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Photosynthetic and respiratory responses of *Gracilaria parvispora* from the southeastern Gulf of California

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Abstract Photosynthetic and respiratory responses (P–E curves) of *Gracilaria parvispora* from the southeast Gulf of California were studied at four temperatures (20, 25, 30, 35 °C) and salinity (25, 30, 35, 40 psu) combinations. The alga showed acclimation in its photosynthetic and respiratory responses to tropical temperature as well as to oceanic salinity. A positive effect of temperature on photosynthetic rate ($P_{\max}$) was observed for all salinities. Photosynthetic rates for treatments at 20 and 25 °C were lower (<9.2 mg O_2 g dry weight (dw)$^{-1}$ h^{-1}) than for treatments at 30 and 35 °C (>12 mg O_2 g dw^{-1} h^{-1}). *G. parvispora* showed limited tolerance to low salinities (25 psu) and low temperatures (20 °C) and the interaction between temperature and salinity was significant (analysis of variance, $P<0.05$). Responses to salinity indicated adaptation to oceanic salinity. Photosynthetic responses were lower at 25 psu than at higher salinities. The lowest $P_{\max}$ values (6.2–8.2 mg O_2 g dw^{-1}h^{-1}) were observed at the lowest salinity (25 psu) regardless of temperature. Compensation and saturation irradiances (26–170 and 57–149 μmol photons m^{-2}s^{-1}, respectively) indicate adaptation to lower irradiances in shallow (1–2 m depth) habitats, where turbidity can be high, and the capacity of shade adaptation has been developed. Results suggest distribution of this species is mainly related to salinity or temperature. The potential mariculture efforts of *G. parvispora* would be limited by low temperatures in winter, and indicate that this species will probably not be able to spread further due to low temperatures (<15 °C) in the upper part of the Gulf of California.

Keywords *Gracilaria parvispora* · Rhodophyta · Gulf of California · Photosynthesis–respiration · Salinity · Temperature

Introduction

The Gulf of California is considered a dynamic and rich environment with high primary productivity levels (Alvarez-Borrego 1983). It has been estimated that about 580 species of macroalgae are present in the area (Zertuche-González et al. 1995), of which 116 are endemic and at least 55 are potentially commercial species (Pacheco-Ruiz and Zertuche-González 1996). According to Espinoza-Avalos (1993), the geographical distribution of macroalgae species in the Gulf of California is closely related to changes in environmental conditions, mainly temperature and sun exposition that prevail in each major geographical area of the Gulf. Recently, some studies have shown the presence of the invasive species *Gracilaria vermiculophylla* (Ohmi) Papenfuss in southeastern coastal lagoons of the Gulf of California (Ochoa-Izaguirre et al. 2007; Orduña-Rojas et al. 2008; Piñon-Gimate et al. 2008). However, molecular and morphological data has confirm the presence of a second invasive species *Gracilaria parvispora* Abbott (García-Rodriguez et al. 2013).

Gracilaria species are an important marine resource exploited worldwide mainly for agar extraction. About 55,000 t dry weight of *Gracilaria* species is extracted annually, with a production of 7,500 t of agar, and a value of 132 million US dollars (McHugh 2002). For the Gulf of California, Norris (1985) reviewed the taxonomy of the genus and found that 16 Gracilariaceae species are present in the area. However, only *Gracilariopsis lemaneiformis* (Bory) Dawson Acleto *et*

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Foldvik is currently exploited at Bahia de Los Angeles, B.C., as raw material to be exported to Japan (Arellano-Carbajal et al. 1999).

Gracilaria parvispora, a species known in Hawaii as "long ogo", is edible red seaweed of great economic value for which several commercial culture systems have been developed (Glenn et al. 1996, 1998; Nelson et al. 2001, 2009). It is estimated that the weekly demand for this alga in Hawaii exceeds 1,000 kg (Paul and Chen 2008). According to Glenn et al. (1999), field growth of this alga is related mainly to ammonia concentration with no evidence of correlation between growth and salinity or temperature. The species has been recently documented to occur along the northwestern Mexico area based on morphological, anatomical, and molecular data (García-Rodriguez et al. 2013). Despite the importance of this *Gracilaria* species, to our knowledge, there are no reports in which physiological responses to abiotic factors, such as temperature and salinity, are examined. In the southeastern Gulf of California the species have a peak in biomass present in June (Orduña and Riosmena, personal observation) and because of their invasive nature a potential use of the species need to be related with critical ecophysiological information.

