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Primary Production and Photosynthetic Quotients of Seaweeds from São Paulo State, Brazil

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Primary production was measured under natural conditions for five common species of seaweeds from the coast of the State of São Paulo, Brazil, using oxygen electrode and pH single-endpoint techniques. Productivity ranged from over 500 μmol O_2 g dw^{-1} h^{-1} (about 6 mg C g dw^{-1} h^{-1}) for *Ulva fasciata* Delile (Chlorophyta), a sheet-like form, to 30 μmol O_2 g dw^{-1} h^{-1} (about 0.36 mg C g dw^{-1} h^{-1}) in *Laurencia papillosa* (C. Agardh) Greville (Rhodophyta), a coarsely-branched form. Intermediate productivities were measured in two other coarsely-branched forms, *Hypnea musciformis* (Wulfen) Lamouroux (Rhodophyta) and *Pterocladia capillacea* (Gmelin) Bornet *et* Thuret (Rhodophyta) and in the thick-leathery species, *Sargassum cymosum* C. Agardh (Phaeophyta). Specific growth rates measured in the field or in continuous-flow seawater systems for commercially-valuable red algae range from 1% day^{-1} in *P. capillacea* to 14% day^{-1} in *H. musciformis*. Primary production and growth rates are in agreement with the functional-form model of Littler and Littler. Available biomass information showed that the maximum standing stocks did not correspond to the growth potential determined from measurements of primary productivity and growth rates, suggesting that levels of standing stocks are determined more by physical factors (wave action) and biological interactions (grazing) than by intrinsic growth rate potentials. The measured ratios of net photosynthetic O_2 release to CO_2 uptake (photosynthetic quotient, PQ), were consistently less than the theoretically expected values of 1.0 to 1.3 (mean measured values: 0.42 to 1.01). The PQ values did not vary according to taxonomic division or functional-form group and were unaffected by experimental nutrient (nitrate + phosphate) enrichment. The continued use of PQ = 1.00 is recommended to facilitate interconvertibility in comparisons between studies of primary production by seaweeds.

Introduction

Although most of the research on Brazilian benthic algal communities has been in taxonomy, some information is available about phenology and *in vitro* growth responses for a few species of commercial red algae harvested for agar (e. g. Oliveira and Sazima 1973, Silva *et al.* 1987, Yokoya and Oliveira 1992, Oliveira and Berchez 1993). There are only three studies that directly measured physiological primary production using gas exchange methods (Kinoshita and Teixeira 1979, Coutinho and Yoneshigue 1988, Coutinho *et al.* 1989). The use of ecosystem models in studies of Latin American plant communities is increasing and measurements of seaweed primary production are urgently needed to apply these models to benthic marine algae (Seeliger 1992).

Although primary production of seaweeds is usually measured using techniques that measure oxygen evolution, carbon units are preferred in ecosystem models. Oxygen production is usually converted into carbon fixation by assuming a 1 : 1 relationship between O_2 evolution and CO_2 uptake, defined as the photosynthetic quotient (PQ). A value of PQ equal to unity assumes hexose production with ammonium as the N source. If this simple physiological portrayal of photosynthesis is replaced by an ecological summation of protoplasm production, including carbohydrates, proteins, lipids, and nucleic acids, with either ammonium or nitrate as N sources, then the predicted PQ is higher, in the range from 1.25 to 1.6 (Ryther 1956, Williams *et al.* 1979, Williams and Robertson 1991).

Most reported PQs have been determined for phytoplankton from measurements of net oxygen exchange and a ^{14}C value between net and gross carbon fixation (Peterson 1980, Turpin 1991). As a result, photosynthetic oxygen release is diminished by concurrent respiratory oxygen consumption. To be useful, PQs should be determined using net measures of both carbon fixation and oxygen evolution. Empirical measurements of PQ are available for only a few species of macroalgae (Arnold and Littler 1985) and, except for a single study using sewage effluents (Kin-

dig and Littler 1980), the effects of environmental factors, such as the N source, have not been investigated. With nitrate as the N source, the PQ values predicted from plant composition would be lower for macroalgae with high C : N ratios than for phytoplankton cells with low C : N. With ammonium as the N source, the upper limit on PQ would be lower.

