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A comparison of nutrient- and light-limited photosynthesis in psammophytic versus epilithic forms of *Halimeda* (Caulerpales, Halimedaceae) from the Bahamas

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Abstract. The relative nutritional status, with respect to phosphorus (P_i) vs. nitrogen (N) limitation, and light-limited photosynthesis (P_s) was examined over a broad range of quantum fluxes (I) for four *Halimeda* species, *Halimeda tuna* (Ellis and Solander) Lamouroux, *H. simulans* Howe, *H. lacrimosa* Howe and *H. copiosa* Goreau and Graham, taken from clear, shallow, Bahamian waters. The results support the hypothesis that psammophytic forms (i.e., sand dwellers anchored by a bulbous rhizoidal system) differ in nutrient status from epilithic forms (i.e., attached to rock by inconspicuous rhizoids). Maximum photosynthetic rates (P_{max}) for the epilithic species *H. lacrimos* and *H. copiosa* decreased ($P<0.05$) following P_i enrichment, but increased ($P<0.05$) following N pulses. Conversely, following brief exposures to P_i, P_{max} in the sand-dwelling forms *H. tuna* and *H. simulans* was elevated ($P<0.05$). These findings suggest that shallow species of *Halimeda* are adapted to take advantage of episodic nutrient pulses, and that partitioning of limiting resources may occur between the various life forms. Shallow water *Halimeda* species appear well adapted to variable light regimes, including low light conditions. In all cases, light-saturated photosyntheses (I_k) occurred at irradiances much lower than the ambient levels available on typical sunny days. Associated with low saturation irradiances were low light requirements for photosynthetic compensation (I_c) and reasonably efficient use of low photon flux densities as indicated by relatively steep slopes (α) of the P_s vs. I curves. Of the four species, *H. copiosa* was the most shade adapted, with considerably higher α values and considerably lower I_c, I_k and photoinhibition values.

Introduction

Members of the green algal genus *Halimeda* (Caulerpales, Halimedaceae) are recognized (e.g., Ginsburg 1956; Milliman 1974; Hillis-Colinvaux 1980, 1986) as major elements of both tropical Atlantic and Pacific reefs. This calcareous genus contains some of the deepest living frondose algae (Hillis-Colinvaux 1977, 1986; Littler et al. 1985, 1986a), often dominating communities on deep reef slopes, such as the zone of *Halimeda* spp. from 90 to 130 m deep for a Bahamian Seamount (Littler et al. 1986a).

In contrast with deep-water *Halimeda* species, other species are abundant on protected back-reef and fore-reef habitats, occurring over a broad depth range on both hard and soft substrata. Some psammophytic (sand-dwelling) forms are associated with shallow seagrasses and mangroves. Natural *Halimeda* populations of 100 plants $\cdot m^{-2}$ are common (Hillis-Colinvaux 1980), and densities up to 500 $\cdot m^{-2}$ are found on some reefs. Recently, immense bank-like mounds composed of living *Halimeda* species and their sediments (dating to 5000 yrs ago) have been discovered (Davies and Marshall 1985). The importance of *Halimeda* as a reef-forming organism was well reviewed over 80 yrs ago (Chapman and Mawson 1906), but has been largely overlooked.

Reefs with large standing stocks of macroalgae usually receive elevated nutrient supplies (Adey et al. 1977), an observation consistent with the idea that growth rates of reef macroalgae may often be nutrient limited. However, the question of which macronutrient element – N, P_i or their interactions – might limit macroalgal productivity in reef ecosystems has seldom been addressed experimentally. Traditionally, N is considered the primary limiting nutrient in tropical marine waters (e.g., Parsons et al. 1977), although recent evidence from geochemical models (Broecker and Peng 1982; Smith 1984) and in situ macroalgal bioassays (Lapointe 1985, 1987) suggests that P_i may be the more important growth-limiting nutrient in carbonate-rich tropical marine waters. A knowledge of photosynthetic responses to P_i and N by species of an abundant calcifier such as *Halimeda* could prove useful to clarify current uncertainties (e.g., see Smith 1984) about the importance of N vs. P_i limitation to algal growth in tropical marine environments.

Two major form-groups exist in the genus *Halimeda,* psammophytic forms that have well-developed, bulbous, rhizome systems, and epilithic forms which have only limited rhizoidal attachment structures. Based upon this morphological divergence in the genus, and the influence of morphology on nutrient-uptake, we hypothesized that different nutrient-related responses may have evolved within this genus. To begin to understand the comparative physiological ecology of this important worldwide reef alga, we examined the relative nutritional status (N vs. P_i limitation) for two psammophytic and two epilithic *Halimeda* species. These studies were conducted with manipulations of ambient light levels to test the role of light as an interacting factor with nutrient limitation.

The following specific questions were addressed:

Do psammophytic forms differ in their relative levels of nutrient limitation from species restricted to hard substrata?

Is there interaction between nutrients and irradiance in the photosynthetic responses of different *Halimeda* species?

Do dark respiration rates (R) and photosynthetic rates at light saturation (P_{max}) vary among various *Halimeda* species?

Do shallow-water populations of *Halimeda* species differ in their light-limited photosynthetic characteristics (α, I_c, I_k)?