Photosynthesis is an effective indicator of plant growth and maximum photosynthesis rate is frequently used to identify preferable abiotic conditions for plant development. Temperature is a major factor controlling the rate of photosynthesis in all plants up to an optimum, beyond which it declines rapidly. Davison (1991) established that low temperatures limit photosynthetic electron transport and carbon fixation and this may reduce the ability of algae to perform photosynthesis efficiently. Hence, the study of these physiological responses of *G. parvispora* would provide valuable information for understand their ecological role as an invader and potential mariculture efforts as potential use. The aim of the present study was to examine photosynthetic and respiratory responses to irradiance, temperature, and salinity of *G. parvispora* collected from a southeast Gulf of California coastal lagoon. The hypothesis tested was that *G. parvispora* from the Gulf of California exhibits broad tolerance to salinity, light, and temperature, similarly to other warm-temperate *Gracilaria* species with strong seasonal growth.

Materials and methods

Samples of *G. parvispora* were collected in June of 2008 from a mixed sandy cobble subtidal habitats at San Lucas Island in Navachiste Bay (25°21′ and 25°35′N, 108°40′ and 109°00′W) southeastern Gulf of California. Tetrasporangial and gametangial populations of *G. parvispora* grow attached to rocks (from the shore to 3-m depth) around small islands located in the bay intermixed with other red algae as dominant elements. Plants ranged from 0.3 to 0.5 m in size, and were green to purple in color, with long cartilaginous branches. Seaweeds were placed in plastic bags with seawater and immediately transported in insulated coolers to the laboratory. Upon arrival, plants were first rinsed with seawater to remove sediment particles and epiphytes, and then cut into 4- to 8-cm segments. Only apical parts of approximately 2 g fresh weight were used in the experiments. The samples were kept for 24–36 h in an acclimation flask, which contained filtered seawater at temperature and salinity of the corresponding experimental condition under low irradiance (20 μmol photons $m^{-2}s^{-1}$) and 12:12 h (light/dark) photoperiod. This period reduces stress before analysis and allows selecting healthy and undamaged branch tips (Dawes 1998). Plants were used within 5 days of collection and the total experiment lasted 5 weeks. Voucher material is housed at the Herbario Ficológico from CIIDIR-IPN, Unidad Sinaloa.

Photosynthetic measurements

The combined effects of temperature and salinity on respiration rate and photosynthesis of the red alga *G. parvispora* were measured at four temperatures (20, 25, 30, and 35 °C) and four salinity levels (25, 30, 35, and 40 psu) using a continuous flow recording respirometer chamber connected to an oxygen electrode . Experimental temperatures corresponded to the natural temperature range at Navachiste Bay (Orduña-Rojas et al. 2008). Two fluorescent light bulbs (Fluorex, 100 W; Lights of America, USA) were used as light source to generate nine irradiance levels of approximately 40, 60, 85, 115, 160, 210, 290, 395, and 610 μmol photons $m^{-2}s^{-1}$ using neutral density filters. Irradiance was measured using a Data Logger Li-1400 and a submersible 4π quantum sensor (LI-COR Inc., USA). Respiration was measured under complete darkness.

On the day of the experimental trial, one plant segment was transferred into the photosynthetic-respirometric chamber (Qubit Systems Inc; Canada) previously filled with filtered seawater (Whatman GF/C) at one of the different temperature–salinity combinations to be tested. The photosynthetic chamber consisted of a translucent acrylic cylinder (0.21-m length and 0.054-m internal diameter; total volume, 600 mL including hose volume) sealed with square acrylic covers at both ends. Each of these two acrylic covers were connected to each other by means of a ½ inch plastic hose that allowed water flux from one side of the cylinder to the other through a recirculation pump (4.5 L min^{-1}). Internally, an acrylic disk acted as a deflector of the inlet water, allowing the water to flow through the interior of the chamber without disturbing the algal segment. The photosynthetic chamber was hermetically closed and placed inside a water bath, previously set at one of the four experimental temperatures and subjected to increasing photon flux densities (PFD) ranging from 0, for dark respiration (R_d) measurement, to 610 μmol photons $m^{-2}s^{-1}$. The temperature of the water bath was maintained constant (±1 °C) using a 100- or 300-W submersible heater. A dissolved-oxygen probe (YSI 5010 BOD) placed hermetically at the upper part of the acrylic cylinder was connected to an oxygen meter (YSI 5010), and the evolved oxygen was measured at 10 min intervals. The oxygen meter was recalibrated for each tested temperature-salinity experimental condition.

