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Morphological Plasticity of *Caulerpa prolifera* (Caulerpales, Chlorophyta) in Relation to Growth Form in a Coral Reef Lagoon

L. Collado-Vides

Lab. Ficología, Facultad de Ciencias, Universidad Nacional Autónoma de México, A. P. 70-620, Coyoacán,
D. F. 04510 Mexico, lcv@hp.fciencias.unam.mx

Caulerpa, a coenocytic marine macroalgae, is a genus characterized by having a prostrate indeterminate axis (stolon) with rhizoids and vertical axes that are potentially independent units as *Caulerpa* can withstand fragmentation and regenerate after a lamina or stolon are cut. This is similar to clonal growth described for vascular plants. A morphometric study was conducted comparing two morphologically distinct populations of *Caulerpa prolifera* growing in contrasting light environments of a coral reef lagoon. Morphometric measurements and dry weight partitioning were analyzed. Results of this study show that significant morphological differences exist. In a shaded environment *C. prolifera* had a higher dry weight (mg/cm^2) than in sunny areas, distance between ramets was longer in shade areas, resulting in an open growth similar to the 'Guerrilla' growth form compared to the 'Phalanx' growth form of sunny sites. In shaded areas the population had fewer lamina per ramet and longer stipes. Morphological differences were analyzed in relation to light intensity. Compact growth, highly branched and thick, small laminas are morphological traits associated with plants in bright habitats. In contrast, thin and longer laminas are more efficient in the capture of light and typify shaded populations. Differences were found at all three levels: clonal fragment, ramets and modules. This suggests that *C. prolifera* has a clonal plant morphology and behavior.

Introduction

Modular plants grow by the iteration of units of construction called modules (White 1979, 1984). Clonal plants are modularly constructed and grow by the production of rhizomes, stolons, or adventitious structures. Due to their extensive lateral growth, clonal plants often experience spatial variation in different environmental conditions (Cain 1994). As the availability of resources is patchy both in space and time, the difficulty in obtaining sufficient resources varies spatially and temporally. In response to changing resource availability, morphological plasticity can lead to different patterns of spacer (internode) production and hence different patterns in the placement of resource acquiring structures and changes in the aspect of the plant.

Clonal plants produce a series of interconnected ramets, each of which occupies a different site (Bell 1984, Sutherland and Stillman 1988). The ability of the plant to modify ramet morphology in response to local environmental conditions will influence its ability to colonize a heterogeneous area (Hutching 1988, de Kroon and Knops 1990) and thus will influence the range of habitats that the species can invade.

Studies show that some clonal plants decrease rhizome or stolon internode lengths and/or increase the frequency of branching in favorable environments (Ashmun and Pitelka 1984, Schmid 1986, Mitchell and Woodward 1988, de Kroon and Knops 1990, Alpert 1991, Marba and Duarte 1998, Collado-Vides and Robledo 1999). These changes in morphology, in clonal plants, have been interpreted in relation to the availability of resources. In this sense, two different growth forms have been described for clonal plants: the 'Guerrilla' or diffuse growth which allows plants to invade new spaces is characterized by plants with a long stolon and less branched ramets, and the 'Phalanx' or compact growth form which is characterized by short and very branched stolons and highly branched ramets. This dichotomy tends to focus on a few closely related selective factors that affect genet proliferation and spread, and competitive ability (Lovett-Doust 1981, Grace 1993).

The genus *Caulerpa* Lamouroux (1809) is widely distributed throughout tropical and subtropical seas (Taylor 1960, Lüning 1990, Suárez *et al.* 1996). The genus is composed of many diverse forms, with the same basic morphological scheme common to all species (Fritsch 1935). It has a prostrate indeterminate axis (stolon) with rhizoids below, and upright axes (laminas or assimilators) that are potentially independent units, as the whole plant can regenerate after a lamina or stolon is cut (Jacobs 1993, 1994). This type of growth form is similar to clonal growth as described by Harper and Bell (1979) for vascular plants. In this analogy, the whole alga is a genet, each independent axis with several ramets is a clonal fragment, and ramets are potentially independent units composed by laminas (modules) stipe and rhizoid cluster, which are the smallest units of a genet that may achieve physiological independence.

