

Response of the tropical red seaweed *Gracilaria cornea* to temperature, salinity and irradiance

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Abstract

The agarophyte *Gracilaria cornea*, collected over 2.5 y in the Florida Keys, shows adaptations to oceanic salinities and subtropical to tropical water temperatures in its photosynthetic and respiratory responses as measured with a respirometer. No seasonal pattern in responses to irradiance, temperature, and salinity were evident between five collections over a 20-month period, indicating the tropical nature of the populations from Bahia Honda and Pigeon Keys. Concentrations of chlorophyll *a* (0.09 to 0.41 mg g d wt⁻¹) and phycoerythrin (0.06 to 0.36 mg g d wt⁻¹) were low and reflect the low nutrient regime of the habitats, especially when compared to laboratory cultured plants. Compensation and saturation irradiances were also low (11–38 and 90–127 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$), indicating acclimation to lower irradiances in their shallow (1–2 m depth) habitats where turbidity can be high. In comparison with other subtropical and warm temperate species of *Gracilaria*, *G. cornea* had lower levels of pigment, but similarly high photosynthetic efficiency, demonstrating shade adaptation; it had only limited tolerance to salinities below 20‰ and temperatures below 15 °C. Thus, *G. cornea* from the Florida Keys in mariculture would require subtropical to tropical temperatures and stable oceanic salinities.

Introduction

In terms of the production of economically valuable phycocolloids, the most important genera of commercial, subtropical and tropical macroalgae are the red seaweeds *Gracilaria*, *Eucheuma*, and *Hypnea* (Dawes, 1998). Further, more studies probably have been carried out on species of *Gracilaria* in regard to the culture and agar production than any other red algal genus (Friedlander & Levy, 1995). This interest is in part due to the rapid growth rates, broad tolerances of many forms, and diversity of species (ca. 97 spp.: Abbot, 1995) that occur in tropical and warm temperate waters of the world (Abbott, 1995; Bird, 1995). *Gracilaria* now accounts for more than 53% of all agar produced worldwide (McHugh, 1991) with a large

portion of the 1000 t agar produced each year being imported into the USA (Jensen, 1993).

Recent reports of successful cultivation of species of *Gracilaria* include such diverse countries as St Lucia (Smith, 1997), Chile (Westmeier et al., 1993), Russia (Titlyanov et al., 1995), Sweden (Haglund & Pedersen, 1993) and the Philippines (Hurtado-Ponce et al., 1992). In Chile, cultivated *G. chilensis* has now replaced wild harvested plants with annual crop yields that exceed 57 000 t wet weight (FAO, 1993). Norris (1985) identified eight species of gracilarioids occurring in the Caribbean and Florida with economic potential in the genera *Gracilaria* and *Polycavernosa*. One of the larger, more robust species is *G. cornea* (formerly *G. debilis*: Dawes, 1974), which yields a high quality agar and is a perennial (Feile-Pelegrin &

Robledo, 1997). Populations of *G. cornea* are known for the northern Yucatan coast of Mexico (Robledo, 1994) and the Florida Keys (Croley & Dawes, 1970).

Although there have been numerous studies measuring growth and changes in proximate constituents and agar for species of *Gracilaria* (Dawes, 1998), there are few studies examining physiological responses to combinations of abiotic factors, particularly light, temperature and salinity (Yakovleva et al., 1997; Dawes, 1998). Measurement of physiological responses have been confined primarily to forms of *G. tikvahiae* (Lapointe et al., 1984; Lapointe & Duke, 1984; Penniman & Mathieson, 1985; Dawes, 1994; formerly *G. foliifera* var. *angustissima*, Friedlander & Dawes, 1984). This species occurs in estuaries from Maine and New Hampshire to Tampa Bay and the Indian River in Florida (Penniman & Mathieson, 1985; Yakovleva et al., 1997) and exhibits broad tolerances to abiotic factors. *G. verrucosa*, another widespread estuarine alga, is similarly tolerant to light, temperature and salinity (Dawes et al., 1978; Yakovleva et al., 1997). There is little information regarding tropical species of *Gracilaria* such as *G. cornea*.

The aim of the present study was to examine pigment concentrations and photosynthetic and respiratory responses to irradiance temperature and salinity in order to determine the tolerances ranges of *Gracilaria cornea* collected in the Florida Keys, because the alga may have potential in Caribbean mariculture. The hypothesis tested was that *Gracilaria cornea* from the Florida Keys will exhibit broad tolerances to salinity, light and temperature, similar to warm temperate species.

