



Agarophyte seaweeds exhibit differential responses to marine heatwaves depending on the species and climatic season

Henrique D. S. Borburema¹ · Gleybson Almeida-Faria¹ · Sávio Lair Cavalcante Silveira¹ ·
Valkíria de Souza Gomes¹ · Fabio Nauer² · Eliane Marinho-Soriano¹

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Abstract

Marine heatwaves (MHWs) are becoming more intense and frequent due to climate change. However, MHWs' seasonal effects on economically relevant seaweeds have been little addressed. Therefore, we analyzed the effects of MHWs simulated for the rainy and dry seasons on the red seaweeds *Gracilaria caudata* and *Gracilaria birdiae* from Brazil. Seaweeds were cultured for two weeks under the mean sea surface temperature (Δ) of the region: 25°C during the coldest months of the rainy season and 28°C during the dry season. Subsequently, they were subjected to mean ($\Delta + 2^\circ\text{C}$), maximum ($\Delta + 4^\circ\text{C}$), and extreme ($\Delta + 6^\circ\text{C}$) intensity MHWs for two weeks. Finally, the temperature was decreased to Δ and the seaweeds were left to recover for two weeks. Thermally stressed seaweeds showed decreased growth and effective quantum yield, with a more pronounced decrease in seaweeds from the dry season, especially *G. birdiae*. Both species resisted the MHWs simulated for the rainy season, whereas *G. birdiae* from the dry season did not tolerate MHWs simulated for this climatic season, and *G. caudata* from the dry season only failed to resist the extreme MHW. Effective and maximum quantum yield, parameters of photosynthetic performance curves, and complementary energy dissipation pathways measured at the end of the recovery time demonstrated that when seaweeds resist MHWs, they can recover. Our results suggest that seaweeds can be more negatively affected by MHWs during the dry season, and *G. caudata* is more interesting for aquaculture in the context of climate change, as *G. birdiae* was less tolerant of the heat stress.

Keywords Climate change · *Gracilaria* · Rhodophyta · Growth · Photosynthesis · Pigments · Seasonality

Introduction

Continuous anthropogenic emissions of greenhouse gases into the Earth's atmosphere have resulted in global environmental changes (IPCC 2023). An increase in atmospheric and oceanic temperatures has been recorded worldwide (Bindoff et al. 2019; IPCC 2023). Global surface temperature increased by about 1.09°C (0.95 to 1.20°C) in 2011–2020 relative to 1850–1900, with higher increases over land (1.59°C [1.34 to 1.83°C]) than over the ocean (0.88°C [0.68

to 1.01°C]) (IPCC 2023). The expected mean global warming based on the SSP5-8.5 scenario by the end of the 21st century (2081–2100) is around 4°C (IPCC 2023). Heatwaves have become more intense and frequent with longer duration over the past decades due to global warming (IPCC 2023). They result in the transfer of heat from the atmosphere to the ocean surface, triggering marine heatwaves (MHWs). MHWs have been defined as anomalously warm events in which sea surface temperatures within a specific area exceed the 90th percentile, based on 30 years of historical baseline data, for at least five consecutive days (Hobday et al. 2016).

MHWs' negative impacts on seaweed communities have been documented in the scientific literature (e.g., Smale and Wernberg 2013). Indeed, MHWs' effects on kelps have been relatively well studied (e.g., Wernberg et al. 2018; Diehl et al. 2021; McPherson et al. 2021; Bunting et al. 2024). Such studies reported reduced growth rates and chlorophyll fluorescence (Bunting et al. 2024), occurrence of tissue necrosis and changes in pigmentation (Diehl et al. 2021),

✉ Henrique D. S. Borburema
henrique.tpb@gmail.com; henrique.borburema@ufrn.br

¹ Department of Oceanography and Limnology, Federal University of Rio Grande do Norte, Via Costeira, Mãe Luiza, Natal, RN 59014-002, Brazil

² Department of Marine Microbiology and Biogeochemistry, NIOZ Royal Netherlands Institute for Sea Research, Den Burg, Netherlands

loss of genetic diversity (Wernberg et al. 2018), and more broadly, large-scale shifts in the structure of kelp forest ecosystems under thermal stress from MHWs (Smale and Wernberg 2013; McPherson et al. 2021). However, reports on MHWs' effects on green and red seaweeds are still scarce in the scientific literature (Nauer et al. 2022), especially in the Southwestern Atlantic. In this sense, Gouvêa et al. (2017) and Nauer et al. (2022) investigated the effects of simulated MHWs on the red seaweeds *Laurencia catarinensis* Cord-eiro-Marino & Fujii and *Hypnea pseudomusciformis* Nauer, Cassano & M.C. Oliveira from Southwestern Atlantic. In both studies, simulated MHWs negatively affected the seaweeds' physiological performance. Nevertheless, ecophysiological studies on a broad range of species are needed to better predict the impacts of extreme climatic events, such as MHWs, on seaweeds, since seaweeds responses to climate change-related stressors are largely species-specific (e.g., Porzio et al. 2011; Kram et al. 2016; van der Loos et al. 2019). Furthermore, MHWs' seasonal effects on seaweeds have been little addressed, which is worrying, since seasonality influences seaweeds responses to thermal stress (e.g., Diehl et al. 2021; Graiff et al. 2021; Franke et al. 2024).

The agar-producing red seaweeds, such as *Gracilaria* species, are ecologically and economically important, but their potential vulnerability to climate change and MHWs is concerning (Segaran et al. 2023). As primary producers, *Gracilaria* species are food for marine consumers, produce oxygen and organic matter in photosynthesis, and participate in nutrient cycling (Hurd et al. 2014; Fernandes et al. 2021). Additionally, they can be a relevant microhabitat for marine organisms (Fernandes et al. 2022). Agarophytes of the genus *Gracilaria* Greville are important sources of agar (Fernandes et al. 2017). Agar is a polysaccharide widely used by several economic sectors, such as the food, pharmaceutical, and biotechnology industries (Bezerra and Marinho-Soriano 2010). For this reason, *Gracilaria* farming is one of the fastest-growing sectors in aquaculture, and the *Gracilaria* genus is the world's third most produced seaweed in aquaculture (FAO 2020). Global *Gracilaria* aquaculture is dominated by China (3,480,850 t in 2019), followed by other countries such as Indonesia (1,223,540 t in 2019), Chile (21,672 t in 2019), and Vietnam (11,330 t in 2019) (Mantri et al. 2023). Currently, global production of agar has reached around 15,000 t per year (Porse and Rudolph 2017). In Brazil, the demand for agar is also considerable, as seaweed imports reached around 2000 t per year between 1999 and 2012 (Marinho-Soriano 2017). In addition to this economic relevance, *Gracilaria* aquaculture provides several ecosystem services of support, cultural, provision, and regulation (Ferreira et al. 2021). Regarding the latter, seaweed aquaculture has received special attention due to its potential to sequester carbon, contributing to the mitigation of global change (Duarte et al. 2017; 2022).

The agarophyte *Gracilaria birdiae* E.M. Plastino & E.C. Oliveira is endemic to Brazil, with a distribution extending from Ceará state (3°S) to Espírito Santo state (20°S), inhabiting intertidal or subtidal rocky substrata (Plastino and Oliveira 2002). Since 2009, small-scale cultivation of *G. birdiae* has been sporadically developed in Northeastern Brazil. This seaweed cultivation has been a complementary source of income for the coastal communities that develop it, thus contributing to the improvement of their quality of life (Marinho-Soriano 2017). Recently, a study based on environmental suitability modeling (i.e., Barbosa-Silva et al. 2023) demonstrated that *G. birdiae* farming could be viable under future conditions (2100) of climate change. However, *G. birdiae*'s tolerance of thermal stress has been little investigated in experimental approaches, which could confirm the trends projected by statistical modeling. *Gracilaria caudata* J. Agardh is another interesting agarophyte for aquaculture activities in Brazil (Faria and Plastino 2016; Faria et al. 2017). It is widely distributed in the Western Atlantic (North and South America and Caribbean islands) and has a record of occurrence in French Polynesia (Guiry and Guiry 2022), which reveals its broad thermal plasticity. Furthermore, recent research demonstrated that *G. caudata* from Northeastern Brazil tolerates a high temperature of 33°C (Chiaramonte et al. 2023), which suggests its potential to cope with thermal stress from MHWs. In addition to small-scale cultivation of *G. birdiae*, both *G. birdiae* and *G. caudata* have been exploited from natural beds in Northeastern Brazil for commercial purposes since 1960 (Marinho-Soriano 2017).