To ensure steady oxygen production rates, prior to experimental trials, one algae segment of similar weight to those used in the experiments was placed into the chamber and the evolved oxygen measured continuously for 1 h in the dark and at each of the PFD tested. It was observed that respiration and photosynthetic responses were constant after a 5-min incubation period. For experimental trials, each PFD lasted for 10 min, and oxygen concentration measurements were taken in the last 5 min. To avoid oxygen oversaturation during the experimental trials, the initial dissolved oxygen concentration was reduced in the water sample by bubbling nitrogen gas. All trials were ended before oxygen concentration reached water saturation limits. At the end of each experimental trial, the algal sample was oven-dried at 60 °C for 36 h for dry weight (dw) determination. Evolved oxygen measurements were normalized to biomass (dw) and expressed as mg O_2 g $dw^{-1}h^{-1}$. The photosynthetic (P) vs. irradiance (E) relationship (P–E curves) was evaluated at each temperature-salinity combination in four replicates.

Photosynthetic–irradiance (P_{max} and α) characteristics were calculated by fitting the data to the following photosynthetic light response model (Jassby and Platt 1976) using STATISTICA 7 software:

$$p_n = p^b_{\max}\tanh\left(a \times E/P^b_{\max}\right) - R_d$$

where P_n is the net production rate (mg O_2 g $dw^{-1}h^{-1}$); $P^b{}_{max}$, the gross maximum photosynthetic rate (mg O_2 g $dw^{-1}h^{-1}$); E, the PFD (μmol photons $m^{-2}s^{-1}$); R_d, the dark respiration rate (mg O_2 g $dw^{-1}h^{-1}$); and α, the initial slope of the light saturation curve or photosynthetic efficiency (mg O_2 g $dw^{-1}h^{-1}$/μmol photons $m^{-2}s^{-1}$). E_k, light saturation parameter (μmol photons $m^{-2}s^{-1}$) was derived from the relationship P_{max}/α, and compensation point (E_c), the compensation irradiance, where net photosynthesis equals respiration (μmol photons $m^{-2}s^{-1}$), was determined as P_n equals zero.

Statistics

A two-way analysis of variance (ANOVA) followed by Bonferroni's post hoc test was performed to verify the significance of differences in photosynthetic and respiratory responses to salinity and temperature of the algae from different salinity-temperature combinations. In addition, a separate one-way ANOVA and Tukey' (HSD) post hoc test were carried out to test for differences among P–E factors (P_{max}, α, E_k, E_c, and R_d), which were calculated for the four different temperatures. Before performing statistical tests, homogeneity of variance and normality were determined using the STATISTICA 7 software (significance was set at $P<0.05$).

Results

Photosynthesis irradiance curves of *G. parvispora* measured at four different temperatures showed a wide range of responses. Increases in photosynthetic rates were observed when irradiance was up to 290 μmol photons $m^{-2}s^{-1}$ for all temperature–salinity combinations, whereas above that irradiance photosynthesis did not change significantly up to 610 μmol photons $m^{-2}s^{-1}$ (Fig. 1). A significant effect of temperature on light-saturated P_{max} was observed, since values increased with increasing temperatures for all salinities. Photosynthetic responses to salinity indicated adaptation to oceanic salinity, since rates were lower at 25 psu than at other salinities tested (Fig. 1). Figure 1 does not include the negative response to 20 psu, where branches degenerated during the acclimation period. The lowest P_{max} values (6.2–8.2 mg O_2 g $dw^{-1}h^{-1}$) were observed at low salinity (25 psu) regardless of temperature. P_{max} values for treatments at 20–25 °C were lower (<9.2 mg O_2 g $dw^{-1}h^{-1}$; Fig. 1a and b) than for treatments at 30–35 °C (>12 mg O_2 g $dw^{-1}h^{-1}$; Fig. 1c and d). The highest light-saturated P_{max} was observed at the temperature–salinity combination of 30 °C and 35 psu (18.8 mg O_2 g $dw^{-1}h^{-1}$).