Materials and methods

This investigation was performed from the research vessel R/V *Columbus Iselin* during an expedition throughout the Bahamas from 8 to 27 August 1986. The specific study sites included Anguilla Island, Cay Sal Banks, Bahamas (23°29.0′ N, 79°29.0′ W) where the epilithic form *Halimeda lacrimosa* Howe was collected on 9 August 1986 from 3 to 4 m deep, growing in unshaded locales on carbonate reef rock. The psammophytic form *H. simulans* Howe was sampled on 10 August 1986 from Elbow Island, Cay Sal Banks, Bahamas (23°57.5′ N, 80°29.0′ W) at a depth of 5 m in unshaded sand pockets. On 11 August 1986, the psammophytic form *H. tuna* (Ellis and Solander) Lamouroux was obtained from the same locale in 7 m of water anchored in carbonate sediments. *Halimeda copiosa* Goreau and Graham (epilithic) was collected on 14 August 1986 from near Staniard Rock off Andros Island, Bahamas (24°51.7′ N, 77°52.3′ W) at a depth of 7 m on dead carbonate reef rock. The *H. copiosa* came from cryptic shaded habitats beneath overhanging ledges and is the only species examined that was collected from a shaded environment. The specimens were held overnight in a metal-free, continuous-flow, seawater system aboard ship under shaded conditions. Voucher materials of all species were preserved in 4% buffered Formalin and deposited in the Algal Collection, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

On the day prior to photosynthetic assays (i.e., the day of collection), the macroalgae were transported to the R/V *Columbus Iselin* where they were cleaned of sediments and epiphytes. Subsequently, replicate whole plants of each alga were soaked in one of three treatments, a factorial design enrichment of N ($NaNO_3$) and P_i (NaH_2PO_4), that consisted of either $+N$, $+P_i$, $+N+P_i$ or a control (no enrichment). Initial concentrations of N and P_i in the enrichment were 160 and 16 μM, respectively. The concentrations used were chosen to saturate the uptake rates and represent the upper range of natural levels encountered in highly enriched environments (e.g., bird islands). Following the overnight (12 h) enrichment, the algae were flushed with 3 changes of fresh seawater 4 h prior to incubation under shaded conditions (50% I_0). Although this enrichment method is based on concepts developed by Smith (1983) for freshwater algae, it has been field tested previously (Lapointe 1987; Lapointe et al. 1987) as a macroalgal photosynthetic bioassay, and the results indicated close correlation with longer-term growth responses.

For all productivity (photosynthesis) measurements that followed the 12-h nutrient enrichment period, four to six replicate incubations per treatment were run. Experimental levels of 6 irradiances and 4 nutrient-pulsed conditions were set up simultaneously in a 6×4 factorial design (total of 96 to 144 samples·species^{-1}) at ambient water temperatures (27.5–28.4 °C) and run between 1000 and 1530 hours with a natural photon-flux density of 1600 ± 92 (Mean ± 1 S.D.) $\mu E \cdot m^{-2} \cdot s^{-1}$ of photosynthetically active radiation (PAR), ranging from a minimum of 1480 to a maximum of 1733 $\mu E \cdot m^{-2} \cdot s^{-1}$. Different layers of neutral density screening were used to produce five experimental light levels (in approximate percent of ambient sunlight): 100.0%, 50.0%, 12.5%, 3.2% and 0.8%. Photon-flux densities were measured in the field with an integrating 2π sensor (Li Cor Model LI-550 printing integrator) throughout the incubation periods. Two layers of heavy duty aluminum foil were wrapped around each respiration bottle to exclude light. Incubations were conducted in one liter glass jars that received continuous cooling and stirring via water-driven magnetic turbines. Dissolved oxygen was measured to 0.01 mg·l^{-1} with an Orbisphere Model 2610 oxygen analyzer and converted to carbon fixed utilizing respiratory and photosynthetic quotients of 1.00 to facilitate comparisons with other studies. Photosynthesis and respiration were normalized to organic dry weight, which was determined by drying the samples to constant weight at 80 °C and ashing them to constant weight at 500 °C. The methods concerning selection of material, handling, incubation and oxygen analysis were within the limits recommended by Littler (1979).

Photosynthetic light saturation values (I_k) were obtained for each species at each nutrient level by determining the intersection of a line drawn parallel to the abscissa and through the point of maximum photosynthesis (P_{max}) with the slope of the light-limited P_s vs. I curve (α). The initial slope (α) of each P_s vs. I curve was determined from the least squares linear regression of all productivity values obtained for the linear portion of the curve (i.e., below 12.7 to 50.8 $\mu E \cdot m^{-2} \cdot s^{-1}$) including dark respiration (8–18 data points). Compensation irradiances (I_c) were calculated as the intersection of the regression line of the initial P_s vs. I response with the abscissa.

P_{max} values used for statistical comparisons represented the mean of the six greatest photosynthetic rates obtained in a particular P_s vs. I curve (total of no less than 24 bottles). Nitrogen and P_i enrichment effects on P_{max} were assessed by two-way ANOVA. Significance reported in the results below implies that the probability of the null hypothesis was <0.05.

Results

It is interesting that among the effects of nutrient enrichment (Table 1), trends were exhibited by the four *Halimeda* species that varied according to both life form and species. For those possessing an extensive, bulbous, rhizoidal, root-like system (*H. tuna* and *H. simulans,* Figs. 1 and 2), P_i pulses had significant enhancement effects ($P<0.05$, two-way ANOVA) on both net P_{max} and R (Table 1). No significant responses ($P>0.05$) in P_{max} or R were shown by either of these two psammophytes following N pulses. Phosphorus and N combined stimulated net P_{max} and R for *H. tuna* and R for *H. simulans* ($P<0.05$).