The genus *Caulerpa* is characterized by extreme morphological variation. Svedelius (1906) and Boergesen (1907) mentioned that factors such as light intensity and degree of water movement possibly influenced morphology in *Caulerpa*. Barilotti (1970) demonstrated that the morphology of *Caulerpa prolifera* (Førsskål) Lamouroux is influenced by light intensity. Also Meinesz (1979a, c), reported morphological variation of *C. prolifera* in relation to season and the ability to regenerate the population by vegetative propagation. Peterson (1972) showed that *Caulerpa racemosa* (Førsskål) J. Agardh, has the ability to change its growth form in different light environments, providing evidence for an environmental rather than genetic control of the wide morphological variation present in this species. In a study of the morphological responses to reduced illumination Calvert (1976) reported interesting morphological modification in response to high or low light intensity in several species of *Caulerpa*. He demonstrated that the radial forms of shallow waters can modify their pattern to a bilateral one in deeper waters. So morphological plasticity has been shown to be environmentally regulated for several species of *Caulerpa*.

Seven species of the genus *Caulerpa* have been recorded from Puerto Morelos reef (Collado-Vides and Robledo 1999). *Caulerpa prolifera* grows in the lagoon, either intermixed with seagrass *Thalassia testudinum* Banks *ex* König or in open patches. As in other clonal plants and in other populations of *Caulerpa prolifera* from the Mediterranean Sea (Meinesz, 1979a, c), differences in internode length, lamina number and lamina size were observed between populations at the study site.

In this study the degree of morphological plasticity between populations in different environments is evaluated. The pattern of this variation in relation to their growth form is described and discussed.

Material and Methods

Study area

Puerto Morelos is part of an extensive reef formation and is located at 20°48' N latitude and 86°52' W longitude on the northeastern Yucatan Peninsula.

Selection of sites

Caulerpa prolifera grows in the reef lagoon, mainly in shallow water with a sandy substrata, either intermixed with the seagrass *Thalassia testudinum* or in open habitats. The general morphology was observed to differ in shaded areas with deeper waters and when intermixed with seagrasses and in sun-exposed shallow waters. Two sites were selected for the study, both in the reef lagoon. One population was in a sun exposed area with a mixture of sandy and cobble substrate at a depth of 0.50 m and exposed to moderate wave action. A second population was in a shaded area within a *Thalassia testudinum* bed with a sandy substratum at 1.50 m depth and low water movement.

The light regime at both sites was recorded. Over a 12 h cycle, light readings were taken simultaneously with two light sensors (PAR, 4π attached to a LiCor 1000 Data Logger, LiCor Inc., Nebraska, USA). Each sensor was fixed within the algal bed to read PAR at the lamina level.

Morphometrics

At each site five quadrat samples (5 x 5 cm) were taken. All *Caulerpa prolifera* inside each quadrat was collected. Special care was taken to collect the whole clonal fragment including all ramets. The material was cleaned of epiphytes and kept in humid conditions.

The following morphometric measures were made (Fig. 1): the distance between consecutive ramets (internode length); the distance between each cluster of laminas in the same stolon. [Because the smallest unit that can be physiologically independent was not known, the term ramet is used in this study as the cluster of laminas growing from a stolon including a cluster of rhizoids (Fig. 1).]; number of lamina per ramet, lamina length, stipe length and lamina thickness.

A photocopy of the fresh material was made and scanned. Automatic calculations for surface area were made using the software for image analysis (SigmaScanPro 4.0, Jandel Scientific Software, San Rafael, CA, USA). Area, as the projected area, was calculated as the number of pixels defining each object and calibrated to cm^2. Shape Factor as 4π * area/Perimeter^2, calculates how circular the object is.

