

**ATOLL RESEARCH BULLETIN
NO. 374**

CHAPTER 10

**PHOTOSYNTHESIS VS. IRRADIANCE CURVES FOR SIX SPECIES OF
MACROALGAE FROM THE SEYCHELLES ISLANDS UNDER
FOUR LEVELS OF NUTRIENT ENRICHMENT**

BY

M. M. LITTLER AND D. S. LITTLER

**ISSUED BY
NATIONAL MUSEUM OF NATURAL HISTORY
SMITHSONIAN INSTITUTION
WASHINGTON, D.C., U.S.A.
June 1992**

CHAPTER 10
PHOTOSYNTHESIS VS. IRRADIANCE CURVES FOR SIX SPECIES OF
MACROALGAE FROM THE SEYCHELLES ISLANDS UNDER FOUR LEVELS OF
NUTRIENT ENRICHMENT

BY

M.M. Littler* and D.S. Littler*

ABSTRACT

The relative nutritional status, with respect to phosphorus (P) versus nitrogen (N) limitation, and light-limited photosynthesis (P_s) was examined over a broad range of quantum fluxes (I) for four species of Chlorophyta (*Codium* sp., *Avrainvillea amadelpha* f. *montagnei*, *Dictyosphaeria cavernosa*, *Udotea orientalis* and two species of Rhodophyta (*Gracilaria crassa*, *G. multifurcata*) taken from Seychelles coastal waters. The results are consistent with the hypothesis that differences in nutrient status among algal forms are related to antecedent habitat history. Maximum photosynthetic rates (P_{max}) for *Codium* sp., *U. orientalis* and *G. multifurcata* from nutrient-poor habitats increased ($P < 0.05$) following nutrient enrichment. However, the species examined from nutrient-rich waters, *A. amadelpha* f. *montagnei*, *D. cavernosa* and *G. crassa*, showed decreases in the initial slope (α) of the P vs. I curve and no significant ($P > 0.05$) increases in P_{max} following nutrient pulses consistent with their previous nutrient environments. The findings suggest that shallow species of tropical macroalgae are adapted to take advantage of episodic nutrient pulses, and that nutrient exposure history can override differences between the various life forms in determining photosynthetic responses to nutrients.

The six shallow water algal species investigated appear well adapted to variable light regimes, including low light conditions. In natural populations of the green alga *A. amadelpha* f. *montagnei*, light-saturated photosynthesis occurred at quite low irradiances ($I_k = 100 \mu E \cdot m^{-2} \cdot s^{-1}$). Associated with low saturation irradiances were low light requirements for photosynthetic compensation ($I_c = 30 \mu E \cdot m^{-2} \cdot s^{-1}$) in this species and reasonably efficient use of low photon flux densities as indicated by a relatively steep slope (α) of the P_s vs. I curve. Conversely, *Codium* sp., *G. crassa* and *G. multifurcata* showed increased photosynthesis as a function of increasing I, with no indication of photoinhibition and relatively shallow α 's.

INTRODUCTION

Large standing stocks of macroalgae on reefs are usually correlated with elevated nutrient supplies (Adey et al. 1977), an observation consistent with the idea that growth rates of tropical reef macroalgae may often be nutrient limited. However, the question of which macronutrient element -- N, P or their interactions -- might limit macroalgal productivity in reef ecosystems has infrequently been addressed experimentally. Traditionally, N is considered the primary limiting nutrient in

* Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560

tropical marine waters (e.g., Parsons et al. 1977), although information from geochemical models (Broecker and Peng 1982, Smith 1984) and recent *in situ* macroalgal bioassays (Lapointe 1985, 1987, 1992, Littler et al. 1991) suggests that P may be the more important growth-limiting nutrient in carbonate-rich tropical marine waters. A knowledge of photosynthetic responses to P and N and light by species of tropical reef algae from contrasting habitats could prove useful to clarify current discrepancies (e.g., see Smith 1984) concerning the role of N versus P limitation to algal stocks in tropical marine environments.

Based upon habitat differences in the Seychelles Islands, and the presumed influence of habitat history on nutrient limitation, we hypothesized that different light and nutrient-related responses would be shown by dominant algae from different island environments. To begin to understand the comparative physiological ecology of Seychelles reef algae, we examined the relative nutritional status (N vs P limitation) for four Chlorophyta and two Rhodophyta 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 macroalgae from enriched waters differ in their relative levels of nutrient limitation from species growing in nutrient-poor habitats?

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

Do dark respiration rates (R) and photosynthetic rates at light saturation (P_{max}) vary among species from different habitats?

Do Seychelles Island reef species differ in their light-limited photosynthetic characteristics (α , I_c , I_k).

METHODS AND MATERIALS

This investigation was performed from the research vessel R/V Alexander A. Nesmeyanov throughout the Seychelles Islands from 1 February to 31 March 1989. The specific study sites included St. Joseph Atoll, Pagoda Island of the Cosmoledo Group (a bird island with Guano), and inner and outer harbor sites off the city of Victoria, Mahé Island (Fig. 1). The specimens were held overnight in metal-free, 106-liter, insulated, plastic containers of ambient seawater 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 Alexander A. Nesmeyanov where they were cleaned of sediments and epiphytes. Subsequently, replicate whole plants of each species were soaked in one of three treatments, a factorial design enrichment of N (NaNO_3) and P (NaH_2PO_4), that consisted of either +N, +P, +N+P or a control (no enrichment). Initial concentrations of N and P 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 under shaded conditions (50% I_0) 4 h prior to incubation. 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, Littler et al. 1988) 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, six replicate incubations per treatment were run. Experimental levels of 7 irradiances and 4 nutrient-pulsed conditions were set up simultaneously in a 7X4 factorial design at ambient water temperatures (27.5-28.4°C) and run between 1000 and 1530 hrs with an average ambient photon-flux density of $2200 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of photosynthetically active radiation (PAR), ranging from a minimum of 1480 to a maximum of $5000 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Incubation chambers were lined with highly reflective aluminum foil to help attain light levels in excess of saturation. Different layers of neutral density screening were used to produce seven experimental light levels (in approximate percent of available sunlight): 100.0%, 50.0%, 25.0%, 12.5%, 3.2%, 0.8% and dark. Photon-flux densities were measured in the field with two integrating 4π sensors (Li Cor Model LI-1000 Data Logger) throughout the incubation periods. Seven layers of neutral density screening and an insulated lid were placed over the 106-liter insulated chamber containing the six incubation jars at the beginning of each run to exclude all light. Incubations were conducted in one liter glass jars that received continuous cooling. Stirring via stir bars on each of the six oxygen electrodes provided vigorous water motion. At five minute intervals, the lid or appropriate layers of screening were removed and dissolved oxygen was recorded at five minute intervals to $0.01 \text{ mg}\cdot\text{l}^{-1}$ 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 70°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 $50.8 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) 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 values obtained in a particular P_s vs. I curve. Nitrogen and P enrichment effects on P_{max} were assessed by two-way ANOVA and Bonferroni t-test of differences. Significance reported in the results below implies that the probability of the null hypothesis was <0.05 .

