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Potential use of Fiji sea grapes, *Caulerpa racemosa* "nama": ecophysiological and biochemical investigations

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Abstract

Caulerpa species are valued for their nutritional benefits and are commercially farmed as sea grapes in several Southeast Asian countries. In Fiji, sea grapes are locally known as Nama and are highly valued and harvested from the wild. Despite their importance, they are not cultivated yet. There is limited understanding of the ecophysiology, particularly regarding their natural growing conditions and how environmental factors, such as light irradiance, influence their physiological and biochemical responses. Conflicting information about taxonomy adds to the complexity of this issue. This study aimed to document environmental conditions at important harvest sites and identify species using DNA barcoding. Primarily, it investigated the effects of varying light irradiances (50, 100, 300, and 600 µmol photons m^{-2} s^{-1}) on photosynthetic performance and recovery abilities of the test organisms. The species identified were *C. racemosa* and *C. oligophylla*. Photosynthetic efficiency remained stable under moderate light (50 µmol photons m^{-2} s^{-1}; F_v/F_m 0.79 ± 0.02) but showed significant photoinhibition under high irradiance (600 µmol photons m^{-2} s^{-1}; F_v/F_m 0.42 ± 0.04). However, full recovery under moderate light was observed (F_v/F_m 0.73 ± 0.03), indicating resilience to light stress. These findings provide important insights into the ecophysiology of Fiji's sea grapes, laying the groundwork for future research on their aquaculture potential. This could reduce pressure on wild populations, ensure sustainability, and create economic opportunities for local and export markets, with special attention to the socio–economic role of sea grapes for local communities, particularly women.

Keywords Chlorophyta, Fiji, Functional foods, Nutritional value, High light intensities, Antioxidant content manipulation

1 Introduction

In a world facing increasing food demand, understanding and optimizing the cultivation of nutritional resources becomes ever more important. Food derived from oceans, lakes and rivers, called blue food, plays a fundamental role in food and nutrition security for billions of people [24. Among blue foods, farmed seaweeds have some of the

lowest environmental impacts [15]. As a nutritious and plentiful food source, seaweeds offers a solution to the challenges of feeding a rapidly growing global population [33]. While its net impact on carbon removal remains under active investigation, seaweed holds potential to contribute to climate mitigation and food security, especially since its cultivation does not require farmland or freshwater and has a lower environmental footprint than many land-based foods [34, 48, 53]). Macroalgae account for 51.2% of the total production in marine and coastal aquaculture [7], whether consumed directly or with derivatives such as alginates or phycocolloids. Macroalgal production stands out as the fastest – growing sector in global marine aquaculture, generating a gross production value exceeding US$ 13 billion annually [13]. However, this production is primarily dominated by a few genera of red and brown macroalgae, with green macroalgae contributing less than 1% [13, 27].

Among the various types of green macroalgae, *Caulerpa* J.V.Lamouroux (1809) is particularly distinctive. The consumed species of *Caulerpa* (Fig. 1) are valued for their unique texture, which includes prostrate, horizontal stems or stolons with rhizomes and edible fronds that have vesiculate ramuli [57]. Species with vesiculate branchlets, like *C. racemosa*, are generally called sea grapes or grape algae, while those with smaller vesiculate branchlets like *C. lentillifera*, are also referred to as green caviar. Both dominate the market and are consumed across the Pacific and Southeast Asia, with an increasing popularity in Western countries [47, 57]. They are characterized by a rich nutritional profile that includes antioxidants, proteins, minerals, vitamins, and they have the potential to be utilized as a promising nutraceutical resource [11,18, 36]. This makes them a valuable and nutritious food option, highly contributing to food security, particularly in the growing populations of coastal tropical regions like Fiji [30, 31, 42]. Sea grapes are typically found in the intertidal and sublittoral regions of tropical shallow water reef areas. Like

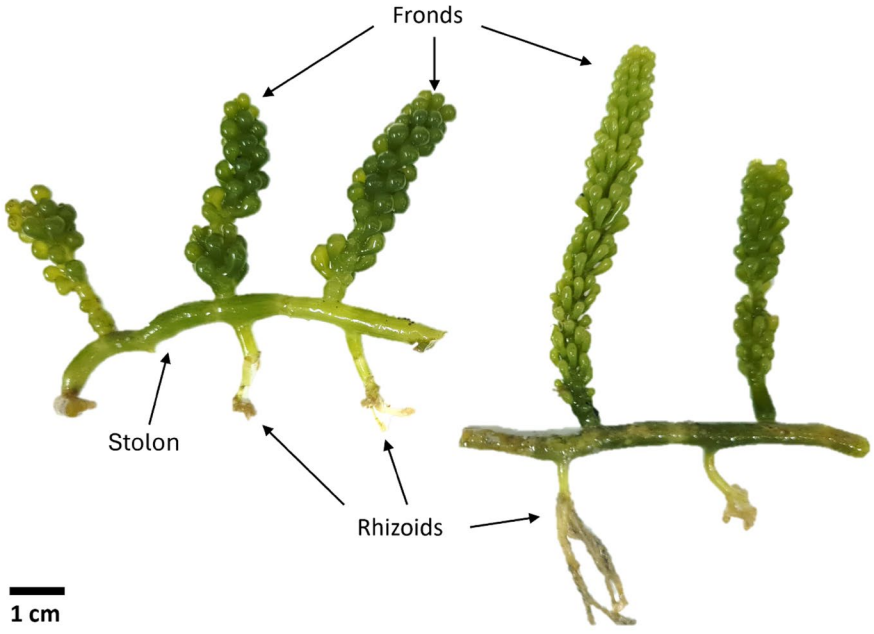

Fig. 1 Sea grapes (*Caulerpa racemosa*) from Fiji with horizontal stolons, rhizoids and the edible fronds with ramuli

other algae found in intertidal areas, sea grapes are well – adapted to environments with rapidly changing and intense abiotic stress factors like light irradiances and temperature.

While *C. lentillifera* is widely cultivated in tropical Asian countries, sea grapes in the South Pacific Islands are predominantly not farmed [57]. In Fiji, a few families and mostly women from the villages of specific regions gather seaweed directly from the wild. The Fijian name for all eaten sea grapes is 'nama' and no distinction is made between the different variations of *Caulerpa* species [48]. Seaweed, including *Caulerpa* species, is traditionally and culturally an important food throughout the Pacific, with consumption practices rooted in local traditions and playing a significant role in the diets and nutrition of Pacific Island communities [5, 26]. South [47] first described the importance of seaweed as a food and income source to Fijian communities.

Morris et al. [28] proposed that production does not meet demands and holds the potential for further expansion with a promising opportunity for an export market. Additionally, they found that 75% of the supply comes from the Yasawa Islands, where 50% of the average weekly income (US$ 49.52) is derived from the trade of *Caulerpa*, highlighting its significant role in supporting rural livelihoods [25, 28].

A study conducted in 2023 further investigated the harvest sites, markets, and supply chains (Mandl, unpublished data). The study identified four sea grape harvesting regions supplying markets in Viti Levu (Fig. 2).

