

The relationships between morphology and photosynthetic parameters within the polymorphic genus *Caulerpa*

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Abstract

The functional form theory predicts that surface area vs. volume ratio ($SA:V$) and maximum productivity (P_{\max}) decrease as morphological complexity of an algal thallus increases. The genus *Caulerpa* demonstrates a tremendous range of morphological forms as well as interspecific plasticity which make it ideal to study intrageneric relationships between photosynthesis and morphology. We used two approaches to assess functional–morphology relationships: 1) an extensive survey of P_{\max} for 15 *Caulerpa* taxa in relation to $SA:V$ from species and forms of the Caribbean and 2) an intensive study of photosynthetic attributes [P_{\max} , photosynthetic efficiency (α), compensation irradiance (I_c), saturation irradiance (I_k)] and respiration (R) for 4 *Caulerpa* taxa from the Indian River Lagoon, Florida, focusing on $SA:V$ and surface area vs. biomass ($SA:B$) ratios. These two sites represent areas of relatively low and high nutrient water respectively. $SA:V$ ratios for Caribbean *Caulerpa* ranged from 0.5 ± 0.10 to $11.7 \pm 3.53 \text{ cm}^2 \cdot \text{cm}^{-3}$ and were highly correlated ($r^2 = 0.74$, $p = 0.01$) to net photosynthetic rates (values from 0.4 to 4.6 $\text{mg C} \cdot \text{g ODW}^{-1} \cdot \text{h}^{-1}$). However, for clumped forms, e.g., *C. sertularioides* var. *brevipes* (J. Ag.) Svedelius, from the Indian River Lagoon, P_{\max} values were lower than predicted possibly due to an auto-shading effect of thin-overlapping branches. In these forms, $SA:B$ ratio was more highly correlated to photosynthetic attributes than $SA:V$ ratio. Our data from the Caribbean, with a mean P_{\max} of $2.23 \text{ mg C} \cdot \text{g ODW}^{-1} \cdot \text{h}^{-1}$, suggest that the genus *Caulerpa*, in low nutrient systems, approaches the lower mid-range of net primary production of other algal forms. Conversely, Indian River Lagoon values are much higher, reaching a maximum of $17.2 \text{ mg C} \cdot \text{g ODW}^{-1} \cdot \text{h}^{-1}$, possibly due to nutrient enriched waters of this system that enhance P_{\max} . Photosynthetic efficiency ranged between 0.007 to 0.042 $\text{mg C g ODW}^{-1} \cdot \text{h}^{-1}$ per $\mu\text{M} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ PAR. P_{\max} was maintained at $2500 \mu\text{M m}^{-2} \cdot \text{s}^{-1}$ and only one species, *C. prolifera* f. *zosterifolia* Børgesen, showed a photoinhibitory effect at $3000 \mu\text{M m}^{-2} \cdot \text{s}^{-1}$. Our data indicate that photosynthetic

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attributes of *Caulerpa* from shallow water in the Indian River Lagoon are characteristic of sun-adapted plants, i.e., high saturation and compensation irradiances, low efficiencies for capturing low photon flux densities and high exposure resistance to elevated light irradiances.

Keywords: *Caulerpa*; Functional–morphology; Photosynthesis; Surface area vs. biomass ratio (SA:B); Surface area vs. volume ratio (SA:V)

1. Introduction

The genus *Caulerpa* is an important component of macroalgal floras in coastal and tropical lagoons and reef systems worldwide. Throughout its range, populations of *Caulerpa* dominate macroalgal standing stocks. In addition to its ecological importance, this genus demonstrates a tremendous range of morphological forms as well as interspecific plasticity.

Morphological and functional adaptations of an organism to its environment play a critical role in the fitness (survival, growth and successful reproduction) of individuals. In this context, Littler (1980) found a close relationship between the thallus morphology and maximum photosynthetic rates (P_{\max}) of 45 species of macroalgae from a wide latitudinal range of distribution. Sheet-like and filamentous forms had higher P_{\max} values than coarse to calcareous forms. Primary production of sheet-like and filamentous algae was closely correlated with dry weight of the thallus while this relationship did not hold as well for the other algal form groups because of the higher proportion of structural mass. Such a between-species comparative approach has proven valid for a broad spectrum of seaweeds (Steneck and Watling, 1982; Littler et al., 1983; Hanisak et al., 1988; Kilar et al., 1989); however, no attempt has been made to test this hypothesis using a diversity of forms within a single genus.

In the present work, we use the morphologically diverse genus *Caulerpa* to explore the functional–morphology model. We follow two approaches; 1) an extensive survey of productivity for 15 *Caulerpa* taxa from a broad range of habitats in the Caribbean in relation to surface area vs. volume ratios (SA:V) and 2) a more detailed and intensive study of photosynthetic attributes such as maximum photosynthetic rates (P_{\max}), photosynthetic efficiencies (α), compensation levels (I_c), saturation irradiances (I_k) and respiration (R) for four *Caulerpa* taxa from the Indian River Lagoon, with additional focus on relationships to surface area vs. biomass ratios (SA:B).

2. Study areas

Samples of *Caulerpa* were collected at the following locations (Fig. 1): San Salvador Island, Bahamas, offshore of the College Centre of the Finger Lakes (24°10'N, 74°30'W). The habitat is a *Thalassia testudinum* bed bathed by the clearest of western Atlantic open-ocean waters (Jerlov Type 1). Carrie Bow Cay, Belize (16°45'N, 88°04'W), located in the Central Province of the Belize Barrier Reef, Central America



Fig. 1. Location of the four study areas.

with pristine waters extremely low in nutrients (Lapointe et al., 1992). Florida Keys, Florida ($24^{\circ}40'N$, $81^{\circ}23'W$), a habitat well documented (Lapointe, 1989) to be under elevated nutrient fluxes. The Indian River lagoon, Florida (extending between $28^{\circ}45'N$, $80^{\circ}50'W$ and $27^{\circ}15'N$, $80^{\circ}10'W$). The Lagoon is a long and shallow coastal system that receives substantial pulses of nutrients from residential and agricultural runoff during rainstorms.

