Seasonal variation in photosynthesis and biochemical composition of *Caulerpa* spp. (Bryopsidales, Chlorophyta) from the Gulf of Mexico

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Photosynthesis, pigment content, soluble carbohydrate, and protein levels of six *Caulerpa* species were examined on a seasonal basis from samples taken along the northern coast of the Yucatan Peninsula, Mexico, between June 1998 and August 1999. For *Caulerpa* ashmeadii, *C. mexicana*, *C. paspaloïdes*, and *C. racemosa* photosynthetic capacity changed depending on seasonal trends in photon flux density and water temperature in the study area. This pattern was not evident in *Caulerpa* prolifera and *C. cupressoides*. Maximum photosynthetic rates of 18.3 ± 0.8 mg O$_2$ g dry weight$^{-1}$ h$^{-1}$ were obtained in *C. mexicana* during the cold season. Photosynthetic efficiency (a) showed a similar pattern to that of $P_{\text{max}}$ coinciding with low irradiances ( photon flux density [PPFD]: 151 ± 67 μmol photons m$^{-2}$ s$^{-1}$) and water temperature (23.8 ± 1.9°C), and the highest levels of dissolved inorganic nitrogen and dissolved reactive phosphorus in the water (9.1 μmol 1$^{-1}$ and 0.5 μmol 1$^{-1}$, respectively). Compensation ($E_c$) and saturation ($E_s$) irradiances were low and ranged from 3 to 35 and 44 to 280 μmol photons m$^{-2}$ s$^{-1}$, respectively. Maximum chlorophyll a and b (Chl a and b) levels occurred in *C. racemosa* and *C. cupressoides* during the cold to rainy seasons. The highest Chl b:a ratios were observed during the coldest months for all studied species. Protein and carbohydrate contents in *Caulerpa* spp. followed an inverse seasonal pattern. In general, high protein levels were observed in the dry season coinciding with increasing light and seawater temperatures.

Photosynthesis in *Caulerpa* spp. from the Yucatan Peninsula coast is affected by high temperatures during the dry and rainy seasons. There is also a seasonal shift in the species proximate constituents indicative of a rapid growth period from January to May and a carbohydrate accumulation period during the rest of the year.

**INTRODUCTION**

Seaweeds are exposed to seasonal variations in abiotic factors that influence their metabolic responses (photosynthesis and growth rates) and proximate constituent levels. Seasonal changes in photosynthetic performance have been demonstrated for temperate and subtropical seaweed species with higher efficiencies related to changes in light intensity, temperature, nutrients, or algal developmental state (Duke et al. 1989; Campbell et al. 1999). The genus *Caulerpa* is widely distributed in tropical and subtropical marine ecosystems throughout the world (Linning 1990). Scientific interest in *Caulerpa* has been growing since the invasion of two *Caulerpa* species into the Mediterranean Sea: *C. taxifolia* (M. Vahl) C. Agardh in 1984 (Meinesz & Boudouresque 1996) and *C. racemosa* (Forsskål) J. Agardh in 1994 (Ceccherelli & Piazzia 2001). Rapid proliferation of *C. taxifolia* in the Mediterranean has been attributed to abnormally vigorous growth, tolerance of relatively low winter temperatures, and efficient vegetative reproduction (Meinesz & Boudouresque 1996). Gayol et al. (1995) showed that winter acclimated *C. taxifolia* easily maintains its basal metabolism requirements and generates significant additional photosynthetic product for storage and/or growth. Garcia et al. (1996b) demonstrated that *C. taxifolia* annual productivity was less affected by seasonal fluctuations in light and temperature, as reported for endemic species from the north-western Mediterranean. Moreover, this species did not exhibit the photoadaptive responses to bathymetric changes in irradiances that have been reported in other algae (Chisholm & Jaubert 1997). It has also been demonstrated that Mediterranean *C. taxifolia* can withstand a temperature of 10°C (Komatsu et al. 1997), and more recently Chisholm et al. (2000) reported a cold tolerance threshold of 9 to 11°C in *C. taxifolia* from Australia.