Specific questions addressed by this study are as follows: Can primary productivity and growth rate for seaweeds from São Paulo State, Brazil, be predicted using the functional-form model (Littler and Littler 1980, Littler *et al.* 1983) that has been applied to North American and Caribbean macroalgal communities? Are the rates for common Brazilian seaweeds comparable to those for the same or similar species elsewhere? Are rates of primary production correlated with the biomass levels observed in the field? What are the effects of nutrient enrichment on rates of primary production? Is PQ affected by nutrient enrichment? What are empirical values of PQ, based on actual simultaneous measurements, so that productivity data can be useful in building realistic ecological models?

Materials and Methods

Seaweeds that visually dominated the biomass were collected at the Praia das Cigarras, in São Sebastião, on the coast of São Paulo State, Brazil (lat. 23°48'39" S, long. 45°24'00" W). The species selected for this study were the green alga *Ulva fasciata* Delile, the brown alga *Sargassum cymosum* C. Agardh, and the red algae *Pterocladia capillacea* (Gmelin) Bornet *et* Thuret, *Hypnea musciformis* (Wulfen) Lamouroux and *Laurencia papillosa* (C. Agardh) Greville. *Hypnea musciformis* occurred as an epiphyte on *Sargassum* spp. These five species represented four functional-form groups (Littler *et al.* 1983): sheet-like (*U. fasciata*), filamentous (*H. musciformis*), coarsely-branched (*P. capillacea* and *L. papillosa*), and thick-leathery (*S. cymosum*).

Plants were collected at low tide and quickly transferred to large (220 L) outdoor continuous-flow (11.5 turnovers per day) seawater tanks. All experiments were performed during July and August (winter) when temperature in the outdoor tanks ranged from 23.0 to 24.4 °C (1 to 2 °C warmer than ambient seawater) and salinity ranged from 32.0 to 33.5‰.

Subsamples for incubation were prepared on the day prior to the experiments. The seaweeds were incubated in light and dark 300 mL glass BOD bottles suspended from PVC plastic poles in the outdoor tanks. Control bottles did not contain seaweeds. The incubation medium was filtered (Whatman No. 1 filter paper) seawater that had been sparged with nitrogen gas to reduce initial oxygen concentrations to ca. 60–70% of saturation. The incubations lasted about 1.3 h (early to mid-afternoon) and incident light intensity was measured every few minutes using a luxmeter (Dr B. Lange, Berlin). Measurements in lux were divided by 50 to obtain approximate photosynthetic photon flux densities (PAR) in μmol quanta $m^{-2}\,s^{-1}$ (Lüning 1981). Mixing was provided by a glass marble at the bottom of each bottle and, every few minutes, the submerged bottles were agitated by hand using the PVC poles.

Oxygen concentrations were measured using a Yellow Springs Instruments Model 51B oxygen meter equipped with a polarographic 5750 BOD probe. The pH was measured using a Micronal Model B374 digital pH-meter calibrated with standard buffer solutions and a buffer at the same salinity as the seawater (Smith and Kinsey 1978). Total alkalinity was measured by titrating 0.01 N HCl to each of the seawater samples and measuring the pH. During all oxygen and pH measurements, mixing was provided by a magnetic stirrer. Following the experiment, the seaweeds were dried to constant weight at 60 °C. Oxygen production was calculated directly from the initial and final readings. The initial and final values of total inorganic carbon (TIC) were calculated using the equations given in Smith and Kinsey (1978), including the calculation of total alkalinity (Culberson *et al.* 1970). Values for the dissociation constants of boric and carbonic acids were obtained from the tables in Skirrow (1975). None of the seaweeds selected deposited $CaCO_3$, so that changes in the total alkalinity due to calcification were negligible during the incubations. Rates of respiration were calculated from concurrent changes in oxygen and total CO_2 in the dark bottles.

The PQ values were calculated as the ratio of net O_2 to net CO_2 exchange. Mean values of PQ were based on oxygen and pH measurements for 3 to 9 samples. If PQ is assumed to equal unity, net primary productivity in oxygen units (μmol O_2 g dw^{-1} h^{-1}) can be multiplied by 0.012 to obtain equivalent carbon units (mg C g dw^{-1} h^{-1}).

In some experiments, the seaweeds in the outdoor tanks were acclimated to nutrient-enriched (5 to 9 days) or low-light (20 days) conditions. Nutrient enrichments consisted of daily midday additions of concentrated aqueous solutions of $NaNO_3$ and NaH_2PO_4 to bring the nitrate concentration up to 230 μM and the phosphate concentration up to 23 μM. To avoid toxic effects due to high water temperature, seawater flow was not interrupted during nutrient pulsing. Nutrient enrichment is known to cause a short-term increase in uptake-associated respiration (Lapointe *et al.* 1984, Turpin 1991). For this reason, photosynthesis and respiration were measured 24 hours after the last nutrient pulse. The low-light treatment used neutral-density screening to reduce the light level to 19% of the incident photon flux density, simulating conditions in the crevices where the experimental species, *Pterocladia capillacea*, was col-

lected. The controls were seaweeds that were acclimated to ambient conditions in the outdoor tanks.