3. Materials and methods

Using a large-scale overview approach, comparisons of net photosynthesis were made for 15 forms of *Caulerpa* (6 replicates each) from San Salvador Island, Carrie Bow Cay and the Florida Keys (see Table 1) to examine the relationships between P_{\max} and $SA:V$

Table 1
Caulerpa taxa from the Caribbean used for the extensive survey on the relationship between P_{\max} vs. SA:V ratio. The localities involved are: San Salvador Island, Bahamas (SS), Carrie Bow Cay, Belize (B) and Florida Keys, Florida (K).

Location	Taxa and Authors	Id.No.*	SA:V Ratio ($\text{cm}^2 \cdot \text{cm}^{-3}$)	\pm SD ($N = 6$)
SS, B, K	<i>C. cupressoides</i> (J. Agardh) Weber-van Bosse [var. <i>lycopodium</i>]	1	0.53	0.10
B, K	<i>C. paspaloides</i> (Weber-van Bosse) Howe [var. <i>compressa</i>]	2	0.65	0.36
B	<i>C. racemosa</i> (J. Agardh) Børgesen [var. <i>occidentalis</i>]	3	0.67	0.19
B, K	<i>C. paspaloides</i> Weber-van Bosse [var. <i>wurdermanii</i>]	4	0.96	0.36
SS, B, K	<i>C. racemosa</i> (Turner) Weber-van Bosse [var. <i>uvifera</i>]	5	1.18	0.49
SS, B, K	<i>C. cupressoides</i> (West) C. Agardh [var. <i>cupressoides</i>]	6	1.47	0.36
B, K	<i>C. racemosa</i> (Kützting) Taylor [var. <i>macrophyssa</i>]	7	1.62	0.17
B, K	<i>C. mexicana</i> (Weber-van Bosse) Taylor [f. <i>laxior</i>]	8	1.66	0.29
K	<i>C. microphyssa</i> (Weber-van Bosse) J. Feldmann	9	1.71	0.41
SS, B, K	<i>C. cupressoides</i> (Montagne) Weber-van Bosse [var. <i>mamillosa</i>]	10	1.87	1.08
SS, B, K	<i>C. mexicana</i> (Sonder) J. Agardh [f. <i>mexicana</i>]	11	1.99	0.52
SS, B, K	<i>C. sertularioides</i> (Weber-van Bosse) Børgesen [f. <i>farlowii</i>]	12	2.92	0.51
B	<i>C. racemosa</i> (Lamouroux) Eubank [var. <i>peltata</i>]	13	5.57	2.33
SS, B, K, IR	<i>C. prolifera</i> Børgesen [f. <i>zosterifolia</i>]	14	8.43	2.59
SS, B, K, IR	<i>C. sertularioides</i> (Gemelin) Howe [f. <i>sertularioides</i>]	15	11.26	0.35

* Identification number is used as a reference for Fig. 2

ratios. Incubations were carried out between 0900 and 1500 in 1.19 l jars under natural environmental conditions. Incident light was measured with a 4π sensor (Li Cor Model LI-1000) and maintained within the range of light saturation but not photoinhibition by using neutral density screening. Methods used were the same as those given in Littler et al., 1983. Linearity runs were used to assure that ratios of thallus weight: water volume: incubation time did not exceed the threshold of limiting factors (Littler, 1979). Mixing was continuous by means of water-driven magnetic turbines and was above the saturation level for water movement. All algae incubated were taken from their habitats of maximum abundance (i.e., in full sunlight from shallow (2–4 m) depths).

Surface area and volume measurements of the 15 *Caulerpa* taxa were made for six different replicate thalli to 0.01 cm^3 by submerging them in an Erlenmeyer flask and measuring the volume of water displaced upward in the constricted neck using a fixed suction microburette. The projected two-dimensional area of each thallus was determined to 0.01 cm^2 with a Li-Cor Model 3100 ± 1 area meter. The total surface area of each thallus was obtained by multiplying the projected surface area of cylindrical thallus portions by π , spherical portions by 3.5 (which compensates for the area of attachment to each stalk) and thin flat portions by 2.

In the more detailed analysis of specific photosynthetic parameters conducted on Indian River material, photosynthesis vs. irradiance curves were studied for four different taxa of *Caulerpa* with different SA:V and SA:B ratios; 1) finely dissected forms were represented by *Caulerpa sertularioides* f. *sertularioides* (Gmelin) Howe and *C. sertularioides* f. *brevipes* (J. Ag.) Svedelius, 2) sheet forms by *Caulerpa prolifera* f. *zosterifolia* Børgesen and 3) thick coarsely branched forms by *C. racemosa* var. *lataevirens* (Montagne) Weber-van Bosse.

Plants for *P* vs. *I* investigations were collected on the day prior to photosynthetic assays. They were transported to the laboratory, cleaned of sediments and epiphytes and cut in pieces of approximately 0.4 g of fresh weight. Thalli were held during the night in a circulating seawater tank at lagoon temperatures to permit wound healing.

Photosynthesis vs. irradiance measurements were conducted on plants incubated in jars immersed in an ambient water-cooled bath (26–33°C) in a 106 l insulated chamber, lined with highly reflective aluminium foil to increase light levels. Seven to nine experimental light levels were obtained with different layers of neutral density screening (30% reduction of available sunlight per layer). Measurements of the respiration rates were done under completely dark conditions. Incubations were all run between 1000 and 1200 to avoid endogenous patterns in photosynthesis.