RESULTS

Maximum net apparent photosynthesis (P_{max}) in *Codium* sp. from the pristine St. Joseph Atoll (Table 1, Fig. 2) was strongly N-limited (N significantly greater than control, $P < 0.05$). Values of samples pulsed with P were consistently higher than the controls but not to a statistically significant degree ($P > 0.05$). The two nutrients combined produced a significant ($P < 0.05$) synergistic increase in net apparent photosynthesis. Net photosynthesis began to show light saturation (I_k) above about $I_k = 250 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in the controls and at lower light levels (150 - $170 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) in the pulsed samples (Table 1). The nutrient-pulsed material had compensation intensities (I_c , Table 1) that were all less than half that of the controls ($80 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). The α values of the pulsed material were consistently higher than that of the control samples (Table 1).

For *Udotea orientalis* from another pristine environment on St. Joseph Atoll, P_{\max} significantly increased ($P < 0.05$) following pulses of N or P, but no P + N synergism occurred (Fig. 3, Table 1). Net apparent photosynthesis became light saturated at around $170\text{--}280 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (I_k) in the control and N-pulsed samples but was substantially higher ($410 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) in the samples pulsed with P alone (Table 1). The nutrient-pulsed samples showed somewhat lower I_c values than the controls, particularly in the case of the N-pulsed material (30 vs. $140 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, Table 1). The α values were similar with the exception of the P-pulsed material which was two to three times lower (Table 1).

In *Avrainvillea amadelpha* f. *montagnei* (Fig. 4, Table 1), from the guano-influenced Pagoda Island, Cosmoledo Atoll, there was no significant ($P > 0.05$) change in P_{\max} for any of the pulsed treatments. Net photosynthesis began to show light saturation at the relatively low I_k of $100 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in the controls and at 310 , 354 and $633 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for N-, P- and N+P-pulsed material, respectively (Table 1). I_c values followed this same trend with lower control values and a much higher I_c in the N+P-pulsed samples. The α values of the nutrient enriched materials were substantially lower, particularly in the case of the N+P-pulsed material, than in the controls (Table 1).

Dictyosphaeria cavernosa, the dominant alga from Pagode Island (Fig. 5), Cosmoledo Atoll, under the direct influence of seabird guano, showed no significant ($P > 0.05$) nutrient stimulation of P_{\max} , with substantial inhibition in the P- and N+P-pulsed samples (Table 1). Net photosynthesis tended to become light saturated at $320\text{--}370 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, except in the case of the N-pulsed samples ($I_k = 540 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). The nutrient-pulsed material had slightly elevated I_c values than the controls (Table 1). The α values, conversely, were nearly twice as high in the controls as in the pulsed material.

Gracilaria multifurcata from Cerf Island outside of Victoria Harbor, Mahe (Fig. 6), had P_{\max} stimulated most by pulses of P (significant at $P < 0.05$) and to a lesser degree by N and N+P. Light saturation of the control (Table 1) was somewhat high compared to the other algal species, as reflected by an I_k of $480 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. The nutrient-pulsed samples showed quite high I_k values ranging from 510 to $870 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Only the N-pulsed samples had substantially higher I_c values than the controls (120 vs. $70 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, Table 1).

In *Gracilaria crassa* (Fig. 7), a dominant in the highly eutrophic shallow waters adjacent to the shoreline of Victoria Harbor, Mahe, all combinations of additions of N, P, or both, significantly ($P < 0.05$) inhibited P_{\max} . Light saturation began to appear earlier in the controls, with an I_k of $380 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ compared with $1200\text{--}1975 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for the pulsed samples. Correspondingly, the new compensation value was much lower for the controls, which had an I_c of 60 compared with $280\text{--}400 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for the pulsed material. Concomitantly, the pulsed samples showed substantially reduced α values compared with the untreated controls (Table 1).

There was a tendency for respiration (R) to decrease following nutrient pulses in most species. However, statistically significant ($P < 0.05$) declines in R were shown only for the pulsed samples of *Udotea orientalis* from St. Joseph Atoll (Table 1).

DISCUSSION

McRoy and Lloyd (1981) have categorized marine macrophytes as comprising two fundamentally different groups: (1) the macroalgae and (2) the seagrasses. The former group, as characterized by these authors, is analogous to filter-feeding animals in terms of extraction of nutrients from the seawater milieu, while secured to two-dimensional substrata by means of a holdfast. Members of the latter group extract nutrients from both the water column and pore waters of the soft, sedimentary,

three-dimensional substrata by means of vascular root-rhizoid systems that also serve for anchoring them. This dichotomy overlooks many siphonaceous algae (=rhizophytes), such as *Udotea orientalis*, prevalent in habitats characterized by sedimentary substrata. Such algae, mainly of the order Bryopsidales, anchored in nutrient-laden pore waters (Littler and Littler 1990), also have extensive root-like and rhizomatous systems for attachment in soft substrata and, because cross walls are minimal, these plants can utilize active transport, rapid turnover and cytoplasmic streaming to translocate nutrients taken up from both the sedimentary pore waters and water column milieu (Williams 1984). *Udotea orientalis* (Fig. 3) did not support the finding of Littler and Littler (1990) that psammophytic rhizophytes tend to exhibit little response to the overall P_s vs. I relationship following nutrient pulses. However, the sedimentary substratum from which this psammophyte was taken on St. Joseph Atoll is especially white aerobic sand free of pigmented organic or other matter. This finding is in agreement with the two epilithic forms, *Codium* sp. and *Gracilaria multifurcata* (Figs. 2 and 5), also from low nutrient waters, where the same result prevailed; i.e., a trend towards overall increases in the nutrient pulsed samples relative to unpulsed control material.

