

Productivity and nutrient relationships in psammophytic versus epilithic forms of Bryopsidales (Chlorophyta): comparisons based on a short-term physiological assay

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Abstract

Members of the green algal order Bryopsidales (= Caulerpales) are important calcifying agents of tropical reefs and comprise two fundamentally different life-form groups: (1) epilithic species with limited attachment structures and (2) psammophytic forms that have extensive subterranean rhizoidal systems. Because the shallow-water habitats of the former have relatively low nitrogen (N) to phosphorus (P_i) ratios compared to the pore waters of the sedimentary carbonate-rich substrata in which the latter are anchored, we hypothesized that epilithic forms should tend to be relatively more limited by N, while psammophytic species should tend to show P_i limitation. In partial support of the hypothesis, light-saturated net photosynthesis (P_{max}) in the epilithic forms, *Halimeda opuntia*, *H. lacrimosa* and *H. copiosa*, tended to be enhanced by N, while P_i was inhibitory or had no effect. In contrast, the psammophytic forms, *Udotea* sp., *U. conglutinata*, *H. monile*, *H. tuna* and *H. simulans*, tended to be stimulated more by P_i , whereas N had little effect. The utility of a bioassay to assess macroalgal nutrient limitation, based on a physiological response (net P_{max}) to short-term nutrient pulses, is demonstrated.

Introduction

Traditionally, nitrogen is considered (Hatcher & Larkum, 1983) to be the nutrient most often limiting tropical marine algal growth. Phosphorus, due to its effective recycling on reefs, generally has been thought (Pilson & Betzer, 1973) less likely to be in short supply. However, geochemical interpretations (Broecker & Peng, 1982; Smith, 1984; Smith & Atkinson, 1984) and recent *in situ* macroalgal bioassays (Lapointe, 1985, 1987, 1989) implicate P_i as the more frequent growth-limiting nutrient in carbonate-rich tropical marine

waters. In such environments, particularly in interstitial pore waters, dissolved P_i (PO_4^{3-}) concentrations become substantially reduced by equilibrium reactions with carbonate fluoroapatite (Gulbrandsen & Roberson, 1973) and P_i is adsorbed readily and bound onto $CaCO_3$, aragonite and calcite crystals (DeKanel & Morse, 1978). Fixation of atmospheric nitrogen by blue-green algae and bacteria associated with sediments (Capone & Taylor, 1980), microalgal turfs (Mague & Holm-Hansen, 1975; Wiebe *et al.*, 1975), macrophyte populations (Capone, 1977; Capone & Taylor, 1977; Capone *et al.*, 1977) and

corals (Crossland & Barnes, 1976) can elevate $N:P_i$ ratios while further accelerating P_i limitation by competing for available orthophosphate (Redfield, 1958; Doremus, 1982).

Members of the green algal order Bryopsidales (sensu Silva, 1982) are recognized (e.g. Chapman & Mawson, 1906; Ginsburg, 1956; Milliman, 1974; Hillis-Colinvaux, 1980, 1986) as major calcifying elements of both tropical Atlantic and Pacific reefs. Bryopsidales can be viewed as composed of two fundamentally different functional groups: (1) epilithic forms that have only limited attachment structures and (2) psammophytic species that have well-developed bulbous rhizoidal systems. The first group extracts nutrients solely from the water-column milieu while secured to two-dimensional hard substrata by means of small holdfasts. Members of the second group also extract nutrients from the water column, but potentially can obtain nutrients from the pore waters of sedimentary three-dimensional substrata by means of their extensive root-like rhizoidal systems that also serve as anchors. It is of interest that typical pore-water levels of N in the tropical western Atlantic range between 120–200 μM (Williams & Fisher, 1985), whereas associated water-column levels are frequently three orders of magnitude lower (Williams, 1984; Lapointe, 1989). This differential, as well as the stripping action of CaCO_3 particles on P_i , results in greatly elevated $N:P_i$ ratios in sedimentary environments. Bryopsidales are siphonaceous algae and, because cross walls are minimal, can utilize active transport together with rapid turnover and cytoplasmic streaming to translocate nutrients (Williams, 1984).