While some sea grape fields are situated offshore in the sublittoral zone, accessible only by boat, other harvesting areas are found within the intertidal zone. However, there remains a substantial lack of environmental data for these areas. Critical information such as biomass density, light conditions, water depth, and general ecological parameters are scarcely documented. Information about the growing conditions of Fiji´s sea

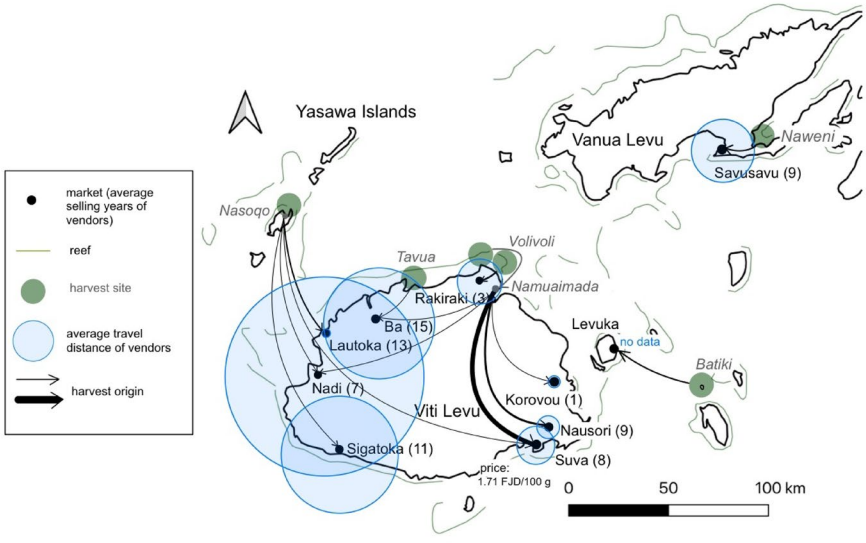

Fig. 2 Map of Fiji depicting Caulerpa ('nama') harvest sites (green dot) and supply chains (black arrows) to municipal markets: The distribution of 'nama' harvest sites across Fiji, focusing on key municipal markets including Ba, Lautoka, Nadi, Sigatoka, Suva, Nausori, Korovou, Rakiraki, Savusavu, and Levuka. Average years of selling experience (in brackets) and distances (distance bar) traveled by vendors to reach these markets depicted. The thickness of arrows represents the number of vendors on each market. Total number of vendors interviewed: $n = 38$. (Mandl, unpublished Data)

grapes is crucial for understanding the algae physiology and ensuring the sustainability of the harvest sites.

Fiji positioned itself as the biggest producer of *Caulerpa* spp. among the Pacific islands, achieving an annual production of 110 tons (fresh weight) and garnering a total revenue of US$ 141,632 [28]. Recent numbers of production after the pandemic do not exist.

Although scientists in the past had recognized the sea grapes growing around Fiji as *Caulerpa racemosa* Forsskäl J. Agardh (1873), recent molecular analyses have shown a different species composition, challenging the previously established understanding [32]. Morphological identification is challenging, because the fronds can be highly plastic and are significantly influenced by environmental conditions [2].

Caulerpa lentillifera is a shade – adapted and light – sensitive seaweed that exhibits signs of photoinhibition, such as reduced maximum quantum yields of photosystem II (F_v/F_m), at light intensities of 100 µmol photons m^{-2} s^{-1} or higher [17, 22]. Similar to other green macroalgae, *C. lentillifera* can swiftly recover to their prior photosynthetic efficiency following exposure to specific stressors (e.g., *Ulva rotunda;* [Franklin et al. 14, 51].

Due to their exposure to environments rich in light and oxygen, which promote the production of free radicals and oxidizing agents, seaweeds have also developed a variety of antioxidants as carotenoids, tocopherols, ascorbic acid, and polyphenols to protect themselves from oxidative damage [10, 20]. These mechanisms further enhance the nutritional properties of edible seaweeds. Several studies have shown the increasing nutritional qualities of sea grapes using high irradiances during cultivation or as post – harvest treatment [46, 50]. *C. lentillifera* has shown significant increases of antioxidant activity (AOA) and total phenolic content (TPC) of up to 228.8 ± 12.4 and 222.2 ± 22.7% of initial values when exposed to irradiances up to 600 µmol photons m^{-2} s^{-1}. However it is not known how the antioxidant level may change after exposing the seaweed to light stress and then allowing the organisms to recover. Whether sea grapes consumed in Fiji exhibit similar nutritional profiles that can be enhanced, also remains to be investigated.

The limited understanding of species composition of Fiji´s sea grapes accompanied by a significant lack of environmental data at harvesting sites, which is crucial for optimizing cultivation and ensuring a sustainable supply underlines the need for further research in this field. Additionally, there is insufficient knowledge regarding the biochemical and ecophysiological responses of sea grapes to light stress, their recovery capabilities, and the impact on antioxidant content. These gaps emphasize the urgent need for thorough research to address these aspects.

The present study was conducted for a comprehensive understanding of sea grapes in Fiji on different levels. Field measurements of environmental parameters and biomass sampling were focused on the main harvesting region, Rakiraki. For eco – physiological and biochemical aspects, the study aims to assess the impact of four light irradiances (50 – 600 µmol photons m^{-2} s^{-1}) on photosynthetic efficiency, antioxidant activity (AOA), and total phenolic content (TPC). Additionally, the study investigates whether sea grapes can recover from potential stress when returned to lower light conditions, and to what extent AOA and TPC levels change post – recovery. Molecular species identification completes the scope of this research.

2 Materials and methods

2.1 Study locations, field measurements and biomass sampling

Most sea grapes sold at the Suva Municipal Market come specifically from Namauimada in Rakiraki (Fig. 2). Consequently, the study was conducted at two sea grape harvesting sites in this area (Fig. 3). The 'Offshore Site' is located off the coast of the Rakiraki district in the Ra province on the northern coast of Fiji's main island, Viti Levu (17°17'29.4"S, 178°10'02.2"E). Here, women from Namauimada Village collect the seaweed, a major supplier of 'nama' at the Suva Municipal Market. The second site, the 'Nearshore Site,' is situated in the intertidal zone of the Volivoli peninsula within the same district (17°19'3"S, 178°11'21"E). Women from Navolau 1 harvest sea grapes here for domestic use. Both sites were visited at the end of October during low tide under sunny weather conditions, during the transition from the dry season to the wet season. Environmental parameters (depth, irradiance at growth depth, temperature, salinity, pH, and O2 levels) were measured at these sites at the end of October 2023. Light irradiances (Photosynthetic Active Radiation, PAR) were measured using a LI – 1400 datalogger with a 4 – π flathead sensor (LI – COR Biosciences, USA). Water temperature, oxygen levels, and pH were measured during low tide using a multimeter (WTW 3430 SET F, Germany). To assess the density of *Caulerpa spp.* fronds at the Offshore Site, a quadrat survey was conducted in January 2023. A series of 1 m^2 quadrats ($n = 5$) were randomly positioned within the sea grape harvesting area, and the fronds within each quadrat were counted. For the laboratory experiments, samples of *Caulerpa spp.* were collected from the Offshore Site and transported to the University of the South Pacific (USP) in Suva (Fig. 3). The collection of plant materials for this study was conducted in accordance with local and national regulations, with permissions from the Ministry of iTaukei Affairs (Reference: MTA-42/2–8) and the Ministry of Education.

