most bleached. The absorption difference spectra measured for *G. dentata* on exposure to different components of solar radiation showed that the bleaching of the photosynthetic pigments in this alga was similar to that in *H. musciformis*. However, the absorbance for the photosynthetic pigments increased at 1 h of exposure under all the radiation types before declining drastically after 2 h of exposure and continued until the end of the exposures. The absorbance was highest in chlorophyll *a* (red peak), followed by chlorophyll *a* (solet band), carotenoids, phycocyanin, and then phycoerythrin with the lowest absorbance. The absorption showed a gradual depletion of the photosynthetic pigments, specifically in the absorption range of the phycoerythrin, phycocyanin, and carotenoids. Furthermore, there was a gradual decrease in absorption at shorter wavelengths, showing a loss in scattering.

DISCUSSION

This study evaluated the effects of solar radiation on pigmentation, survival, and photosynthetic oxygen production in three red algal species. As photoautotrophic organisms are capable of oxygenic photosynthesis, solar radiation is one of the main elements influencing the growth of red algae. Red algae make a carpet of seaweed that resembles moss, usually seen in the lower portion of the shore and exposed during low tide. Red algae are delicate organisms that thrive in the sub-littoral zone, close to the low watermark, or in rock pools. Here, they are not exposed to the kind of extended exposure where enough solar energy can reach the plants to produce biomass at a net positive rate. As such, it makes sense to use them to evaluate how increasing levels of solar radiation affect living things.

Sensitivity to solar radiation

The present investigation found that upon exposure to different wavelengths of solar irradiation, *H. musciformis*, *G. dentata*, and *C. clavulatum* exhibited varied sensitivities. Reduced photosynthetic oxygen production and decreased absorption maxima peaks were the results of solar radiation bleaching photosynthetic pigments and breaking down proteins.

The same photosynthetic pigments were generally present in *C. clavulatum*, *H. musciformis*, and *G. dentata* (Figure 2). This may indicate the relative order of photosynthetic capacities, attributable to the differences

in their absorbance rates, with *C. clavulatum* having the greatest, followed by *G. dentata* and then *H. musciformis*. As the thalli were exposed to different components of solar radiation, their absorbance gradually diminished, indicating that the photosynthetic pigments were being bleached. The thalli exposed to unfiltered solar radiation had the lowest optical densities after 3 h of exposure (Figures 3 and 4). According to Yang et al. (2020), most phytoplankton organisms cannot withstand unfiltered solar radiation and when exposed to excessive sunlight, their photosynthetic pigments become bleached, and they quickly perish. In contrast, the majority of higher plants are adapted to full sunlight. Hence, the observations in our study are in agreement with the report by Yang et al. (2020).

The kinetics of bleaching and the pace at which pigments corresponding to those peaks are being bleached are indicated by changes in the absorption peaks. The absorption at the peaks of the photosynthetic pigments in the three red algae varied significantly ($P < 0.05$) (Appendices 1 and 2), indicating that the pigments had been bleached by the sun's UV and visible light. In certain marine diatoms and cyanobacteria, exposure to solar radiation has been observed to easily bleach photosynthetic pigments, with significant implications for solar energy utilization, resulting in decreased ATP and NADPH availability and potential impairment of biomass production (Yang et al., 2020).

Role of carotenoids

In *C. clavulatum* and *H. musciformis*, an increase in absorption rate occurred within the initial hour of exposure to various radiation conditions, including PAR+UVA+UVB, PAR+UVA, PAR, and unfiltered solar radiation. This increase may be attributed to the high presence of carotenoids, because carotenoids provide direct protection of photosystem II reaction centers against photooxidation and serve as effective radical-trapping antioxidants (Kozono et al., 2018; Saccon et al., 2020). Carotenoids can react with and neutralise singlet state oxygen. They quench the triplet state of chlorophyll *a*, which is one of the main sources of undesired energy for the intracellular production of singlet-state oxygen (Bautista-Saraiva et al., 2018).

Zhang et al. (2020) have demonstrated that specific carotenoids are active in phytoplankton and take part in the xanthophyll cycle. The xanthophyll cycle is a series of reactions that dissipate excess light energy and prevent photoinhibition (Yang et al., 2020). Therefore, during the first hour, the presence of carotenoids might have prevented photobleaching of the other photosynthetic pigments, thereby causing an increase in their absorbance.

Impact of UV radiation

The red algae used in this study were all susceptible to different forms of solar radiation, with UV being the most harmful. The photosynthetic pigments were one of the primary targets for UV damage; phycocyanin and phycoerythrin were bleached first, then carotenoids, and finally chlorophyll *a*. The high sensitivity of these organisms to UV radiation lends credence to worries about rising solar UVB radiation stressing phytoplankton and other algae (Yang et al., 2020). Majority of phytoplankton organisms use gravity and light as their primary signals to choose a specific depth within the water column; however, some have been found to orient in relation to UV radiation according to Yang et al. (2020). Since red algae are sessile and found in the sublittoral and littoral zones, they would be much more affected by radiation than other organisms. Such organisms cannot move to lower levels (with less UVB); therefore, an increase in the ratio of UVB to PAR will increase the UVB stress, which will negatively impact their growth and development.

Photosynthesis and respiration

Solar radiation negatively impacted both photosynthesis and respiration, with the findings of this study confirming that excessive solar exposure led to decreased oxygen production and potential impairment of metabolic processes. While respiration in some Mediterranean macroalgae seems less affected, this study results indicated significant inhibition in red algae, revealing a need for further investigation into the effects of solar radiation on various species in varying geographic locations. Since photosynthesis is the process that drives the growth of red algae, solar radiation resources are necessary for their production. However, exposure to excessive direct solar radiation reduced both dark respiration and photosynthesis; meaning direct solar irradiation was injurious to the algae studied. Zúñiga et al. (2020) have reported that respiration is largely unaffected in the Mediterranean macroalgae, but photosynthesis is inhibited primarily in red, brown, and green benthic algae. The findings of this study confirm the devastating effects of solar radiation on photosynthesis in red algae and further indicate that respiration could also be adversely affected. Hence, elevated solar radiation could have detrimental impacts on red algae and similar organisms. Both the primary light reaction and the dark reaction of photosynthesis are specifically impacted by UV radiation.