Contrastingly, P_{max} in the two epilithic forms (haptophytes), *Halimeda lacrimosa* and *Halimeda copiosa* from the Bahamas (Littler et al. 1988), increased consistently in thalli which had been pulsed with N, whereas P was inhibitory ($P < 0.05$). Conversely, treatment with P resulted in higher P_{max} in both of the psammophytic *Halimeda* species investigated, ($P < 0.05$), suggesting (Littler et al. 1988) that epilithic and psammophytic *Halimeda* species may tend to differ in their nutrient status with regard to N and P requirements. The P-limitation previously observed in psammophytic species corresponds with the observed high N:P ratios of sediment pore waters in carbonate-rich sediments (Rosenfeld 1979; Berner 1974), which could result in the P-limited state Littler et al. (1988) observed. Alternatively, epilithic forms, which must rely more on water-column N and P availability, appear (Littler and Littler 1990) to be more N-limited, possibly because of lower N:P ratios characteristic of shallow tropical waters. In contrast, our data for *U. orientalis*, a rhizophyte from an exceptionally pristine sedimentary environment, did not show differential P vs. N limitation (Fig. 3).

The demonstration of the P-limited nutrient condition for *Gracilaria multifurcata* also differs from the above and from 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 is frequently more important than N in regulating phytoplankton productivity (Myers and Iverson 1981). Several recent macroalgal studies (Lapointe 1985, 1986, 1987, Littler et al. 1988, Littler and Littler 1990) also showed P limitation in tropical macroalgae. This supports the opinion held by geochemists (Broecker and Peng 1982, Smith 1984) and, in particular, Redfield (1958) that the oceans as a whole are P-limited ecosystems. In contrast, our data for *Codium* sp., agree with those for other epilithic algae (see Topinka and Robbins 1976, Chapman and Craigie 1977, Hanisak 1979) and for a similar rock grower, *Halimeda 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} tended to decrease R (Table 1). This observation is inconsistent with the idea that R is elevated when short-term pulses of nutrient enrichment are quickly metabolized into photosynthetic and respiratory machinery, as found in experimental studies with other macroalgae (Lapointe et al. 1984). An increased R normally is attributable to increased metabolic cost associated with energetic requirements for nutrient uptake across membrane surfaces, as originally shown by Syrett (1953), or to increased P_{max} machinery, as evidenced during sun/shade acclimation.

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 tropical whole-algal photosynthetic attributes such as rates of maximum light-saturated photosynthesis, compensation irradiance, saturation irradiance, the initial slope of the photosynthesis-irradiance curve and dark respiration is available only for a several species of *Halimeda* (Littler et al. 1988). Thalli of shallow *Halimeda* species in clear tropical waters often exhibit light-saturated photosynthesis at irradiances that are much lower than levels available on typical sunny days. With a measured light attenuation for clear Seychelles waters of about 0.4% of photosynthetically active surface irradiance per meter of depth, the deepest specimens we collected (7-m deep) would have been growing in up to 97% of the light energy available at the surface. Our results indicate photosynthesis in some shallow tropical macroalgae can reach a maximum under relatively low light energies and that many species appear well adapted to variable light regimes, including low-light conditions, as particularly illustrated by *Avrainvillea amadelpa* f. *montagnei* (Fig. 4). 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 six species we studied, *A. amadelpa* f. *montagnei* clearly emerges as the most shade adapted, with considerably higher α values and relatively low I_c and I_k values.

In comparison to our data, five uncalcified temperate chlorophyta (Arnold and Murray 1980) had initial P_s vs. I slopes (α) that ranged from 0.018 mg C·g dry wt⁻¹·h⁻¹ per $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ 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 0.012 mg C·g ODW⁻¹·h⁻¹ per $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ to 0.034. In other words, the full range found for selected genera was exceeded within this small study group of six taxa. *Codium* sp. increased markedly in α following pulses of nutrients, whereas the other species tended to show lower α values following pulses of either nutrient or both. Arnold and Murray (1980) recorded compensation intensities ranging from 6.1 to 11.4 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and saturation intensities from 50.3 to 81.9 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for five temperate chlorophytes; all were photoinhibited in full sunlight. In comparison, the ranges we obtained for untreated Seychelles algae were considerably higher (e.g., I_c from 30 to 140 and I_k from 100 to 480).

Previously published net photosynthetic rates for other tropical species (i.e., *Halimeda*, Littler and Littler 1990) 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 comparable to the mean of 3.5 and range of 1.3 to 4.6 mg C·g ODW⁻¹·h⁻¹ determined for untreated controls of the six species investigated here. Our highest rates of photosynthesis did not necessarily come from thalli previously exposed to high nutrient levels. Other published values (see Littler et al. 1986b) for common tropical 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.

In a parallel exploratory study, Littler et al. (1991) characterized some of the environmental features of the same habitats studied here and the reader is referred to that work for detail. Seawater nutrient samples were taken at midday next to the algal thalli used in the photosynthesis/nutrient assays reported here. Total inorganic nitrogen was lowest at St. Joseph Atoll (0.64 μM) followed by Victoria Harbor (0.77), Cerf Island (1.29) and the guano enriched Pagode Island, with a very high level of 5.48 μM (Littler et al. 1991). Orthophosphate levels followed the same trend with the lowest total inorganic phosphorus at St. Joseph Atoll (0.11 μM) followed by Cerf Island (0.12), Victoria Harbor (0.22) and Pagode Island (with the highest value of 0.50 μM). Novozhilov et al. (1992) also noted that the waters of Victoria Harbor and near the bird rookeries of Cosmoledo Atoll contain elevated levels of nutrients which they likewise attributed to sewage discharges and bird excrements, respectively. Our photosynthetic assays coincide closely with the predicted trends in nutrient levels and are consistent with the hypothesis that macroalgae from enriched waters differ in their relative levels of nutrient limitation from species growing in nutrient-poor habitats. This finding is in agreement with more extensive bioassay studies for tropical macroalgae (see Littler et al. 1991,

Lapointe et al. 1992). It appears that tropical macroalgae are not only adapted to large variations in the 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).