Photon-flux densities (PFD) were measured in situ during the incubation period with a submerged spherical quantum sensor (Li-Cor Model LI-1000 Data Logger). Algae were incubated in 1.19 l incubation jars with stirring provided by high-speed stir bars on each of six oxygen electrodes; four replicates and two blank-controls were incubated per run. Dissolved oxygen concentration was recorded two times per irradiance level with an Orbisphere Model 2610 oxygen analyzer, once photosynthetic rates had stabilized.

The photosynthetic light saturation values (I_k) were obtained for each species by determining the intersection of a line drawn parallel to the abscissa and through the mid region of the points of maximum photosynthesis (P_{\max}) with the slope (α) of the light-limited *P* vs. *I* curve. The initial slope of each *P* vs. *I* curve was determined from

the least squares linear regression of all productivity values obtained for the linear portion of the curve including dark respiration. The compensation irradiance (I_c) was calculated as the intersection of α with the abscissa.

Changes in O_2 concentration were converted to $mg\ C\ fixed \cdot g\ dry\ wt^{-1} \cdot h^{-1}$ by standard methods (Strickland, 1960), assuming a photosynthetic quotient of 1.00. Oxygen production and respiration were normalised to organic dry weight after drying ($60^\circ C$) and ashing ($500^\circ C$) to constant weight.

Analysis of covariance (Zar, 1974) was used to compare the different linear regression lines using the Systat Statistics-package program Systat-Statistics for Windows, 1992.

4. Results

4.1. Synoptic study of 15 *Caulerpa* taxa from wide-ranging habitats

4.1.1. Surface area: volume measurements

Surface area: volume ratios for the 15 Caribbean taxa of *Caulerpa* (Table 1) ranged from 0.5 ± 0.10 to $11.7 \pm 3.53\ cm^2 \cdot cm^{-3}$. The three highest, *C. sertularioides* f. *sertularioides*, *C. prolifera* f. *zosterifolia* and *C. racemosa* var. *peltata* comprised one group and were significantly greater ($P < 0.01$, ANOVA) than the rest which formed a second group (Table 1). The first group had a mean SA:V ratio of about 8 (range = 6–11), whereas the second group had a mean SA:V ratio of 2 (range = 0.5–3). The group with lower SA:V ratios were larger, thicker and more coarsely branched forms.

4.1.2. Net photosynthetic measurements

Net photosynthetic rates varied by a factor of four (0.4 to $4.6\ mg\ C \cdot g\ ODW^{-1} \cdot h^{-1}$) for the 15 Caribbean taxa (Fig. 2) and increased as a function of increasing SA:V ratios. Differences between the lowest and highest SA:V values were highly significant ($p < 0.001$, ANOVA). The photosynthetic rates based on organic dry weight of thallus fell into two groupings (Fig. 2) which are consistent with those based on SA:V ratios. The regression of P_{max} versus SA:V ratios for all Caribbean taxa was significant (Fig. 2, $r^2 = 0.74$, $p = 0.01$).

4.2. Detailed study of four *Caulerpa* taxa from the Indian River Lagoon

4.2.1. Surface area: biomass and surface area: volume ratios

Surface area: volume and surface area: biomass ratios do not follow the same interspecific patterns (Table 2); *C. sertularioides* f. *brevipes* had the highest SA:V ratio, more than twice the value registered for *C. sertularioides* while the latter species had the highest SA:B ratio. Also, interspecific differences calculated on a volume basis are more pronounced than the values based on organic biomass; *C. sertularioides* had a 10-fold higher SA:V ratio than *C. racemosa* and was 1.25 times that of *C. prolifera*. Surface area: biomass differences among taxa were less pronounced; *C. sertularioides* had double the ratio of *C. racemosa* and was higher than *C. prolifera* by a factor of 1.6.

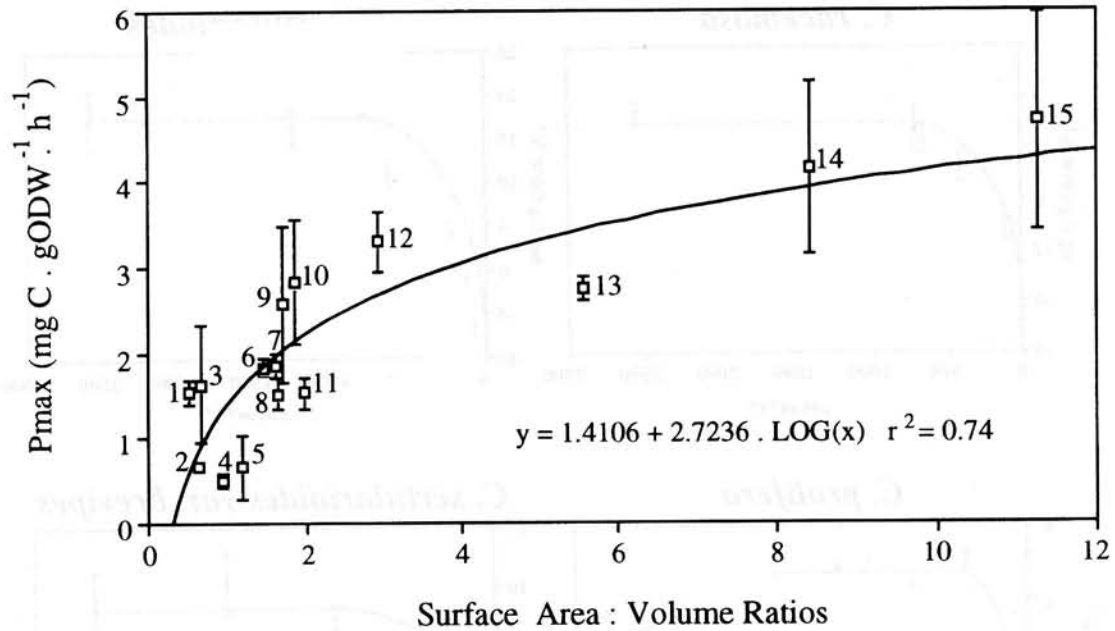


Fig. 2. Regression analysis of net photosynthetic ratios for 15 Caribbean taxa. Numbered points indicate mean values and standard deviation of the taxa bearing the same numbers in Table 1. Standard deviation values for SA:V ratios are provided in Table 1.