Effects of light and temperature on photosynthesis and respiration rates have also been studied in other *Caulerpa* spp. on both instantaneous and seasonal bases. To date, variations in their photosynthetic responses have been attributed to differences in physiology, morphology, or the environmental conditions in which the algae grow. Laboratory experiments with two varieties of *Caulerpa racemosa*, *C. racemosa* var. *clavifera* (Turner) Weber–van Bosse (Gattuso & Jaubert 1985) and *C. racemosa* var. *uwifera* (C. Agardh) J. Agardh (Riechert & Dawes 1986), have indicated acclimation to varying irradiances and higher photosynthetic capacities at temperatures between 20 and 30°C. Similarly, higher net photosynthesis has been reported during the summer in Florida Keys populations of *Caulerpa paspaloïdes* (Bory de Saint-Vincent) Greville (O’Neal & Prince 1988). In the same study, winter acclimated thalli were found to utilize low light more efficiently than summer acclimated thalli without significant differences in net photosynthesis over a temperature range of 19–30°C.

In a Mediterranean coastal lagoon in southern Spain, *Caulerpa prolifera* (Forsskål) J.V. Lamouroux is reported to have adjusted its metabolism to the annual water temperature course with maximum photosynthetic rates in late spring and early summer (Terrados & Ros 1992). Intrageneric relationships between photosynthesis and morphology have also been studied for Caribbean *Caulerpa* species. Garcia et al. (1996a) characterized shallow-water tropical/subtropical *Caulerpa*
populations as mostly sun-adapted plants, whereas Collado-Vides & Robledo (1999) found both sun and shade tolerant species among distinct growth forms in seven Caulerpa species growing in reefs and lagoons of the Mexican Caribbean reef system.

Sixteen Caulerpa species have been described from the Atlantic coast of Mexico, and at least six of these dominate tropical macroalgal standing stocks year round (Ortega et al. 2001). To date, no studies have been performed on how environmental variables affect the physiology and biochemical composition of these Caulerpa species indigenous to the Gulf of Mexico. This study assesses seasonal variations in photosynthesis, respiration, and biochemical composition rates given the hypothesis that Caulerpa species will exhibit little to no seasonal variation in photosynthetic rate, pigment, carbohydrate content, and protein content.

MATERIAL AND METHODS

Site location and sample collection

The Yucatan Peninsula, Mexico, located along the southeast margin of the Gulf of Mexico, is a limestone platform characterized by marked seasonal differences in environmental conditions. It experiences a rainy or wet season between July and October with abundant tropical rainfall, high air temperatures, and storms. A cold season occurs from November to February, with lower rainfall and temperatures and prevailing northerly winds. A third, dry, season occurs between March and June and is characterized by sunny days and calm water conditions. This seasonal pattern may influence the physiological performance and biochemical constituents of seaweed species found in this tropical region.

Monthly sampling of Caulerpa was performed between June 1998 and August 1999 off the coast of Dzilam de Bravo (21°23′N, 88°57′W), in the state of Yucatan, Mexico. The sandy bottoms in this area are covered by six Caulerpa species: C. ashmeadii Harvey; C. cupressoides (Vahl) C. Agardh; C. mexicana Sonder ex Kützing; C. prolifera (Forsskål) J.V. Lamouroux; C. paspalooides (Bory de Saint-Vincent) Greville; and C. racemosa (Forsskål) J. Agardh. These algae form patches and grow at 2 to 4 m depth together with the sea grasses Thalassia testudinum König and Syringodium filiforme Kützing. Algae samples for laboratory analysis were randomly collected every 2 months during the sampling period, with a total of six to eight sampling events for photosynthesis and nine sampling events for biochemical analyses. Plants were transported in cool boxes with seawater to the laboratory. The thallus blade (ramet) of each species (5–7 cm long) was removed, gently brushed, and placed in sterile aerated seawater (34%o and 27°C) under low irradiances (< 30 μmol photons m⁻² s⁻¹) and a 12:12 light:dark photoperiod.