ACKNOWLEDGEMENTS

We sincerely appreciate the valuable assistance in the field and laboratory provided by Barrett Brooks. Woody Lee helped with the organizational logistics, for which we are grateful. Funding for the study originated from a Smithsonian Institution Research Opportunities Award, a grant from the Smithsonian Marine Station at Link Port and the Assistant Secretary for Research Discretionary Fund. This study is Contribution No. 307 of the Smithsonian Marine Station at Link Port, Florida.

REFERENCES

- Adey, W.H., P.J. Adey, R. Burke and L. Kaufman. 1977. The Holocene reef systems of eastern Martinique, French West Indies. *Atoll Res. Bull.* 218: 1-40.
- Arnold, K.E. and S.N. Murray. 1980. Relationships between irradiance and photosynthesis for marine benthic green algae (Chlorophyta) of differing morphologies. *J. Exp. Mar. Biol. Ecol.* 43: 183-192.
- Berner, R.A. 1974. Kinetic models for the early diagenesis of nitrogen, phosphorus, and silicon in anoxic marine sediments. In: Goldberg, E.D. (ed.) *The Sea*. Vol 5. Wiley, New York, pp 427-450.
- Broecker, W.S. and T.H. Peng. 1982. *Tracers in the sea*. Eldigio Press, New York.
- Chapman, A.R.O. and J.S. Craigie. 1977. Seasonal growth in *Laminaria longicuris*: relations with dissolved inorganic nutrients and internal reserves of nitrogen. *Mar. Biol.* 40: 197-205.
- Hanisak, M.D. 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. 1980. Ecology and taxonomy of *Halimeda*: primary producer of coral reefs. *Adv. Mar. Biol.* 17: 1-327.
- Jensen, P.R., R.A. Gibson, M.M. Littler and D.S. Littler. 1985. Photosynthesis and calcification in four deep-water *Halimeda* species (Chlorophyceae, Caulerpales). *Deep-Sea Res.* 32: 451-464.
- Lapointe, B.E. 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, B.E. 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, B.E. 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, B.E., M.M. Littler and D.S. Littler. 1987. A comparison of nutrient-limited productivity in macroalgae from a Caribbean barrier reef and from a mangrove ecosystem. *Aquat. Bot.* 20: 243-255.
- Lapointe, B.E., K.R. Tenore and C.J. Dawes. 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.
- Lapointe, B.E., M.M. Littler and D.S. Littler. 1992. Nutrient availability to marine macroalgae in siliciclastic versus carbonate-rich coastal waters. *Estuaries* 15(1): 76-83.
- Littler, M.M. 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, M.M., D.S. Littler and P.R. Taylor. 1983. Evolutionary strategies in a tropical barrier reef system: functional-form groups of marine macroalgae. *J. Phycol.* 19: 229-237.
- Littler, M.M., D.S. Littler, S.M. Blair and J.N. Norris. 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, M.M., D.S. Littler and B.E. Lapointe. 1986b. Baseline studies of herbivory and eutrophication on dominant reef communities of Looe Key National Marine Sanctuary. NOAA Technical Memorandum, NOS MEMD 1, Washington, D.C.
- Littler, M.M., D.S. Littler and B.E. Lapointe. 1988. A comparison of nutrient- and light-limited photosynthesis in psammophytic versus epilithic forms of *Halimeda* (Caulerpales, Halimedaceae) from the Bahamas. *Coral Reefs* 6: 219-225.
- Littler, M.M. and D.S. Littler. 1990. Productivity and nutrient relationships in psammophytic versus epilithic forms of Bryopsidales (Chlorophyta): comparisons based on a short-term physiological assay. *Hydrobiologia* 204/205: 49-55.
- Littler, M.M., D.S. Littler and E.A. Titlyanov. 1991. Comparisons of N- and P-limited productivity between high granitic islands vs. low carbonate atolls in the Seychelles Archipelago: a test of the relative-dominance paradigm. *Coral Reefs* 10: 199-209.
- Mazzella, L. and R.S. Alberte. 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, C.P. and D.S. Lloyd. 1981. Comparative function and stability of macrophyte-based ecosystems. In: Longhurst, A.R. (ed.) *Analysis of marine ecosystems*. Academic Press, New York, pp 473-489.
- Meyer, J.L., E.T. Schultz and G.S. Helfman. 1983. Fish schools: an asset to corals. *Science* 220: 1047-1049.

- Myers, V.B. and R.I. Iverson. 1981. Phosphorus and nitrogen limited phytoplankton productivity in northeastern Gulf of Mexico coastal estuaries. In: Estuaries and nutrients. Humana, Clifton, New Jersey, pp 569-582.
- Novozhilov, A.V., Y.N. Chernova, I.A. Tsukurov, V.A. Denisov and L.N. Propp. 1992. Characteristics of oceanographic processes on reefs of the Seychelles Islands. Atoll Res. Bull. No. 366: 1-36.
- Parsons, T.R., M. Takahashi and B. Hargrave. 1977. Biological oceanographic processes. Pergamon Press, New York.
- Ramus, J. 1981. The capture and transduction of light energy. In: Lobban, C.S. and M.J. Wynne (eds.) The biology of seaweeds. Univ. of California Press, Berkeley, pp 458-492.
- Redfield, A.C. 1958. The biological control of chemical factors in the environment. Am. Sci. 46: 205-221.
- Rosenfeld, J.K. 1979. Interstitial water and sediment chemistry of two cores from Florida Bay. J. Sed. Petrol. 49: 989-994.
- Ryther, J.H. and W.M. Dustan. 1971. Nitrogen, phosphorus, and eutrophication in the coastal marine environment. Science 171: 1008-1013.
- Smith, S.V. 1984. Phosphorus versus nitrogen limitation in the marine environment. Limnol. Oceanogr. 29: 1149-1160.
- Smith, V.H. 1983. Light and nutrient dependence of photosynthesis by algae. J. Phycol. 19: 306-313.
- Syrett, P.J. 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, J.A. and J.V. Robbins. 1976. Effects of nitrate and ammonium enrichment on growth and nitrogen physiology in *Fucus spiralis*. Limnol. Oceanogr. 21: 659-664.
- Vince, S. and I. Valiela. 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.
- Williams, S.L. 1984. Uptake of sediment ammonium and translocation in a marine green macroalga *Caulerpa cupressoides* (Chlorophyta). J. Phycol. 29: 374-379.
- Zimmerman, R.C. and J.N. Kremer. 1984. Episodic nutrient supply to a kelp forest ecosystem in Southern California. J. Mar. Res. 42: 591-604.
-