After all morphometric measures were made, the material was separated into parts (lamina, stipe, stolon, and rhizoid). The rhizoids were immersed in a 5 % solution of phosphoric acid to remove the sand. Then all parts were dried (10 h at 60 °C). The dry weights of all parts were determined. Based on growth analysis

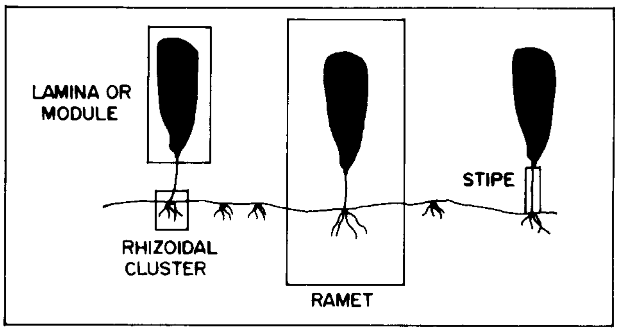

Fig. 1. Schematic representation of the clonal parts of a clonal fragment showing the module or lamina, ramet, stipe and rhizoidal cluster.

(Pearcy *et al.* 1989), the following morphological parameters were calculated:

1. Total dry weight per quadrat: All algal material in each quadrat.
2. Lamina dry weight: Dry weight of individual laminas.
3. Total lamina dry weight: The dry weight of all the laminas in each quadrat.
4. Total stipe dry weight: The dry weight of all the stipes in each quadrat.
5. Total rhizoid dry weight: The dry weight of all the rhizoids in each quadrat.

From those calculations the following parameters were obtained:

1. Lamina weight ratio (BWR): lamina dry weight/ total of all parts dry weight.
2. Specific lamina area (SLA): lamina surface area/ lamina dry weight.
3. Stipe weight ratio (SWR): stipe dry weight/total of all parts dry weight.
4. Rhizoid weight ratio (RWR): rhizoid dry weight/ total of all parts dry weight.
5. Photosynthetic weight (PW): lamina and stipe dry weight.
6. Photosynthetic/Non photosynthetic weight ratio (PNPWR): lamina and stipe dry weight/rhizoid dry weight.

Statistical analyses were performed to evaluate the differences in values between sample sites. One-way ANOVA tests were used to compare the populations.

Results

The light regimes of the two environments studied were significantly different, ($p < 0.049$) (Fig. 2). The sunny site had a mean of 751 µmol quanta m^2/s (s. e. 99, max 2346, min 0) and the shady site of 512 µmol quanta m^2/s (s. e. 66, max 1540, min 0).

Morphological differences were found between populations living in open shallow sunny areas, and deeper, shade environments amid seagrass beds.

The clonal fragment and ramet level

Caulerpa prolifera grows from a running stolon and rhizoid clusters, either attached to rocks or anchored in sand. From the upright stipes, erect laminas with different levels of branching arise (Fig. 1).

Significant morphological differences were found between populations. In shaded areas *C. prolifera* was found to have a higher dry weight per unit area than in sun exposed areas. Nevertheless the distance between consecutive ramets along the stolon (internode length) was longer in the shade environment, suggesting a less compact growth form from that shown by populations in sunny areas. Hence greater dry weight per unit area characterized the population in the shade environment, while the growth form was more compact in the sunny area populations. The shaded area population had fewer laminas per ramet and longer stipes than that found in the sunny population (Table I).