Environmental factors

Incident light and seawater temperature were recorded continuously (1 and 2 h intervals, respectively) at the study site using submersible data loggers (HOBO, Onset Computer Corp., Pocasset, MA) tied to an anchor bolt hammered into the limestone substrate. Instant daily temperatures were recorded and mean monthly temperatures were calculated by averaging all values obtained for a 30 day period. Light readings taken during the sunlight period (13 h) were converted from lux to photon flux density (PFD, 400–700 nm, in μmol photons m⁻² s⁻¹) using an equation derived from a linear regression obtained through use of a LI-COR 4700 quantum sensor (LI-COR Inc., Lincoln, NE). Seawater samples were taken at the study site during each plant collection for nutrient analysis. Salinity, dissolved inorganic nitrogen (DIN = sum of N-NO₃ + N-NO₂ + N-NH₄), dissolved reactive phosphorus (DRP = P-PO₄), and suspended particulate matter (SPM) were determined as described by Strickland & Parsons (1972).

Photosynthesis

Photosynthesis was estimated from the photosynthesis vs irradiances relationships determined from data obtained using the light–dark bottle technique. Photosynthesis–irradiances curves (P vs E) were measured 1 day after collection. Two clean ramets of each Caulerpa sp. weighing between 50 to 100 mg (depending on the species) were placed in each of six 60 ml BOD bottles containing filtered seawater from the study site; two blank bottles were used as controls. Oxygen evolution was measured for 1 h at each irradiance with a YSI (mod. 58) oxygen meter (YSI Inc., Yellow Springs, OH) in an ambient cooled water bath at 26 ± 1°C. Irradiances were generated by a halogen lamp (500 W) with neutral density filters providing a range of 0 to 800 μmol photons m⁻² s⁻¹. Photosynthesis–irradiances parameters (P_{max}, E_{c}, E_{a}, α) and respiration rates (R_d) were determined for each sample using computer-generated graphics. Respiration rates were measured for bottles incubated under completely dark conditions. Net photosynthesis (hereafter referred to as P_{net}) was calculated from the mean value of the three highest photon flux densities that resulted in a light saturated rate of photosynthesis. Alpha (α), the initial slope of the P–E curve, was calculated using a linear regression of 3–5 points. All data for the light-limited portion of the P–E curve which exhibited no deviations from a linear increase (r² = 0.9) were used. Upon completion of the experimental run, all samples were dried and weighed and oxygen evolution was expressed as mg O₂ g dry weight⁻¹ (d wt⁻¹) h⁻¹ standardized to 300 ml to allow comparison with other published data. Mean values for each season (rainy, cold, and dry) were obtained by averaging monthly values obtained for each species.

Pigment analysis and proximate tissue constituents

Chlorophyll a and b (Chl a and b) were extracted on the day of collection by grinding algal fragments (n = 10) of 100 to 150 mg fresh weight in a mortar using liquid nitrogen. Extraction was done with acetone (80% vol/vol) in the dark and at low temperatures. Extracts were centrifuged (1650 g) for 10 min and absorption determined at 665 nm (Chl a) and 647 nm (Chl b) using a Shimadzu (UV-1601) spectrophotometer (Shimadzu Corporation, Tokyo, Japan). Pigment concentrations were determined using published extinction coefficients and equations (Jeffrey & Humphrey 1975). Percentage dry weight of 100 to 200 mg fresh weight branches (n = 8) was calculated from each collection after blotting dry, weighing, drying for 24 h at 60°C, and reweighing. Similarly, 14 clean branches were dried, placed in test vials, and stored for proximate analysis. Total soluble carbohydrates (Dubois et al. 1972) were determined using a method based on the reduction of an aliquot of each extract with a solution of sodium bisulfite (Jorgensen 1973) in the presence of a ferrocyanide reagent (Fiske & Subbarow 1925).
1956) and protein (Lowry et al. 1951) were determined for all bimonthly samples. Dried samples were ground and the powder screened through No. 40 mesh to enhance extraction of soluble carbohydrate and protein. All values are presented as percentage dry weight.