Table 1. Photosynthetic and dark respiratory characteristics in relation to various nutrient conditions (α = mg C·g organic dry weight (ODW)⁻¹·h⁻¹ per $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). Asterisks indicate values that are significantly different for only P_{max} and R (* = P < 0.05, ANOVA using Bonferroni *t* tests of differences) from the controls. The α , I_c and I_k values were time-series dependent and not analyzed statistically.

Species and treatment	P _{max}	R	α	I _c	I _k
	(mg C·gODW ⁻¹ ·h ⁻¹)			($\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	
<i>Codium</i> sp.					
Control	3.18±0.097	-1.93±0.64	0.021	80	250
+Nitrogen	6.51±1.97*	-2.21±1.68	0.052	37	150
+Phosphorus	4.40±0.38	-1.07±0.43	0.032	20	150
+N+P	4.80±0.36*	-1.25±0.32	0.038	23	170
<i>Udotea orientalis</i>					
Control	1.31±0.42	-3.53±1.36	0.018	140	220
+Nitrogen	3.23±0.92*	-1.51±0.32*	0.021	30	170
+Phosphorus	2.50±0.57*	-1.56±0.30*	0.007	80	410
+N+P	2.09±0.30	-1.66±0.70*	0.013	120	280
<i>Avrainvillea amadelpha</i> f. <i>montagnei</i>					
Control	2.56±0.55	-1.62±1.29	0.034	30	100
+Nitrogen	3.15±0.56	-0.82±0.13	0.012	50	310
+Phosphorus	3.24±0.33	-0.92±0.18	0.010	64	354
+N+P	2.53±0.49	-0.94±0.11	0.006	148	633
<i>Dictyosphaeria cavernosa</i>					
Control	4.09±1.46	-3.87±2.61	0.021	140	320
+Nitrogen	4.43±0.24	-2.20±0.98	0.012	165	540
+Phosphorus	2.63±1.45	-3.51±2.82	0.014	170	350
+N+P	3.24±1.03	-3.33±0.91	0.011	150	370
<i>Gracilaria multifurcata</i>					
Control	5.06±0.59	-0.89±0.26	0.012	70	480
+Nitrogen	5.43±0.88	-0.73±0.41	0.006	120	870
+Phosphorus	6.55±0.78*	-0.75±0.05	0.015	60	510
+N+P	6.07±0.79	-0.55±0.08	0.008	40	750
<i>Gracilaria crassa</i>					
Control	4.56±0.78	-0.88±0.19	0.014	60	380
+Nitrogen	3.42±0.66*	-1.15±0.40	0.003	400	1300
+Phosphorus	3.15±0.90*	-1.02±0.20	0.002	280	1975
+N+P	3.57±0.65*	-0.88±0.28	0.004	280	1200