Initial saturation irradiance (E_k) ranged from 87 to 249 μmol photons $m^{-2}s^{-1}$, and E_c varied from 26 to 170 μmol photons $m^{-2}s^{-1}$ (Table 1). In general, E_c values obtained at 25 psu were different from values at other salinities and tended to be higher as temperatures and salinities increased. E_c values for 25 psu were always higher than values at other salinities at a given temperature, and these differences were statistically significant (ANOVA, $P<0.05$). Photosynthetic efficiency, as expressed by α, ranged from 0.09 to 0.16 mg O_2 g $dw^{-1}h^{-1}$/μmol photons $m^{-2}s^{-1}$, and only small differences were observed depending on the temperature–salinity combination. No statistically significant differences ($P<0.05$) in α were observed for the 25 °C treatment (Table 1). At other temperatures, statistically significant differences were observed mostly between 25 psu and the other salinities.

Similarly to P_{max}, R_d rates increased with temperature. Higher R_d were observed for 35 °C treatments (10.4–14.8 mg O_2 g $dw^{-1}h^{-1}$), and lower rates (2.1–4.3 mg O_2 g $dw^{-1}h^{-1}$) were recorded for the lowest temperature (20 °C; Table 1). The interaction between temperature and salinity was found to be significantly different ($P<0.05$; Table 2). Mid temperatures produced variable R_d rates, ranging from