Because (1) sedimentary carbonate-rich pore waters have relatively high $N:P_i$ ratios (Berner, 1974; Rosenfeld, 1979) compared with the lower $N:P_i$ ratios characteristic of shallow tropical waters (Lapointe, 1989), and (2) based upon the above morphological divergences and the influence of morphology on nutrient-uptake (e.g. Rosenberg & Ramus, 1984), we predicted that different nutrient-related responses may have developed within the order. As a working hypothesis, psammophytic members should show a tend-

ency to be relatively more limited by P_i whereas epilithic forms should tend to show N limitation. This study reexamines previous data (Littler *et al.*, 1988) on the photosynthetic responses for psammophytic and epilithic forms of four Bahamian Bryopsidales under four combinations of nutrient enrichment and tests the above hypothesis for four other Bryopsidales from a different system (i.e. the Florida Keys).

Methods and materials

The field studies reported here were conducted during 20–23 December 1988 from a boat dock in South Pine Channel adjacent to Little Torch Key 38 km east of Key West, Florida, USA. This habitat shows a seasonal trend in dissolved inorganic nitrogen (Lapointe, 1989) with water-column winter minima and summer maxima as follows: $\text{NH}_4^+ = 0.03\text{--}1.20 \mu\text{M}$, $\text{NO}_3^- = 0.25\text{--}2.10 \mu\text{M}$. Concentrations of PO_4^{3-} were almost undetectable throughout the year, generally $<0.12 \mu\text{M}$.

For the experiments conducted in the Florida Keys, whole plants of the epilithic form, *Halimeda opuntia* (L.) Lamour. were contrasted with the psammophytic species *H. monile* (Ellis & Solander) Lamour., collected from 1 m deep within a few meters of each other on the west side of South Pine Channel next to the site of incubation on Little Torch Key ($24^\circ 40' 00'' \text{N}$, $81^\circ 23' 30'' \text{W}$). Additionally, two other sympatric psammophytes, *Udotea* sp. nov. (*abbottiorum*, Littler & Littler, 1990) and *U. conglutinata* (Ellis & Solander) Lamour., were collected (1 m deep) from north of South Pine Channel on the largest of the western Content Keys group. All sedimentary substrata consisted primarily of white, sand-sized fragments of *Halimeda* segments that did not appear to be anaerobic; the epilithic carbonate substratum consisted of Miami Oolite. Additional comparative data were reassessed from our earlier studies in the Bahamas (Littler *et al.*, 1988) using the same techniques. The relative nutritional status of Bahamian Bryopsidales, with respect to N versus P_i limitation at P_{max} , was

examined for two psammophytes, *Halimeda tuna* (Ellis & Solander) Lamour. and *H. simulans* Howe, and for two epilithic forms, *H. lacrimosa* Howe and *H. copiosa* Goreau & Graham, taken from clear, shallow (3–7 m deep) waters (Jerlov type I).

On the day of collection in all cases, the macroalgae were cleaned of sediments and epiphytes and replicate whole plants were soaked overnight in one of four treatments that consisted of enrichment with either N (NaNO_3), P_i (NaH_2PO_4), N + P_i or a control (no enrichment). Initial enrichment concentrations were $160 \mu\text{M} - \text{N}$ and $16 \mu\text{M} - \text{P}_i$ in order to saturate (Lapointe, 1989) the uptake rates. These concentrations represent the upper range of natural levels encountered in eutrophic environments (e.g. bird islands) and the mid range found in Caribbean sediment pore waters (i.e. $120\text{--}200 \mu\text{M} - \text{N}$, Williams & Fisher, 1985). Following the 12 h overnight period of enrichment, the algae were flushed with 3 changes of seawater 4 h prior to incubation in full sunlight. This enrichment assay for nutrient limitation has been found (Littler *et al.*, 1986, 1988; Lapointe, 1987, 1989; Lapointe *et al.*, 1987) to correlate closely with longer-term growth responses for macroalgae.