4.2.2. *P* vs. *I* curves

Maximum photosynthetic rates attained in the photosynthesis vs. irradiance curves (Fig. 3) followed the same tendency encountered in the synoptic study; *Caulerpa sertularioides* and *Caulerpa sertularioides f. brevipes* had the highest values, 80% and 60% higher (significant differences; $p < 0.001$, ANOVA), respectively than either *C. prolifera* or *C. racemosa* (Fig. 4a).

The slopes (α) of the light response experiments were significantly different ($p < 0.001$, ANCOVA; $p < 0.05$, multiple comparisons, Tukey Test) for some of the taxa. *Caulerpa sertularioides* showed 30% more efficiency (α) in the capture of low light intensities than *C. sertularioides var. brevipes*, which in turn was more than twice as efficient as either *C. racemosa* or *C. prolifera* (Table 3; Fig. 4b).

Irradiances above $2500 \mu\text{M} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ were attained during *Caulerpa prolifera* incubations and resulted in the only photoinhibition effect recorded (Fig. 3).

Table 2

Surface area vs. volume ($\text{cm}^2 \cdot \text{cm}^{-3}$) and surface area vs. biomass ($\text{cm}^2 \cdot \text{g ODW}^{-1}$) relationships for *Caulerpa* taxa from the Indian River Lagoon

	Surface Area:Volume ($\text{cm}^2 \cdot \text{cm}^{-3}$)	Surface Area:Biomass ($\text{cm}^2 \cdot \text{g ODW}^{-1}$)
<i>C. sertularioides</i>	11.6	366
<i>C. sertularioides f. brevipes</i>	35.6	280
<i>C. prolifera</i>	8.4	220
<i>C. racemosa var. laetevirens</i>	1.2	153

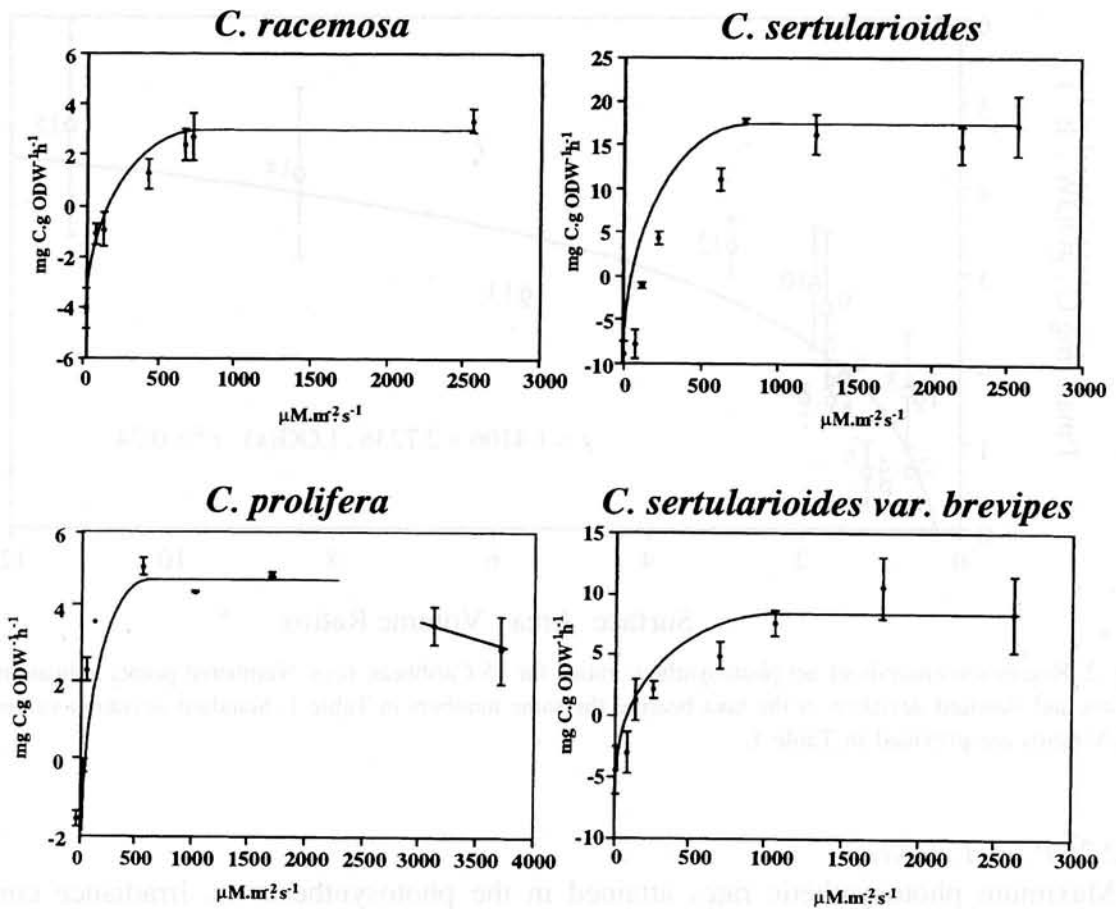


Fig. 3. Photosynthesis vs. irradiance curves of the four *Caulerpa* from the Indian River Lagoon. See details on the different photosynthetic parameters and number of replicates in Table 3.