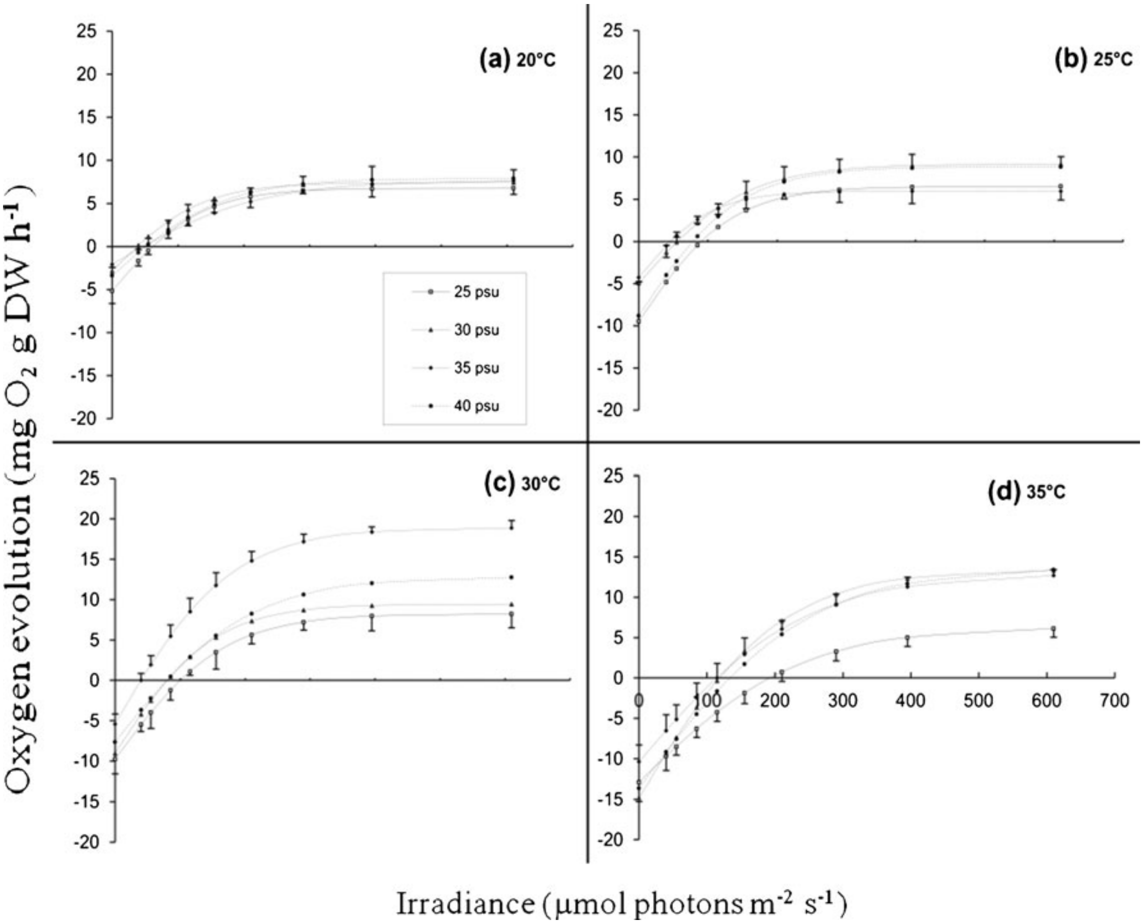

Fig. 1 *G. parvispora* P–E curves in response to four temperature–salinity combinations (mean±SD; n=4)

4.2 to 9.4 mg O_2 g $dw^{-1}h^{-1}$, depending on the temperature–salinity combination.

Discussion

Gracilaria parvispora from the southeast Gulf of California showed high photosynthetic and respiratory responses at high temperatures (30 and 35 °C; Fig. 1, Table 1) indicating that populations of this species are adapted to tropical water temperatures and oceanic salinity unlike other more warm–temperate *Gracilaria* species. This rejects the hypothesis tested that *G. parvispora* from the Gulf of California exhibits broad tolerance to salinity, light, and temperature, similar to other warm–temperate *Gracilaria* species. P vs. E data indicate that this species is adapted to low irradiance (E_c, E_k, α). Since populations occur in shallow habitats in the Navachiste Bay, this suggests that these populations are adapted to both deep and shallow waters with high turbidity. Also, strongly suggest that this species is limited in their geographical distribution in relation to temperature and salinity experiments.

McLachlan and Bird (1986) reported that maximum growth for warm species of *Gracilaria* occurred between 25 and 30 °C and suggested that temperatures above 30 °C are lethal. Levy and Friedlander (1990) found the optimal growth temperature for five *Gracilaria* strains at 25 °C with a sharp decrease at higher temperatures. In addition, Wang et al. (1984) reported that seawater temperatures above 30 °C caused growth of some *Gracilaria* species to cease. On the other hand, Yokoya et al. (1999) found that *G. vermiculophylla* from Japan tolerated a wide range of temperature variation (5–30 °C). These authors argued that the eurythermal response of this species is in accordance with observations that *Gracilaria* species from temperate waters tend to be eurythermal.

However, these observations disagree with our observations on *G. parvispora* from the Gulf of California. In the present study, the maximum light-saturated $P_{\max}$ on *G. parvispora* were observed at 30 and 35 °C, which are the typical summer temperatures in the collecting area from June to September (Orduña-Rojas et al. 2008), whereas $P_{\max}$ decreased almost to half at lower temperatures (25 and 20 °C).

Table 1 *Gracilaria parvispora* photosynthesis–irradiance saturation curve fit parameters data at four temperatures and four salinity combinations. Mean and standard deviation (±1 SD) from four replicates are given for $P_{\max}$ and R_d, maximum photosynthesis and dark respiration (in mg O_2 g dw h^{-1}); E_c and E_k, compensation and saturation point (in μmol photons $m^{-2}s^{-1}$); and α, slope of linear part of curve (in mg O_2 g dw h^{-1}/μmol photons $m^{-2}s^{-1}$)