Statistical comparisons of productivity and PQ data were made using the Bonferroni a posteriori multiple classification analysis (SAS Institute Inc. 1985, General Linear Models) to identify significant differences at the $P < 0.05$ level.

Results and Discussion

Figure 1 shows net photosynthesis (oxygen evolution) for several seaweed species on cloudy and sunny days. The highest productivity (> 500 μmol O_2 g dw^{-1} h^{-1} on sunny days) was measured in the sheet-like *Ulva fasciata*. Lower productivities (< 200 μmol O_2 g dw^{-1} h^{-1}) were measured in the coarsely-branched red algae and in thick-leathery *Sargassum cymosum*.

Dark respiration in control thalli of the five seaweed species is shown in Table I. Sheet-like *Ulva fasciata* and filamentous *Hypnea musciformis* had higher rates of dark respiration than the coarsely-branched red algae or thick-leathery *Sargassum cymosum*. Net photosynthesis was at least twice dark respiration, even on cloudy days. Slightly higher ratios of net photosynthesis to respiration (up to 11) were measured on sunny days (Table I).

The production rates of these Brazilian seaweed species are within the ranges measured for the same or similar species in North America and the Caribbean (*e. g.* Littler *et al.* 1983). The only other primary productivity measurements for seaweeds from São Paulo State are those of Kinoshita and Teixeira (1979) for *Pterocladia capillacea*. Using simulated *in situ* incubations, they reported rates of net production equivalent to 328 to 645 μmol O_2 g dw^{-1} h^{-1}. Even higher production rates of about 600 to 2000 μmol O_2 g dw^{-1} h^{-1} have been reported for *P. capillacea* from a region of upwelling further north in Rio de Janeiro State (Coutinho and Yoneshigue 1988, Coutinho *et al.* 1989). Two populations of *Ulva fasciata* from this region were reported to have rates of primary production ranging from 1800 to 4000 μmol O_2 g dw^{-1} h^{-1} (Coutinho *et al.* 1989). These photosynthetic rates are considerably higher than rates reported for the same or similar species in this study or in North America and the Caribbean. The lower productivities measured in the coarsely-branched red algae and in the thick-leathery *Sargassum cymosum*, in comparison with the sheet-like *U. fasciata*, were consistent with the functional-form model (Littler and Littler 1980, Littler *et al.* 1983). The fact that PQ did not increase in response to nutrient (nitrate + phosphate) enrichment (Williams and Robertson 1991) suggests that the control plants were also utilizing nitrate as the nitrogen source.

Table I. Dark respiration (μmol O_2 g dw^{-1} h^{-1}) and ratios of net photosynthesis (P_n) to respiration (R) in five seaweed species from Brazil, arranged according to functional-form group. P_n : R measured on cloudy days (average PAR about 350 to 650 μmol quanta m^{-2} s^{-1}) and on sunny days (average PAR during incubation about 970 to 1,260 μmol quanta m^{-2} s^{-1}). Mean ± SD (n = 3 to 12).

Species	Dark respiration, R	P_n : R
Sheet		
Ulva fasciata	90.2 ± 23.3	2–6 (cloudy) 7 (sunny)
Filamentous		
Hypnea musciformis	67.8 ± 21.5	2 (cloudy)
Coarsely-branched		
Pterocladia capillacea	24.2 ± 9.2	4–9 (sunny)
Laurencia papillosa	14.9 ± 4.4	2 (cloudy)
Thick-leathery		
Sargassum cymosum	26.9 ± 8.9	4–10 (cloudy) 11 (sunny)

Available biomass-based growth rates for Brazilian seaweeds are presented in Table II. All of the species are red algae and most are in the coarsely-branched functional-form group. Filamentous, finely-branched *Hypnea musciformis* showed the highest maximum growth rates under all growth conditions (Table II). In the sea (*in situ*), the highest growth rates in this species were measured in plants that were protected from herbivory by fish and nudibranchs (*Aplysia* sp.; Berchez *et al.* 1989). Although growth rates measured under low light, high nutrient laboratory conditions (*e. g.* Berchez and Oliveira 1990 b, Yokoya and Oliveira 1992) are difficult to relate to the natural environment, high growth rates have been observed *in vitro* (Table II). The highest rates were found in the filamentous forms, *H. musciformis* and *Hypnea cornuta*. The thick-leathery form *Meristiella echinocarpa* showed the lowest rate among the species in this study (Yokoya and Oliveira 1992). More growth measurements are needed for seaweeds representing different functional-form groups.