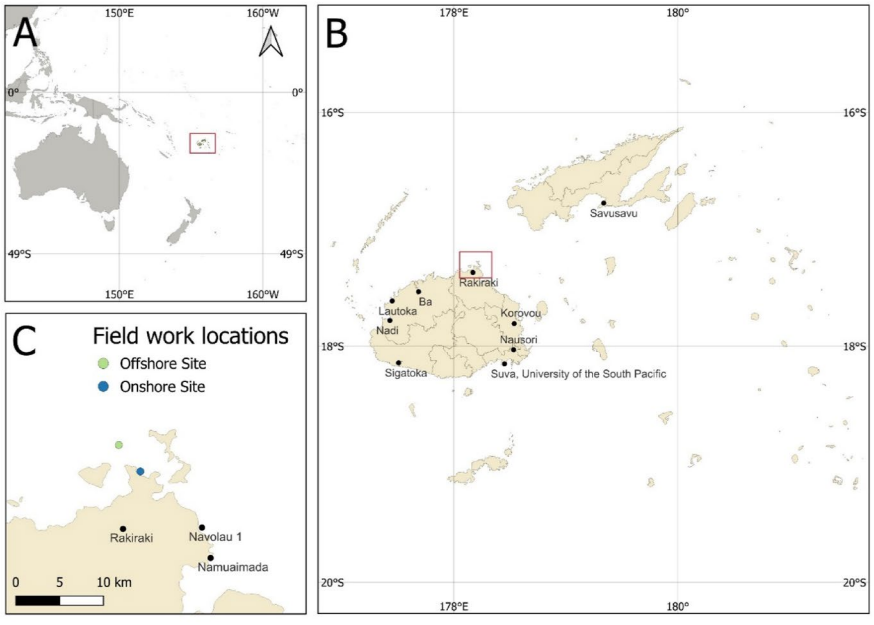

Fig. 3 **A** Location of Fiji within Oceania, the red square marks the Republic of Fiji; **B** Map of Fiji with the locations of markets on main island Viti Levu and the second biggest island, Vanua Levu; the red square marks the north of the Ra province; **C** Map of field work locations at the northern coast of the Ra province with the Offshore Site (green dot) and the Onshore Site (blue dot), including the two villages Namauimada and Navolau 1 and the city Rakiraki

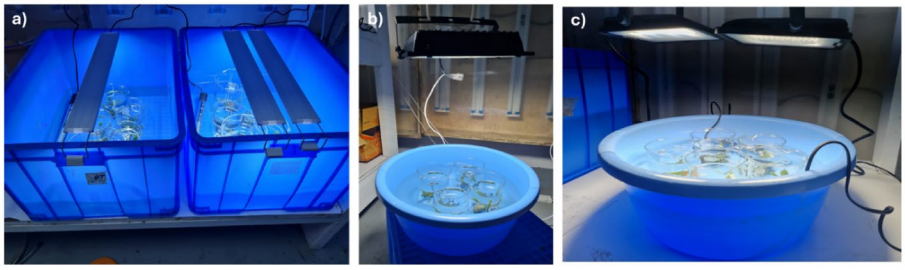

Fig. 4 Experimental set – up for *Caulerpa racemosa* from Fiji. Four treatments with **a** 50 (left) and 100 µmol photons m^{-2} s^{-1} (right); **b**, **c** Set – ups of the 300 and 600 µmol photons m^{-2} s^{-1} treatment, respectively

Table 1 Irradiance treatments of photosynthetically active radiation (PAR) in µmol photons m^{-2} s^{-1} for four treatments, including the corresponding light source. Values are shown as mean ± sd across all measurements in the experimental beakers

Targeted irradiance [µmol photons m^{-2} s^{-1}]	Light source	Mean ± SD	Minimum	Maximum
50	14 W, Yao Rui Aquarium Supplies, China	51.6 ± 5.1	44.2	60.6
100	14 W, Yao Rui Aquarium Supplies, China	97.6 ± 13.8	78.6	117.3
300	200 W, Elements	305.1 ± 8.4	292.7	314.5
600	50 W, Philips	604.9 ± 19.6	590.9	635.2

2.2 Experimental set–up

Laboratory experiments were conducted in 1 L glass beakers filled with seawater collected from Laucala Bay, located on the eastern side of Suva. To maintain a salinity of 34 PSU, additional sea salt (Coral Pro Salt, Red Sea, Israel) was added when needed, particularly after rainfall. All beakers were maintained in water baths to ensure a stable and uniform temperature of 25.0 ± 0.5 °C. The measured pH averaged 8.3 ± 0.2. Water in the beakers was stirred daily and changed every second day. Before the start of the experiments, the sea grapes were cut into single fronds with a length of 4–6 cm, each attached to stolons measuring 2–3 cm in length and acclimatized for 4 days in a 60 L aquarium (60 × 40 × 25 cm) at 25 °C illuminated with an irradiance of 50 µmol photons m^{-2} s^{-1}. The fronds ($n = 4 – 5$) were exposed to different light irradiances (50, 100, 300, and 600 µmol photons m^{-2} s^{-1}) under a 12:12 light – dark photoperiod for 13 days, using light – emitting diodes (14 W, Yao Rui Aquarium Supplies, China; Fig. 4a) and LED floodlights (200 W, Elements; 50 W, Philips; Fig. 4b, c) to achieve the targeted irradiance levels for each experimental treatment (Table 1). A LI – COR with a 2 – π flathead sensor (LI – COR Biosciences, USA) was used to adjust the experimental irradiance. Temperature, salinity, and pH were regularly monitored to maintain constant conditions in the beakers. For subsequent analyses, the samples were taken from the beakers, and excess water was removed by gently dabbing the fronds with paper tissues.

2.3 Measurement of photosynthetic efficiency

The photosynthetic efficiency was measured using a portable Diving – PAM chlorophyll fluorometer (Walz, Germany). The maximum quantum yield of photosystem II (PSII) (F_v/F_m) was measured in Caulerpa frond thallus parts that were dark – adapted for 7 min. For the light stress experiment (will also be referred to as such below), F_v/F_m values were taken on the initial day of the experiment, as well as on days 1, 3, 10, and 13.

To examine the potential of recovery after potential light induced physiological stress, another experiment was conducted, mirroring the setup of the first. In the following, this experiment is referred to as the recovery experiment. Sea grapes were transferred after 10 days to additional recovery aquaria illuminated with an irradiance of 50 µmol photons m^{-2} s^{-1}. F_v/F_m measured just before the transfer and after 7 days under recovery conditions. After each measurement, the middle section of the frond was excised and frozen at – 20 °C until all samples were collectively freeze-dried (see 2.4).

2.4 Preparation of sample extract

This method was adapted from [4], with slight modifications. The sea grapes were kept at – 80 °C for 24 h and then freeze – dried for 24 h at 1 mbar (Zirbus technology, Germany). Until further processing, the samples were stored in a dark place for two months. The freeze – dried samples were ground to powder for 45 s using a FastPrep – 24 (MP Biomedicals, Germany). 0.0125 g dry weight (DW) of the samples was dissolved in 250 µL ethanol (70%) and extracted in a water bath (47 °C) for 4 h, being vortexed hourly. The samples were then centrifuged (2500 g, 20 °C) for 5 min.

2.5 Measurement of antioxidant activity/$ABTS^{\bullet+}$ assay

Antioxidant activity (AOA) was measured using a modified $ABTS^{\bullet+}$ assay (2,2′ – azino – bis – 3 – ethylbenzthiazoline – 6 – sulphonic acid) based on the method by [40] with modifications as described in previous studies [4, 46, 50]. A stock solution of 2.45 mM ABTS•+ was prepared by oxidizing 7.0 mM ABTS with potassium disulfate ($K_2S_2O_8$) for 16 h. The working solution was freshly prepared by diluting the stock solution with absolute ethanol until a stable absorbance of 0.7 ± 0.02 at 734 nm was reached, measured using a UV/VIS spectrophotometer (Thermo Scientific Genesys 140/150, Fisher Scientific GmbH, Germany). For the assay, 1 mL of the ABTS•+ working solution was mixed with 10 µL of the sample extract, and absorbance at 734 nm was recorded after 6 min. Trolox was used as a standard, and AOA was expressed as Trolox Equivalents (TE mmol per 100 g dry weight). All reagents were obtained from Sigma-Aldrich/Merck KGaA, Germany.