For all net productivity (photosynthesis) measurements that followed the 12 h nutrient-enrichment period in Florida material, 14 replicate incubations per treatment were run for a total of 56 samples \cdot species $^{-1}$ at ambient water temperatures ($24.0\text{--}24.2^\circ\text{C}$) between 0820 and 1700 hrs in full sunlight with a natural photon flux density of $2332 \mu\text{mol m}^{-2} \text{s}^{-1}$ of photosynthetically active radiation (PAR), ranging from a minimum of 1035 to a maximum of $3673 \mu\text{mol m}^{-2} \text{s}^{-1}$. Photon irradiance was measured in the field with an integrating 4π sensor (LiCor Model LI-550 printing integrator) throughout the incubation periods. 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 a photosynthetic quotient of 1.00 to facilitate compari-

sons. Photosynthesis was 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).

Results

In the nutrient enrichment treatments (Fig. 1), trends were exhibited by the four Bahamian Bryopsidales that varied according to both life form and species. For those possessing an extensive, subterranean, rhizoidal, root-like system (*Halimeda tuna* and *H. simulans*, Fig. 1), P_i pulses had significant ($p < 0.05$, two-way ANOVA) enhancement effects on net P_{max} . No significant

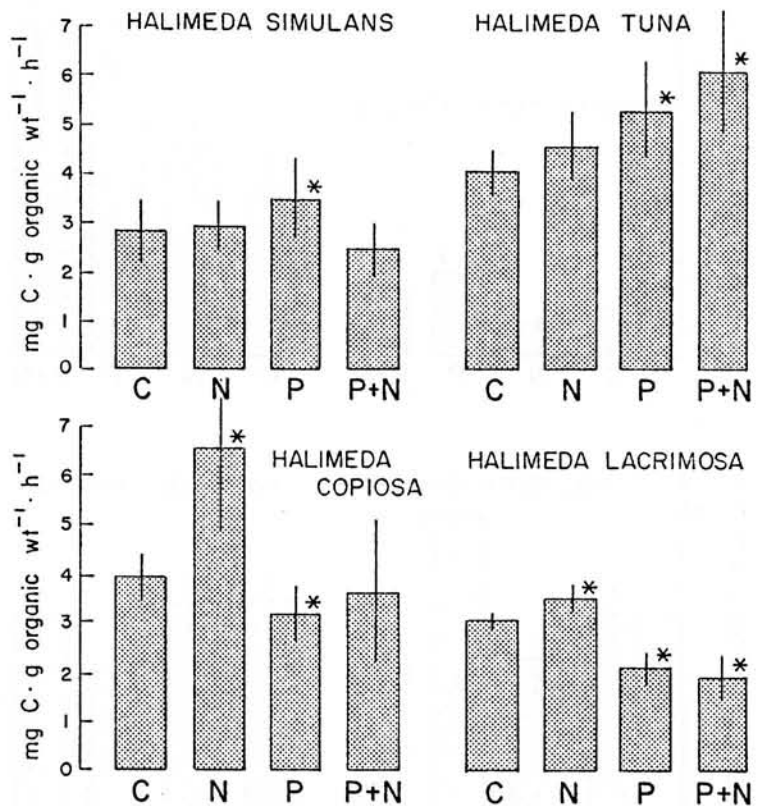


Fig. 1. P_{max} of the Bahamian psammophytes, *Halimeda simulans* and *H. tuna*, and two epilithic forms, *H. copiosa* and *H. lacrimosa*, in response to enrichment by NO_3^- and/or PO_4^{3-} . C = control. Values represent means ± 1 SD ($N = 4\text{--}6$). Reanalyzed from Littler *et al.* (1988). Asterisks indicate values that are significantly different from the controls ($p < 0.05$, two-way ANOVA).

responses in P_{\max} ($p > 0.05$) were shown by either of these two Bahamian psammophytes following N pulses. Phosphorus and nitrogen combined stimulated net P_{\max} (significant at $p < 0.05$) for *H. tuna* as well.

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

The productivity of the two calcareous psammophytes, *Udotea conglutinata* and *Udotea* sp. (*abb.*), in Florida (Fig. 2) emulated the pattern established for psammophytes in the Bahamas

(Fig. 1). There was substantial (significant at $p < 0.05$, two-way ANOVA) stimulation of P_{\max} following pulses of P_i , but not N, in both species. In *U. conglutinata*, the combination of N + P_i had no significant effect ($p > 0.05$), while in *Udotea* sp. (*abb.*), N + P_i significantly ($p < 0.05$) elevated P_{\max} . Correspondingly, the psammophyte *Halimeda monile* from Florida (Fig. 2) also showed a significant ($p < 0.05$) increase in P_{\max} following exposure to P_i whereas pulses of N alone and N + P_i together had no significant effects ($p > 0.05$). In the rock dwelling *H. opuntia* from Florida (Fig. 2), there was significant ($p < 0.05$) inhibition of P_{\max} due to enrichment with P_i , but no significant ($p > 0.05$) changes in P_{\max} subsequent to pulses of either N or N + P_i .