Respiration rates were surprisingly similar for the different species (Table 3, Fig. 4c); except that *Caulerpa prolifera* with $0.82 \text{ mg C. g ODW}^{-1} \cdot \text{h}^{-1}$ had 40% lower rates than *C. sertularioides*.

The I_c for *C. sertularioides* was 75% and 55% lower than those for *C. racemosa* and *C. prolifera*, respectively. For the same species I_k was only 62% and 46% of the values for the above two species. Both parameters, I_c and I_k , tended to be inversely related to the respiration rates (Table 3).

5. Discussion

The P_{\max} data for the 15 Caribbean *Caulerpa* taxa supported the functional form theory which predicts that $SA:V$ ratio and P_{\max} would decrease as morphological complexity of the thallus increases. Because the forms selected represented portions of a morphological continuum, each taxon was not expected to be statistically different from all others. However, forms near opposite ends of the $SA:V$ ratio spectrum did show significant differences in the direction predicted.

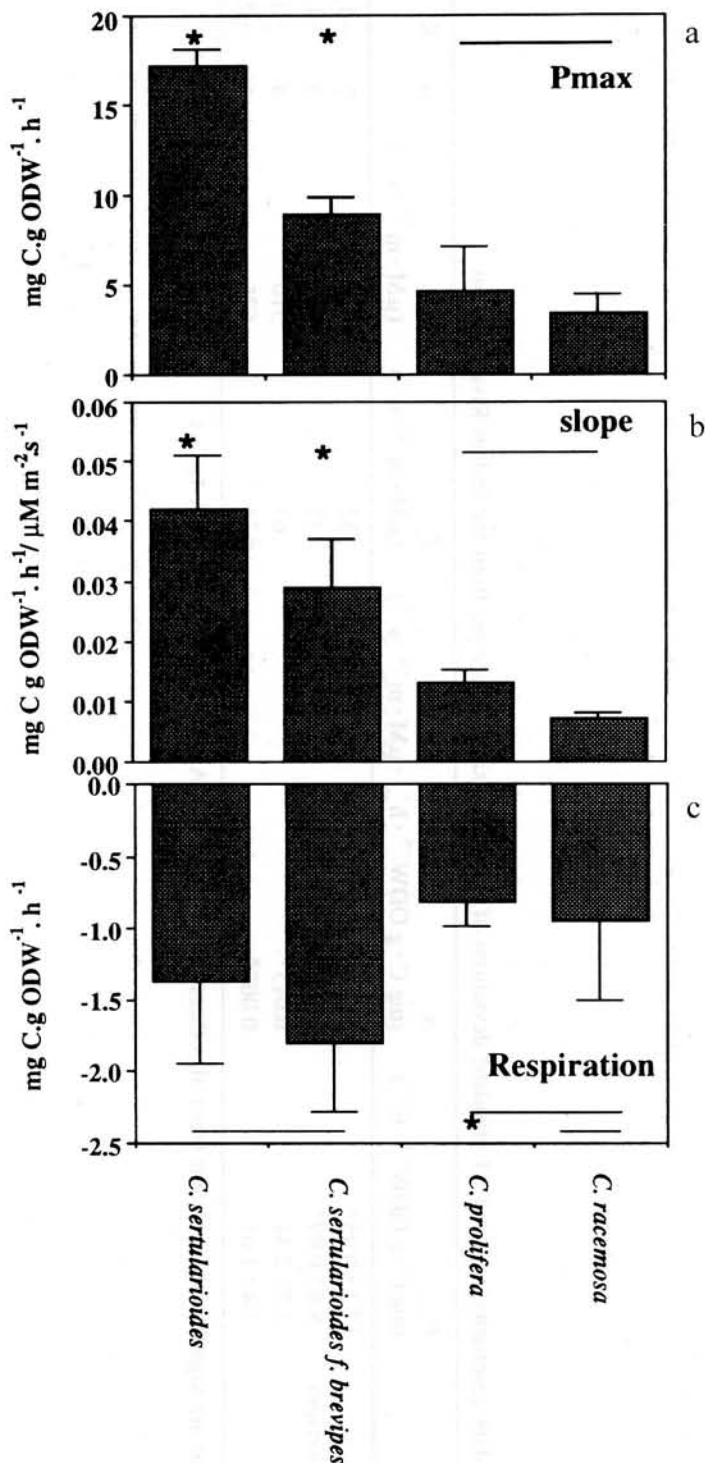


Fig. 4. (a) Maximum photosynthetic rates (P_{max}) of the four taxa studied. Asterisks indicate significant differences between groups ($P < 0.001$, ANOVA, multiple comparisons $P < 0.05$, Tuckey Test). (b) Slopes corresponding to the linear part of the photosynthesis vs. irradiance curves for the different taxa of *Caulerpa* studied. Statistical differences between regression lines were tested through a covariance analysis ($P < 0.001$, ANCOVA, multiple comparisons, $P < 0.05$, Tuckey test). (c) Respiration rates for *Caulerpa*. Asterisks indicate significant differences between groups ($P < 0.001$, ANOVA, multiple comparisons, $P < 0.005$, Tuckey Test).

Table 3
Photosynthetic and dark respiration values (± 1 standard deviation) of the four taxa of *Caulerpa* from the Indian River Lagoon

	P_{\max} (mg C · g ODW ⁻¹ · h ⁻¹)	α (mg C · g ODW ⁻¹ · h ⁻¹ · $\mu\text{M} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	I_c ($\mu\text{M} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	I_k ($\mu\text{M} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	n	R
<i>C. sertularioides</i>	17.2 ± 0.95*	0.042*	32	350	7	-1.37 ± 0.57
<i>C. sertularioides f. brevipes</i>	8.8 ± 0.99*	0.029*	37	490	3	-1.08 ± 0.48
<i>C. prolifera</i>	3.7 ± 2.41	0.013*	63	310	4	-0.82* ± 0.16
<i>C. racemosa</i>	3.4 ± 1.01	0.007*	134	675	4	-0.94 ± 0.56

* Indicate values that are significantly different from all others ($P < 0.01$, ANOVA for P_{\max} and ANCOVA for α).