In this study, we analyzed the effects of simulated MHWs on the physiological responses of the agarophytes *G. birdiae* and *G. caudata* from typical climatic seasons in Northeastern Brazil, namely, the rainy and dry seasons. Based on the literature previously cited, we hypothesized that (i) both species could be resistant and resilient to the simulated MHWs, exhibiting recovery after heat stress; (ii) *G. caudata* has a higher thermal tolerance than *G. birdiae*; and (iii) MHWs simulated for the dry season have stronger negative effects than those simulated for the rainy season, as more stressful environmental conditions occur during the dry season.

Materials and methods

Seaweed collection and laboratory cultures

Gracilaria caudata and *G. birdiae* specimens were collected during low tide from a natural bed in the intertidal zone of Mãe Luiza beach (5° 48' 4.86'' S and 35° 10' 45.11'' W), Rio Grande do Norte state, Northeastern Brazil, in October 2023 (dry month) and March 2024 (rainy month). Based on Köppen's Climate Classification System, the climate of

the seaweed collection site is tropical humid and hot (Alvares et al. 2013). At the seaweed collection region, only two seasons occur: a rainy season from March to August (autumn/winter) and a dry season from September to February (spring/summer) (Carneiro et al. 2011; Borburema et al. 2022a).

After field collection, seaweeds were transported to the laboratory of marine macroalgae in the Department of Oceanography and Limnology of the Federal University of Rio Grande do Norte. In the laboratory the sediment on the seaweeds was removed by washing with tap water followed by washing with filtered seawater. Afterward, the macrofauna was removed using tweezers and branches with epiphytes were discarded. Seaweeds (biomass around 3 g L⁻¹) were maintained in 10-L transparent glass aquaria containing from 4 to 5 L of culture medium: filtered seawater (salinity of 38) enriched with nutrient solution of von Stosch (VSES/2 = 4 mL L⁻¹). The von Stosch solution was prepared as described by Edwards (1970) and modified with a 50% reduction of vitamin concentration (Yokoya 2000). Seaweeds were maintained under ambient temperature from 23 to 25°C, photon flux density of 70–100 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ provided by daylight fluorescent tubes, and a light:dark cycle of 12:12 h (typical in tropical zones). The culture medium was bubbled intermittently (30:30 min) with compressed air sterilized by filtering and replaced weekly for nutrient replenishment. Seaweeds remained in these conditions for 21 days as an acclimation period. During this period, the tetrasporophytic phase of seaweeds was identified under optical microscopy by observing tetrasporangia scattered over the thallus surface (Plastino and Oliveira 2002) (Fig. S1) and selected for the experiments. Tetrasporophytes were selected for the marine heatwave experiments, as this life history phase is predominant in natural beds of *G. birdiae* in Northeastern Brazil (Carneiro et al. 2011) and of *G. caudata* along the Brazilian coast (Faria and Plastino 2016).

Experimental design

Visibly healthy seaweeds were subjected to one marine heatwave experiment for each climatic season (i.e., dry and rainy seasons). Tetrasporophytic branches (3 cm in primary axis length, Fig. S1) were cultured for 14 days under the mean sea surface temperature (Δ) of the seaweed collection region: 28°C during the dry season and 25°C during the coldest months (June–August) of the rainy season (Borburema et al. 2020). Afterward, the water temperature was increased (1°C every hour) to simulate MHWs in three independent treatments: mean-intensity heatwave ($\Delta + 2^\circ\text{C}$), maximum-intensity heatwave ($\Delta + 4^\circ\text{C}$), and extreme-intensity heatwave ($\Delta + 6^\circ\text{C}$) (Nauer et al. 2022). In a fourth treatment, the water temperature was maintained at Δ as a control. These treatments were carried out for 14 days.

Subsequently, the water temperature was decreased in the simulated marine heatwave treatments to reach the control temperature (Δ), and seaweeds were left to recover for 14 days. Thus, each experiment lasted 42 days. Each treatment had four independent replicates ($n = 4$), and each replicate was composed of four apical branches cultured in 500 mL Erlenmeyer flasks containing 400 mL of culture medium (as described in the previous section). Thus, each experiment was composed of 32 Erlenmeyer flasks (two species $\times$ four treatments $\times$ four replicates). The experimental design established for each climatic season was succinctly schematized in Figure S2. An initial biomass of 600 ± 0.08 mg was established for *G. birdiae* per replicate, while 158 ± 0.04 mg was established for *G. caudata*. This difference is explained by the morphological differences between *G. birdiae* and *G. caudata*, as the latter has less thick branches. Throughout the experiments, the culture medium was bubbled intermittently (30:30 min) with compressed air sterilized by filtering and replaced weekly. The photoperiod and photon flux density were the same as in the acclimation period, and the Erlenmeyer flasks were repositioned daily to provide the same light condition to all replicates. The treatments were established in four independent water baths (50-L transparent glass aquaria containing water warmed by a heating device adjusted by a thermostat). The culture medium temperature was monitored daily with a handheld thermometer in all replicates of the treatments. The experiments were carried out with seawater from Mãe Luiza beach. Each experiment was carried out with seawater from the same collection.

The mean sea surface temperature (Δ) of the seaweed collection region was based on temperature data from a 16-year temporal series (monthly averages, January 2007–December 2022). Temperature data were obtained by the MODIS (Moderate Resolution Imaging Spectroradiometer) sensor coupled to NASA's AQUA satellite. Marine heatwave intensity (i.e., mean, maximum, and extreme) was based on Nauer et al. (2022), who characterized MHWs for the Brazilian coast using the free software package “heatwaveR” (Schlegel and Smit 2018) in the R program. Those authors used daily mean sea surface temperatures of temporal series from 1982 to 2020 to estimate the duration, intensity, and frequency of MHWs for localities of the coastline in Brazil. As in our study, they also followed the definition of MHW given by Hobday et al. (2016) (see introduction).

Growth rates

Throughout the experiments, seaweeds were weighed weekly when the culture medium was replaced. Seaweeds were weighed on an analytical balance, and before weighing, they were gently blotted dry with paper towels to remove excess water. Relative growth rates (RGR: % day⁻¹) were estimated using the equation recommended by Yong et al.

(2013): $RGR = [(W_f/W_i)^{1/t} - 1] \times 100$, where W_i and W_f are the initial and final wet weights, respectively, and t is the culture period. RGR data are shown for the conditions: before heatwaves (BHW, on the 14th experimental day), under heatwaves (UHW, on the 28th experimental day), and recovery (R, on the 42nd experimental day).

Photosynthetic performance

In vivo variable chlorophyll *a* fluorescence measurements were obtained from the replicates ($n = 4$) using a submersible pulse-amplitude-modulated (PAM) fluorometer (Diving-PAM-II, Walz, Germany) to calculate several of the photosynthetic parameters. The effective quantum yield ($\Delta F/F_m'$) of photosystem II (PSII) was calculated weekly. The formula $\Delta F/F_m' = (F_m' - F_t)/F_m'$ was applied, where F_t is the current steady-state fluorescence of light-adapted photosynthetic organisms and F_m' is the maximum fluorescence under actinic light during a saturating pulse (Schreiber et al. 1995). F_t was measured under a very low photon fluence rate of red light ($0.3 \mu\text{mol photons m}^{-2} \text{s}^{-1}$), and F_m' during a saturating pulse ($1500 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) of 0.6 s. During the fluorescence measurements, the branches were placed in a glass Petri dish containing filtered seawater. The fluorescence measurements were always performed from the apical parts of the branches. Effective quantum yield data are shown for the following conditions: BHW, UHW, and R.