2.6 Measurement of total phenolic content/folin assay

For determining the total phenolic content, the Folin – Ciocalteu method (TPC) described by [1] used with minor adjustments. A 10% (v/v) Folin – Ciocalteu solution was mixed with 150 µL of sample using a vortexer. 1200 µL Na_2CO_3 solution (700 mM) were added and incubated for 45 min in the dark at room temperature. The samples were then centrifuged (3 min, 5000 rpm and 20 °C), and the absorbance was measured at 765 nm using the same UV/VIS spectrophotometer described in Sect. 2.5. As a standard gallic acid was used and results were expressed as 100 mg Gallic acid equivalents (GAE) g^{-1} DW. The source of the chemicals was as described in Sect. 2.5.

2.7 Statistical analyses

All statistical analyses and graphical outputs were done using R with RStudio [37, 55] and the package tidyverse [55]. Outliers were identified and excluded from further analyses using Grubbs' test through the webpage GraphPad (https://www.graphpad.com/quickcalcs/Grubbs1.cfm, accessed on 23.04.2024; $p < 0.05$). Outlier analysis revealed

Table 2 Primer sequences used for DNA barcoding of Caulerpa spp. From Fiji

Primer	Sequence (5´– 3´)
tuf_A forward	ATGATWACNGGHGCNGCWCAAATGG
tuf_A backward	TTGTTCKAACATAAAATTGWGGTC

Table 3 List of the reagents per sample for PCR including the manufacturer and the volume used for amplification. * VWR Taq dna – polymerase 2X mastermix, 2,0 mM $mgcl_2$

Reagents	Manifacturer	Vol.(µL) per sample
Sterile water (PCR grade, DEPC – water)	Carl Roth, Germay	7.5
Master mix (2x) *	VWR, Germany; Avantor, Poland	10.0
Magnesiumchlorid (25mM)	Roboklon, Germany	0.5
Primer forward (10µM)	Biomers, Germany	1.0
Primer reverse (10µM)	Biomers, Germany	1.0
Master mix volume		**20.0**
DNA template		**2.0**
Total volume		**22.0**

no more than one outlier per set of five replicates, which was excluded. The normality of the datasets was assessed using QQ plots and the Shapiro – Wilk test ($p > 0.05$), while Levene's test was used to verify the homogeneity of variance ($p > 0.05$). A two – way Analysis of Variance (ANOVA) was conducted to investigate the effects of the main factors, light irradiance, and exposure time on different response variables (F_v/F_m, TPC, AOA). For between – subject effects (between the treatments on each experimental day) a one – way ANOVA with light treatment as independent variable was run with a Tukey's honestly significant difference (HSD) post – hoc test.

Quantitative data are expressed as mean values with the corresponding standard deviations. In case the normality assumption was not met, a Kruskal – Wallis test followed by a Dunn – Bonferroni post – hoc test was applied. If Levene's test indicated significant variance differences, a Welch one – way ANOVA was performed, followed by the Games – Howell post hoc test.

2.8 Species identification

No primary identification of the species was performed. Instead, an attempt was made to determine which of the species described by Paul et al. [32] was present. The DNA samples from Sites 1 and 2 were extracted from four freeze – dried samples each using the Quick – DNA™ Plant/Seed Miniprep Kit (ZYMO RESEARCH Europe GmbH, Germany). PCR amplification was performed using a thermocycler (Biometra T – advanced, Analytik Jena, Germany) with a tuf_A primer (Biomers, Germany; Table 2). The tuf_A gene, known for its relatively conserved nature, is commonly used to identify and classify green algae [12, 44, 45]. Details regarding the used reagents used in this study are summarized in Table 3. The following PCR conditions were applied: polymerase activation at 95 °C/2 min, followed by denaturation 95 °C/30 sec; primer annealing at 55 °C/30 sec; extension at 72 °C/45 sec; and an end elongation at 72 °C/5 min, with a total of 40 cycles. PCR products were purified by gel electrophoresis and extracted using a DNA gel extraction kit (Monarch®, New England BioLabs Inc., Germany). The samples were subjected to commercial sequencing (StarSeq Mainz, Germany). Results were compared using BLAST analysis in the NCBI database.

Table 4 Environmental data derived from the multimeter (WTW 3430 SET F, Germany) during low tide from the offshore site, located off the Coast of the Rakiraki district, Northeast of viti levu, and from the nearshore site, located in the intertidal zone of volivoli beach in the same district (29.11.2023) ± SD

	Daytime	Depth, low tide (m)	Irradiance (µmol photons m^{-2} s^{-1}), mean ± SD	Temperature (°C)	pH	Salinity (PSU)	O_2 (%)
Offshore Site (*Caulerpa racemosa*)	1:00 PM	0.8 – 1.3	1055.1 ± 172.0	29.5	8.3	31.9	103.4
Nearshore Site (*Caulerpa oligophylla*)	10:00 AM	0.1 – 0.2	1491.5 ± 158.9	28.9	8.4	31.6	127.6
		0.1 – 0.2, covered with *Gracilaria* sp	625.8 ± 166.4	–	–	–	–
		exposed	2479.0 ± 85.6	–	–	–	–

Fig. 5 **a** Sea grapes at the Offshore Site, located off the coast of the Rakiraki district, northeast of Viti Levu, Fiji **b** Sea grapes at the Nearshore Site, located at Volivoli beach in the Rakiraki district, submerged and partially covered with *Gracilaria spec.* **c** Fully exposed sea grapes at the Nearshore Site

3 Results

3.1 Species identification

Using DNA barcoding, a different species was identified at each of the two sampling sites. The results revealed that at the Offshore Site, the harvesting location responsible for supplying a majority of the sea grapes to the Suva market, the sampled species matched *Caulerpa racemosa* (Forsskål) J.Agardh (1873) with a similarity score of 99.0%. At the Nearshore Site, the identified species matched *Caulerpa oligophylla* Montagne (1842) with a similarity score of 99.3%. A voucher specimen was not collected or stored for this study (no new species were identified).

3.2 Field measurements

Environmental parameters, including depth, irradiance (at growing depth), temperature, salinity, pH, and O2 levels, were recorded for both study sites and are presented as a snapshot in Table 4. At the Offshore Site, sea grapes were completely submerged and partially covered (Fig. 5a), with water depths ranging from 0.8 to 1.3 m at low tide. In contrast, at the Nearshore Site, sea grapes were partially or completely exposed (Fig. 5c), often overgrown by the red alga *Gracilaria* sp (Fig. 5b). The highest irradiance levels were recorded for the exposed sea grapes at the Nearshore Site, with a PAR of 2479.0 ± 85.6 µmol photons m^{-2} s^{-1}. However, differences in measurement timing (time of day) should be considered when comparing sites. The quadrat survey conducted at the Offshore Site revealed a density of 332.5 ± 83.2 fronds per m^2.