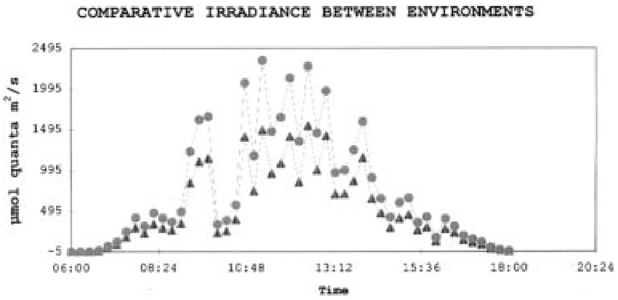

Fig. 2. Comparative irradiance between sites ● = light, ▲ = shade. A 12 h cycle of data collection of photosynthetic active radiation (PAR) measured with a 4π sensor attached to a LiCor Data Logger.

Table I. Morphometric parameters of the habit of *C. prolifera*, and statistical analysis.

	Density	D/RAM.	Blade #	ST. L	ST. W	RH. W.	BL. W.	Total
Light								
Mean	0.0368	2.4591	2.6214	6.2315	0.2408	0.0146	0.2966	0.5522
S. E.	0.00681	0.1622	0.1474	1.0181	0.04122	0.00351	0.06132	0.10222
S. D.	0.01523	1.5215	1.4959	9.9233	0.09217	0.00786	0.13713	0.22857
Shade								
Mean	0.09548	3.8703	1.9091	11.407	0.4984	0.027	0.9068	1.4322
S. E.	0.01334	0.3196	0.1652	0.6906	0.10517	0.01197	0.11629	0.20009
S. D.	0.02982	1.9441	1.0958	8.4868	0.23516	0.02676	0.26003	0.44742
$P < 0.05$	0.00400	0.0001	0.005	0.000	0.05203	0.34938	0.002	0.00443
F	15.34500	18.906	8.100	19.864	5.20000	0.98800	21.542	15.345

ANOVA $P < 0.05$. Density = dry weight/quadrat area (5 × 5 cm.). D/RAM = distance between ramets. Blade # = number of blades per ramet. ST. L = stipe length. ST. W = stipe dry weight. RH. W. = rhizoid dry weight. BL. W. = blade dry weight. Total = total biomass.

Table II. Morphometric parameters of blades and statistical analysis.

	Thickness	Length	Weight	Area	SLA	Shape
Light						
Mean	0.4029	2.5284	0.018	2.3654	128.87	0.6051
S. E.	0.0084	0.1310	0.0011	0.1723	5.1569	0.0141
S. D.	0.0819	1.2770	0.0115	1.6798	50.264	0.1416
Shade						
Mean	0.24423	4.26688	0.03169	3.96811	179.064	0.50909
S. E.	0.01220	0.16063	0.00219	0.18108	21.5323	0.01039
S. D.	0.15001	1.97395	0.02693	2.22518	264.593	0.12773
$p < 0.05$	0.0001	0.0001	0.0001	0.0001	0.025	0.0001
F	91.848	55.564	20.702	42.315	8.442	31.205

ANOVA $p < 0.05$. Thickness = blade thickness in mm. Length = blade length in cm. Weight = blade dry weight in g. Area = projected area in cm^2, SLA = specific lamina (blade) area: blade area/blade weight (cm^2/g). Shape = shape factor.

The growth form of the shade population is more open, with long stipes that carry the laminas above the understory, avoiding shading by the seagrass canopy. The sunny population is characterized by a compact growth, with short stipes and a large number of laminas potentially resulting in selfshading.

Lamina morphometrics or the module level

As at the ramet and clonal levels, significant morphological differences were found in laminas from both sites (Table II). Smaller, thicker laminas were characteristic of the light environment, these laminas had a lower individual surface area (Table II). The greater weight of shade laminas is due to their larger size, but the SLA indicates smaller values in the light population (Table II). An interesting morphological change is related to lamina shape. Laminas from the shade habitat were elongated (Fig. 3, Shape factor of 5 ± 0.14), but in the high light population the laminas become smaller, shorter and wider (shape factor of 6 ± 0.12). This results in a reduction of surface area (Fig. 3).