Surface area: volume ratios provide an integrative measure of morphological complexity that has functional significance (see also Hanisak et al., 1988) relating the potential for the exchange of energy and nutrients of an organism. Thus, species with high $SA:V$ ratios have higher P_{\max} values due to the enhanced availability of environmentally limiting factors (e.g., light, CO_2 and nutrients) to primary production.

Among most seaweeds, net photosynthesis correlates well with $SA:V$ ratios. In agreement, the strong correlation between P_{\max} and $SA:V$ ratio (Fig. 2) was shown to be highly interrelated among diverse forms of *Caulerpa*. From these results we conclude that the functional–form model (Littler and Littler, 1980) is valid within the polymorphic genus *Caulerpa*, as well as across broad taxonomic groups.

Although the light environment is widely acknowledged as an important ecological factor in the distributions and abundances of marine algae (e.g., Ramus, 1981; Mazzella and Alberte, 1986), comprehensive information for tropical/subtropical whole plant photosynthetic parameters, such as P_{\max} , I_c , I_k , α and R , is available only for several species of Bahamian *Halimeda* (Littler et al., 1988), six species of macroalgae from the Seychelles (Littler and Littler, 1992) and five dominant macroalgae from North Inlet Estuary, South Carolina (Continho and Zingmark, 1987).

Published net photosynthetic rates (see Littler et al., 1986) for common tropical macroalgal species incubated under full ambient irradiances range from 0.3 mg C · g ODW⁻¹ · h⁻¹ for crustose forms to 13.4 mg C · g ODW⁻¹ · h⁻¹ for thin frondose forms. When focusing only on macroalgae from pristine low-nutrient systems (see Littler et al., 1988; Littler and Littler, 1990, 1992) values ranged from 0.8 to 6.4 mg C · g ODW⁻¹ · h⁻¹, with a mean of 3.15 mg C · g ODW⁻¹ · h⁻¹. Our data from the Caribbean, with a mean P_{\max} of 2.23 mg C · g ODW⁻¹ · h⁻¹ suggest that the genus *Caulerpa* in low nutrient systems produces somewhere near the lower mid-range of algal forms. Nevertheless, when considering data from the Indian River Lagoon, values ascend to a maximum of 17.2 mg C · g ODW⁻¹ · h⁻¹ which is considerably higher and agrees with the hypothesis that macroalgae from nutrient enriched waters should show higher (less nutrient limited) P_{\max} values.

We hypothesised that $SA:B$ ratio might prove to be as meaningful a morphometric parameter as $SA:V$ ratio for taxa within the same genus from the same environment, and that examination of the more detailed functional relationships of photosynthetic attributes such as α , I_k , I_c and R , in relation to morphology, would be instructive. This prompted the intensive approach using the four taxa of *Caulerpa* from the Indian River Lagoon. These results show a significant correlation between P_{\max} and $SA:B$ ratio (Fig. 5a), while P_{\max} did not correlate well with $SA:V$ ratio ($p > 0.5$). This abnormal lack of correlation could be due to the auto-shading effect of thin-overlapped branches of *C. sertularioides* var. *brevipes* which results in light being a limiting factor for productivity in this form. The thin subtropical form *C. van-bosseae* Setch. and Gardn. from the Gulf of California, when incubated in its natural clumped form, also showed (Littler and Littler, 1984) unusually low photosynthetic rates, even though it had a high $SA:V$ ratio. As pointed out by Littler and Arnold (1980), the advantages of high surface:volume ratios are negated in the clumped form by overlapping diffusion gradients and self shading.

Values of α for *Caulerpa* species from the Indian River Lagoon range between 0.007