Discussion

The photosynthetic response at light-saturation (P_{\max}) to nutrient enhancement is a parameter with considerable potential to reveal the type and degree of nutrient limitation in marine macroalgae. Field studies have shown that rates of P_{\max} in a freshwater microalga (Auer & Canale, 1982) and a freshwater macrophyte (Schmitt & Adams, 1981) are correlated with cellular levels of P_i . If this correlation applies to macroalgae, then prior pulsing of N and P_i followed by subsequent determination of P_{\max} could be used as a diagnostic field assay to examine the degree of nutrient limitation to primary productivity in coastal environments. Such utility is demonstrated by the present bioassay in addressing the question of whether or not psammophytic forms of Bryopsidales differ in their relative levels of nutrient limitation from members of the order that only attach to hard substrata.

The results for the four Bahamian species of *Halimeda* (Fig. 1) suggested that psammophytic forms tend to differ in nutrient status from epilithic forms. Similar Belizean experiments on epilithic *H. opuntia* also showed significant ($p < 0.05$, two-way ANOVA) stimulation of P_{\max} following pulses of N but not P_i , even though the two populations examined came from quite dif-

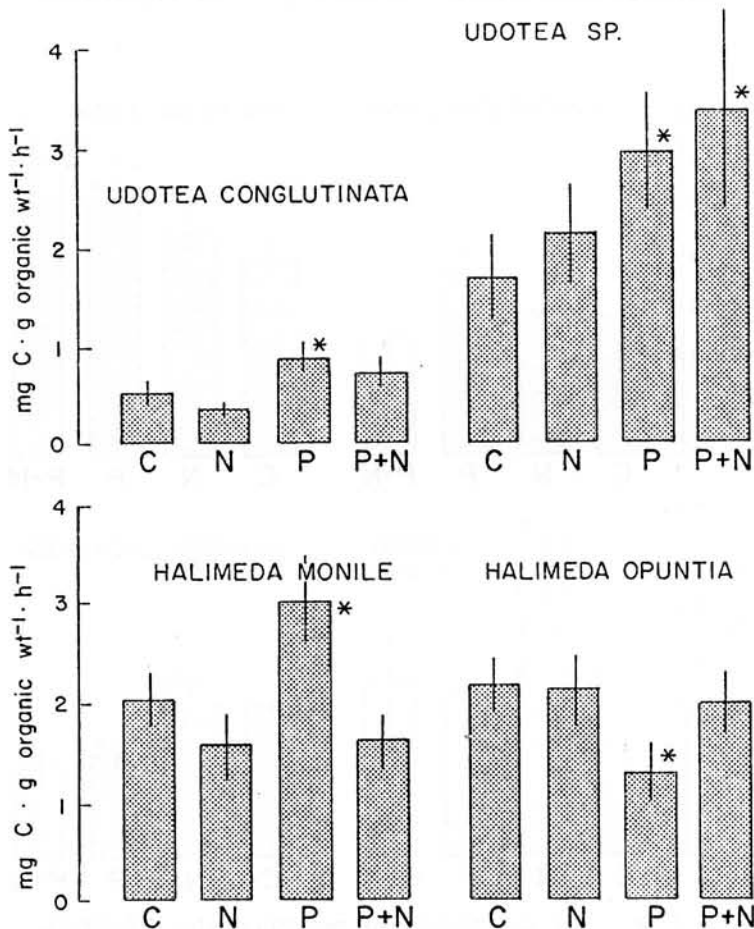


Fig. 2. P_{\max} of the Florida psammophytes, *Udotea conglutinata*, *Udotea* sp. and *Halimeda monile*, and the epilithic alga, *Halimeda opuntia*, in response to NO_3^- and/or PO_4^{3-} enrichment. C = control. Values represent means \pm 1 SD ($N = 14$). Asterisks indicate values that are significantly different from the controls ($p < 0.05$, two-way ANOVA).