Thin, regular shaped and long laminas from long stipes are characteristics of populations in shade environments. In contrast, thick, irregularly shaped and short laminas from short stipes are characteristics of populations in sunny environments.

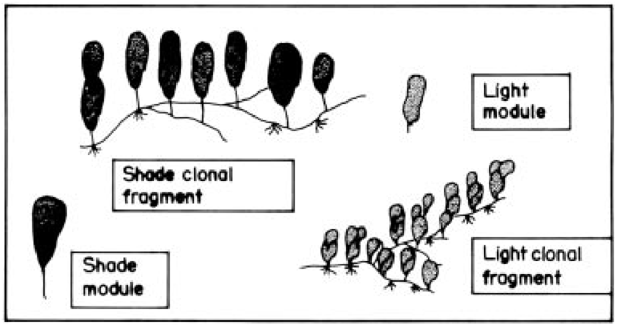

Fig. 3. Schematic representation of clonal fragments of *Caulerpa prolifera* showing differences between shade and sunny clonal fragments.

Dry weight partitioning

Photosynthetic tissue weight (the sum of lamina and stipe dry weight) and stipe weight ratio were significantly different between the two populations (Table III). This suggests that the distribution of dry weight between lamina, stipe and rhizoids differs between the populations compared. Shade populations invest more in photosynthetic area.

Discussion and Conclusion

The capacity to change size, form, and physiological behavior is an essential feature of living organisms, and variation is well known in plants. This is the way organisms acclimate and/or adapt to different environmental conditions and, hence, amplify their distribution or avoid competition by diversification. This capacity of change in clonal plants has been widely described (Slade and Hutchings 1987a, b, de Kroon and Schieving 1990, Hutching and Mogie 1990). Decreased rhizome or stolon internode length and/or increased clonal branching in response to favorable environments is thought to be beneficial, since it should allow resource acquiring parts of plants to become concentrated in the most rewarding areas of habitat, maximizing their acquisition of resources (Hutchings and Mogie 1990).

The results of this study show that morphological plasticity exists in *Caulerpa prolifera*. The distance between consecutive ramets and the branching pattern varies between sun-exposed and shade environments, as demonstrated by the morphometric study (Tables I and II). A longer distance between consecutive ramets is found in shade environments combined with low lamina branching. Total dry weight is higher

Table III. Dry weight partitioning and statistical analysis.

	BWR	SWR	RWR	PW	PNPWR
Light					
Mean	0.53442	0.43898	0.02658	0.5374	41.8522
S. E.	0.02393	0.02134	0.00556	0.10041	6.43566
S. D.	0.05351	0.04772	0.01244	0.22452	14.3905
Shade					
Mean	0.64407	0.33831	0.01761	1.4052	87.6907
S. E.	0.04181	0.03673	0.00697	0.19528	23.6683
S. D.	0.09348	0.08213	0.01559	0.43667	52.9240
$p < 0.05$	0.052	0.045	0.344	0.004	0.099
F	5.18	5.616	1.011	15.617	3.493

ANOVA $p < 0.05$. BWR = blade weight ratio (blade weight/total weight). SWR = stipe weight ratio (stipe weight/total weight). RWR = rhizoid weight ratio (rhizoid weight/total weight). PW = photosynthetic weight (blade + stipe weight). PNPWR = photosynthetic-non photosynthetic weight ratio (PW/rhizoid weight).

in populations of shady versus populations of sunny environments where the distance between consecutive ramets is shorter and lamina branching is higher. This morphological contrast is similar to the 'Guerrilla' and 'Phalanx' growth forms described for vascular plants (Lovett-Doust 1981, Grace 1993).