**Statistical analysis**

Normality and homogeneity of variance were first determined using Kolmogorov–Smirnov and Bartlett tests, respectively. Variables were log transformed to meet these assumptions when necessary. One-way analysis of variance (ANOVA) was used to test for significant differences between photosynthetic parameters, pigment content, carbohydrate levels, and protein levels with respect to months. An *a posteriori* Student’s Newman Keuls test was used to compare means between groups found to be significantly different with the ANOVA. Chemical constituents (carbohydrate, protein, and pigment content) and environmental variables (seawater temperature, irradiances, and nutrients) were correlated using a Pearson correlation (Zar 1984).

**RESULTS**

Incident light and seawater temperature exhibited similar seasonal patterns (Fig. 1). Mean seawater temperature in the area was 28.2 ± 2.4°C. Maximum temperature was registered in August 1998 (31.4 ± 1.5°C) and minimum in January 1999 (23.8 ± 1.9°C). From June to October 1998 (rainy season), temperature averaged 30.2 ± 1.0°C, while from November 1998 to February 1999 (cold season) temperature averaged 25.7 ± 1.3°C. From March to June 1999 (dry season) temperature averaged 27.6 ± 1.6°C, increasing to 30.3 ± 0.6°C during the following rainy season (July and August 1999).

Low irradiances (PFD: 151 ± 67 μmol photons m⁻² s⁻¹) occurred in November 1998 reflecting the prevalence of cloudy days and high turbidity (SPM 161 mg l⁻¹). In contrast, maximum irradiances levels (PFD: 559 ± 186 to 660 ± 342 μmol photons m⁻² s⁻¹) were obtained from March to June (dry season), coinciding with clear skies and low turbidity (SPM: 23 mg l⁻¹), and averaged 641 ± 55 μmol photons m⁻² s⁻¹. Mean PFD for the rainy season was 446 ± 87 μmol photons m⁻² s⁻¹, and for the cold season it was 512 ± 290 μmol photons m⁻² s⁻¹. A gradual decrease in salinity was observed from August to January (35.6 to 29.5%), coinciding with the rainy and cold seasons, followed by an increase from February to a peak in May (36.7%). Nutrients peaked during the cold season at 9.1 μmol l⁻¹ DIN and 0.5 μmol l⁻¹ DRP.

Photosynthesis followed a seasonal cycle with significantly higher net photosynthesis values during the cold season (Fig. 2). For *C. prolifera* and *C. cupressoides*, this pattern was not evident since photosynthesis ranged from 7.4 ± 0.6 to 9.3 ± 0.5 mg O₂ g d wt⁻¹ h⁻¹, with no significant differences between seasons (F₂,15 = 2.67, P > 0.05; F₂,15 = 0.21, P > 0.05, respectively). A maximum photosynthetic rate of 18.3 ± 0.8 mg O₂ g d wt⁻¹ h⁻¹ was recorded for *C. mexicana* during the cold season (F₂,15 = 23.36, P < 0.001) and a minimum rate of 3.3 ± 0.5 mg O₂ g d wt⁻¹ h⁻¹ for *C. racemosa* in the rainy and dry seasons (F₂,15 = 13.45, P > 0.001, Fig. 2A–F). *Caulerpa prolifera* maximum photosynthesis was positively correlated to water temperature (r = 0.53, P < 0.05), while photosynthesis in *C. mexicana* was negatively correlated (r = −0.57, P < 0.05) partially explaining the high Pmax rates found during the cold season. *Caulerpa* spp. collected during the cold season also had higher respiration rates, with higher values for *C. ashmeadii* (−7.0 ± 0.9 mg O₂ g d wt⁻¹ h⁻¹) and *C. mexicana* (−8.0 ± 1.0 mg O₂ g d wt⁻¹ h⁻¹). For *C. paspaloides*, no significant differences in respiration were found between seasons (F₂,15 = 0.51, P > 0.05). Respiration rates for all the examined *Caulerpa* species were positively correlated with incident light (C. racemosa, r = 0.61; C. ashmeadii, r = 0.57; C. cupressoides, r = 0.66; C. mexicana, r = 0.49; C. paspaloides, r = 0.51; C. prolifera, r = 0.50; P < 0.05). Photosynthetic efficiency (α) showed maximum values during the cold season (November to January), a pattern similar to that of Pmax. These physiological descriptors were significantly, positively correlated in *C. racemosa*, r = 0.72; C. ashmeadii, r = 0.74; C. cupressoides, r = 0.76; C. mexicana, r = 0.81; and *C. paspaloides*, r = 0.86 (P < 0.05), but not in
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Fig. 2. Seasonal patterns of light saturated photosynthesis (bars) and dark respiration (●) in (A) C. mexicana; (B) C. prolifera; (C) C. cupressoides; (D) C. paspalooides; (E) C. ashmeadii; and (F) C. racemosa. Standard deviations indicated. Bars with the same letters are not significantly different (P < 0.05).