Photosystem I appears to be far less sensitive to UVB; whereas, photosystem II reaction centres are inactivated by UVB (Terada et al., 2021). Since photosystem II efficiency was directly correlated with CO₂ assimilation,

any damage to the photosystem II reaction centre will certainly affect photosynthesis adversely. Even though some uncertainty exists regarding the main mechanism of photosystem II inactivation, it has been demonstrated that it might be due to structural alterations in the polypeptide matrix at the water oxidation catalytic site (Liu and Blankenship, 2019). UVB can also prevent the production of some photosynthetic pigments, such as chlorophyll *a*, as well as reduce the activities of Rubisco and ATP-synthase (Ji and Gao, 2021) and, consequently, lead to reduction in photosynthesis.

Specific reaction to solar radiation

Unfiltered solar radiation significantly caused a reduction in the amount of photosynthetic oxygen produced. This reduction was greatest in *C. clavulatum*, where, after 49 min of exposure, net oxygen production was zero (Figure 1A). Although photosynthesis is driven by light energy, too much light can harm the photosynthetic apparatus and prevent PS II-level photosynthetic electron transport (Liu and Blankenship, 2019; Terada et al., 2021). Therefore, excessive solar radiation reaching the habitat of red algae (sub-littoral zone, close to the low watermark or in rock pools) could have devastating consequences on marine photosynthetic productivity and oxygen production, which could negatively impact both terrestrial and aquatic life.

When exposed to short durations of UVB, UVA, and PAR, the production of photosynthetic oxygen in red algae decreases faster than protein degradation and reduction in absorption maxima of photosynthetic pigments (Danquah et al., 2023). Similarly, Quintano et al. (2019) observed reduction in photosynthetic pigments in the agarophyte (*Gelidium corneum*); while in *Cladophora glomerata*, *Spirogyra* species and *Sirodotia delicatula*, Bautista-Saraiva et al. (2018) found that prolonged UV exposure caused the photosynthetic capacity of the cells to decline faster than the changes in protein analysis and absorption maxima. This indicates that UV-induced photo-bleaching happens only after prolonged exposure, whereas structural changes within the photosynthetic apparatus are induced by relatively short exposure times, which affect energy transfer within the antenna complex. Indeed, Li et al. (2023) have found that brief exposure of the diatom *Thalassiosira pseudonana* to high fluence rates of UVB radiation suppresses photosynthetic oxygen production greater than prolonged exposure period at low fluence rates, indicating the potential for a repair mechanism.

Among the wavelength bands of solar radiation, UVB irradiation appeared to have the most drastic effect, followed by UVA, while visible radiation had the least negative effect, though the differences between them

were not statistically significant ($P > 0.05$). There are instances when the UVA region functions similarly to UVB and instances when it functions similarly to visible radiance. These reactions could be caused by the absorption spectra of different photosensitizers overlapping, which could explain why there are not many noticeable variations. Terada et al. (2021) have demonstrated that many species suffer photoinhibition or even photodamage in response to intense solar radiation, especially UV radiation, even though visible radiation also plays a role. For instance, in some cyanobacteria, the inhibition of photosynthesis occurs even more quickly than the effects on other physiological functions like motility and orientation (Voronova, 2019). *H. musciformis* was the most resistant species to solar radiation, followed by *G. dentata* and *C. clavulatum* according to photosynthetic oxygen production rate. *H. musciformis* resistance could be due to its structural makeup, as it sometimes takes the form of dense, cushion-like patches or loose, bushy clumps. Moreover, it possesses an abundance of branchlets that bear tetrasporangia, which are awl-shaped or spine-shaped branchlets that have cytotraps about 650 μm in diameter. These morphological structures allow it to retain some water in its thallus, which lessens the impact of solar radiation on it. Pliego-Cortés et al. (2019) have argued that increased production of UV-screening materials, such as mycosporine-like amino acids (MLAA) in algae, may be responsible for their resistance to solar radiation. MLAA are water-soluble iminocarbonyl derivatives of mycosporines, which appear to be particularly distributed throughout the aquatic biota and absorb maximally in the range of 310–360 nm (Bautista-Saraiva et al., 2018; Quintano et al., 2019). The presence of MLAA in the red algae studied was not determined. Therefore, there is a need to find out the basis of resistance in *H. musciformis*.

Conclusion

The red algae were under stress from all the different components of solar radiation, such as reduced photosynthesis, thalli protein destruction, and photobleaching of photosynthetic pigments. The organisms were most stressed by UVB and unfiltered solar radiation, albeit to differing degrees. The detrimental effects of excessive solar radiation on marine red algae are confirmed by this study, with that being a major threat to the primary producers of the marine ecosystem.

Given the significant role of red algae in oxygen production and the marine food web, the observed reductions in photosynthetic efficiency could have cascading effects on marine biodiversity and ecosystem stability. The ability of these organisms to serve as bioindicators of solar radiation stress suggests their

potential use in environmental monitoring programs aimed at mitigating the impacts of climate change and UV radiation exposure.

Further research is needed to investigate the mechanisms underlying algal resistance and adaptation to solar radiation, particularly in species such as *H. musciformis*. This understanding could provide insights into the resilience of marine ecosystems and inform conservation efforts in the face of increasing solar radiation exposure.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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