Materials and methods

Collections. Attached *Gracilaria cornea* was collected in May, June and December 1996 and September and December 1997 at Pigeon Key (24°42'12" N, 81°09'18" W) or Bahia Honda Key (24°39'12" N, 81°16'51" W) in Florida Keys. The two sites were similar in substrate (limestone with thin covering of sand), depth (0.7–1 m MLW), and hydrological features (moderate wave activity, oceanic exposure, tidal currents). Temperature and salinity were measured with every collection and were identical for the two sites. The plants were returned in coolers to the laboratory, cleaned of epiphytes, rinsed in antibiotic solution (Dawes & Koch, 1991) and sterile seawater, and placed in a culture chamber for 2 to 3 d (24 °C, 20

Table 1. Concentrations of chlorophyll *a* and phycoerythrin (mg g d wt⁻²) for freshly collected *Gracilaria cornea* from the Florida Keys (± 1 S.D.). n = number of replicates.

Date	Chlorophyll <i>a</i>		Phycoerythrin	
	mg chla g d wt ⁻²	n	mg PE g d wt ⁻²	n
May 1996	0.41 (0.11)	9	–	–
June 1996	0.33 (0.05)	10	0.39 (0.08)	10
Dec. 1996	0.24 (0.03)	6	0.16 (0.03)	6
Sep. 1997	0.14 (0.01)	6	0.19 (0.02)	6
Dec. 1997	0.09 (0.03)	6	0.06 (0.05)	6

or 30 ‰ salinity sterile seawater, 12/12 h L/D period, 40 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$). The 2 to 3 d period insured that healthy, undamaged branch tips could be selected and do not affect possible seasonal responses (Dawes, 1998).

Pigment. Chlorophyll *a* (80% acetone) and phycoerythrin (0.1 M phosphate buffer) were extracted (n = 6 to 10) by grinding 3 cm branches in the dark and cold. The extracts were centrifuged (2250 \times g) in the cold for 5 min and absorption determined at 665 nm for chlorophyll *a* and 565 nm for phycoerythrin using Bausch & Lomb (model 20) or Gilford (model 250) spectrophotometers. Extinction coefficients used were 11.9 for chlorophyll *a* and 12.4 for phycoerythrin (Dawes, 1998).

Photosynthesis and respiration. Factorial experiments were used to measure the effects of salinity, temperature, and irradiance on the rates of photosynthesis and respiration using a Gilson Respirometer (Model GRP-20; Dawes, 1985). Each reaction flask held two clean 2.5 to 3.0 cm long branch tips of *Gracilaria cornea*, 10 mL of either 20 or 30 ‰ salinity (n = 8), and 0.9 mL of a CO₂ generating solution producing a 1% atmosphere (Dawes, 1985). Readings were corrected for possible manometric fluctuations using 4 to 5 blank flasks. Respiratory and photosynthetic rates (0, 100, 200, 400, 600 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$) were measured for 1 h each at 15, 25 and 35 °C (± 0.1 °C). All measurements expressed in $\mu\text{L O}_2 \text{ g d wt}^{-1} \text{ h}^{-1}$ were converted to $\text{mg O}_2 \text{ g d wt}^{-1} \text{ h}^{-1}$ 300 mL^{-1} . Conversion from μL to mg O_2 was done by multiplying the former by 1.4286 (STP). For temperatures other than 275 °K, 1.4286 is multiplied by a factor (273 divided by °T + 273, where T = temperature used in °C).