C. prolifera (r = 0.31; P > 0.05) (Fig. 3). Maximum $P_{\text{max}}$ and $\alpha$ values also coincided with the highest DIN and DRP levels in the water. Compensation irradiances ($E_c$) were low (3 to 35 $\mu$mol photons m$^{-2}$ s$^{-1}$), as were saturation irradiances ($E_k$ = 44 to 280 $\mu$mol photons m$^{-2}$ s$^{-1}$) (Table 1).

The two examined photosynthetic pigments followed the same seasonal pattern (Fig. 4). Chlorophyll $a$ content was positively correlated with Chl $b$ in all species ($P < 0.05$). Maximum Chl $a$ and $b$ levels occurred in C. cupressoides (15.9 ± 1.5 and 19.3 ± 2.7 mg g dwt$^{-1}$, respectively) and C. racemosa (23.2 ± 3.3 and 12.9 ± 2.4 mg g dwt$^{-1}$, respectively) during the cold (November) to rainy (July) seasons. For C. paspalooides, maximum values occurred during the cold (January) to dry (March) seasons (15.8 ± 0.7 and 13.9 ± 2.0 mg g dwt$^{-1}$, respectively). Minimal chlorophyll levels were found in C. prolifera and C. ashmeadii, with overall concentrations of 7.5 and 8.4 mg Chl $a$ g dw t$^{-1}$ and 4.7 and 6.3 mg Chl $b$ g dw t$^{-1}$, respectively. The highest Chl $b$:$a$ ratios were observed during the coldest months (November, January) for all the studied species.

Protein and carbohydrate contents in Caulerpa spp. followed an inverse seasonal pattern (Fig. 5). In general, high protein levels were observed in the dry season (March–April) coinciding with increasing light and seawater temperatures. Caulerpa paspalooides had the highest protein content (12.1 ± 0.3% dry weight), whereas C. ashmeadii and C. racemosa had the lowest content (1.6 ± 0.1%). Total soluble carbohydrates increased during the rainy and cold seasons in all species. Maximum carbohydrate content was found in C. prolifera during November (30.2 ± 1.0%). A significant reduction in carbohydrates was observed in all species during March and April, with the lowest soluble carbohydrate content found in
C. asheaddi (3.4 ± 0.9%). A significant negative correlation between protein and carbohydrate content was found for C. mexicana (r = −0.40) and C. paspaloides (r = −0.46) (P < 0.05).