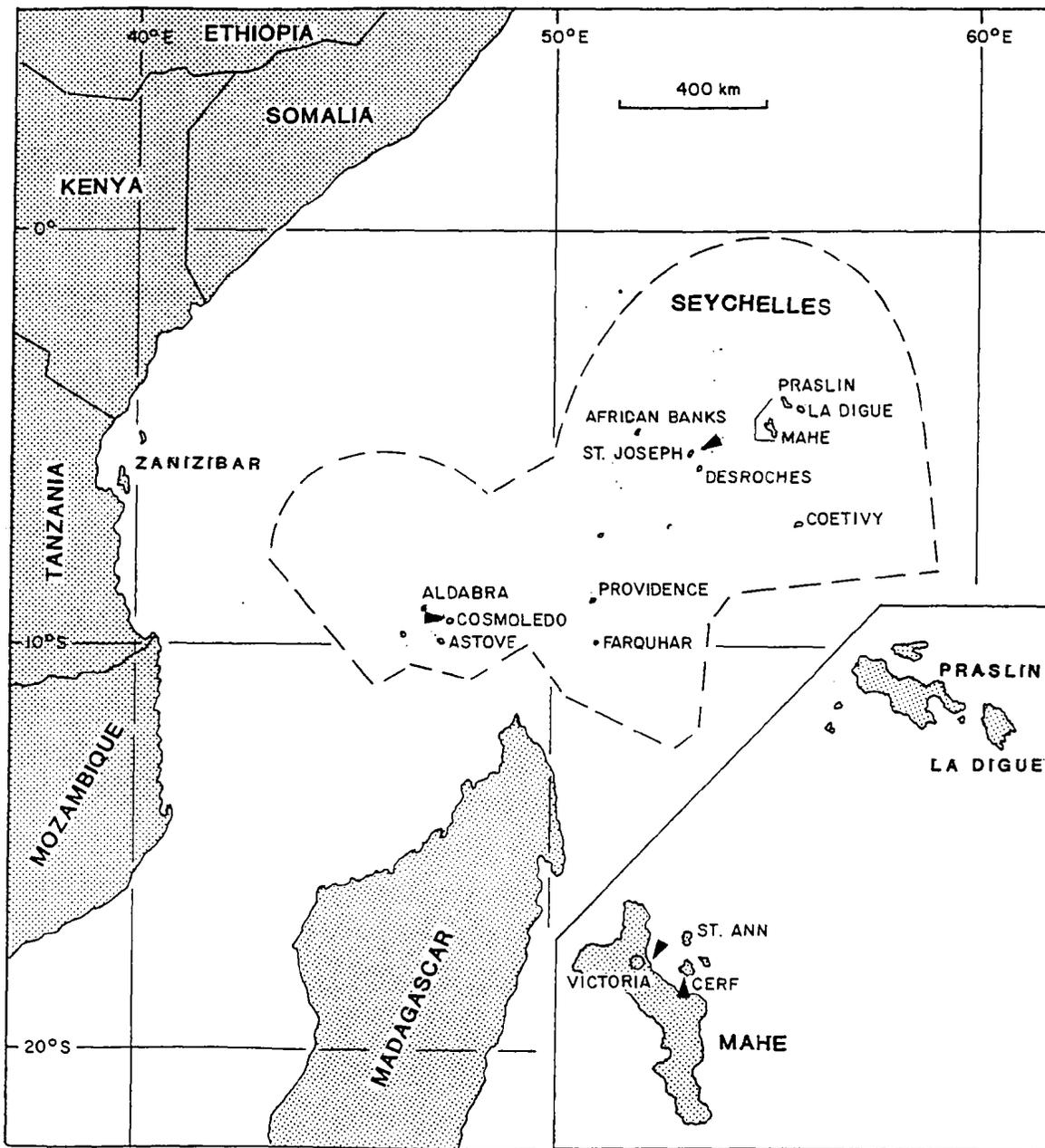


Figure 1. Map showing the locations (arrows) of the four study areas. The collection sites on St. Joseph Atoll and Cerf Island are relatively oligotrophic compared to the eutrophic sites on the guano-influenced Pagoda Island, Cosmoledo Atoll, and the sewage-influenced Victoria Harbor, Mahé. Inset shows the group of granitic islands in larger detail.

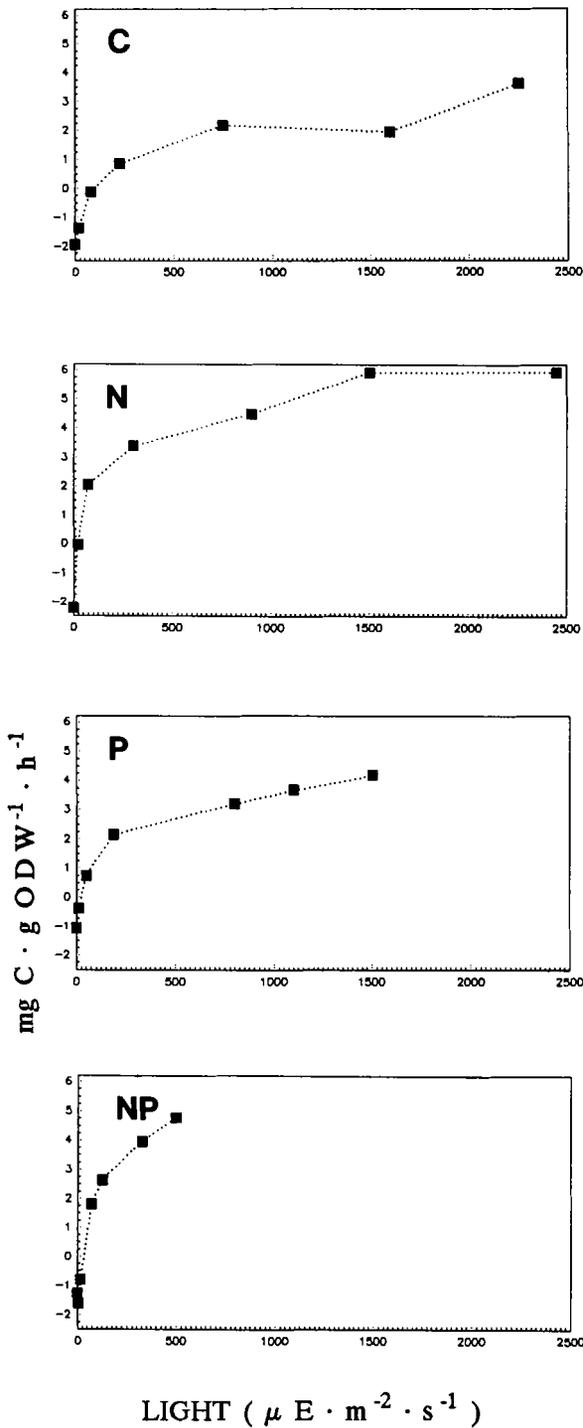


Figure 2. P_s versus I response of *Codium* sp. in relation to four nutrient treatments. (C) Control (no nutrients added), (N) Nitrogen (NaNO_3) added, (P) Phosphorous (NaH_2PO_4) added and (NP) Both N and P added.