In contrast, P_i pulses inhibited net P_{max} ($P<0.05$, Table 1) for the rock growers *Halimeda lacrimosa* and *H. copiosa.* Phosphorus in combination with N also inhibited P_{max} in *H. lacrimosa.* Pulses of N had a significant enhancement effect ($P<0.05$) on P_{max} in *H. lacrimosa,* and greatly stimulated (significant at $P<0.05$) both P_{max}

Table 1. Photosynthetic and dark respiratory characteristics (±1 standard deviation) of the four *Halimeda* species in relation to various nutrient conditions (α = mg C · g^{-1} organic dry weight (ODW) · h^{-1}/μE · m^{-2} · s^{-1}). Asterisks indicate values that are significantly different (* = $P<0.05$, ** = $P<0.01$, *** = $P<0.001$, two-way ANOVA) from the controls

Species and treatment	P_{max}	R	α	I_c	I_k
	(mg C · g ODW^{-1} · h^{-1})			(μE · m^{-2} · s^{-1})	
Psammophytic forms					
Halimeda tuna					
Control	3.90±0.53	−0.35±0.02	0.075	4.8±0.6	60.2±11.0
+Nitrogen	4.42±0.81	−0.23±0.10	0.048**	5.0±1.7	84.0±11.6*
+Phosphorus	5.28±1.30*	−0.52±0.11*	0.054*	9.3±2.2**	96.8±10.5***
+Both	6.08±1.58**	−0.65±0.25*	0.052	12.4±3.7*	102.9±72.4
Halimeda simulans					
Control	2.47±0.70	−0.42±0.08	0.089	4.7±1.3	25.5± 2.1
+Nitrogen	2.84±0.57	−0.49±0.05	0.065**	7.8±0.8**	42.1± 7.1**
+Phosphorus	3.34±0.99*	−0.63±0.04**	0.064***	12.5±4.4**	57.6± 4.8***
+Both	2.46±0.64	−0.60±0.04**	0.051***	12.2±2.6**	79.2±19.8**
Epilithic forms					
Halimeda lacrimosa					
Control	3.17±0.22	−0.86±0.17	0.123	7.1±1.3	32.5± 5.8
+Nitrogen	3.52±0.29*	−0.78±0.16	0.094	8.3±0.4	47.0±13.6
+Phosphorus	2.19±0.37***	−0.74±0.08	0.074**	9.9±0.9*	23.9± 2.3*
+Both	1.95±0.41***	−0.48±0.13*	0.085*	5.7±1.1	22.5± 3.6*
Halimeda copiosa					
Control	3.89±0.58	−0.22±0.12	0.161	1.8±0.7	19.9± 7.3
+Nitrogen	6.49±1.62**	−0.90±0.03***	0.334***	2.8±0.3**	11.8± 0.7**
+Phosphorus	3.09±0.58*	−0.45±0.03**	0.147	3.9±1.5**	20.4±10.0
+Both	3.62±1.58	−0.52±0.30	0.155	4.0±1.2**	18.2± 6.4

and R in *H. copiosa* (Table 1). There was a general tendency in both species of psammophytes, as well as in one of the rock growers (*H. copiosa*), for increases in respiration associated with nutrient pulses that increased P_{max}. The various nutrient enrichments generally caused significant shifts in the P_s vs. I curves towards the higher irradiances (Figs. 1–4); i.e., I_c and I_k almost always occurred at higher light energies following nutrient pulses, regardless of whether P_{max} was stimulated or inhibited.

Respiration rates for the unenriched control samples (Table 1) ranged from a high of 0.86 mg C respired · g organic dry wt^{-1} · h^{-1} for *Halimeda lacrimosa* to a low of 0.22 in the case of *H. copiosa*. *Halimeda simulans* and *H. tuna* were intermediate and respired at rates of 0.42 and 0.35 mg C · g organic dry wt^{-1} · h^{-1}, respectively. Maximum net photosynthetic rates of untreated thalli (controls) ranged from 3.90 (*H. tuna*) and 3.89 (*H. copiosa*) to 2.47 mg C · g organic dry wt^{-1} · h^{-1} (*H. simulans*), with *H. lacrimosa* photosynthesizing at 3.17 mg C · g organic dry wt^{-1} · h^{-1} (Table 1). In one of the species, highest untreated photosynthetic rates occurred at 1600 μE · m^{-2} · s^{-1} (i.e., *Halimeda simulans*, Fig. 2), while two species reached their peak at 800 μE · m^{-2} · s^{-1} (*H. tuna*, *H. lacrimosa*, Figs. 1 and 3). *Halimeda copiosa* (Fig. 4) had very low light requirements (150 μE · m^{-2} · s^{-1}) to reach maximum steady-state rates of photosynthesis.

Photosynthetic responses of the control material to subsaturating irradiances differed among these four species. *Halimeda copiosa* (Fig. 4) showed the largest effect reaching light saturation (I_k, Table 1) at only 19.9 μE · m^{-2} · s^{-1}. The other three species neared saturation from 25.5 to 60.2 μE · m^{-2} · s^{-1}. *Halimeda simulans* (Fig. 2) was the least responsive to changes in irradiance and, as was found also for *H. lacrimosa* (Fig. 3), was not inhibited when exposed to the highest irradiance (i.e., nearly full sunlight) for five hours. *Halimeda tuna* showed mild inhibition in direct sunlight, whereas net photosynthesis in *H. copiosa* was drastically reduced following exposure to irradiances beyond 200 μE · m^{-2} · s^{-1}.

There was a slight increase in respiration or photo-inhibition at the highest irradiances in *Halimeda lacrimosa* (Fig. 3) and a large increase in the shade-collected *H. copiosa* (Fig. 4). The psammophytes, *Halimeda tuna* and *H. simulans*, showed no inhibitory interactions between light and the combination of the two nutrients beyond P_{max} (Figs. 1 and 2). Nutrient effects were consistently most pronounced for the two psammophytes (Figs. 1 and 2) at the lowest irradiance level (significant at $P<0.05$).