DISCUSSION

Caulerpa spp. from the coast of the northern Yucatan Peninsula exhibited marked seasonality in photosynthetic capacity and biochemical constituents. The oxygen production rate was largely species dependent, but a degree of environmental and seasonal variation was evident (Fig. 2). $P_{\text{max}}$ values reported for Caulerpa species from the Yucatan Peninsula coast are somewhat higher than or similar to those reported for other Caulerpa species listed in Table 1. However, in some instances, such as C. racemosa, they are clearly lower when compared to C. racemosa var. clavifera (Gattuso & Jaubert 1985) or C. racemosa from the Mexican Caribbean (Collado-Vides & Robledo 1999). On the contrary, C. mexicana had the highest $P_{\text{max}}$ rates, comparable to those recorded for C. taxifolia in the Mediterranean (Gacia et al. 1996b).

Maximum photosynthesis ($P_{\text{max}}$) values were observed during the cold season, a period of reduced light and lower temperatures. In contrast, low photosynthetic rates were observed during the dry and rainy seasons, when light and temperature increased. A similar seasonal trend has been reported in the Florida Keys for C. paspaloides in which thalli collected during winter photosynthesized more efficiently at low light intensities than thalli collected in the summer (O’Neal & Prince 1988). Respiration rates were low during the rainy season, which coincides with high seawater temperatures, and increased during the cooler temperatures prevailing in January. Since low respiration rates correspond to periods of storage (summer), it appears that photosynthesis and respiration rates in the studied species are affected by high temperatures during the dry and rainy months, which probably result in low growth rates for some Caulerpa species during this season.

The effect of temperature on photosynthesis and respiration changes during an annual cycle, in some cases it indicates thermal sensitivity and an adaptation of metabolic rates to the seasonal water temperature course (Luning 1990). Caulerpa taxifolia is an example of this. This seaweed has successfully colonized different areas in the Mediterranean Sea by adjusting its physiology and growth characteristics to the new environment. In the present study, no significant changes in the annual photosynthesis course were observed for C. prolifera and C. cupressoides. These findings suggest that both species exhibited metabolic adaptation to seasonal changes in abiotic factors. In this sense, maximum photosynthesis ($P_{\text{max}}$) and dark respiration ($R_d$) in C. prolifera increased linearly with water temperature between 10 and 30°C and 10 and 35°C, respectively, year round in the Mediterranean (Terrados & Ros 1992). In contrast, C. asheaddi, C. paspaloides, and C. racemosa did not correlate with any of the environmental parameters that most strongly affect seaweed productivity; i.e. light availability, water temperature, and nutrient availability (Duke et al. 1989).

When compared to other Caulerpa species, the relatively high $P_{\text{max}}$ rates, together with low $E_a$ and $E_s$ values, suggest that Caulerpa species from the Yucatan Peninsula coast seem to be adapted to low light environments. These low $E_a$ and $E_s$ values, and the high efficiency at low light incoming irradiiances, although common to other species of the genus Caulerpa (Terrados & Ros 1992; Gacia et al. 1996a; Chisholm & Jaubert 1997; Collado-Vides & Robledo 1999), suggest that species from the Gulf of Mexico behave like shade-adapted plants. The strong positive relationship between $P_{\text{max}}$ and $\alpha$ indicates that Caulerpa spp. with high photosynthetic efficiency at low light also tend to exhibit high photosynthetic

Table 1. Photosynthesis parameters in different Caulerpa species. $P_{\text{max}}$ and $R_d$ (mg O$_2$ g dw$^{-1}$ h$^{-1}$), $E_a$ and $E_s$ (μmol photons m$^{-2}$ s$^{-1}$).