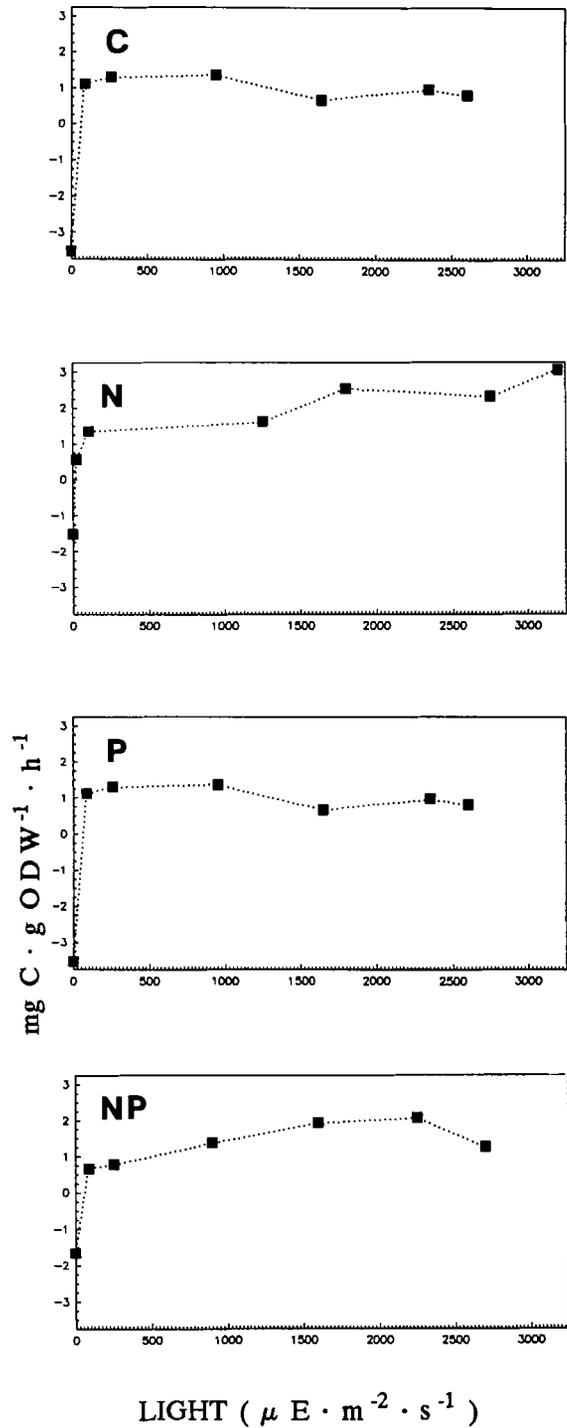


Figure 3. P_s versus I responses of *Udotea orientalis* in relation to four levels of nutrients. Features are the same as those indicated in Fig. 1.

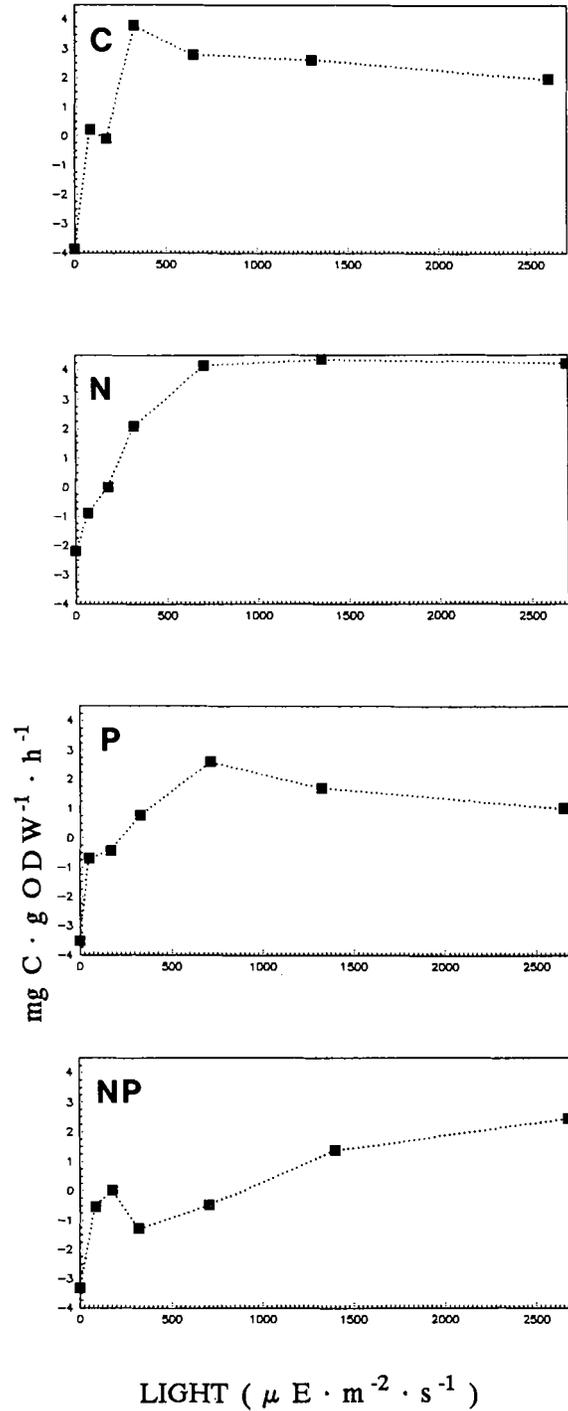
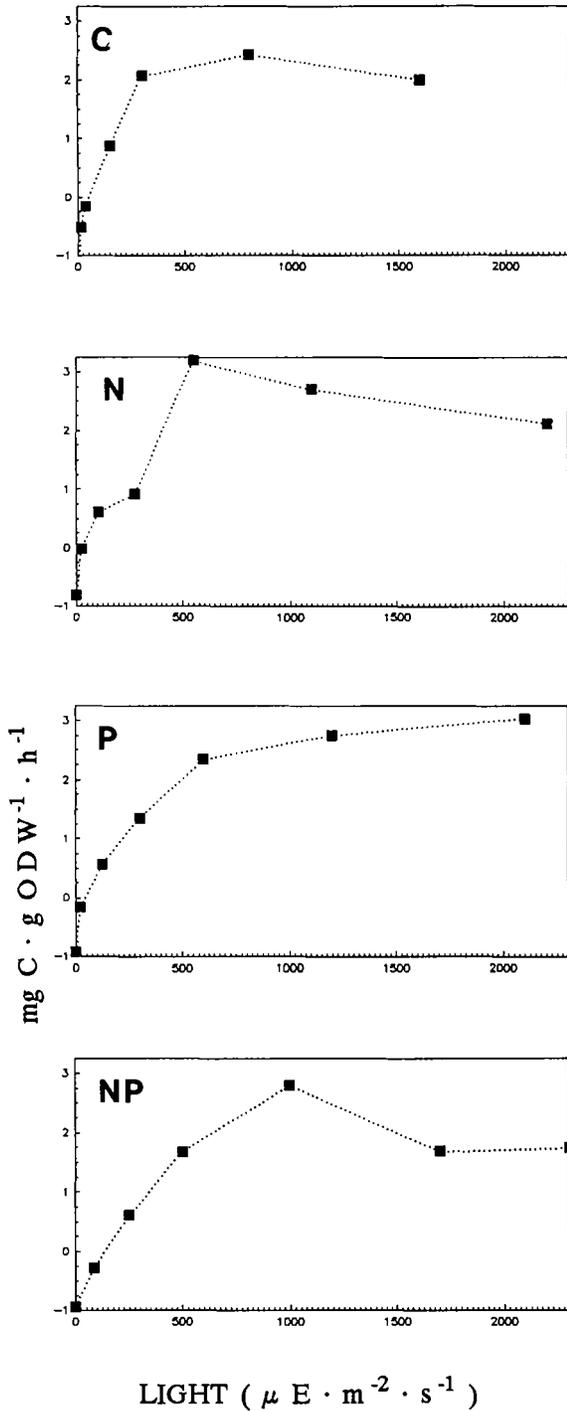


Figure 4. P_s versus I responses of *Avrainvillea amadelpha* f. *montagnei* in relation to four levels of nutrients. Features are the same as those indicated in Fig. 1.