ferent dissolved nutrient regimes (i.e. Twin Cays N & P_i ~3 fold > Curlew Cay (Lapointe *et al.*, 1987). Trends from our Bahamian (Littler *et al.*, 1988) and Belizean (Lapointe *et al.*, 1987) studies and the new findings on *Halimeda* and *Udotea* from the Florida Keys can be summarized as follows. In partial support of the hypothesis, P_{max} in psammophytes tended to be stimulated by pulses of P_i, while high levels of N consistently had no effect. In contrast, epilithic species tended to be stimulated more by N enrichment, whereas high levels of P_i inhibited P_{max} or had little effect.

The demonstration of a P_i-limited nutrient regime for the sand dwellers *Halimeda tuna*, *H. simulans*, *H. monile*, *Udotea* sp. (*abb.*) and *U. conglutinata* contrasts with studies in temperate coastal environments along eastern North America where N was the primary growth-limiting nutrient of both phytoplankton (Ryther & Dunstan, 1971; Vince & Valiela, 1973) and epilithic macroalgae (Topinka & Robbins, 1976; Chapman & Craigie, 1977; Hanisak, 1979). However, nutrient bioassays using phytoplankton off Florida's northern Gulf coast (Myers & Iverson, 1981), as well as epilithic macroalgal assays near the site studied here (Lapointe, 1989), have shown that P_i can be more important than N in regulating primary productivity. Lapointe (1989) recorded water-column dissolved inorganic N : P_i ratios of less than 10 during winter in South Pine Channel, which should result in N limitation (Ryther & Dunstan, 1971; Smith, 1984); however, this was not the case in any of the Florida Bryopsidales (i.e. mostly psammophytes) we examined (Fig. 2).

The recent series of studies using epilithic Phaeophyta and Rhodophyta from the Florida Keys (Lapointe, 1985, 1986, 1987, 1989) also documented mostly P_i limitation. This agrees with predictions based on geochemistry (Redfield, 1958; Broecker & Peng, 1982; Smith, 1984) that the productivity of oceanic ecosystems should most often be P_i limited. In contrast, our data for the rock-dwellers *Halimeda lacrimosa* and *H. copiosa* agree with those for other epilithic algae (see Topinka & Robbins, 1976; Chapman & Craigie, 1977; Hanisak, 1979; Hatcher & Larkum, 1983) and for the closely related rock-

dweller, *H. opuntia* from Belize (Lapointe *et al.*, 1987), which also demonstrated photosynthetic enhancement primarily by N enrichment.

These findings support the hypothesis that the two life-forms characteristic of Bryopsidales may show differential limitation by inorganic N or P_i, corresponding to the ratios present in their respective environments, while having the ability to take advantage of episodic nutrient pulses. The trend toward P_i-limitation observed in the psammophytic species corresponds with the observed (Berner, 1974; Rosenfeld, 1979) high N : P_i ratios of sediment pore waters in carbonate-rich sediments, which could result in the P_i-limited state we recorded. The lack of inhibitory responses to either nutrient shown by the psammophytic forms might be related to relatively high half-saturation constants (K_s, the nutrient concentration at which half the maximum uptake rate is achieved). Values of K_s as high as 107 μM – N have been documented (Williams, 1984) for psammophytic Bryopsidales, strongly indicating adaptation to the presence of high nutrient levels. Macrophytes adapted to using only water-column nutrients, which occur in concentrations several orders of magnitude lower, should have correspondingly lower K_s values (Williams, 1984). The epilithic forms that must rely on water-column N and P_i availability tended to be more N-limited, possibly because of the much lower N : P_i ratios characteristic of shallow tropical waters.

It is difficult to generalize concerning nutrient limitation in marine macroalgae since previous nutrient-exposure history and life form are among the important parameters. Because episodic nutrient pulses are both sporadic and frequent in nature (Meyer *et al.*, 1983; Zimmerman & Kremer, 1984) and, as shown here, different functional groups respond differently (see also Rosenberg & Ramus, 1984), the degree and type of nutrient limitation in benthic macrophytes is dependent on a spectrum of variables.

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