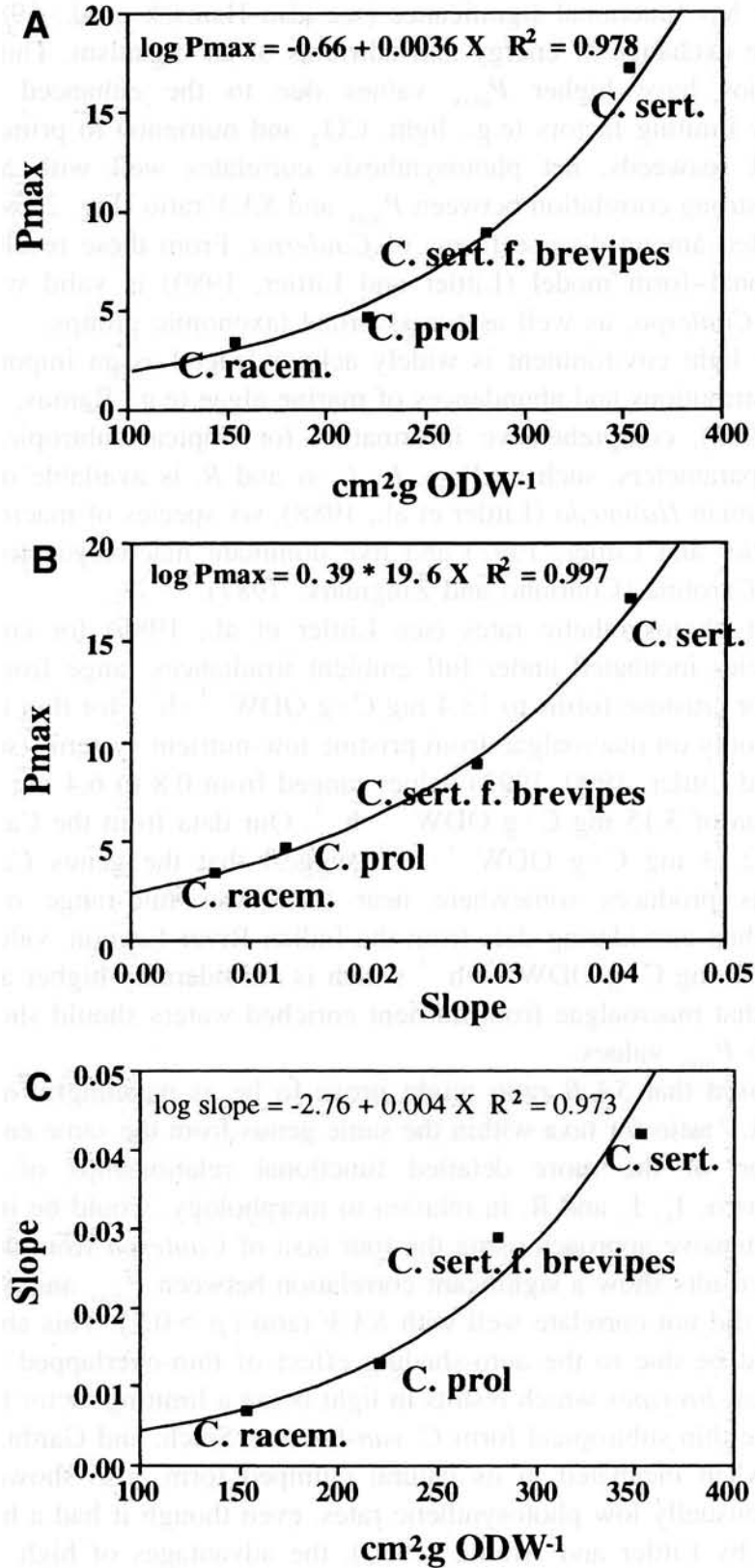


Fig. 5. (a), (b) and (c). Correlations between maximum photosynthetic rates (P_{\max}) in mg C · g ODW⁻¹ · h⁻¹ and SA:B ratios in cm² · g ODW⁻¹ of the algae, P_{\max} and initial slope of the P vs. I curve (α) in mg C · g ODW⁻¹ · h⁻¹ $\mu\text{M} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ PAR, and initial slope vs. SA:B ratios of the algae.

to $0.042 \text{ mg C} \cdot \text{g ODW}^{-1} \cdot \text{h}^{-1}$ per $\mu\text{M} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ PAR, and fall within the lower range given for five fleshy temperate Chlorophytes (Arnold and Murray, 1980); from $0.018 \text{ mg C} \cdot \text{g ODW}^{-1} \cdot \text{h}^{-1}$ per $\mu\text{M} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ PAR for optically dense *Codium fragile* to $0.129 \text{ mg C} \cdot \text{g ODW}^{-1} \cdot \text{h}^{-1}$ per $\mu\text{M} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ PAR for thin sheet-like *Ulva rigida*. Nevertheless, low α values have also been recorded for tropical and subtropical uncalcified macroalgae (Continho and Zingmark, 1987; Littler and Littler, 1992); α from 0.012 to 0.034 and 0.005 to 0.036 (assuming a DW: ODW of 10) $\text{mg C} \cdot \text{g ODW}^{-1} \cdot \text{h}^{-1}$ per $\mu\text{M} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ PAR, respectively. This suggests a common trend of low efficiency at capturing low light intensities for macroalgal species of low latitudes exposed to high irradiances, as is characteristic of sun-adapted plants (Parsons et al., 1977; Carpenter, 1985).

Maximum photosynthetic rates (P_{max}) and slopes (α) of the P vs. I curve were strongly correlated in all four taxa studied (Fig. 5b). The taxa with more efficient productivities at low light levels were also the ones that attained higher productivities (P_{max}) per unit of biomass under saturating light conditions. Both P_{max} and α decreased at similar rates correlated with increased coarseness ($< SA:B$) of the algae (Fig. 5a, 5c). Similarly, the photosynthesis vs. irradiance response for 5 species of seagrasses and 20 species of marine macroalgae showed (Enrquez, 1993) a good correlation between P_{max} and α and both parameters were also related to the $SA:B$ ratio (coarseness) of the plant. Coarseness was thought (Enrquez, 1993) to determine photosynthetic efficiency in marine macrophytes and the P_{max} correlation to coarseness was mainly explained by autocorrelation with α .

Arnold and Murray (1980) measured photosynthesis-irradiance relationships for 5 species of temperate macroalgae and found photoinhibition occur at full sunlight ($1405 \mu\text{M m}^{-2} \cdot \text{s}^{-1}$ PAR) for all of them except for thick, optically dense *Codium fragile*. None of the four *Caulerpa* species studied showed a decline in the P vs. I curve indicating photoinhibition did not occur in the brightest levels encountered, as was also the case for two sun-exposed species of *Halimeda* from the Bahamas (Littler et al., 1988). Moreover, *Caulerpa* species from the Indian River Lagoon maintained P_{max} at $2500 \mu\text{M m}^{-2} \cdot \text{s}^{-1}$. Conversely, *Caulerpa prolifera* incubated at $3000 \mu\text{M m}^{-2} \cdot \text{s}^{-1}$ was photoinhibited probably due to the combination of both higher absolute irradiance and exposure time (Belay, 1981; Pahl-Wostl and Imboden, 1990; du Preez et al., 1990). Nevertheless, some data reported on P vs. I response of *Caulerpa* species from tropical/subtropical systems differ from ours. *Caulerpa cupressoides* from Cuba was photoinhibited at $500 \mu\text{M m}^{-2} \cdot \text{s}^{-1}$ when incubated at 34°C due to the interaction of high light and unusually high temperature (Buesa, 1990). *Caulerpa racemosa* var. *uvifera* from shallow waters in Tampa Bay, showed decreased P_{max} at irradiances above $200 \mu\text{M m}^{-2} \cdot \text{s}^{-1}$ (Riechert and Dawes, 1986), probably due to several days acclimation under relatively low light conditions ($200 \mu\text{M m}^{-2} \cdot \text{s}^{-1}$). The species studied from the Indian River Lagoon are well adapted to the temperature ranges and high light intensities they encounter. Therefore, our results suggest adapting mechanisms of high light resistance for tropical macroalgae, as has been reported for algal turf and phytoplankton communities (Furnas and Mitchell, 1988; Carpenter, 1985).