On the last experimental day, after measuring F_t and F_m' to calculate the effective quantum yield, the seaweeds were dark-acclimated for 15 min. Then, light pulses (0, 25, 45, 65, 90, 125, 190, 258, 420, 628, 822, 1150, and $1500 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) were applied in 20 s intervals to construct relative electron transport rate (rETR) $\times$ photon fluence rate (PAR) curves. From the first light pulse, the maximum quantum yield of PSII was calculated using the formula $F_v/F_m = (F_m - F_o)/F_m$, where F_m is the maximum fluorescence during a saturating pulse on dark-acclimated photosynthetic organisms, and F_o is the basal fluorescence (Schreiber et al. 1995; Enríquez and Borowitzka 2011). Relative electron transport rates were calculated by multiplying the effective quantum yield by the appropriate PAR values ($rETR = \Delta F/F_m' \times PAR$) (Schreiber et al. 1995; Enríquez and Borowitzka 2011). Relative electron transport rate vs. photon fluence rate curves were fitted using the KaleidaGraph program, according to the mathematical model log-normal. From each curve, the maximum relative electron transport rate ($rETR_{\text{max}}$), the light utilization coefficient (α), and the initial saturation irradiance for photosynthesis (I_k) were calculated.

For each treatment, complementary energy dissipation pathways in PSII were investigated. The photochemical pathway was calculated as $Y(II) = (F_m' - F_t)/F_m'$, whereas the non-regulated non-photochemical quenching of light

energy ($Y(NO)$) was determined using the formula $Y(NO) = F_t/F_m'$, and the regulated non-photochemical quenching of light energy ($Y(NPQ)$) was calculated using the formula $Y(NPQ) = F_t/F_m' - Y(NO)$. $Y(NO)$ reflects the fraction of energy that is passively dissipated in the form of heat and fluorescence, mainly due to closed PSII reaction centers, while $Y(NPQ)$ corresponds to the fraction of energy dissipated in the form of heat via the regulated photoprotective non-photochemical quenching mechanisms (Schermer et al. 2013). Overall, the total energy is conserved as $Y(II) + Y(NPQ) + Y(NO) = 1$.

Pigment content

At the end of the experiments, a biomass of 80 mg of wet weight (WW) was powdered in liquid nitrogen for each replicate ($n = 4$) of the treatments. Phycoerythrin (PE), phycocyanin (PC), and allophycocyanin (APC) were extracted in 1 mL of 50 mM sodium phosphate (Na_2HPO_4) buffer (pH 5.5) overnight at 4°C and in darkness (Souza and Yokoya 2016). Afterward, the samples were centrifuged at $14,000\times g$ for 20 min at 4°C. Absorbances of the supernatants were measured by spectrophotometry (Shimadzu UV-1800, $\lambda = 498.5, 614, \text{ and } 651$), and the phyco-biliprotein concentrations in the seaweeds ($\mu\text{g g}^{-1}$ of WW) were determined using the equations proposed by Kursar et al. (1983). A biomass of 20 mg of WW for each replicate ($n = 4$) was used to extract total carotenoids (Car) and chlorophyll *a* (Chl *a*) in 1 mL of N,N-dimethylformamide overnight at 4°C and in darkness (Borburema et al. 2022b). After extraction, absorbances in N,N-dimethylformamide were measured by spectrophotometry ($\lambda = 480, 647, \text{ and } 664 \text{ nm}$), and the Car and Chl *a* concentrations in the seaweeds ($\mu\text{g g}^{-1}$ of WW) were determined by applying the equations of Wellburn (1994).

Statistical analyses

Data normality and homoscedasticity were checked applying Shapiro–Wilk and Levene tests, respectively. Relative growth rate and effective quantum yield data were compared among species, seasons, and treatments over time (i.e., BHW, UHW, and R) by applying three-way repeated-measures ANOVAs (Table S1). The other photosynthetic responses and pigment contents were compared among species, seasons, and treatments by applying three-way ANOVAs (Table S2). Tukey's *post-hoc* tests were performed when the ANOVAs revealed significant differences. All statistical analyses were carried out in the software R (version 4.4.0), and the significance value adopted was 0.05 ($\alpha = 5\%$).

Results

Growth rates

Gracilaria caudata from the rainy season showed a mean RGR between 5 and 7% day⁻¹ BHW. After 14 days under simulated MHWs, its RGR decreased significantly under maximum and extreme MHWs: control = $\Delta + 2^\circ\text{C} > \Delta + 4^\circ\text{C} > \Delta + 6^\circ\text{C}$ (Fig. 1A). After 14 days for the seaweed's recovery, *G. caudata* exhibited a decrease of RGR in the control, $\Delta + 2^\circ\text{C}$, and $\Delta + 4^\circ\text{C}$. The seaweed showed a higher decrease of RGR under $\Delta + 4^\circ\text{C}$ when compared to $\Delta + 2^\circ\text{C}$ (Fig. 1A). The RGR of *G. caudata* subjected to $\Delta + 6^\circ\text{C}$ did not differ significantly between UHW and R (Fig. 1A). Meanwhile, *G. caudata* from the dry season showed a similar RGR among treatments before heatwaves (Fig. 1B). Under heatwaves, its RGR decreased significantly at $\Delta + 4^\circ\text{C}$ and $\Delta + 6^\circ\text{C}$, with a more pronounced decrease under $\Delta + 6^\circ\text{C}$ (Fig. 1C). After 14 days for recovery, specimens subjected to $\Delta + 2^\circ\text{C}$ showed RGR similar to the UHW condition, while specimens subjected to $\Delta + 4^\circ\text{C}$ had a significant

significantly at $\Delta + 2^\circ\text{C}$ and $\Delta + 4^\circ\text{C}$ when compared to the control (Fig. 1B). *Gracilaria caudata* from the dry season subjected to an extreme-intensity heatwave (i.e., $\Delta + 6^\circ\text{C}$) had a null RGR after 14 days under thermal stress (Fig. 1B). The specimens subjected to $\Delta + 2^\circ\text{C}$ exhibited a subtle recovery, whereas specimens subjected to $\Delta + 4^\circ\text{C}$ had a null RGR after the recovery time (Fig. 1B). The $\Delta + 6^\circ\text{C}$ treatment was considered lethal to *G. caudata* from the dry season, as its RGR was continuously null (Fig. 1B) and the specimens did not show an effective quantum yield in R (Fig. 2B).

Gracilaria birdiae from the rainy season exhibited a similar RGR among treatments before heatwaves (Fig. 1C). Under heatwaves, its RGR decreased significantly at $\Delta + 4^\circ\text{C}$ and $\Delta + 6^\circ\text{C}$, with a more pronounced decrease under $\Delta + 6^\circ\text{C}$ (Fig. 1C). After 14 days for recovery, specimens subjected to $\Delta + 2^\circ\text{C}$ showed RGR similar to the UHW condition, while specimens subjected to $\Delta + 4^\circ\text{C}$ had a significant