Discussion

McRoy and Lloyd (1981) have contrasted marine macrophytes into two fundamentally different groups: (1) the macroalgae and (2) the seagrasses. The former group, as characterized by these authors, is analogous to filter-

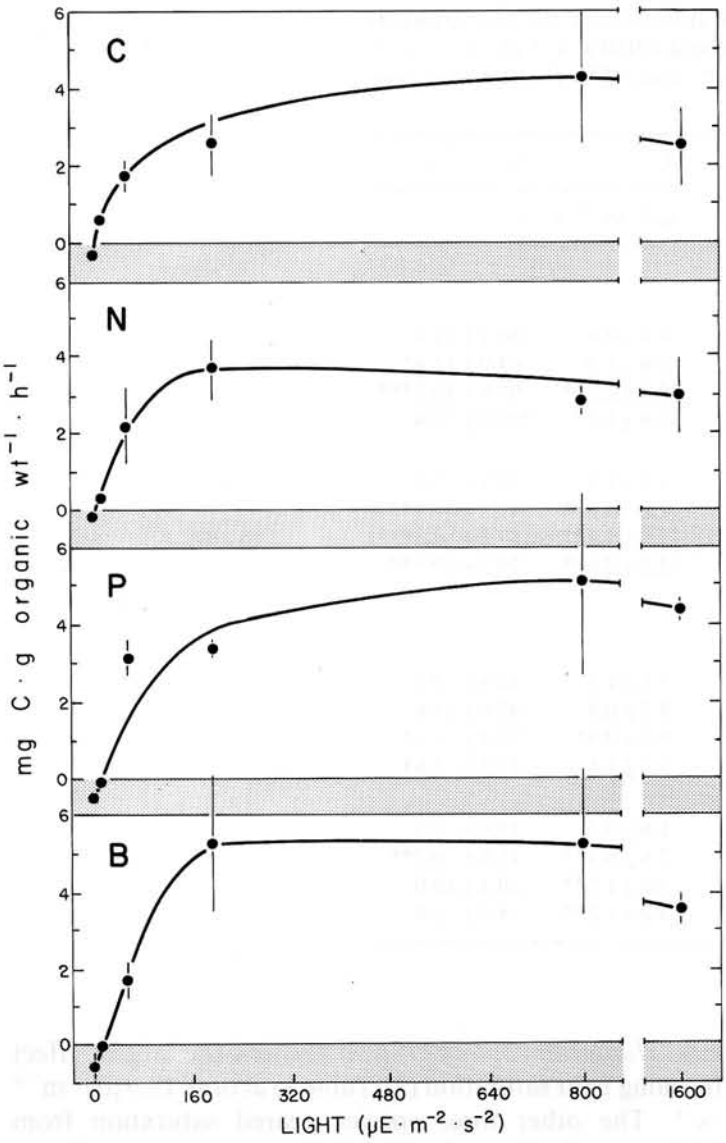

Fig. 1. P_s vs. I response of *Halimeda tuna* in relation to four nutrient treatments. (*C*) Control (no nutrients added). (*N*) Nitrogen ($NaNO_3$) added, (*P*) Phosphorus (NaH_2PO_4) added and (*B*) both *N* and P_i added. The vertical lines at each point indicate ± one standard deviation (S.D.), unless the diameter of the point exceeds the ±S.D.

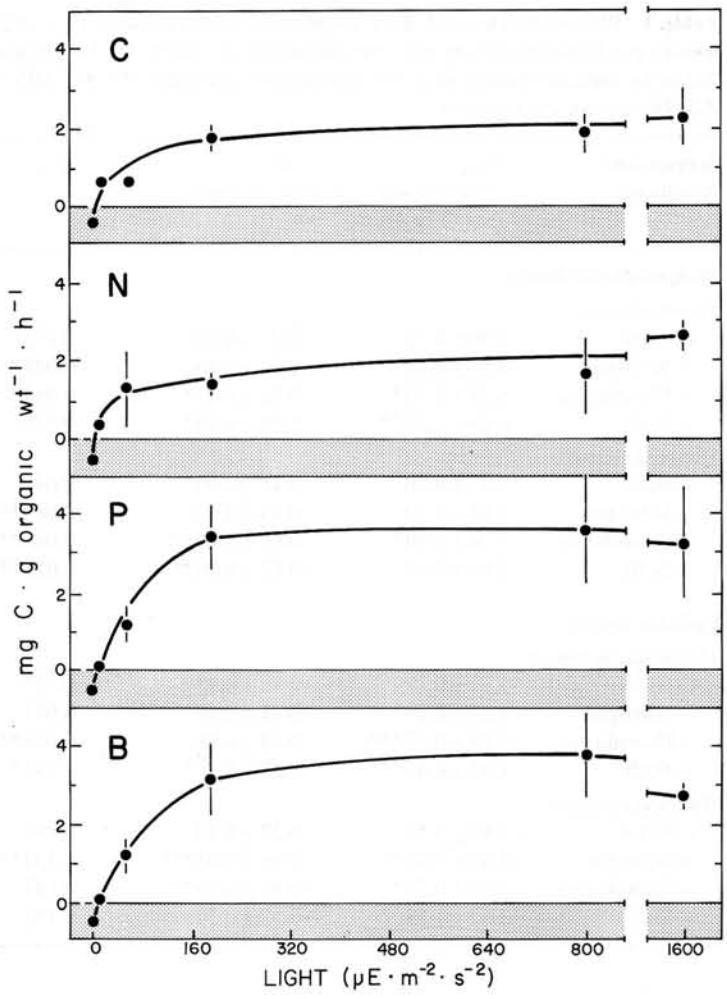

Fig. 2. P_s vs. I responses of *Halimeda simulans* in relation to four levels of nutrients. Features are the same as those indicated in Fig. 1

feeding animals in terms of extraction of nutrients, while secured to two-dimensional substrata by means of a holdfast. Members of the latter group extract nutrients from both the water column and soft, sedimentary, three-dimensional substrata by means of vascular root-rhizoid systems that also serve for anchoring them. This dichotomy overlooks many siphonaceous algae prevalent in habitats characterized by sedimentary substrata. Such algae, mainly of the order Caulerpales, also have extensive root-like and rhizomatous systems for attachment in soft substrata and, because cross walls are minimal, hypothetically these plants can utilize active transport, rapid turnover and cytoplasmic streaming to translocate nutrients taken up from both the sedimentary pore water and water column milieu.