3.3 Photosynthetic efficiency

In the light stress experiment, which was carried out for 13 days, F_v/F_m values were significantly affected by exposure time ($F(4, 84) = 33.18$, $p < 0.001$)) and irradiance treatment ($F(3, 84) = 71.59$, $p < 0.001$), as well as by the interaction of both factors ($F(11, 84) = 17.43$, $p < 0.001$). Initial F_v/F_m of sea grapes (0.75 ± 0.05) decreased with increasing irradiances (Fig. 6). The photosynthetic efficiency of sea grapes at treatments of 50 and 100 µmol photons m^{-2} s^{-1} remained consistent throughout the experiment, with over 90% of the initial photosynthetic efficiency maintained. Photosynthetic efficiency of sea grapes exposed to 300 µmol photons m^{-2} s^{-1} declined to ~70% efficiency by day 3 and unfortunately mostly withered by day 10. Data from this treatment and day were not included in the statistical analyses. Algae exposed to 600 µmol photons m^{-2} s^{-1} experienced a rapid decrease of F_v/F_m to 0.42 ± 0.04 and then stabilized, maintaining levels between 40% and 60% of the initial value thereafter.

In the recovery experiment, exposure time and irradiance treatment affected F_v/F_m values significantly ($F(2, 36) = 15.35$, $p < 0.001$; $F(3, 36) = 26.03$, $p < 0.001$). Initial F_v/F_m values of sea grapes averaged 0.79 ± 0.02. Following 10 days of exposure to irradiance treatments, sea grapes exposed to 50 µmol photons m^{-2} s^{-1} maintained almost 70% of the initial value (0.56 ± 0.17), while those treated with 100 µmol photons m^{-2} s^{-1} maintained approximately 85% of the initial photosynthetic efficiency (Fig. 7). Sea grapes exposed to 300 µmol photons m^{-2} s^{-1} decreased to 60% of the initial (0.50 ± 0.06), and those exposed to 600 µmol photons m^{-2} s^{-1} showed retention of ~45% of the initial value (0.33 ± 0.07). After the 7 days recovery period, sea grapes under 50, 300 and 600 µmol photons m^{-2} s^{-1} showed a significant increase in F_v/F_m ($p_{50} = 0.056$; $p_{30\,0} = 0.002$; $p_{600} = < 0.001$), sea grapes of every treatment recovered to ~92% of the initials with F_v/F_m values of 0.73 ± 0.03 (Fig. 7).

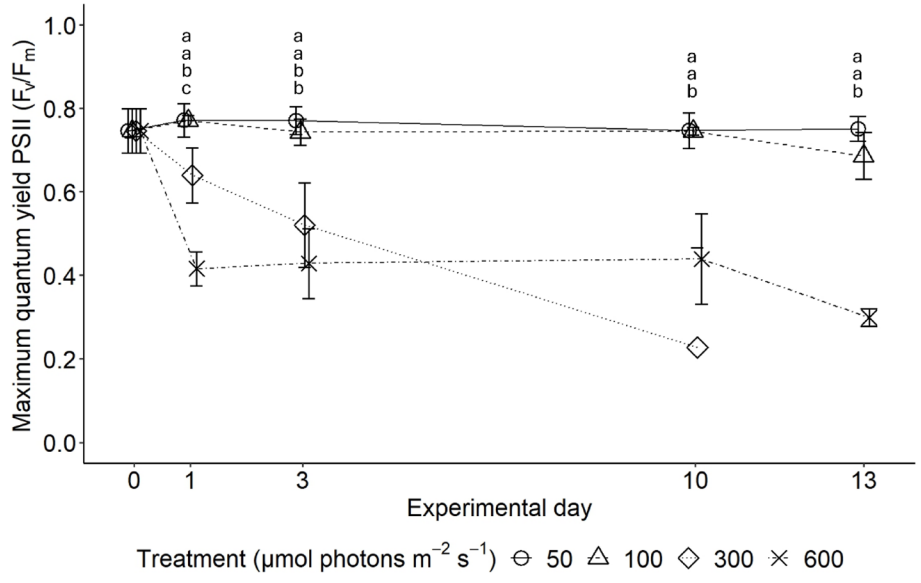

Fig. 6 Maximum quantum yield of PSII (F_v/F_m) of sea grape (Caulerpa racemosa) fronds under four different irradiances (50, 100, 300, 600 µmol photons m^{-2} s^{-1}) over an experimental run of 13 days. Values are expressed as mean ± SD, $n = 4–5$. Different letters indicate significant differences between irradiance treatments per day (One – way ANOVA with post – hoc test, $p < 0.05$) and are assigned to treatments in the graph from top to bottom

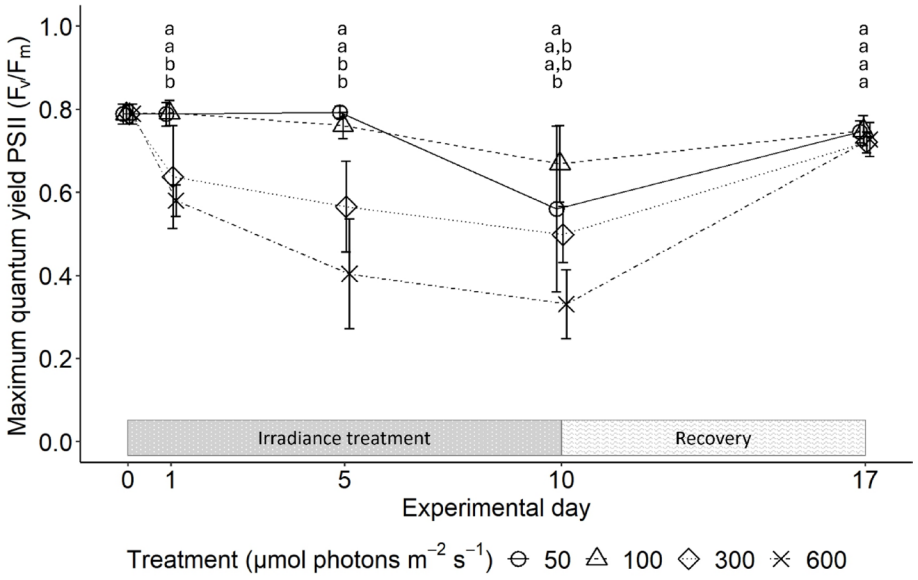

Fig. 7 Change of maximum quantum yield of PSII (F_v/F_m) of *Caulerpa racemosa* exposed to four different irradiance treatments (50, 100, 300, 600 µmol photons m^{-2} s^{-1}). The potential of recovery under 50 µmol photons m^{-2} s^{-1} after exposure to different treatments has been investigated. Dark gray and light gray bars indicate the time of exposure to the different treatment irradiances or recovery, respectively. Data are mean values ± SD ($n = 4-5$). Different letters indicate significant differences between treatments (one – factor ANOVA followed by Tukey's HSD, $P < 0.05$) and are assigned to treatments in the graph from top to bottom

3.4 Antioxidant activity

For the light stress experiment, antioxidant levels of the sea grapes were significantly affected by exposure time ($F(4, 40) = 3.14$, $p = 0.024$). Irradiance treatment ($F(3, 40) = 1.45$, $p = 0.243$) and interaction of both ($F(10, 40) = 1.37$, $p = 0.232$) had no significant impact. *Caulerpa racemosa* showed an initial value of 292.01 ± 10.99 mmol TE 100 g^{-1} DW (Fig. 8). There are no significant differences between initial values and values at day 13 ($p_{50} = 0.99$; $p_{100} = 0.79$; $p_{600} = 0.10$). Regarding the recovery experiment, AOA did not change significantly over time ($F(4, 49) = 2.47$, $p = 0.057$) or with varying treatment ($F(3, 49) = 0.39$, $p = 0.762$). Also, the interaction of both factors was not significant ($F(12, 49) = 1.01$, $p = 0.457$) (Fig. 9).