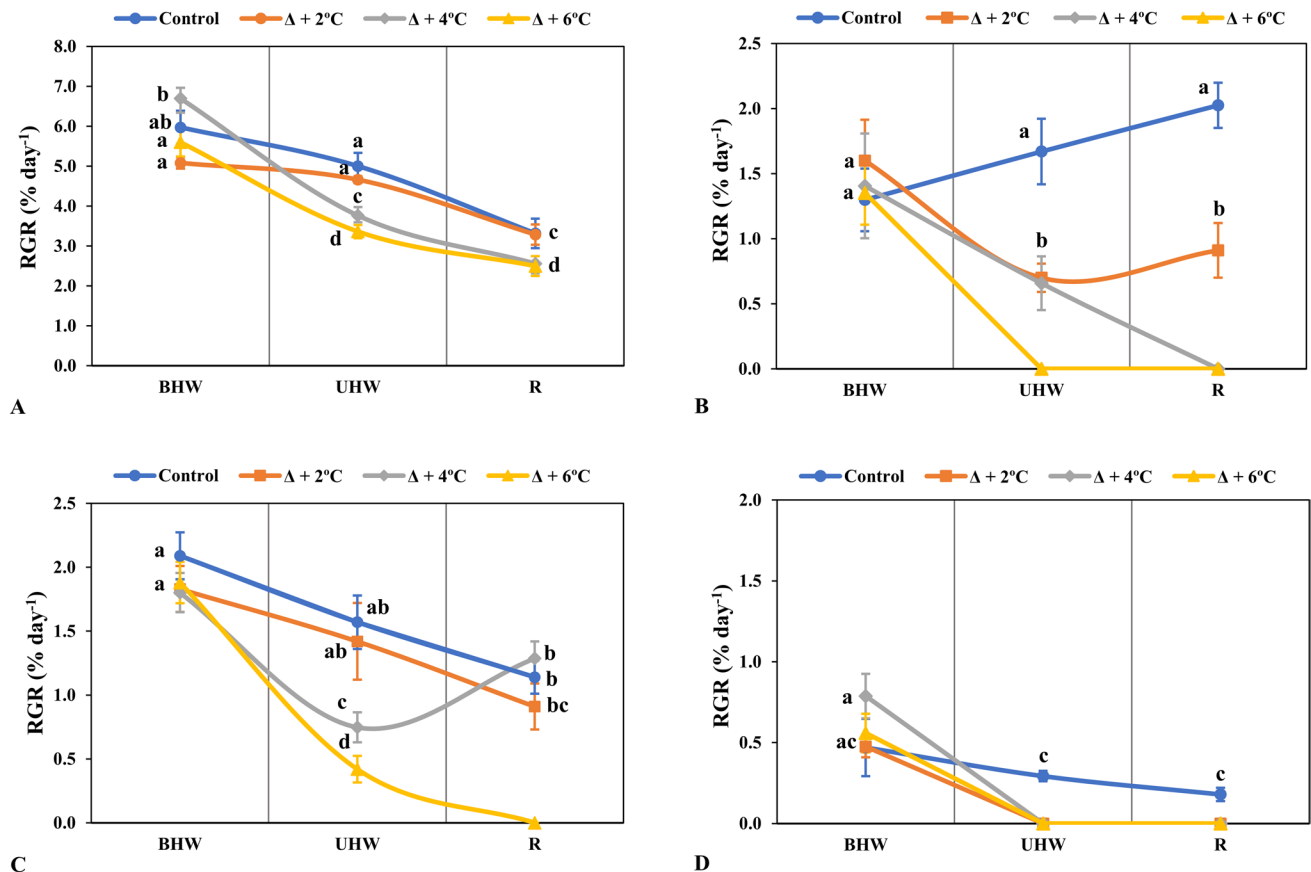


Fig. 1 Relative growth rate (RGR: % day⁻¹) of *Gracilaria caudata* (A and B) and *Gracilaria birdiae* (C and D) from the rainy (A and C) and dry (B and D) seasons cultured in experiments of simulated marine heatwaves (MHWs): $\Delta + 2^\circ\text{C}$, $\Delta + 4^\circ\text{C}$, and $\Delta + 6^\circ\text{C}$ refer to mean-, maximum-, and extreme-intensity MHWs, respectively. BHW, UHW, and R represent “before heatwaves” (14th experimental day), “under heatwaves” (28th experimental day), and “recovery” (42nd experimental day), respectively. Seaweeds cultured in the con-

trol were not subjected to simulated MHWs. Δ refers to the mean sea surface temperatures during the dry season (28°C) and the coldest months of the rainy season (25°C). Symbols are means and bars are standard deviations based on four replicates ($n = 4$). Different letters report statistical differences ($p < 0.05$) among treatments of the same species from the same climatic season by Tukey's tests after applying three-way repeated-measures analyses of variance (ANOVAs)

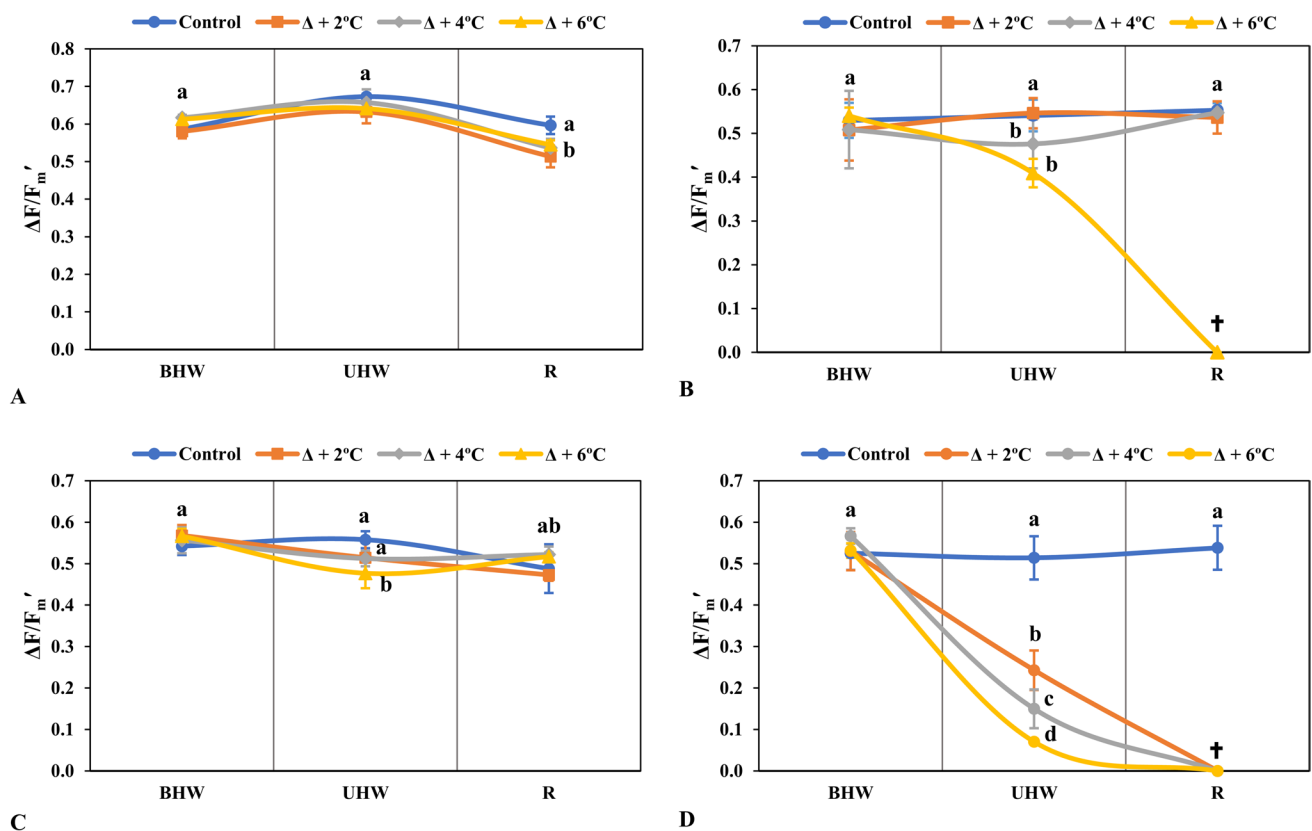


Fig. 2 Effective quantum yield ($\Delta F/F_m'$) of *Gracilaria caudata* (A and B) and *Gracilaria birdiae* (C and D) from the rainy (A and C) and dry (B and D) seasons cultured in experiments of simulated marine heatwaves (MHWs): $\Delta + 2^\circ\text{C}$, $\Delta + 4^\circ\text{C}$, and $\Delta + 6^\circ\text{C}$ refer to mean-, maximum-, and extreme-intensity MHWs, respectively. BHW, UHW, and R represent “before heatwaves” (14th experimental day), “under heatwaves” (28th experimental day), and “recovery” (42nd experimental day), respectively. Seaweeds cultured in the con-

trol were not subjected to simulated MHWs. Δ refers to the mean sea surface temperatures during the dry season (28°C) and the coldest months of the rainy season (25°C). Symbols are means and bars are standard deviations based on four replicates ($n = 4$). Different letters report statistical differences ($p < 0.05$) among treatments of the same species from the same climatic season by Tukey’s tests after applying three-way repeated-measures analyses of variance (ANOVAs). Lethality is reported by crosses (+)

recovery, and specimens subjected to $\Delta + 6^\circ\text{C}$ exhibited a null RGR (Fig. 1C). Simulated MHWs for the dry season had a strong negative effect on *G. birdiae* from this season. Under heatwaves, all specimens subjected to MHWs showed a null RGR (Fig. 1D). Their RGRs were continuously null in R (Fig. 1D), and the specimens did not show an effective quantum yield after the recovery time (Fig. 2D). For these reasons, treatments of simulated MHWs were considered lethal to *G. birdiae* from the dry season. Between species, *G. caudata* exhibited higher RGRs than *G. birdiae* in both climatic seasons (Fig. 1 and Table S1).