In support of the hypothesis that differences in the nutrient status of the two form groups (psammophytic vs. epilithic) would be revealed, the two psammophytic species (*Halimeda tuna* and *H. simulans*) tended to exhibit little effect on the overall P_s vs. I response following the nitrogen pulses (Figs. 1 and 2), whereas, there was a trend toward an overall increase shown by these psymmophytes throughout the total P_s vs. I response in the P_i-pulsed samples relative to the *N*-pulsed material. This contrasts markedly with the two epilithic forms *H. lacrimosa* and *H. copiosa* (Figs. 3 and 4), where the opposite result prevailed; i.e., a trend towards overall decreases in the P_i-pulsed samples relative to material pulsed with either *N* or P_i+N.

P_{max} in the rock growers, *Halimeda lacrimosa* and *H. copiosa* (Table 1), consistently increased in thalli which had been pulsed with *N*, whereas P_i was inhibitory ($P<0.05$, two-way ANOVA). Conversely, treatment with P_i resulted in higher P_{max} in the two psammophytes ($P<0.05$). This suggests that epilithic and psammophytic *Halimeda* species differ in their nutrient status with regard to *N* and P_i requirements. The P_i-limitation observed in the psammophytic species corresponds with the observed high $N:P_i$ ratios of sediment pore water in carbonate-rich sediments (Rosenfeld 1979; Berner 1974), which could result in the P_i-limited state we observed. Alternatively, the epilithic forms, which must rely more on water-column *N* and P_i availability, appear to be more *N*-

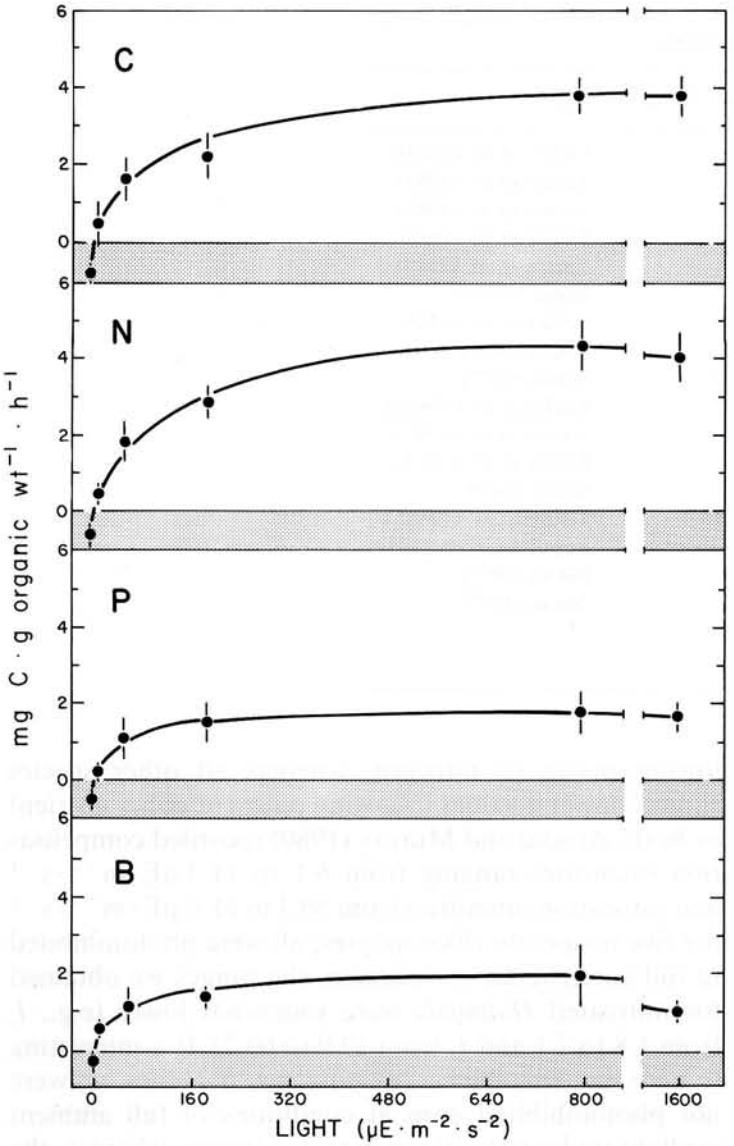

Fig. 3. P_s vs. I responses of *Halimeda lacrimosa* in relation to four levels of nutrients. Features are the same as those indicated in Fig. 1