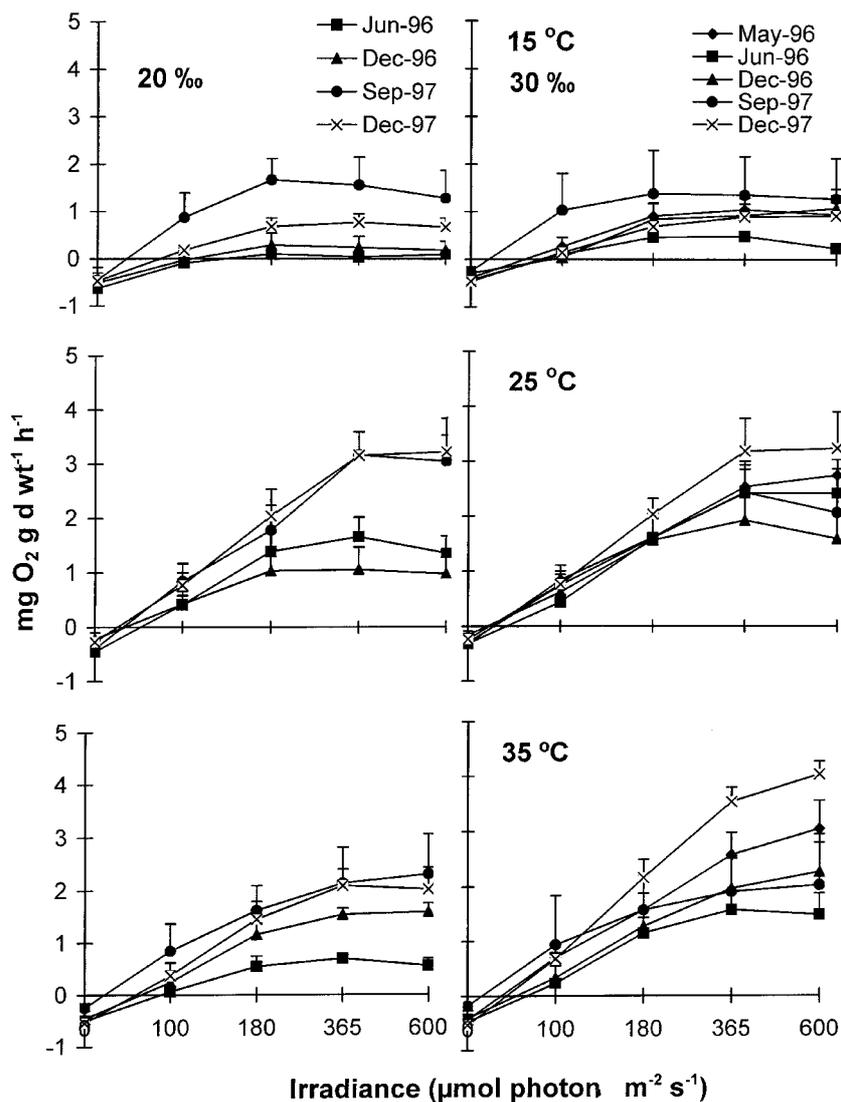


Figure 1. Photosynthetic and respiratory responses of *Gracilaria cornea* collected in the Florida Keys on five occasions and acclimated to 20‰ and 30‰ salinities for 3 d. All responses ($n=8$) were measured using a Gilson Respirometer. ± 1 S.D. Bars are included.

In addition, a YSI oxygen meter (Model 51B) was used to carry out extended (0 to 1200 or 1600 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$) photosynthetic-irradiance (P-I) curves within 2 d of collection. Two clean branch tips (4 to 5 cm long) were placed in 60 mL BOD bottles containing filtered, 30‰ salinity seawater. Temperature was maintained at 25 °C (± 1.0 °C) in a water bath. Irradiance was from a 1000 W (GE Projection Bulb) and reduced using neutral density filters. All measurements are presented as $\text{mg O}_2 \text{ g d wt}^{-1} \text{ h}^{-1}$ standard-300 mL BOD bottle⁻¹. Photosynthetic-irradiance characteristics (I_c , I_k , P_{max} , α) were de-

termined for each sample using computer generated graphs.

Statistics. One way ANOVA's were used to test for differences between P-I factors (I_c , I_k , P_{max}) calculated for the 5 samplings. Homogeneity of variance and normality were first determined using the Sigma Stat program (significance when $P < 0.05$). Logarithmic transformation was unnecessary.

Table 2. Photosynthesis-irradiance data for *Gracilaria cornea* from the Florida Keys kept at 23 °C and 30‰ salinity. Mean and standard deviation (± 1 S.D.) are given for I_c and I_k (compensation and saturation point photon fluxes in $\mu\text{mol photon m}^{-2} \text{s}^{-2}$), α (slope of linear part of curve), PI (photoinhibition; in $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) and P_{max} ($\text{mg O}_2 \text{ g d wt}^{-1} \text{ h}^{-1}$). All responses were measured using a YSI Oxygen Meter. * = Significant differences for P-I factors ($P < 0.05$). n = number of replicates.

Date	n	I_c	I_k	P_{max}	α	PI
1996						
May	6	11 (3.0)*	107 (25)	4.0 (0.9)	0.04 (0.01)	1100
June	6	34 (4.4)	127 (56)	3.8 (0.7)	0.03 (0.01)	900
December	9	25 (2.4)	91 (10)	4.3 (0.9)	0.05 (0.01)	1100
1997						
September	6	38 (20.6)	112 (12)	3.7 (0.6)	0.03 (0.00)	1000
December	7	31 (3.0)	90 (10)	3.6 (0.7)	0.04 (0.01)	1200

Results

Water temperatures ranged from a high of 30.5 in June to a low of 24 °C in December 1997, while salinities ranged from a high of 37‰ in May and June to a low of 33‰ in December 1996 at both Pigeon Key and Bahia Honda Key in the Florida Keys. Chlorophyll *a* ranged from 0.413 mg g d wt^{-1} in May 1996 to a low of 0.091 mg g d wt^{-1} in December 1997, while phycoerythrin levels were lower with a range of 0.389 mg g d wt^{-1} in June to 0.06 mg g d wt^{-1} in December 1997 (Table 1). In general, freshly collected plants were a dull brown-red in color for all collections.