| Species     | $P_{\text{max}}$ | $-R_d$ | $E_a$ | $E_s$ | Reference |
|-------------|------------------|--------|-------|-------|-----------|
| C. racemosa | 14.2$^1$         | 3.8$^1$| 18–143| 6–37  | Gattuso & Jaubert 1985 |
| C. racemosa | 0.1–0.3$^1$     | 0.01–0.03$^1$| 100–200| 25    | Riechert & Dawes 1986 |
| C. racemosa | 19.9             | 9.0    | 178   | –     | Collado-Vides & Robledo 1999 |
| C. prolifera | 8.5              | 9.1    | 0.3–7.8 | 24–280 | The present study |
| C. prolifera | 4.4–16.3        | 0.5–7.8| 33–237 | 6–18  | The present study |
| C. prolifera | 1.2–6.6         | 0.1–1.0| 11–112 | 2–37  | Terrados & Ros 1992 |
| C. prolifera | 6.9              | 1.2    | –     | 28    | Enriquez et al. 1995 |
| C. prolifera | 3.7$^2$         | 0.8$^2$| 310   | 63    | Gacia et al. 1996a |
| C. prolifera | 25.2            | 6.0    | 147   | –     | Collado-Vides & Robledo 1999 |
| C. prolifera | 6.3–9.8         | 0.3–4.2| 49–98 | 4–19  | The present study |
| C. prolifera | 3.9–11.7        | 1.2–7.0| 60–135 | 7–15  | The present study |
| C. prolifera | 35.7            | 12.8   | 206   | –     | Collado-Vides & Robledo 1999 |
| C. prolifera | 3.5–16.9        | 1.2–6.2| 53–237 | 6–18  | The present study |
| C. prolifera | 13.4            | 4.5    | 152   | –     | Collado-Vides & Robledo 1999 |
| C. prolifera | 3.4–18.3       | 1.0–8.7| 97–195 | 6–35  | The present study |
| C. prolifera | 2.8–6.1$^1$    | 0.2–0.5$^1$| 122–238 | 9–20  | Gayol et al. 1995 |
| C. prolifera | 3.2–18$^2$     | 0.3–1.3$^2$| 68–166 | 1.8–11| Gacia et al. 1996b |
| C. prolifera | 1.1–3.8$^3$    | 0.2–0.3$^3$| 218–310 | 9–21  | Chisholm & Jaubert 1997 |
| C. prolifera | 0.5–5.3$^3$    | 0.8–2.8$^3$| 28–80  | 9–32  | Chisholm et al. 2000 |

1 mg O$_2$ mg Chl a$^{-1}$ h$^{-1}$.
2 mg O$_2$ g$_{\text{org}}$ dw$^{-1}$ h$^{-1}$.
3 Calculated from data expressed in μmol O$_2$ g dw$^{-1}$ h$^{-1}$.
rates under light saturation conditions (Fig. 3). Similarly, the maximum photosynthetic rates ($P_{\text{max}}$) and slopes ($\alpha$) of the $P$ vs $E$ curves were strongly correlated in $C$. prolifera, $C$. racemosa, $Caulerpa$ sertularioides, and $C$. sertularioides var. brevipes from the Caribbean (Gacia et al. 1996a). Enriquez et al. (1995) also found a good correlation between $P_{\text{max}}$ and $\alpha$, and both parameters were also related to tissue thickness in 20 Mediterranean marine macroalgae species. In the same study, thickness was thought to determine photosynthetic efficiency in marine macrophytes, and the $P_{\text{max}}$ correlation to tissue thickness was mainly explained by autocorrelation with $\alpha$.

In general, the lower total Chl ($a + b$) content from March to May, when ambient PFD is high, rather than in November, when ambient PFD is low, observed in the present study suggests sun shade behaviour. In this case the higher pigment concentration is a result of low irradiances caused by increased turbidity and higher inorganic nitrogen levels in the water. Conversely, the decrease in photosynthetic pigment from January to May, during the cold to dry seasons, correlates with high light regimes and intensive growth (Campbell et al. 1999). A relative Chl $b$ enrichment in September and November in $C$. cupressoides (Chl $b:a$ ratios of 1.22 and 1.27, respectively) and during January in $C$. paspaloides (Chl $b:a$ ratio 1.27) suggests that both species exhibit a sun shade adaptation similar to higher plants and green algae. Yokohama (1983) suggested that a higher Chl $b$ proportion is favourable for growth under low light based on the argument that Chl $b$ absorbs shortwave light more efficiently than Chl $a$. Photoacclimation to irradiance in $C$. racemosa var. uvifera is based on changes in pigment and chloroplast structure (Riechert & Dawes 1986).