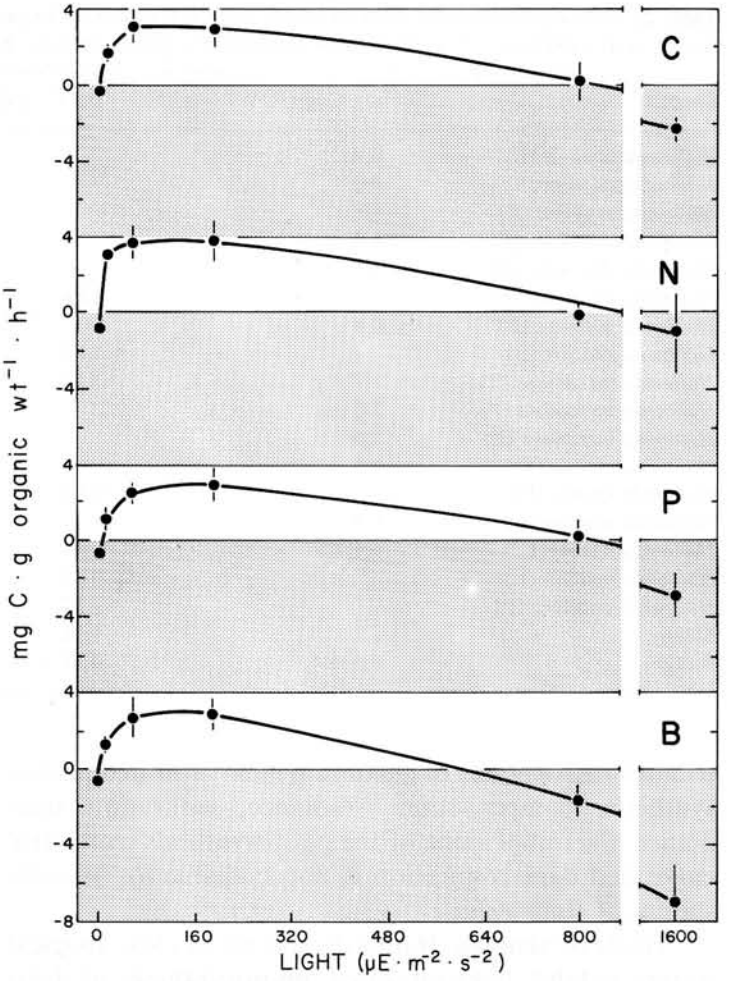

Fig. 4. P_s vs. I responses of *Halimeda copiosa* in relation to four levels of nutrients. Features are the same as those indicated in Fig. 1

limited, possibly because of lower $N:P_i$ ratios characteristic of shallow tropical waters.

The demonstration of the P_i-limited nutrient regime for *Halimeda tuna* and *H. simulans* contrasts with studies in the coastal marine environment along eastern North America where N was considered the primary nutrient limiting growth of both phytoplankton (Ryther and Dunstan 1971; Vince and Valiela 1973) and macroalgae (Topinka and Robbins 1976; Chapman and Craigie 1977; Hanisak 1979). However, nutrient bioassays along Florida's northern Gulf coast have shown that P_i is frequently more important than N in regulating phytoplankton productivity (Myers and Iverson 1981). Several recent macroalgal studies (Lapointe 1985–1987) also showed P_i limitation in tropical macroalgae. This supports the opinion held by geochemists (Brocker and Peng 1982; Smith 1984) and, in particular, Redfield (1958) that the oceans as a whole are P_i-limited ecosystems. In contrast, our data for *H. lacrimosa* and *H. copiosa* agree with those for other epilithic algae (see Topinka and Robbins 1976; Chapman and Craigie 1977; Hanisak 1979) and for a similar rock grower, *H. opuntia,* from Belize, which also demonstrated (Lapointe et al. 1987) photosynthetic enhancement only by N enrichment.

In most cases, exposure to nutrient pulses that increased P_{max} also increased R. This observation is consistent with the idea that short-term pulses of nutrient enrichment can release *Halimeda* species from nutrient limitations, and that these essential components can be quickly metabolized into photosynthetic and respiratory machinery, as found in experimental studies with other macroalgae (Lapointe et al. 1984). An increased R is attributable to increased metabolic costs associated with energetic requirements for nutrient uptake across membrane surfaces, as originally shown by Syrett (1953), or to increased P_{max} machinery, as in sun/shade acclimation.

Several studies of shallow *Halimeda* species (Borowitzka and Larkum 1976; Buesa 1977; Hillis-Colinvaux 1980; Littler et al. 1983, 1986b; Lapointe et al. 1987) and one study of deep *Halimeda* species (Jensen et al. 1985) have determined photosynthetic rates. Although the light environment is generally 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 photosynthetic at-

Table 2. Field-determined net photosynthetic rates for *Halimeda* species. All values at ambient sunlight except Jensen et al. (1985) at ~1% of ambient sunlight (P = psammophytic, E = epilithic)

Species	mg C·g ODW^{-1}·h^{-1}	mg C·g dry wt^{-1}·h^{-1}	Source
Halimeda copiosa (E)	0.9		Littler et al. (1983)
Halimeda copiosa (E)	0.9		Jensen et al. (1985)
Halimeda cryptica (E)	1.5		Jensen et al. (1985)
Halimeda discoidea (P)	1.0′		Littler et al. (1983)
Halimeda discoidea (P)	1.3		Jensen et al. (1985)
Halimeda discoidea (P)		1.84	Buesa (1977)
Halimeda goreauii (E)	0.8		Littler et al. (1983)
Halimeda gracilis (E)		1.84	Buesa (1977)
Halimeda incrassata (P)		1.43	Buesa (1977)
Halimeda incrassata (P)	2.3		Littler et al. (1986b)
Halimeda lacrimosa (E)	1.6		Jensen et al. (1985)
Halimeda monile (P)	1.6		Littler et al. (1983)
Halimeda monile (P)		0.58	Buesa (1977)
Halimeda opuntia (E)	6.4		Littler et al. (1986b)
Halimeda opuntia (E)	4.4		Lapointe et al. (1987)
Halimeda opuntia (E)		0.73	Buesa (1977)
Halimeda simulans (P)		1.12	Buesa (1977)
Mean	2.1	1.26	
Range	0.8–6.4	0.58–1.84	

tributes such as rates of maximum light-saturated photosynthesis, compensation irradiance, saturation irradiance, the initial slope of the photosynthesis-irradiance curve and dark respiration is not available for a single species of *Halimeda*.