Variability of photosynthetic and respiratory responses of the 8 replicates of *Gracilaria cornea* exposed to 0 to 600 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ was low as shown by the error bars of Figure 1. The lowest responses occurred in 15 °C, particularly for plants collected in June (Figure 1) whether held in 20 or 30‰ salinity. In contrast, plants collected in September showed the highest response at all irradiances except under 600 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ when held at 15 °C. Photosynthetic responses were similar for all samplings when plants were exposed to 25 and 35 °C. Only those collected in September and December 1997 and exposed to 20‰ showed higher responses at 25 °C.

Responses to salinity indicated adaptation to oceanic salinity. Except for the September (15, 25 °C) and December (25 °C) collections, photosynthetic responses were lower in 20‰ than 30‰ salinity. Figure 1 does not include the negative response to 15‰ salinity, where branches degenerated during the 2- to 3-d

exposure. Regardless of temperature, no seasonal pattern was evident for the five collections for plants exposed to 30‰ salinity.

Photosynthetic responses increased with irradiance up to 180 to 365 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ for all collections, temperatures and salinities. Only plants held at 35 °C and 30‰ salinity did not peak at 600 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ in the respirometer. In general, oxygen production was low with higher P_{max} values of 3.0 to 3.5 $\text{mg O}_2 \text{ g d wt}^{-1} \text{ h}^{-1}$ 300 mL^{-1} .

Photosynthetic responses to increasing irradiances, as measured with an oxygen meter, produced no significantly different P-I characteristics for all five collections of *Gracilaria cornea* (Table 2) except for I_c . The mean compensation point ranged from a high of 38 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ in September 1997 to a significantly lower value to 11 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ in May 1996. Saturation irradiance (I_k) as determined from the intercept of the linear portion of the curve with P_{max} , was similar for May, June and September, but lower for the two December collections. The rate of oxygen production (P_{max}) was slightly higher than that calculated from the manometric studies, but similar between collections, ranging from 3.6 to 4.3 $\text{mg O}_2 \text{ g d wt}^{-1} \text{ h}^{-1}$ 300 mL^{-1} . Photosynthetic efficiency, as expressed by α , was similar for all four collections, ranging from 0.03 to 0.05 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ per $\text{mg O}_2 \text{ g d wt}^{-1} \text{ h}^{-1}$ 300 mL^{-1} . Photoinhibition occurred above 900 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ for all collections.

Table 3. Optimum levels of irradiance, temperature, and salinity for growth or photosynthesis by macroalgae from subtropical or tropical open ocean habitats.

	Irradiance ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Temp. ($^{\circ}\text{C}$)	Salinity (‰)	Location
Chlorophyceae				
15 species	–	15–30	–	Florida ¹
<i>Caulerpa paspaloides</i>	38 to 111	20 to 32	32	Florida ²
<i>Halimeda</i> (4 species)	160 to 800	–	–	Bahamas ³
Phaeophyceae				
5 species	–	15 to 27	–	Florida ₁
<i>Padina tetrastromatica</i>	–	23 to 28	27 to 32	India ⁴
<i>P. gymnospora</i>	70 to 90+	–	27 to 32	Florida ⁵
<i>Cystoseira barbata</i>	400 to 1700	20 to 30	17 to 47	French Mediterranean ⁶
Rhodophyceae				
18 species	–	18 to 24	–	Florida ¹
<i>Hypnea musciformis</i>	126 to 540+	24 to 32	–	Florida ⁷
	87 to 430+	24 to 30	20 to 40	Florida ⁸
<i>Eucheuma uncinatum</i>	168 to 756+	24 to 30	28 to 40	Gulf of California ⁹
<i>E. denticulatum</i>	252 to 588+	20 to 28	30 to 40	Philippines ⁹
<i>E. nudum</i>	168 to 588+	20 to 32	30 to 40	Florida ⁹
<i>E. isiforme</i>	168 to 672+	24 to 32	30 to 40	Florida ⁹
	–	20 to 30	30 to 40	Florida ¹⁰
<i>Bryothamnion triguetrum</i>	–	29 to 32	27 to 35	Cuba ¹¹
<i>Gracilaria cornea</i>	100 to 800	25, 35	30	Florida ¹²

¹ Mathieson & Dawes, 1986; ² O'Neil & Prince, 1988; ³ Littler et al., 1988; ⁴ Subbaraju et al., 1982 (growth studies); ⁵ Dawes & Kovach, 1992; ⁶ Baghdadi et al., 1990; ⁷ Durako & Dawes, 1980 (oceanic populations); ⁸ Dawes et al., 1976 (oceanic populations); ⁹ Dawes, 1979; ¹⁰ Dawes & Koch, 1988; ¹¹ Areces & Araujo, 1996 (growth studies); ¹² this study.