Temperature (°C)	Salinity (psu)	$P_{\max}$	R_d	E_k	E_c	α
20	25	6.7 ± 0.37^{a}	4.3 ± 0.87^{c}	131 ± 5^{a}	66 ± 6^{a}	0.09 ± 0.01^{a}
	30	7.4 ± 0.75^{ab}	2.8 ± 0.60^{ab}	89 ± 17^{a}	26 ± 9^{b}	0.11 ± 0.02^{a}
	35	7.6 ± 1.13^{ab}	2.1 ± 0.45^{a}	227 ± 14^{b}	39 ± 7^{b}	0.04 ± 0.01^{b}
	40	7.9 ± 0.98^{b}	3.3 ± 0.93^{bc}	187 ± 68^{b}	48 ± 6^{c}	0.07 ± 0.04^{ab}
25	25	6.5 ± 1.06^{a}	9.2 ± 0.12^{b}	135 ± 28^{a}	92 ± 11^{a}	0.12 ± 0.04^{a}
	30	9.1 ± 0.89^{b}	4.9 ± 0.10^{a}	87 ± 24^{a}	47 ± 7^{bc}	0.15 ± 0.04^{a}
	35	6.0 ± 1.07^{a}	4.2 ± 0.48^{a}	105 ± 45^{a}	42 ± 7^{c}	0.12 ± 0.05^{a}
	40	8.8 ± 0.41^{b}	8.7 ± 0.52^{b}	151 ± 70^{a}	54 ± 4^{b}	0.13 ± 0.05^{a}
30	25	8.2 ± 1.73^{a}	9.4 ± 1.58^{c}	162 ± 17^{a}	102 ± 10^{a}	0.11 ± 0.01^{a}
	30	9.4 ± 0.96^{b}	9.0 ± 0.77^{bc}	124 ± 34^{a}	64 ± 5^{b}	0.15 ± 0.03^{b}
	35	18.8 ± 0.90^{c}	5.3 ± 1.20^{a}	164 ± 7^{b}	33 ± 5^{d}	0.15 ± 0.0^{b}
	40	12.7 ± 1.26^{d}	7.6 ± 1.11^{b}	123 ± 10^{a}	77 ± 4^{c}	0.16 ± 0.01^{b}
35	25	6.1 ± 1.13^{a}	12.8 ± 2.4^{ab}	236 ± 64^{a}	170 ± 6^{a}	0.08 ± 0.01^{a}
	30	13.3 ± 2.07^{b}	14.8 ± 1.94^{b}	209 ± 36^{ab}	121 ± 10^{b}	0.13 ± 0.02^{c}
	35	12.7 ± 1.46^{b}	10.3 ± 2.06^{a}	249 ± 36^{b}	108 ± 9^{c}	0.09 ± 0.02^{ab}
	40	13.4 ± 0.88^{b}	13.5 ± 2.31^{ab}	240 ± 27^{ab}	130 ± 9^{b}	0.11 ± 0.02^{bc}

Significant differences ($P<0.05$) among salinities at different temperature tested are indicated by different superscript letters

Salinity is one of the most important environmental factors affecting local distribution of seaweeds (Koch and Lawrence 1987; Dawes 1998). In this work, light-saturated $P_{\max}$ were strongly affected by low salinity at all temperatures tested. When plants were exposed to high temperatures (30 and 35 °C) and salinities (35 and 40 psu), high photosynthetic rates was recorded, whereas low rates were observed at low temperatures and salinities; this indicates the effect of the interaction between temperature and salinity on the $P_{\max}$ of *G. parvispora*. Dawes et al. (1978) found that photosynthetic responses of *G. verrucosa* (Hudson) Papenfuss were higher at 30 than at 10 psu. We could not find the photoinhibition because the design of the experiment and time used to perform the experiments.

Other algae species have shown a decrease in $P_{\max}$ due to reducing salinity levels (Simon et al. 1999; Koch and Lawrence 1987). According to Gessner and Schramm (1971), this decrement in photosynthetic rate at low salinities in seaweeds is associated with ionic loss, particularly Cl^{-} when marine algae are exposed to hypo-osmotic conditions. Poophrong et al. (2008) mentioned that algae growing in estuarine conditions have a broad potential for salinity changes, especially in hyposaline conditions, because their photosynthetic activity is still higher than that of the algae from ocean saline habitats. *G. parvispora* was intolerant to low salinity and low temperature, unlike the estuarine species *Gracilaria tikvahiae* McLachlan (Penniman and Mathieson 1985; Dawes 1994), *G. verrucosa* (Dawes et al. 1978), and *G. vermiculophylla* (Yokoya et al. 1999, Rueness 2005). This reinforces the idea that *G. parvispora* behaves as an oceanic plant with low tolerance to brackish waters.