The morphological plasticity found in the populations compared can be discussed in the context of availability of light because significant differences were found in this abiotic parameter. In the shade population, increasing distance between consecutive ramets allows *Caulerpa prolifera* to grow into clearings between the shoots of *Thalassia testudinum*. In the open-sun population, a decrease in the distance between consecutive ramets and an increase in lamina branching results in a compact growth form where potentially selfshading occurs. Stipes are shorter, laminas are thicker and irregular in shape decreasing SLA exposed to light. These observations are consistent with other morphological modifications reported for different species of *Caulerpa*. Molinier (1953) distinguished 3 morphological categories for *Caulerpa prolifera*, where small lamina are found in shallow waters, similar observations were made by Meinesz (1979a, b) where long lamina were found in deeper waters but also in shallow waters growing under a rock or covered by seagrasses.

These contrasting characteristics have been observed in vascular plants grown either in shade or high light environments. High light causes a stronger development of the palisade and spongy mesophyll regions, resulting in thicker leaves (Boardman 1977). In marine environments, the relationship between morphology and light capture or selfshading has been discussed in the context of the ecological significance of the variation by analyzing tradeoffs among different morphs (Littler and Littler 1980). In the Caribbean Sea several studies have shown that the turf type of growth is a form affording protection against an excess of light as it results in selfshading (Hay 1981, 1986, Beach and Smith 1996). It is suggested here that in the case of *Caulerpa prolifera*, the compact or 'Phalanx' growth form, of the open sun population, potentially affords selfshading. In contrast shade populations show an open or 'Guerrilla' type of growth form which potentially avoids selfshading. This has been observed by Peterson (1972) in his experiments on the effect of light variation on the growth of *Caulerpa racemosa*. He found that the number of ramuli per mm of assimilator increased, and the length of the assimilator decreased in higher light intensities, resulting in a crowding of the growth form which is consistent with the general observations analyzed above.

Although we did not measure water velocities, during the field work it was clearly more difficult to work in the shallow open sunny area because water movement was stronger than in the *Thalassia testudinum* beds. In this regard the shorter distance between consecutive ramets, more branched ramets and shorter laminas observed in the sunny shallow sites compared with the open or 'Guerrilla' growth form of shade sites might also be related to hydrodynamic conditions, as turf forming algae can reduce water velocities (Hurd and Stevens 1997). Morphological characteristics, such as frond size, have been shown to affect dislodgment and survival in high turbulence environments, such as the intertidal zone (Carrington 1990). This means that more than one parameter (light) may be causing the morphological plasticity found in this study. Nevertheless it is noteworthy that morphological plasticity is coherently found at all clonal plant levels and follows a pattern of 'Guerrilla' growth form at the shaded deeper environment compared to the 'Phalanx' growth form at the sunny shallow one.

Marine algae have a modular construction, and many of them also show the clonal type of growth, and their emergent properties analyzed in vascular plants can also be found in algae (Collado-Vides 1997). Perennation by basal systems, dispersal by fragmentation and other mechanisms resulting from clonal architecture are widely present among the species of the genus *Caulerpa*. Meinesz (1979a, c) described in great detail the clonal type of growth of *Caulerpa prolifera* making clear that fragmentation is the main, if not only, way of growth of the population where the basal system (stolon) by a sequence of events regenerates a new, vegetatively produced, population. The morphological plasticity allows this species to live in different light environments by acclimation to each light regime. Sexual reproduction in *C. prolifera* has been observed several times (Dostal 1928), Schussing (1929), but in the occidental basin of the Mediterranean Sea it is imperfect and only vegetative growth is successful and affords the growth and maintenance of the population (Meinesz 1979b). Based on vegetative growth, renovation of the total thalli during an annual year period by the progressive growth from the apical stolon, and by the senescence of distal parts, Meinez (1979a) classifies *Caulerpa prolifera* as a pseudo-perannial plant. This combination of morphological and reproductive traits is widespread in clonal plants and is part of their success in nature (Cook 1983). It is suggested that an understanding of the ecological and evolutionary consequences of being clonal (Schmid 1990) should be included in the study of the biology, ecology and evolution of the species of the genus *Caulerpa*.

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