Discussion

The hypothesis is rejected. Photosynthetic and respiratory responses of *Gracilaria cornea* demonstrate that the Florida Keys populations are adapted to oceanic salinity and tropical water temperatures unlike more temperate species. Further, the populations show low compensation and saturation points and high photosynthetic efficiency (α) indicating adaptation to low submarine irradiance. The responses suggest that any mariculture efforts using this species will require stable, high salinities, subtropical to tropical water temperatures and reduced irradiance.

Compared with subtropical and warm temperate species of *Gracilaria*, chlorophyll *a* concentrations were generally low. For example, all collections of *G. cornea* collected between May 1996 and December 1997 had lower chlorophyll *a* (0.09 to 0.41 mg) compared to Tampa Bay estuarine populations of *G. verrucosa* (0.6 to 1.6 mg; Dawes et al., 1978). However chlorophyll *a* concentrations were higher or similar to two Tampa Bay populations of *G. tikvahiae* (0.26

to 0.37 mg, Dawes, 1994) and cultured sporelings (0.05 to 0.24 mg, Friedlander & Dawes, 1984) of the same species. Phycoerythrin concentrations were also low (0.06 to 0.39 mg) compared with the same populations of *G. tikvahiae* (0.37 to 0.52, Dawes, 1994; 0.16 to 0.56 mg, Friedlander & Dawes, 1984). The pigment concentrations probably reflect low concentrations of nitrogen compounds in the oceanic water of the Florida Keys. In contrast, cultured plants become deeply pigmented (unpublished data) similar to *G. tikvahiae* (Dawes, 1994).

Gracilaria cornea responded positively to low irradiance and demonstrated shade adaptation, that is having low I_c (11–38 μmol) and low I_k (90–112 μmol) values along with a high photosynthetic efficiency ($\alpha = 0.03$ to 0.05). Further, its photosynthetic responses declined at irradiances above 1000 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$. This is also in contrast to *G. tikvahiae* collected in the Great Bay Estuary in New Hampshire (no photoinhibition at 1440 $\mu\text{mol photon}$: Penniman & Mathieson, 1985) and *G. verrucosa* collected as drift plants in Tampa Bay (no photoin-

hibition at 2000 $\mu\text{mol photon}$: Dawes et al., 1978). Finally, *G. cornea* was intolerant of low salinity and low temperature, unlike the estuarine species *G. tikvahiae* (Penniman & Mathieson, 1985; Friedlander & Dawes, 1984; Dawes, 1994) and *G. verrucosa* (Dawes et al., 1978).

Although the data are limited, optimum photosynthetic response of *Gracilaria cornea* to irradiances were similar to other tropical macroalgae (Table 3). In particular, optimum irradiances were between 100 and 800 $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$ and photoinhibition occurred above 1000 $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$, which is similar to *Eucheuma* spp. (Dawes, 1979), *Hypnea musciformis* (Dawes et al., 1976) and *Halimeda* spp. (Littler et al., 1988). Further, the P vs I data suggest that this species is acclimated to low irradiance (I_c , I_k , α), although the populations occur in shallow (0.5 to 1 m) habitats in Florida Keys suggesting adaptation to deeper as well as the turbid water.

High photosynthetic and low respiratory rates were measured in *G. cornea* exposed to 25 and 35 °C, but the rates were low at 15 °C. This response to temperature is similar to that of other tropical seaweeds (Table 3), but not the 37 subtropical Florida macroalgae surveyed by Mathieson and Dawes (1986), where the red algae showed the narrowest range (18–24 °C). As stated earlier, the populations sampled in the Florida Keys were adapted to oceanic conditions, did not tolerate salinity of 15‰, and showed a lower response to 20‰ than 30‰. Although not tested here at a salinity above 30‰, the species probably has a similar tolerance range as *Eucheuma isiforme*, which also occurs there (e.g. 20 to 40‰; Dawes, 1979). The response of *G. cornea* to salinity is also similar to other species widespread in exposed tropical waters (e.g. *Padina* spp., *Bryothamnion triquetrum*; Table 3).

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