Maximum light-saturated photosynthesis rate (18.8 mg O_2 g $dw^{-1}h^{-1}$) was observed at 30 °C and 35 psu, which corresponds to typical summer environmental conditions in the collection area from June to September, followed by rates obtained at 35 °C (*ca.* 13 mg O_2 g day dw$^{-1}h^{-1}$). Phooprong et al. (2007) found similar rates for *Gracilaria salicornia* from

Table 2 *G. parvispora* two-way ANOVA for the combined effect of temperature and salinity for light-saturated $P_{\max}$ and R_d

Variable	$P_{\max}$				R_d			
	DF	MS	F	*P* values	DF	MS	F	*P* values
Temperature	3	121.601	60.590	0.0000	3	277.480	95.882	0.0000
Salinity	3	74.562	37.152	0.0000	3	38.982	13.47	0.0000
Interaction of a×b	9	35.371	17.624	0.0000	9	7.757	2.68	0.0112

Thailand at 30–35 °C (16–19.6 mg O_2 g $dw^{-1}h^{-1}$), but reported lower rates at these conditions for plants from Japan (9.9–12.4 mg O_2 g $dw^{-1}h^{-1}$). According to these authors, these differences in photosynthetic responses may be related to the environmental conditions of their natural habitats, since Thailand is located near the equator where the climate is more tropical than in Japan. Dawes et al. (1998) found similar results with the tropical species *G. cornea* from Florida, in which the optimum temperature for photosynthetic responses was found to be between 25 and 35 °C. A wide variation in E_k responses to irradiance by different species of *Gracilaria* has been published. For example, *G. lemaneiformis* was light saturated at about 90 μmol photons $m^{-2}s^{-1}$ (Santelices and Fonck 1979), whereas for *G. tikvahiae* from New Hampshire, saturation occurred at 240 μmol photons $m^{-2}s^{-1}$ (Penniman and Mathieson 1985) and below 50 μmol photons $m^{-2}s^{-1}$ in culture (Bird et al. 1979). On the other hand, higher E_k values were reported by Phooprong et al. (2007, 2008) for three populations of *G. salicornia* from Thailand and Japan (144–557 μmol photons $m^{-2}s^{-1}$), and for *G. vermiculophylla* from Japan (208–498 μmol photons $m^{-2}s^{-1}$). For *Gracilaria bursa-pastoris* (Gemlin) Silva and *Gracilaria dura* (C. Agardh) J. Agardh, values of 343 and 300 μmol photons $m^{-2}s^{-1}$, respectively, have been reported from the Mediterranean coast of France (Plus et al. 2005). The compensation and saturation irradiance values reported for *G. parvispora* here are similar to those reported by Dawes et al. (1998) for tropical *Gracilaria cornea* from Florida and by Orduña-Rojas et al. (2002) for the same species from Yucatan, Mexico, and suggest, as has been pointed out by these authors, that *G. parvispora* plants are shade plants but tolerant of high irradiances with high efficiency for light gathering in turbid waters.

High dark respiration rates were recorded in *G. parvispora* exposed to high temperatures (30 and 35 °C) but the rates were low at 25 and 20 °C, similarly to what was observed for P_{max}. These respiration rate responses to temperature have been observed in other *Gracilaria* species. For example, Ganzon-Fortes (1999) found that respiratory rates of *Gelidiela acerosa* (Forssk.) Feldmann and Hamel in tide-pool and subtidal plants were similar at 22 and 28 °C and were 7–100 times lower than the rates at 34 °C. Phooprong et al. (2007, 2008) mentioned a twofold increase in respiration rates of *G. salicornia* when temperature increases from 20 to 30 °C as well as in *G. vermiculophylla* with a temperature increase from 5 to 25 °C at three salinity levels (10, 20, and 30 psu). Dawes et al. (1998) reported higher respiration rates for tropical *G. cornea* from Florida at 25–35 °C than at 15 °C. Temperature has fundamental effects on chemical reactions and usually the rates of photosynthesis and respiration double for every 10 °C rise in temperature (Davison 1991, Lobban and Harrison 1997). On the other hand, Simon et al. (1999) found that hypo- and hypersaline treatments reduced the P_{max} and increased dark respiration in *Grateloupia doryphora* (Montagne) Howe. Respiration rates obtained in the present study were higher than those reported for other *Gracilaria* species, nevertheless the same two- to threefold increase was obtained between low (20 and 30 °C) and high (25 and 35 °C) temperatures. This probably reflects higher metabolism for tropical plants compared to temperate ones.

In conclusion, photosynthesis in *G. parvispora* from the Gulf of California is negatively affected by low temperatures and low salinities, therefore these environmental conditions could probably limit the spread of this species further into the Gulf of California, since low temperatures occur during the winter season in the northern part of the Gulf. On the other hand, the low tolerance of this plant to low salinities indicates that possible culture efforts of this species should be confined to open water areas where oceanic salinities prevail.

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