3.5 Total phenolic content

The initial TPC values were 189.45 ± 6.75 mg GAE 100 g DW^{-1}. In the light stress experiment, the analysis showed no significant effects of treatment ($F(3, 38) = 0.07$, $p = 0.974$), exposure time ($F(4, 38) = 0.97$, $p = 0.436$), or their interaction ($F(11, 38) = 1.25$, $p = 0.291$). There were no significant differences between initial values and those measured on day 13 ($p_{50} = 0.90$; $p_{100} = 1.00$; $p_{600} = 1.00$) (Fig. 10). In the recovery experiment, both exposure time and treatment significantly affected TPC (exposure time: $F(4,43) = 2.70$, $p = 0.043$; treatment: $F(3,43) = 4.92$, $p = 0.005$), but their interaction was not significant ($F(11,43) = 1.62$, $p = 0.128$). The treatment with 600 µmol photons m^{-2} s^{-1} showed a significant increase in TPC after 10 days ($p = 0.047$), though no significant difference after the recovery period was detected (Fig. 11). Samples treated with 100 µmol photons m^{-2} s^{-1} showed a significant decrease in TPC after recovery ($p = 0.046$). No other significant changes in TPC were found.

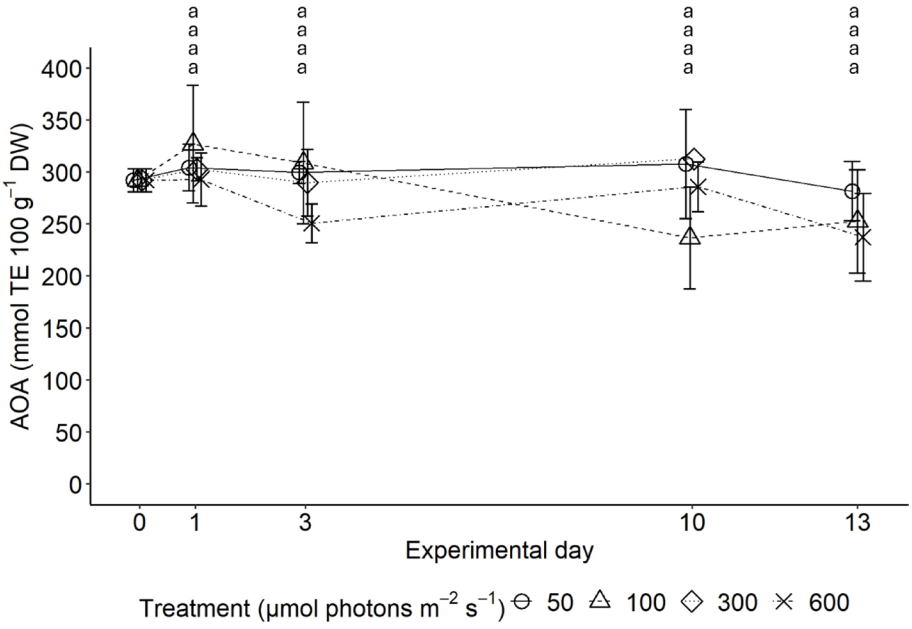

Fig. 8 Antioxidant activity (AOA, Trolox equivalents (mmol TE 100 g^{-1} dry weight (DW)) of sea grape (*Caulerpa racemosa*) fronds under four different irradiances (50, 100, 300, 600 µmol photons m^{-2} s^{-1}) over an experimental run of 13 days. Values are expressed as mean ± SD, $n = 3–4$. Letters indicate significant differences between irradiance treatments per day (One – way ANOVA with post – hoc test, $p < 0.05$) and are assigned to treatments in the graph from top to bottom

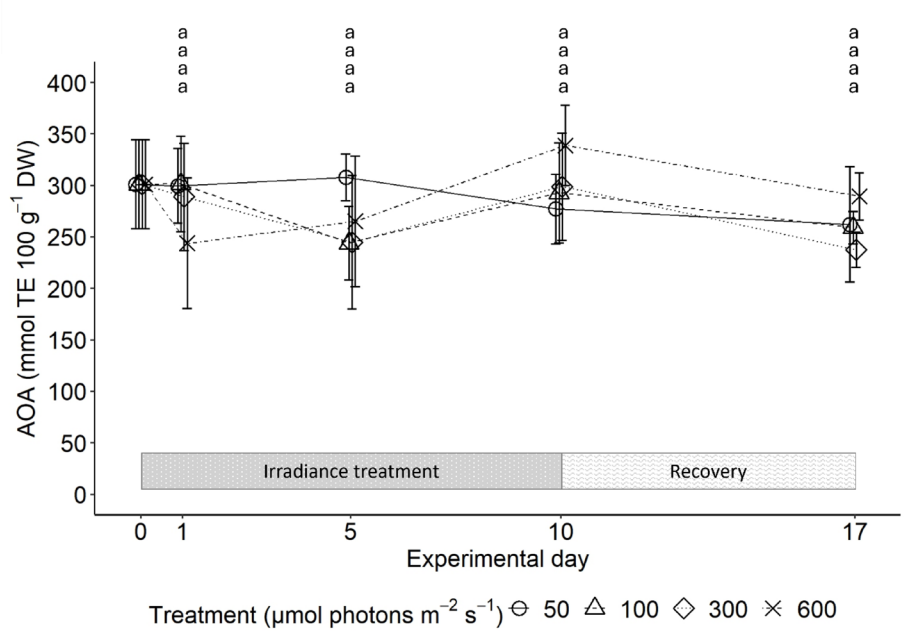

Fig. 9 Change of Antioxidant activity (AOA, Trolox equivalents (mmol TE 100 g^{-1} dry weight (DW)) of *Caulerpa racemosa* exposed to four different irradiance treatments (50, 100, 300, 600 µmol photons m^{-2} s^{-1}). The potential of recovery under 50 µmol photons m^{-2} s^{-1} after exposure to different treatments has been investigated. Dark gray and light gray bars indicate the time of exposure to the different treatment irradiances or recovery, respectively. Data are mean values ± SD ($n = 3 – 4$). Letters indicate significant differences between treatments (one – factor ANOVA followed by Tukey's HSD, $P < 0.05$) and are assigned to treatments in the graph from top to bottom

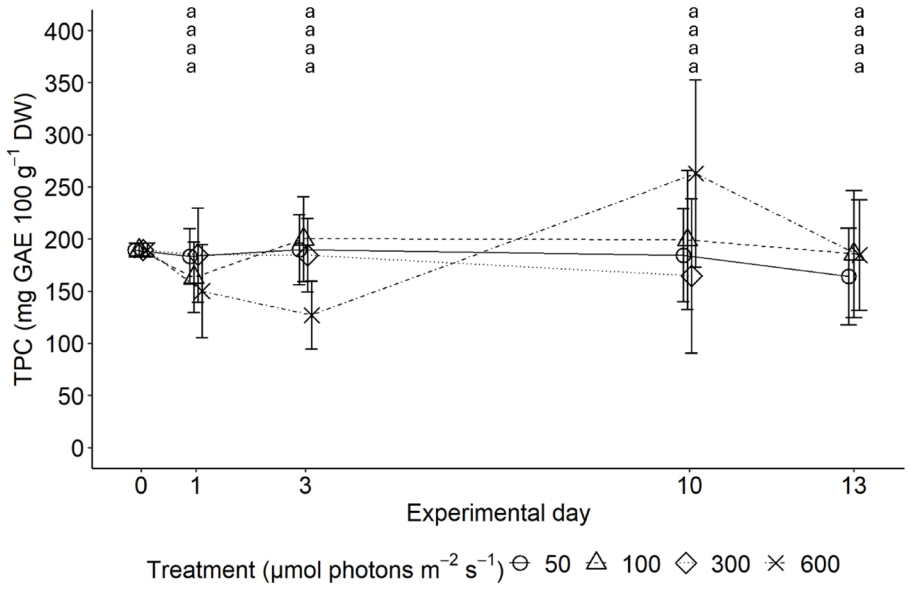

Fig. 10 Total phenolic content (TPC, Gallic acid equivalents (mg GAE 100 g^{-1} DW) of sea grape (*Caulerpa racemosa*) fronds under four different irradiances (50, 100, 300, 600 µmol photons m^{-2} s^{-1}) over an experimental run of 13 days. Values are expressed as mean ± SD, $n = 3–4$. Letters indicate significant differences between irradiance treatments per day (One – way ANOVA with post – hoc test, $p < 0.05$) and are assigned to treatments top down according to order in the graph