Thalli of shallow *Halimeda* species in clear tropical waters exhibit light-saturated photosynthesis at irradiances that are much lower than levels available on typical sunny days (Figs. 1–4). With a measured light attenuation for clear Bahamian waters of about 0.4% of photosynthetically active surface irradiance per meter of depth (Littler et al. 1986a), the deepest unshaded specimens we collected (7-m deep) would have been growing in up to 97% of the light energy available at the surface. These results indicate photosynthesis in *Halimeda* reaches a maximum under relatively low light energies and that the genus is well adapted to variable light regimes, including low-light conditions, as particularly illustrated by *H. copiosa*. Concomitant with low saturation irradiances are low light requirements for photosynthetic compensation and reasonably efficient use of low photon flux densities as indicated by the steep slopes of the P_s vs. I curves. Of the four *Halimeda* species we studied, *H. copiosa* clearly emerges as the most shade adapted, with considerably higher α values and relatively low I_c and I_k values.

In comparison to *Halimeda*, five uncalcified Chlorophyta (Arnold and Murray 1980) had initial P_s vs. I slopes (α) that ranged from 0.018 mg C·dry wt^{-1}·h^{-1}/μE·m^{-2}·s^{-1} for the thick optically dense alga *Codium fragile* (Sur.) Har. to 0.129 for the thin sheet-like *Ulva rigida* C. Ag. Our α values for untreated material ranged from 0.075 mg C·g ODW^{-1}·h^{-1}/μE·m^{-2}·s^{-1} in *H. tuna* to 0.161 for *H. copiosa*. In other words, nearly the full range found for selected genera was found within this one highly plastic genus. *Halimeda copiosa* increased markedly to an α of 0.334 (significant at $P<0.001$) following pulses of nitrogen, whereas all other species showed lower α values following pulses of either nutrient or both. Arnold and Murray (1980) recorded compensation intensities ranging from 6.1 to 11.4 μE·m^{-2}·s^{-1} and saturation intensities from 50.3 to 81.9 μE·m^{-2}·s^{-1} for five temperate chlorophytes; all were photoinhibited in full sunlight. In comparison, the ranges we obtained for untreated *Halimeda* were somewhat lower (e.g., I_c from 1.8 to 7.1 and I_k from 19.9 to 60.2). It is interesting to note that two species (*H. simulans, H. lacrimosa*) were not photoinhibited even at conditions of full ambient sunlight under natural nutrient conditions; whereas, the deeply pigmented *H. tuna* and the shade dweller *H. copiosa* were photoinhibited beyond 800 μE·m^{-2}·s^{-1} during the 5-h incubation period; inhibition tended to be increased following nutrient pulses.

Previously published net photosynthetic rates for *Halimeda* species (Table 2) have ranged from 0.8 to 6.4 mg C·g organic dry wt^{-1}·h^{-1}, with a mean of 2.1 mg C·g ODW^{-1}·h^{-1}. This is lower but comparable to the mean of 3.4 and range of 2.5 to 3.9 mg C·g ODW^{-1}·h^{-1} determined for untreated controls of the four species investigated here. Our highest rates of photosynthesis came from thalli previously exposed to high nutrient levels and ranged to 6.5 (mean of 4.9) mg C·g ODW^{-1}·h^{-1}. These differences could reflect a seasonal component because our measurements were made in summer (see Hudson 1985), while previous data (Table 2) resulted from determinations made from fall to spring. Other published values (see Littler et al. 1986b) for common Caribbean macroalgal species incubated in 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. These data suggest that *Halimeda*, as a group, lies somewhere near the lower midrange in productivity.

In summary, it appears that *Halimeda* is not only adapted to large variations in its light environment, but can take advantage of episodic nutrient pulses, possibly such as those documented for temperate kelp forests (Zimmerman and Kremer 1984) and tropical photosynthetic corals (Meyer et al. 1983).

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References

Adey WH, Adey PJ, Burke R, Kaufman L (1977) The Holocene reef systems of eastern Martinique, French West Indies. Atoll Res Bull 218:1–40

Arnold KE, Murray SN (1980) Relationships between irradiance and photosynthesis for marine benthic green algae (Chlorophyta) of differing morphologies. J Exp Mar Biol Ecol 43:183–192

Berner RA (1974) Kinetic models for the early diagenesis of nitrogen, phosphorus, and silicon in anoxic marine sediments. In: Goldberg ED (ed) The sea, vol 5. Wiley, New York, pp 427–450

Borowitzka MA, Larkum AWD (1976) Calcification in the green alga *Halimeda*. II. The exchange of Ca^{2+} and the occurrence of age gradients in calcification and photosynthesis. J Exp Bot 27:864–878

Broecker WS, Peng TH (1982) Tracers in the sea. Eldigio Press, New York

Buesa RJ (1977) Photosynthesis and respiration of some tropical marine plants. Aquat Bot 3:203–216

Chapman ARO, Craigie JS (1977) Seasonal growth in *Laminaria longicruris:* relations with dissolved inorganic nutrients and internal reserves of nitrogen. Mar Biol 40:197–205

Chapman F, Mawson D (1906) On the importance of *Halimeda* as a reef-forming organism: with a description of the *Halimeda*-limestones of the New Hebrides. J Geol Soc Lond 62:702–711

Davies PJ, Marshall JF (1985) *Halimeda* bioherms – low energy reefs, northern Great Barrier Reef. Proc 5th Int Coral Reef Symp 5:1–7

Ginsburg RN (1956) Environmental relationships of grain size and constituent particles in some south Florida carbonate sediments. Bull Am Assoc Petrol Geol 40:2384–2427