It is generally assumed that both pigment concentration and the accessory-to-primary antenna pigments ratio vary inversely with ambient PFD in green algae. Low Chl ($a + b$) contents and high Chl $a:b$ (low Chl $b:a$) ratios have been found in sun-acclimated species, while shade species are char-
charaterized on the basis of their low Chl \(a:b\) (high Chl \(b:a\)) ratio (Rosenberg & Ramus 1982). *Caulerpa mexicana*, *C. ashmeadii*, and *C. prolifera* can thus be characterized as shade species based on their high, year round Chl \(b:a\) ratios. Differences in tissue thickness and Chl \(a\) content have been shown to account for most differences in light absorption properties across a broad spectrum of marine macrophytes (Enriquez et al. 1995). In the present study, however, species with higher chlorophyll content, such as *C. cupressoides* and *C. racemosa*, did not necessarily increase their photosynthetic efficiency or their maximum photosynthetic rate.

Some studies in the *Caulerpa* genus have shown a correlation between photosynthetic rates and thallus morphology (Gacia et al. 1996a; Collado-Vides & Robledo 1999). Because *C. paspaloides* thallus morphology is more complex than that of *C. mexicana* and *C. prolifera* (e.g. fronds bearing three or four ranks of pinnules vs flattened fronds with opposite pinnules in *C. mexicana* and undivided blades in *C. prolifera*), it could be expected that *C. paspaloides* would exhibit lower light utilization efficiencies and maximum photosynthetic rates; these parameters, however, were similar to those of *C. mexicana*.

*Caulerpa* species had high carbohydrate levels during the rainy and cold seasons and high protein levels in the dry months, indicating that the most active growth period probably occurs during these months. Durako & Dawes (1980) indicated that an increase in protein levels correlates to rapid growth. In addition, increasing total soluble carbohydrate levels are inversely related to growth. At times when growth is high, total carbohydrates tends to be lower, modifying the protein to carbohydrate ratios. The importance of nitrogen in the seasonal growth cycle of an alga has much to do with its life strategy, i.e. annual or perennial. In perennial species, nutrient availability does not govern growth onset, though it does play an important role in the seasonal cycle (Kain 1989). In this sense, a shift between higher nutrient concentration during November and higher protein content in March–April was observed in all the studied species.

An increase in the carbon storage reserves was observed during the cold season in all the studied *Caulerpa* species. The decrease in carbohydrate contents from November to March suggests that stored photosynthetic products are used for cold season maintenance, similar to the pattern found in *C. prolifera* from the Mediterranean (Terrados & Ros 1992).

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**Fig. 5.** Protein (bars) and carbohydrate (●) content in bimonthly samples of *Caulerpa* species in relation to season: Rainy (grey bars); cold (stripped bars); and dry (white bars). (A) *C. mexicana*; (B) *C. prolifera*; (C) *C. cupressoides*; (D) *C. paspaloides*; (E) *C. ashmeadii*; and (F) *C. racemosa* (no data are shown for November and March because no thalli were found during these months). Standard deviations indicated. Bars with the same letters are not significantly different (\(P < 0.05\)).
However, the seasonal pattern in this study differs slightly, with higher carbohydrate levels in September to November, which may reflect the warmer waters of the Yucatan Peninsula region.

In conclusion, photosynthesis in Caulerpa from the Yucatan Peninsula is mostly affected by high temperatures during the dry and rainy seasons. The relatively high \( P_{\text{max}} \) rates, in comparison to other Caulerpa species, together with low \( E_t \) and \( E_r \) values, indicate an acclimation to low light environments, suggesting that Caulerpa species from the Gulf of Mexico behave as shade-adapted plants. Based on Chl \( b:a \) ratios, however, \( C.\) cupressoides and \( C.\) paspalooides exhibit a sun shade adaptation. A seasonal shift in the proximate constituents of the studied Caulerpa species indicates a rapid growth period from January to May and a carbohydrate accumulation period during the rest of the year.

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