Respiration rates of *Caulerpa* from the Indian River Lagoon were two to three times higher than the rates reported in the literature for other species of the same genus

(O'Neal and Prince, 1988; Terrados and Ros, 1992; Gacia et al., 1996). High respiration could be associated with high metabolism due to exposure to elevated dissolved nutrient levels characteristic of the Indian River Lagoon (Hand et al., 1988). Elevated nutrient availability could likewise explain the extremely high P_{\max} values found in species of *Caulerpa* from this location compared to the 15 Caribbean *Caulerpa* (Fig. 2).

Ranges of I_c and I_k recorded for the spectrum of *Caulerpa* forms studied (Table 3) are within the same range that others reported for subtropical and tropical species (I_c from 12 to 207 $\mu\text{M} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ PAR, I_k 100 to 866 $\mu\text{M} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ PAR; Continho and Zingmark, 1987; Buesa, 1990; Littler and Littler, 1992), but are higher than those of Arnold and Murray (1980) for 5 temperate zone macroalga species from California (I_c from 6.11 to 11.4 $\mu\text{M} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ PAR, I_k from 100 to 866 $\mu\text{M} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ PAR). Low

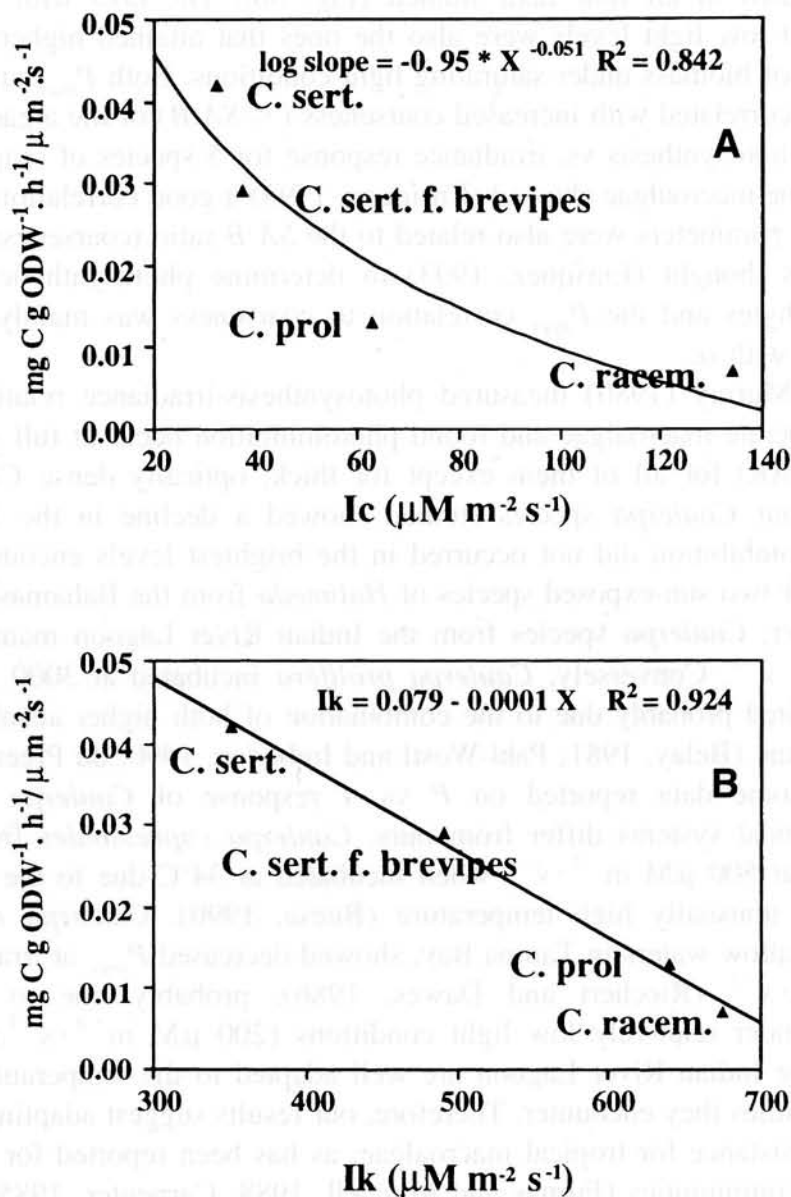


Fig. 6. (a) and (b). Correlations between slope of the P vs. I curve (α), compensation irradiance (I_c) and saturation irradiance (I_k).

saturation irradiances (I_k) were correlated with low light requirements for photosynthetic compensation (I_c) and reasonably efficient use of low photon flux densities as indicated by the steep slopes (α) of the P vs. I curves (see also Fig. 6a, 6b). This is probably due to the increase in the basal metabolism necessary to sustain a more active photosynthetic rate at low light levels (Enríquez, 1993). Finally, these results characterise shallow-water tropical/subtropical *Caulerpa* populations as mostly sun-adapted plants (Parsons et al., 1977) with high saturation and compensation irradiances, low efficiencies for capturing low photon flux densities and high resistance to exposure to elevated light irradiances.

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