Photosynthetic performance

Gracilaria caudata from the rainy season showed a similar effective quantum yield ($\Delta F/F_m'$) between BHW and UHW in all treatments (Fig. 2A). However, after 14 days for recovery, the $\Delta F/F_m'$ of *G. caudata* subjected to MHWs decreased significantly (Fig. 2A). Regarding *G. caudata* from the dry

season, a significant decrease in $\Delta F/F_m'$ was registered in the specimens subjected to $\Delta + 4^\circ\text{C}$ and $\Delta + 6^\circ\text{C}$ (Fig. 2B). The specimens subjected to $\Delta + 4^\circ\text{C}$ had a recovery of $\Delta F/F_m'$, whereas those thermally stressed under $\Delta + 6^\circ\text{C}$ did not show a recovery, exhibiting a null $\Delta F/F_m'$ in R (Fig. 2B). *Gracilaria birdiae* from the rainy season only exhibited a significant decrease in $\Delta F/F_m'$ under $\Delta + 6^\circ\text{C}$, recovering it in R (Fig. 2C). However, simulated MHWs for the dry season had a marked negative effect on $\Delta F/F_m'$ of *G. birdiae* from this climatic season. The specimens showed a significant reduction of $\Delta F/F_m'$ under MHWs: control $> \Delta + 2^\circ\text{C} > \Delta + 4^\circ\text{C} > \Delta + 6^\circ\text{C}$ (Fig. 2D). After 14 days for the seaweed’s recovery, these specimens did not show an effective quantum yield (Fig. 2D). Between species, *G. caudata* exhibited higher $\Delta F/F_m'$ than *G. birdiae* in both climatic seasons (Fig. 2 and Table S1).

In relation to the photosynthetic parameters measured at the end of the experiments (i.e., after the recovery time), the maximum quantum yield (F_v/F_m) of the seaweeds from

both climatic seasons did not vary significantly among treatments (Table 1, Table S2). A significant difference was found between species (Table S2), with *G. caudata* exhibiting a higher F_v/F_m than *G. birdiae* in both climatic seasons (Table 1). Regarding the $rETR \times PAR$ curves, *G. caudata* from the rainy season showed similar photosynthetic performance among treatments (Fig. 3A), as the light utilization coefficient (α) and maximum relative electron transport rate ($rETR_{max}$) did not differ significantly among treatments (Table 1). On the other hand, *G. caudata* from the dry season exhibited decreasing $rETR \times PAR$ curves according to the treatments of simulated MHWs (i.e., control $> \Delta + 2^\circ C > \Delta + 4^\circ C$, Fig. 3B). This pattern also was observed for α and $rETR_{max}$ (Table 1). *Gracilaria birdiae* from the rainy season decreased its photosynthetic performance under treatments of simulated MHWs as well (Fig. 3C), as specimens thermally stressed by two weeks showed a lower α after the recovery time (control $> \Delta + 2^\circ C = \Delta + 4^\circ C = \Delta + 6^\circ C$) (Table 1). The initial saturation irradiance for photosynthesis (I_k) of both *Gracilaria* species varied from 1482 ± 63 to $1847 \pm 92 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ (Table 1), revealing that both *Gracilaria* species are high-light plants. Concerning the complementary energy dissipation pathways,

the photochemical pathway (Y[II]), the non-regulated non-photochemical quenching of light energy (Y[NO]), and the regulated non-photochemical quenching of light energy (Y[NPQ]) did not vary significantly among treatments (Fig. 4, Table S2). Significant differences were found between species for Y(II) and Y(NPQ) (Table S2). *Gracilaria caudata* exhibited a higher Y(II), while *G. birdiae* showed a higher Y(NPQ) in both climatic seasons (Fig. 4).

Pigment content

The most abundant pigment registered in *G. caudata* and *G. birdiae* from both climatic seasons was phycoerythrin (Table 2). The treatments of MHWs simulated for the rainy season did not significantly affect the pigment content of *G. caudata* (Table 2). On the other hand, *G. caudata* from the dry season showed a decreased content of phycoerythrin, chlorophyll *a*, and total carotenoids in the $\Delta + 4^\circ C$ treatment when compared to the control (Table 2). Similar to *G. caudata* from the rainy season, the pigment content of *G. birdiae* from this climatic season was not significantly affected by the MHWs, except for the phycocyanin content, which increased significantly in the $\Delta + 2^\circ C$ treatment (Table 2).

Table 1 Photosynthetic parameters of *Gracilaria caudata* and *Gracilaria birdiae* subjected to seasonal experiments of simulated marine heatwaves (MHWs). Control refers to the mean sea surface temperature (Δ) of the seaweed collection region: $28^\circ C$ during the dry season and $25^\circ C$ during the coldest months of the rainy season. $\Delta + 2^\circ C$, $\Delta + 4^\circ C$, and $\Delta + 6^\circ C$ refer to the mean, maximum, and extreme MHWs, respectively. F_v/F_m : maximum quantum yield; α : light utilization

coefficient; I_k : initial saturation irradiance for photosynthesis; $rETR_{max}$: maximum relative electron transport rate. Values are means with standard deviations based on four replicates ($n = 4$). Different superscript letters represent a significant difference ($p < 0.05$) among treatments of the same species from the same climatic season by Tukey's tests after applying three-way analyses of variance (ANOVAs). Lethal treatments are reported by crosses (+)

Species	Season	Treatment	F_v/F_m	α (electrons photons $^{-1}$)	I_k ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$)	$rETR_{max}$
<i>Gracilaria caudata</i>	Rainy	Control	0.600 ± 0.09^a	0.053 ± 0.005^a	1653 ± 60^{ac}	88 ± 6^a
		$\Delta + 2^\circ C$	0.511 ± 0.08^a	0.048 ± 0.003^a	1754 ± 87^c	85 ± 5^a
		$\Delta + 4^\circ C$	0.544 ± 0.06^a	0.051 ± 0.004^a	1847 ± 92^b	93 ± 7^a
		$\Delta + 6^\circ C$	0.535 ± 0.02^a	0.053 ± 0.002^a	1591 ± 26^a	85 ± 4^a
	Dry	Control	0.553 ± 0.01^a	0.105 ± 0.006^a	1498 ± 36^a	157 ± 6^a
		$\Delta + 2^\circ C$	0.536 ± 0.03^a	0.089 ± 0.003^b	1511 ± 14^a	136 ± 7^b
		$\Delta + 4^\circ C$	0.548 ± 0.00^a	0.059 ± 0.001^c	1636 ± 72^b	97 ± 4^c
		$\Delta + 6^\circ C$	+	+	+	+
<i>Gracilaria birdiae</i>	Rainy	Control	0.470 ± 0.04^a	0.089 ± 0.005^a	1482 ± 63^a	133 ± 13^a
		$\Delta + 2^\circ C$	0.488 ± 0.04^a	0.076 ± 0.004^b	1645 ± 63^b	126 ± 11^a
		$\Delta + 4^\circ C$	0.503 ± 0.11^a	0.081 ± 0.002^b	1740 ± 34^b	141 ± 7^a
		$\Delta + 6^\circ C$	0.506 ± 0.02^a	0.080 ± 0.001^b	1751 ± 71^b	141 ± 6^a
	Dry	Control	0.538 ± 0.05^a	0.097 ± 0.001	1652 ± 33	160 ± 5
		$\Delta + 2^\circ C$	+	+	+	+
		$\Delta + 4^\circ C$	+	+	+	+
		$\Delta + 6^\circ C$	+	+	+	+