Figure 5. P_s versus I responses of *Dictyosphaeria cavernosa* in relation to four levels of nutrients. Features are the same as those indicated in Fig. 1.

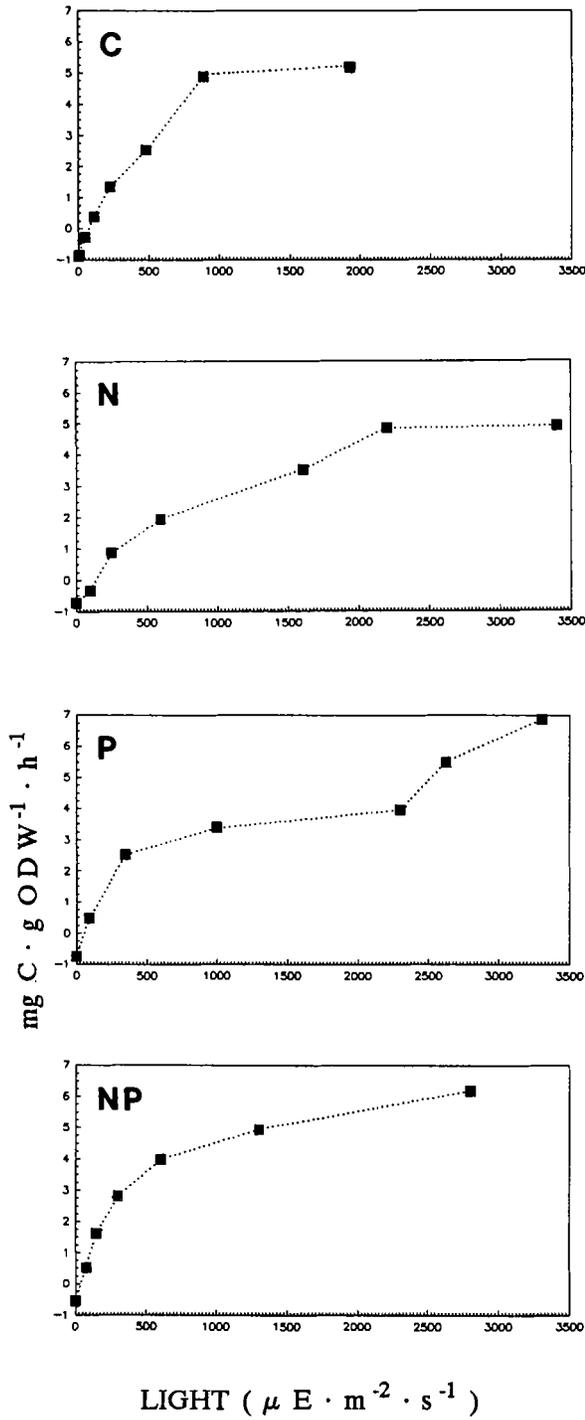


Figure 6. P_s versus I responses of *Gracilaria multifurcata* in relation to four levels of nutrients. Features are the same as those indicated in Fig. 1.

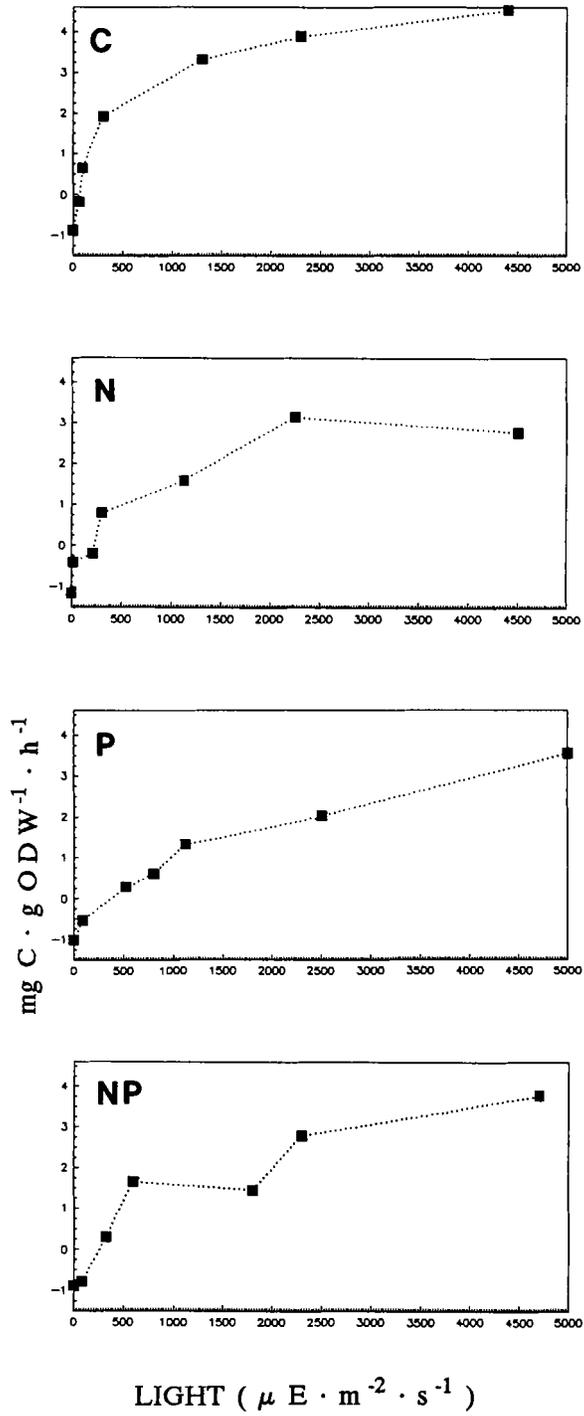


Figure 7. P_s versus I responses of *Gracilaria crassa* in relation to four levels of nutrients. Features are the same as those indicated in Fig. 1.