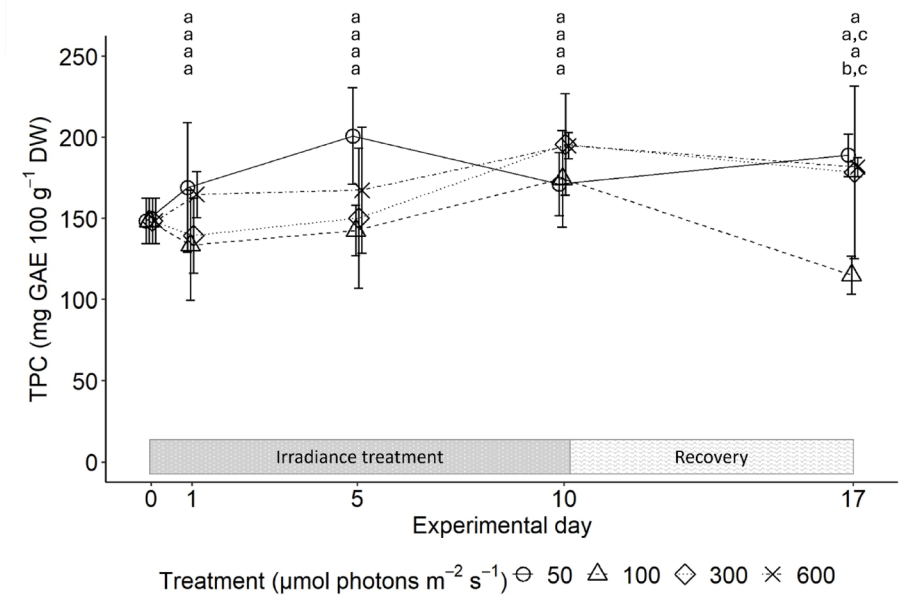

Fig. 11 Change of total phenolic content (TPC, Gallic acid equivalents (mg GAE 100 g^{-1} DW) of *Caulerpa racemosa* exposed to four different irradiance treatments (50, 100, 300, 600 µmol photons m^{-2} s^{-1}). The potential of recovery under 50 µmol photons m^{-2} s^{-1} after exposure to different treatments has been investigated. Dark gray and light gray bars indicate the time of exposure to the different treatment irradiances or recovery, respectively. Data are mean values ± SD ($n = 3 – 4$). Letters indicate significant differences between treatments (one – factor ANOVA followed by Tukey's HSD, $P < 0.05$) and are assigned to treatments top down according to order in the graph

4 Discussion

This study provided insights into environmental conditions at important harvest sites and identified sea grape species through DNA barcoding. It also assessed the effects of light irradiance on the physiological state of sea grapes, including their photosynthetic performance, recovery abilities, and impact on antioxidant and phenolic content.

4.1 Taxonomy

Sea grapes collected from the Offshore Site, where they are harvested by local women for the markets, were identified via DNA barcoding as *Caulerpa racemosa*. This result is notable given recent DNA analyses of Fijian sea grapes, where three different *Caulerpa* species (*C. oligophylla*, *C. macra*, and *C. chemnitzia*) were identified, with *C. oligophylla* and *C. macra* found around Rakiraki 32], but none identified as *C. racemosa*. The species collected at the Nearshore Site was identified as *C. oligophylla*, which in turn aligns with these findings. Even with the use of molecular methods, the significant phenotypic plasticity and the presence of hybrids in some *Caulerpa* species continue to cause problems regarding their classification and identification. Despite progressions in taxonomy and phylogeny, there is still confusion in species delineation and identification, resulting in the description of nearly 400 species, varieties, forms, ecotypes, and ecads [57]. Taxa associated with *C. racemosa* (Forsskal) J. Agardh and *C. peltata* J. V. Lamouroux belong to the taxonomically most challenging group within *Caulerpa*, collectively known as the *C. racemosa–peltata* complex, covering over 30 described varieties and growth forms. However, recent molecular studies have revealed the complex to include at least six distinct species – level entities [55], yet only a few taxonomic revisions have been suggested. This leads to a situation, where over 250 GenBank sequences predominantly remain labeled either as *C. racemosa* or *C. peltata*, emphasizing problems of the accurate identification of sequences despite the availability of molecular data [2]. Due to the complicated phylogeny in this Genus, it could well be that a BLAST analysis is not sufficient to reveal the true identity. In future studies in Fiji this should be considered accordingly.

4.2 Photosynthetic efficiency

The photosynthetic efficiency of unstressed, acclimatized sea grapes had initial F_v/F_m values of 0.75 ± 0.05 and 0.79 ± 0.02, which falls within the same range as values reported for *C. lentillifera* (0.70 ± 0.03 and 0.74 ± 0.04), though slightly higher on average [4, 50]. The results of the light stress experiment indicate that Fiji´s sea grapes thrive best under irradiances of 50 and 100 µmol photons m^{-2} s^{-1}, as implied by the maintenance of their F_v/F_m values for 13 days. This suggests the sea grapes remained healthy and unaffected by the irradiances. Similar responses were seen by Stuthmann et al. [50] after exposing *C. lentillifera* for 14 days to similar irradiances, where F_v/F_m remained > 88% of the initial. In the present study, sea grapes exposed to 300 µmol photons m^{-2} s^{-1} seemed to show gradual declines in F_v/F_m until day 3 (Fig. 6) but unfortunately withered after 10 days, which could be due to pre-stress or contamination. Those treated with 600 µmol photons m^{-2} s^{-1} showed a rapid drop in F_v/F_m of almost 50% after just one day and remained relatively stable thereafter. These findings align with Horstmann [19], who classified *C. racemosa* as shade – adapted low-light plants and are further supported by physiological data presented by Robledo and Freile-Pelegrín [41] which indicate low light requirements for effective photosynthesis in certain *C. racemosa* varieties. In

conditions of high light exposure, the sudden decrease in F_v/F_m serves as an indicator of photoinhibition [16], a phenomenon well – documented in various temperate species of the genus *Caulerpa* [52], including *C. lentillifera* [17, 50]. This response to high light exposure is also influenced by spectral composition, which can affect photoinhibition dynamics. However, the spectrum of the aquarium lamps used in this study could not be determined, representing a limitation that should be considered when interpreting the results.

The ability of seaweed to recover from light stress could be seen in the recovery experiment. Sea grapes from treatments of 300 and 600 µmol photons m^{-2} s^{-1} showed a significant increase in F_v/F_m after the recovery period of 7 days. The decrease in photosynthetic efficiency observed in the 50 µmol photons m^{-2} s^{-1} treatment at day 10 (Fig. 7) could be due to microalgal contamination. The full recovery of all samples demonstrates the ability of macroalgae to restore their previous photosynthetic efficiency after being exposed to stress. Similarly, *C. lentillifera* has demonstrated immediate and full recovery of F_v/F_m values within 24 h after transfer to recovery conditions [51]. This response serves as a mechanism for intertidal macroalgae to cope with fluctuating and intense abiotic stressors, such as light, and has also been observed in other green algae of the intertidal, like *Ulva rotundata* [14].