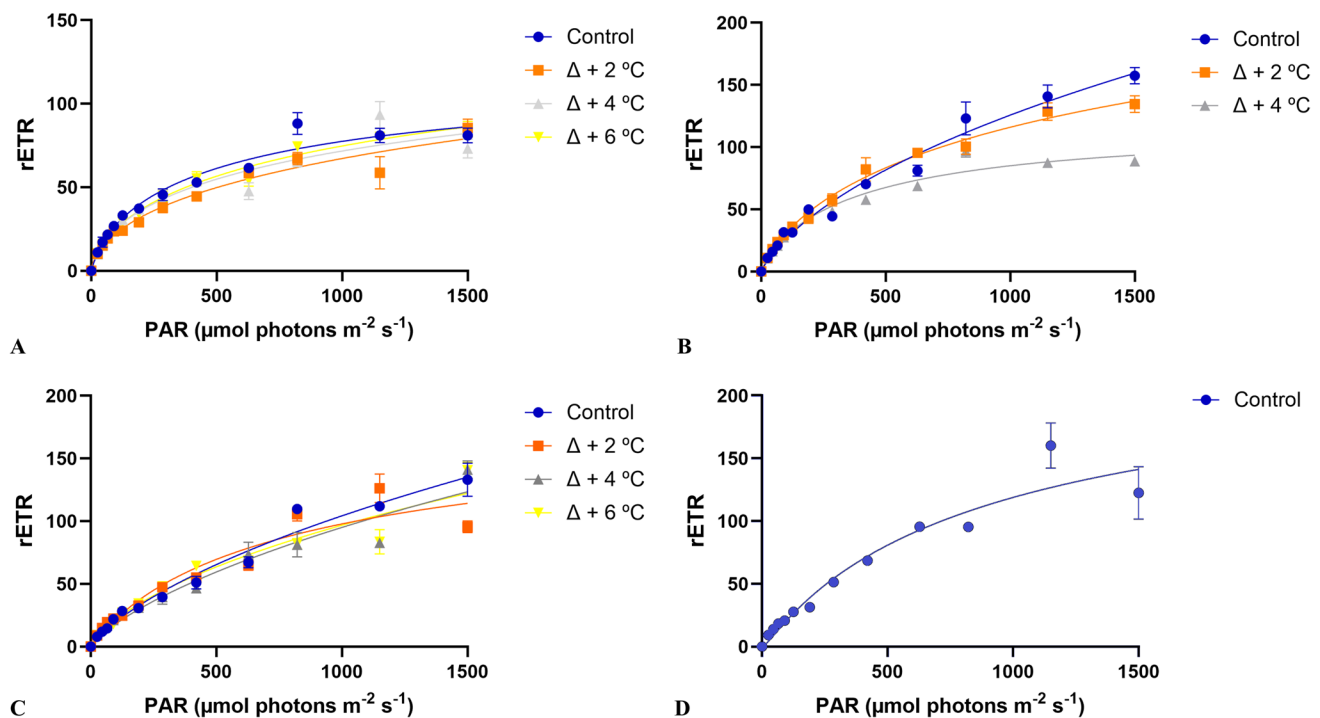


Fig. 3 Relative electron transport rate (rETR) × photon fluence rate (PAR) curves of *Gracilaria caudata* (A and B) and *Gracilaria birdiae* (C and D) from the rainy (A and C) and dry (B and D) seasons cultured in experiments of simulated marine heatwaves (MHWs): $\Delta + 2^{\circ}\text{C}$, $\Delta + 4^{\circ}\text{C}$, and $\Delta + 6^{\circ}\text{C}$ refer to mean-, maximum-, and extreme-intensity MHWs, respectively. Seaweeds cultured in the

control were not subjected to simulated MHWs. Δ refers to the mean sea surface temperatures during the dry season (28°C) and the coldest months of the rainy season (25°C). Symbols are means and bars are standard deviations based on four replicates ($n = 4$). rETR × PAR curves were fitted using the KaleidaGraph program according to the mathematical model lognormal

Discussion

Agarophyte seaweeds exhibited differential responses to simulated MHWs depending on the species and climatic season. In our experiments, *G. caudata* showed better physiological performance (growth and several photosynthesis-related parameters) than *G. birdiae*, confirming our second hypothesis. Furthermore, both seaweeds were more negatively affected by the MHWs simulated for the dry season, which confirmed our third hypothesis. Our first hypothesis, “both species could be resistant and resilient to the simulated MHWs, exhibiting recovery after heat stress,” was partially confirmed. Both seaweeds were resistant and resilient to the MHWs simulated for the rainy season (Figs. 2, 3, and 4A and C, Tables 1 and 2). However, the extreme-intensity MHW (34°C) simulated for the dry season was lethal to *G. caudata*, and all MHWs simulated for this climatic season were lethal to *G. birdiae* (Figs. 2, 3, and 4B and D, Tables 1 and 2). The hypothesized resistance of *G. birdiae* was mainly based on the predictive study performed by Barbosa-Silva et al. (2023). Those authors projected an increase of environmentally suitable areas for *G. birdiae* farming under climate change in Brazil by applying statistical modeling. However, in that study, other global change-related environmental

variables were considered, namely, maximum nitrate and minimum and maximum salinity. Studies have demonstrated the importance of global change-related research to investigate how multiple stressors can interact and affect marine species, since several synchronous or asynchronous environmental drivers influence each other (e.g., Rich et al. 2018; Borburema et al. 2022c, 2024). Thereby, *G. birdiae*’s higher thermal tolerance (around 33°C) projected by Barbosa-Silva et al. (2023) may be related to the interaction of environmental drivers. Thus, our study reveals the need for future multifactorial ecophysiological approaches, including salinity and nutrient variation, to better elucidate the effects of thermal stress on *G. birdiae*. Concerning seaweed resilience, our results demonstrated that when *G. caudata* and *G. birdiae* resist heat stress, they can recover. Multiple photosynthesis-related parameters (i.e., $\Delta F/F_m'$, F_v/F_m , and complementary energy dissipation pathways) support this finding.

Our research highlighted the relevance of a climate change-related experimental approach to consider seasonal effects, as seaweeds from the dry season were less tolerant of heat stress than seaweeds from the rainy season, especially *G. birdiae*. This seaweed did not tolerate mean-, maximum-, and extreme-intensity MHWs simulated for the dry season (temperatures of 30 , 32 , and 34°C , respectively).