Hanisak MD (1979) Growth patterns of *Codium fragile* spp. *tomentosoides* in response to temperature, irradiance, salinity, and nitrogen source. Mar Biol 50:319–332

Hillis-Colinvaux L (1977) *Halimeda* and *Tydemania:* distribution, diversity and productivity at Enewetak. Proc 3rd Int Coral Reef Symp 1:365–370

Hillis-Colinvaux L (1980) Ecology and taxonomy of *Halimeda:* primary producer of coral reefs. Adv Mar Biol 17:1–327

Hillis-Colinvaux L (1986) *Halimeda* growth and diversity on the deep fore-reef of Enewetak Atoll. Coral Reefs 5:19–21

Hudson JH (1985) Growth rate and carbonate production in *Halimeda opuntia:* Marquesas Keys, Florida. In: Toomey DF, Nitecki MH (eds) Paleoalgology: contemporary research and applications. Springer, Berlin Heidelberg New York, pp 257–263

Jensen PR, Gibson RA, Littler MM, Littler DS (1985) Photosynthesis and calcification in four deep-water *Halimeda* species (Chlorophyceae, Caulerpales). Deep-Sea Res 32:451–464

Lapointe BE (1985) Strategies for pulsed nutrient supply to *Gracilaria* cultures in the Florida Keys: interactions between concentration and frequency of nutrient pulses. J Exp Mar Biol Ecol 93:211–222

Lapointe BE (1986) Phosphorus-limited photosynthesis and growth of *Sargassum natans* and *Sargassum fluitans* (Phaeophyceae) in the western North Atlantic. Deep-Sea Res 33:391–399

Lapointe BE (1987) Phosphorus- and nitrogen-limited photosynthesis and growth of *Gracilaria tikvahiae* (Rhodophyceae) in the Florida Keys: an experimental field study. Mar Biol 93:561–568

Lapointe BE, Littler MM, Littler DS (1987) A comparison of nutrient-limited productivity in macroalgae from a Caribbean barrier reef and from a mangrove ecosystem. Aquat Bot 28:243–255

Lapointe BE, Tenore KR, Dawes CJ (1984) Interactions between light and temperature of the physiological ecology of *Gracilaria tikvahiae* (Gigartinales: Rhodophyta). I. Gross photosynthesis and respiration. Mar Biol 80:161–170

Littler MM (1979) The effects of bottle volume, thallus weight, oxygen saturation levels, and water movement on apparent photosynthetic rates in marine algae. Aquat Bot 7:21–34

Littler MM, Littler DS, Taylor PR (1983) Evolutionary strategies in a tropical barrier reef system: functional-form groups of marine macroalgae. J Phycol 19:229–237

Littler MM, Littler DS, Blair SM, Norris JN (1985) Deepest known plant life discovered on an uncharted seamount. Science 227:57–59

Littler MM, Littler DS, Blair SM, Norris JN (1986a) Deep-water plant communities from an uncharted seamount off San Salvador Island, Bahamas: distribution, abundance, and primary productivity. Deep-Sea Res 33:881–892

Littler MM, Littler DS, Lapointe BE (1986b) Baseline studies of herbivory and eutrophication on dominant reef communities of Looe Key National Marine Sanctuary. NOAA Technical Memorandum, NOS MEMD 1, Washington, DC

Mazzella L, Alberte RS (1986) Light adaptation and the role of autotrophic epiphytes in primary production of the temperate seagrass, *Zostera marina* L. J Exp Mar Biol Ecol 100:165–180

McRoy CP, Lloyd DS (1981) Comparative function and stability of macrophyte-based ecosystems. In: Longhurst AR (ed) Analysis of marine ecosystems. Academic Press, New York, pp 473–489

Meyer JL, Schultz ET, Helfman GS (1983) Fish schools: an asset to corals. Science 220:1047–1049

Milliman JD (1974) Recent sedimentary carbonates. Marine carbonates, part I. Springer, Berlin Heidelberg New York

Myers VB, Iverson RI (1981) Phosphorus and nitrogen limited phytoplankton productivity in northeastern Gulf of Mexico coastal estuaries. In: Estuaries and nutrients. Humana, Clifton, NJ, pp 569–582

Parsons TR, Takahashi M, Hargrave B (1977) Biological oceanographic processes. Pergamon Press, New York

Ramus J (1981) The capture and transduction of light energy. In: Lobban CS, Wynne MJ (eds) The biology of seaweeds. University of California Press, Berkeley, pp 458–492

Redfield AC (1958) The biological control of chemical factors in the environment. Am Sci 46:205–221

Rosenfeld JK (1979) Interstitial water and sediment chemistry of two cores from Florida Bay. J Sed Petrol 49:989–994

Ryther JH, Dustan WM (1971) Nitrogen, phosphorus, and eutrophication in the coastal marine environment. Science 171:1008–1013

Smith SV (1984) Phosphorus versus nitrogen limitation in the marine environment. Limnol Oceanogr 29:1149–1160

Smith VH (1983) Light and nutrient dependence of photosynthesis by algae. J Phycol 19:306–313

Syrett PJ (1953) The assimilation of ammonia by nitrogen-starved cells of *Chlorella vulgaris*. I. A correlation of assimilation with respiration. Ann Bot London 17:1–19

Topinka JA, Robbins JV (1976) Effects of nitrate and ammonium enrichment on growth and nitrogen physiology in *Fucus spiralis*. Limnol Oceanogr 21:659–664

Vince S, Valiela I (1973) The effects of ammonium and phosphate enrichments on chlorophyll *a*, pigment ratio and species composition of phytoplankton of Vineyard Sound. Mar Biol 19:69–73

Zimmerman RC, Kremer JN (1984) Episodic nutrient supply to a kelp forest ecosystem in Southern California. J Mar Res 42:591–604