4.3 AOA and TPC

The ability of sea grapes to respond to increased light stress with a corresponding increase in antioxidant levels could not be proven in this study. This is in contrast to findings of [46], who were able to simultaneously increase AOA and TPC of *C. lentillifera* by exposing it to increased irradiances, which confirms that phenolic compounds play a major role in the antioxidant capacity of *Caulerpa* [30].

Most studies on the antioxidant content of *C. racemosa* have employed different methods like the 2,2 – diphenyl – 1–picrylhydrazyl or DPPH [46] or the ferric reducing ability of plasma FRAP [3]; or different drying processes (shade–/sun – drying) and solvents (chloroform, hexane, methanol), making direct comparisons difficult. However, [56] reported that *C. racemosa* exhibited significantly higher antioxidant activity and TPC compared to *C. lentillifera*. Interestingly, in the present study, the initial AOA values of *C. racemosa* from Fiji, after acclimatization at a light intensity of 50 µmol photons m^{-2} s^{-1}, were over 300 mmol TE 100 g^{-1} DW – double the AOA found in comparable studies of *C. lentillifera*, which reported values around 150 mmol TE 100 g^{-1} DW using the same method [50]. In their studies, Stuthmann et al. also found that AOA of sea grapes exposed to 600 µmol photons m^{-2} s^{-1} reached a saturation point after one week, achieving 229% of the initial value and a significant increase in TPC with rising irradiance, reaching 180–198% of the initial values.

A possible reason for the overall high AOA in the present study is that the sea grapes from Fiji were pre – stressed and already saturated with antioxidants, which could explain the high initial values and the lack of significant change in antioxidant levels over time, even under high irradiances. This saturation is consistent with the very high PAR measured in situ at the growing sites, which exceeded 1000 µmol photons m^{-2} s^{-1}, likely inducing a sustained antioxidant response in the sea grapes. During the dry season, irradiances could be even higher. In the Mediterranean Sea, the invasive *C. racemosa* has been shown to experience similarly high irradiances with around 1300 µmol photons

$m^{-2}\ s^{-1}$ [39]. For comparison, *C. lentillifera* in culture ponds in Vietnam were exposed to a PAR of 600 µmol photons $m^{-2}\ s^{-1}$ in the summer months. This indicates that species of the *C. racemosa* – complex may be more adaptable to varying light conditions compared to *C. lentillifera*, which is very sensitive to high solar radiation [17, 46, 50]. *C. racemosa* in the Mediterranean Sea is well – known for its adaptability and photosynthetic flexibility, allowing it to thrive in diverse environments, from fully exposed areas to depths of up to 60 m [39]. This adaptability extends to the existence of distinct Caulerpa morphotypes, which display structural and photophysiological acclimation in response to varying light conditions. Collado-Vides and Robledo [8] reported that *C. sertularioides* thalli subjected to high irradiance develop altered morphology and exhibit lower light compensation and saturation points compared to those found in more shaded reef habitats. These findings highlight the capacity of Caulerpa species to undergo both physiological and morphological adjustments to different light environments. In natural settings with intense light irradiances, other factors exist to reduce the light exposure for sea grapes. For instance, [19] found that *C. racemosa* in the Philippines is frequently shaded by seaweeds like *Sargassum* and *Turbinaria*, and the *Caulerpa* thalli are often covered with a layer of mud particles, which likely serves as a filter for light exposure on the fronds, as evidenced by the rapid death of exposed algae when removed from the mud. It is likely that the sediment covering the sea grapes in Fiji also serves as an irradiance filter, as well as the *Gracilaria* specimens that cover them at the Nearshore Site (Fig. 5b).

4.4 Socioeconomic implications

To further highlight the socio – economic importance of the sea grapes for the coastal communities, it is essential to consider their crucial role in ensuring food security. In the South Pacific, there is increasing pressure on local food systems, with an influx of processed, imported foods from Western countries leading to greater dependency and the erosion of local markets [6, 9]. Sea grapes, as a sustainable, local food source, hold significant potential in reversing this trend.

Sea grape harvesting has traditionally been a woman's role, deeply rooted in local customs [23]. As the industry explores modern techniques like aquaculture to increase profit, it is vital to ensure that these developments do not undermine local communities, particularly women, by shifting economic benefits to external entities or disregarding traditional practices. In other regions, men have benefited disproportionately from the introduction of modernization and technology required for controlled cultivation, often as a result of unequal access to resources, training, and decision – making power [21, 29, 38].

Further, it is important to consider that challenges in the sea grape industry in Fiji may not derive from supply or harvesting issues, but rather from gaps in support chains and market access [35] – issues that aquaculture alone would not resolve and could potentially exacerbate, if not managed carefully.

Ultimately, the future of the sea grape industry needs to be shaped by the local communities to ensure not only longevity and sustainability of the development but also for ethical considerations, particularly considering the historical marginalization of women and the potential for unequal distribution of benefits. Any decisions should prioritize the local communities' interests, and external stakeholders must engage with them, ensuring that their voices are heard, and their traditions respected [54].

5 Conclusion

Notably, Fiji's sea grapes are not only nutritious and more resilient to high light intensities than *C. lentillifera* but are also cherished by locals as a traditional and flavorful food. The harvesting communities in Fiji understand that making collection sustainable is important for a stable supply.

However, relying only on wild harvests could pose dangers for the communities involved. Climate change with rising temperatures, elevated sea levels, and extreme weather events could make ongoing dependence on wild harvest more uncertain and risky.

Given the physiological resilience of Fiji´s sea grapes to varying light conditions and their ability to recover from light – induced stress, sea grapes present a promising opportunity for mariculture. Controlled cultivation in nearshore environments could ensure a stable supply, reducing pressure on natural populations and opening possibilities for export.

Sea grapes are not currently advertised or offered as a local traditional food. This gap could present an excellent opportunity for communities to enhance the market value of sea grapes by promoting their traditional use, potentially supporting local economies and expanding market opportunities.

Further research is essential to fully understand the challenges and opportunities of sea grape aquaculture in Fiji, improving cultivation techniques and ensuring sustainable resource management together with the Fijian people. By balancing these risks and opportunities, Fiji's sea grapes could play a central role in both ecological conservation and economic development in coastal communities.

Author contributions

Milena Söhnen: Conceptualization (lead), Investigation (lead), Visualization (lead), Methodology (lead), Investigation (equal), Writing – Original Draft Preparation; Karin Springer: Conceptualization (supporting), Writing – Review & Editing (equal), Supervision (equal); Andreas Kunzmann: Writing – Review & Editing (equal), Supervision (equal), Funding Acquisition (lead); Rajesh Prasad: Review & Editing (equal), Supervision (equal); Hannah Mandl: Conceptualization (supporting), Investigation (supporting), Visualization (supporting), Investigation (supporting), Writing – Original Draft Preparation (supporting); Beatrice Brix da Costa: Visualization (supporting), Methodology (supporting). All authors reviewed the manuscrtipt.

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Data availability

Data is provided on figshare: 10.6084/m9.figshare.29110160 .

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

Plant identification and voucher specimen statement

The plant material used in this study was identified by the author through DNA barcoding. No new or unclassified species were involved. A voucher specimen has not been deposited; however, it is available upon request from Dr. Rajesh Prasad.

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