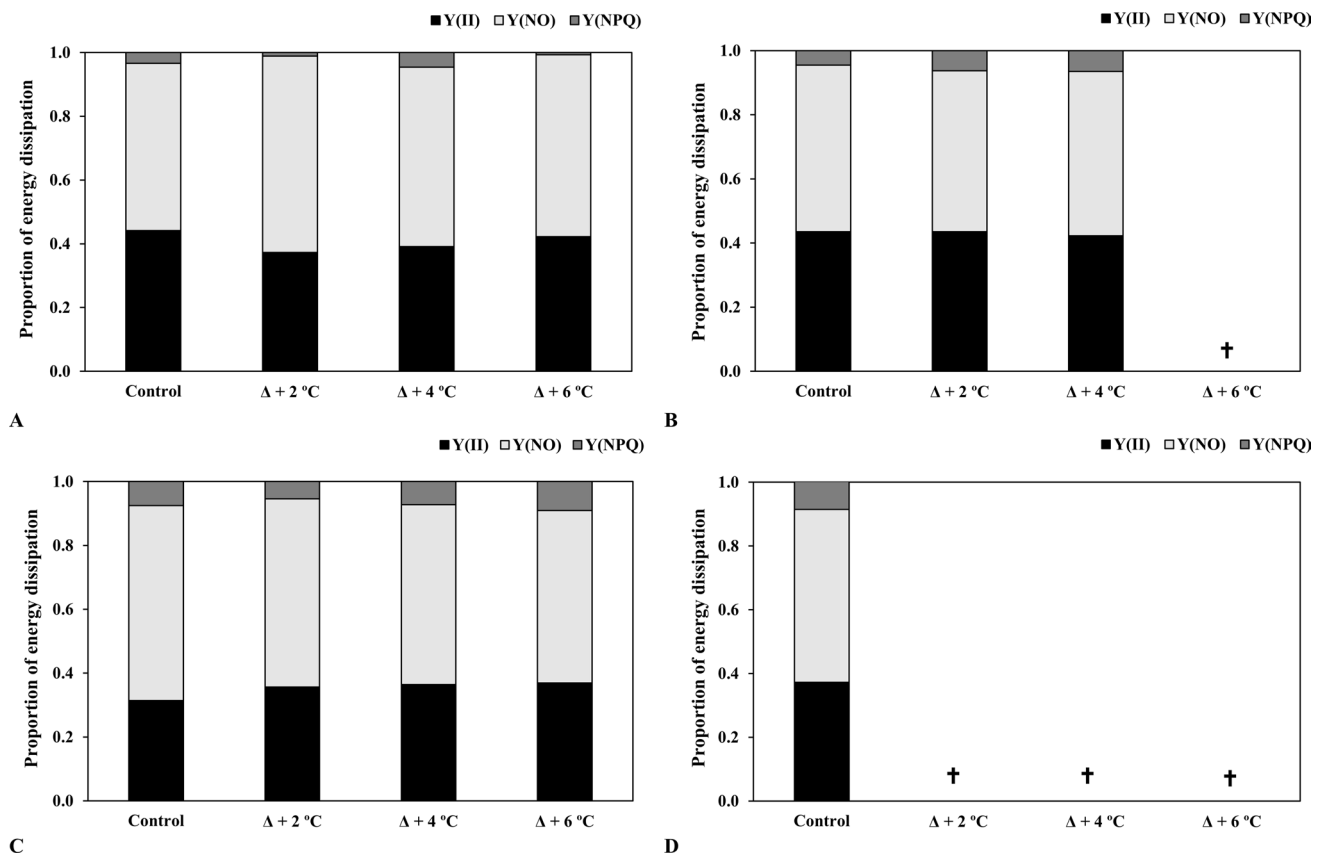


Fig. 4 Complementary energy dissipation pathways in PSII of *Gracilaria caudata* (A and B) and *Gracilaria birdiae* (C and D) from the rainy (A and C) and dry (B and D) seasons cultured in experiments of simulated marine heatwaves (MHWs): Δ + 2 °C, Δ + 4 °C, and Δ + 6 °C refer to mean-, maximum-, and extreme-intensity MHWs, respectively. Seaweeds cultured in the control were not subjected to simulated MHWs. Δ refers to the mean sea surface temperatures dur-

ing the dry season (28 °C) and the coldest months of the rainy season (25 °C). Columns represent the proportion of energy dissipation based on four replicates (n = 4). Y(II) is the photochemical pathway, Y(NO) is the non-regulated non-photochemical quenching of light energy, and Y(NPQ) is the regulated non-photochemical quenching of light energy. Lethal treatments are reported by crosses (+)

Nevertheless, it tolerated MHWs simulated for the rainy season (temperatures of 27, 29, and 31 °C). This decoupling, that is, tolerance of *G. birdiae* specimens from the rainy season under 31 °C and lethality in specimens from the dry season between 30 °C and 32 °C, may be explained by environmental effects. As stated in the “Materials and Methods” section, seaweeds were collected in the dry and rainy seasons for the respective experiments (i.e., one for each climatic season). This experimental approach includes ecological realism, as environmental effects were considered to test the temporal hypothesis. The environmental conditions are more favorable for seaweeds during the rainy season in Northeastern Brazil. They are subjected to lower temperatures and salinities and to enrichment with nutrients, such as nitrate, ammonium, and orthophosphate (Carneiro et al. 2011). The nutrient enrichment and reduced salinity are caused by increased rainfall, which rises from approximately 27 mm month⁻¹ over the dry season to 427 mm month⁻¹ over the rainy season (Carneiro et al. 2011). Seaweeds

increase their growth, produce reproductive structures, and store metabolites under more favorable conditions (Carneiro et al. 2011; Hurd et al. 2014; Bezerra et al. 2024; Borburema et al. 2024). The stored metabolites can be used by seaweeds as energy and antioxidant compounds to tolerate stressors when subjected to detrimental conditions (Lobban and Harrison 1997). Thereby, very likely, *G. birdiae* specimens from the rainy season could better cope with the thermal stress derived from MHWs due to metabolic reserves. Growth data confirm these observations, as *G. caudata* and *G. birdiae* from the rainy season showed higher RGRs than those from the dry season before heatwaves (Fig. 1). The tolerance of *G. birdiae* to a temperature of 31 °C is consistent with that reported by Fernandes et al. (2017), who cultivated *G. birdiae* under temperatures from 26.25 °C to 31.93 °C in an outdoor experiment. The tolerance of *G. caudata* up to 32 °C is also consistent with results reported by Chiamonte et al. (2023), who registered a tolerance of *G. caudata* from Northeastern Brazil of up to 33 °C. So, our study documents

Table 2 Pigment content ($\mu\text{g g}^{-1}$ of wet weight) of *Gracilaria caudata* and *Gracilaria birdiae* subjected to seasonal experiments of simulated marine heatwaves (MHWs). Control refers to the mean sea surface temperature (Δ) of the seaweed collection region: 28°C during the dry season and 25°C during the coldest months of the rainy season. $\Delta + 2^\circ\text{C}$, $\Delta + 4^\circ\text{C}$, and $\Delta + 6^\circ\text{C}$ refer to the mean, maximum, and extreme MHWs, respectively. PE: phycoerythrin; PC:

phycocyanin; APC: allophycocyanin; Chl *a*: chlorophyll *a*; Car: total carotenoids. Values are means with standard deviations based on four replicates ($n = 4$). Different superscript letters represent a significant difference ($p < 0.05$) among treatments of the same species from the same climatic season by Tukey's tests after applying three-way analyses of variance (ANOVAs). Lethal treatments are reported by crosses (+)

Species	Season	Treatment	PE	PC	APC	Chl <i>a</i>	Car
<i>Gracilaria caudata</i>	Rainy	Control	298 ± 65 ^a	37 ± 11 ^a	20 ± 16 ^a	182 ± 33 ^a	21 ± 5 ^a
		$\Delta + 2^\circ\text{C}$	359 ± 90 ^a	34 ± 6 ^a	14 ± 2 ^a	234 ± 65 ^a	22 ± 5 ^a
		$\Delta + 4^\circ\text{C}$	461 ± 70 ^a	55 ± 8 ^a	27 ± 23 ^a	221 ± 41 ^a	25 ± 5 ^a
		$\Delta + 6^\circ\text{C}$	390 ± 97 ^a	37 ± 19 ^a	14 ± 10 ^a	199 ± 32 ^a	19 ± 4 ^a
	Dry	Control	540 ± 97 ^a	16 ± 3 ^a	29 ± 8 ^a	46 ± 5 ^a	19 ± 3 ^a
		$\Delta + 2^\circ\text{C}$	467 ± 76 ^{ab}	19 ± 2 ^a	20 ± 2 ^a	83 ± 8 ^b	21 ± 3 ^a
		$\Delta + 4^\circ\text{C}$	362 ± 17 ^b	16 ± 1 ^a	22 ± 3 ^a	29 ± 2 ^c	4 ± 0.4 ^b
		$\Delta + 6^\circ\text{C}$	+	+	+	+	+
	Rainy	Control	304 ± 69 ^a	79 ± 21 ^a	47 ± 36 ^a	183 ± 53 ^a	24 ± 6 ^a
		$\Delta + 2^\circ\text{C}$	442 ± 47 ^a	132 ± 33 ^b	38 ± 7 ^a	203 ± 36 ^a	26 ± 8 ^a
		$\Delta + 4^\circ\text{C}$	324 ± 90 ^a	124 ± 21 ^{ab}	41 ± 25 ^a	188 ± 42 ^a	24 ± 5 ^a
		$\Delta + 6^\circ\text{C}$	427 ± 104 ^a	79 ± 12 ^a	54 ± 33 ^a	165 ± 36 ^a	15 ± 2 ^a
<i>Gracilaria birdiae</i>	Dry	Control	317 ± 42	63 ± 7	110 ± 33	46 ± 7	19 ± 2
		$\Delta + 2^\circ\text{C}$	+	+	+	+	+
		$\Delta + 4^\circ\text{C}$	+	+	+	+	+
		$\Delta + 6^\circ\text{C}$	+	+	+	+	+

the upper thermal tolerance limit of *G. caudata* from Northeastern Brazil at 34°C. This result is also congruent with Miranda et al. (2012), who recorded lethality in *G. caudata* (as *Hydropuntia caudata*) from Northeastern Brazil at 35°C.

In our study, before heatwaves, *G. birdiae* exhibited mean growth values (0.5–2.2% day⁻¹, Fig. 1C and D) similar to those documented by Fernandes et al. (2017). Regarding *G. caudata*, the higher mean growth varied from 5.07 to 6.69% day⁻¹ (rainy season and before heatwaves [25°C], Fig. 1A). This range is within that reported by Chiaramonte et al. (2023) for *G. caudata* from Bahia and Ceará states (both in Northeastern Brazil) cultured at 25°C. Both species decreased their growth under increasing temperatures of MHWs, with a more pronounced effect on *G. birdiae*. This pattern of decreased growth under increasing temperatures was consistent with results found by Ursi et al. (2013) for *G. birdiae* experimentally cultivated under natural conditions in the sea of Southeastern Brazil. In that study, red strains of *G. birdiae* from Northeastern Brazil showed decreasing growth between October 2002 and March 2003, when mean seawater temperatures increased from 26°C to approximately 30°C. However, when mean seawater temperatures decreased from 30°C to approximately 22°C (between March 2003 and September 2003), the red strains of *G. birdiae* recovered, showing increasing growth. Overall, all seaweeds decreased growth over time (i.e., from the 14th experimental day [BHW] to the 42nd experimental day

[R], Fig. 1), except for *G. caudata* and *G. birdiae* from the dry season cultured in the control, which maintained stable growth (Tukey's test: $p > 0.05$, Fig. 1B and D). This pattern of decreasing growth over experimental time is known for *Gracilaria* species, as reported by Faria et al. (2017) for *G. caudata* cultured under two irradiances for 28 days, Fernandes et al. (2017) for *G. birdiae* cultivated in the sea and shrimp farming ponds for 60 days, and Trigueiro et al. (2017) for *Gracilaria domingensis* (Kützinger) Sonder ex Dickie cultivated in a shrimp pond at two depths for 21 days. Nevertheless, in general, the growth of thermally stressed seaweeds was more reduced over time than that of seaweeds cultured in the control, which highlights the negative interactive effect between treatments and experimental time on seaweeds (Table S1).

Regarding photosynthetic performance before heatwaves, *G. caudata* and *G. birdiae* showed effective quantum yield ($\Delta F/F_m'$) values similar to those already documented in the scientific literature for the *Gracilaria* genus (e.g., Faria et al. 2017; Trigueiro et al. 2017; Marchi and Plastino 2020). All seaweeds decreased $\Delta F/F_m'$ under simulated heatwaves, except *G. caudata* from the rainy season, and heatwaves simulated for the dry season had a higher negative effect on the seaweeds (Fig. 2). Other red seaweeds exhibited a decrease in photosynthetic performance under heat stress, such as the closely related seaweed *Gracilariopsis lemaneiformis* (Bory) E.Y. Dawson, Acleto & Foldvik (also

Gracilariaceae) (Jiang et al. 2022; Gao et al. 2024) and *H. pseudomusciformis* (Gigartinales) (Nauer et al. 2022). *Gracilaria caudata* from the rainy season did not decrease its photosynthetic performance under simulated MHWs (Fig. 2A), as stated above, although it had decreased growth under heat stress (Fig. 1A). Seaweeds produce reactive oxygen species (ROS) under stressful conditions (Lesser 2006; Hurd et al. 2014). ROS trigger damage to the cell's macromolecular structures, including DNA, proteins, and phospholipids, which can induce cell apoptosis (Lesser 2006; Borburema et al. 2022c). Thus, seaweeds need to produce antioxidant compounds to protect their cellular structures from ROS (Lesser 2006; Borburema et al. 2022c). *Gracilaria* species produce several antioxidant compounds, which was already demonstrated by different assays (e.g., Martins et al. 2013; Torres et al. 2019). Therefore, *G. caudata* from the rainy season may have maintained high photosynthetic performance under simulated MHWs to provide energy for the metabolic processes of antioxidant defenses at the expense of growth. Photosynthetic responses measured at the end of the experiments demonstrated a recovery in the photosynthesis of seaweeds that resisted the heat stress, such as $\Delta F/F_m'$ (Fig. 2), F_v/F_m (Table 1), and complementary energy dissipation pathways (Fig. 4). However, *G. caudata* from the dry season showed decreasing $rETR \times PAR$ curves according to the intensity of MHWs (Fig. 3B). This result is certainly related to the decreasing Chl *a* content in *G. caudata* from the dry season subjected to the mean- and maximum-intensity MHWs (Table 2), as $rETR$ measures are derived from Chl *a* fluorescence. The only consistent effect of simulated MHWs on seaweed pigment content was the decrease in Chl *a* and phycoerythrin of *G. caudata* from the dry season (Table 2). Similar results were reported by Gao et al. (2024) for *Gp. lemaneiformis* experimentally subjected to a marine heatwave.

In conclusion, our data demonstrated that both *G. caudata* and *G. birdiae* from the rainy season resisted the mean-, maximum-, and extreme-intensity marine heatwaves simulated for this climatic season. Regarding seaweeds from the dry season, *G. caudata* only failed to resist the thermal stress of the extreme marine heatwave simulated for the dry season (34°C), while all marine heatwaves simulated for this climatic season were lethal to *G. birdiae*, very likely due to the environmental history/effect, as discussed above. Several photosynthesis-related results revealed the recovery (i.e., resilience) of seaweeds when they resisted the marine heatwaves. In our study, *G. caudata* exhibited better physiological performance than *G. birdiae*, especially under heat stress, as *G. caudata* thermally stressed by simulated marine heatwaves exhibited higher growth and photosynthetic performance (i.e., $\Delta F/F_m'$, F_v/F_m , and $Y[II]$) compared to *G. birdiae*. Thereby, *G. caudata* has proven to be a more interesting species for aquaculture activities in the context of

climate change. The higher recorded tolerance of *G. caudata* to heat stress is consistent with field observations, where *G. caudata* inhabits mainly the upper and middle intertidal, while *G. birdiae* occurs mainly in the lower intertidal. Seaweeds that occupy upper intertidal zones are subjected to more stressful conditions than those that occupy lower intertidal zones. Thus, *G. caudata* can better cope with thermal stress derived from marine heatwaves.

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Author's contributions **H.D.S. Borburema:** Conceptualization; Design of the work; Acquisition; Analysis; and Interpretation of data; Writing—original draft. **G. Almeida-Faria:** Acquisition; Analysis; and Interpretation of data. **S.L.C. Silveira:** Acquisition of data. **V.S. Gomes:** Acquisition of data. **F. Nauer:** Acquisition; Analysis; and Interpretation of data; Writing—review and editing. **E. Marinho-Soriano:** Funding acquisition; Resources; Supervision; Writing—review and editing. All authors approved the version to be published and agreed to be accountable for all aspects of the work.

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Availability of data and material The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors declare no conflict of interest.

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