The available information about standing stocks of seaweeds from São Paulo State is shown in Table III. In general, the maximum standing stock does not correspond to the growth potentials determined from the measurements of primary productivity and growth rates. The highest biomasses (> 4 kg fw m^{-2}). have been measured in thick-leathery *Sargassum cymosum* and in the coarsely-branched *Pterocladia capillacea* (Table III). The standing crops of *Ulva* sp. and filamentous *Hypnea musciformis* are highly variable, but can accumulate biomasses in excess of 1 kg fw m^{-2} in local areas that are protected from grazing and wave action. The high biomass of the jointed-

Table II. Biomass-based growth rates (% day^{-1}) measured for some Brazilian red seaweeds, arranged according to functional-form group. Growth rates were for plants incubated in the sea ('*in situ*') on ropes or nets, for plants in an outdoor continuous-flow seawater system ('tank' culture), and in laboratory cultures ('*in vitro*'). Outdoor tank cultures were unenriched or pulsed daily with nitrate or ammonium (up to 400 μM), with or without phosphate (up to 10 μM). Laboratory cultures were in Provasoli's Enriched Seawater under 35–40 μmol quanta $m^{-2} s^{-1}$ (Yokoya and Oliveira 1992) or 32–190 μmol quanta $m^{-2} s^{-1}$ (Berchez and Oliveira 1990 b), with an 18 h : 16 h, light : dark cycle.

Species	Growth rate (% day^{-1})	Conditions	Reference
Filamentous			
Hypnea cornuta (Lamouroux) J. Agardh	38.9[c]	*in vitro*	Yokoya and Oliveira 1992
Hypnea musciformis (Wulfen) Lamouroux	2.0–14.0[a]	*in situ*	Schenkman 1980
H. musciformis	0–60.2[d]	*in situ*	Berchez *et al.* 1989
H. musciformis	0–13.6[b]	*in situ*	Berchez and Oliveira 1990 a
H. musciformis	23.2[c]	*in vitro*	Yokoya and Oliveira 1992
H. musciformis	0.5–13.4[b]	*in situ*	Berchez 1990
Coarsely-branched			
Gracilaria verrucosa (Hudson) Papenfuss	2.4–8.0[a]	*in situ*	Assad-Ludewigs 1984
G. verrucosa	0.9–4.2[b]	tank	Oliveira *et al.* 1990
G. verrucosa	12.0[c]	*in vitro*	Yokoya and Oliveira 1992
Gracilaria sp.	16.2[c]	*in vitro*	Yokoya and Oliveira 1992
Gymnogongrus griffithsiae (Turner) Martius	0.3–1.0[b]	tank	Oliveira *et al.* 1990
Pterocladia capillacea (Gmelin) Bornet *et* Thuret	0–1.1[b]	tank	Oliveira *et al.* 1990
P. capillacea	2.0–9.0[a]	*in vitro*	Berchez and Oliveira 1990 b
P. capillacea	8.5[c]	*in vitro*	Yokoya and Oliveira 1992
Solieria filiformis (Kützing) Gabrielson	0.2–1.1[b]	tank	Oliveira *et al.* 1990
Thick-leathery			
Meristiella echinocarpa (Areschoug) Cheney	8.1[c]	*in vitro*	Yokoya and Oliveira 1992

[a] $r = (\ln W_1 - \ln W_0) \cdot 100/t$, where W_1 and W_0 represent final and initial fresh weights (g) and t represents the elapsed time, in days.
[b] $r = ([W_1/W_0)^{1/t} - 1] \cdot 100$
[c] $r = \log_2 (W_1/W_0) \cdot 100/t$
[d] $r = (W_1 - W_0) \cdot 100/(W_0 \cdot t)$

calcareous red alga, *Jania* sp. (Table III), includes the calcium carbonate. Seasonal biomass data for seaweeds from Pernambuco State in northeastern Brazil have also been published (Silva *et al.* 1987). The results suggest that, in most locations, the upper limit of standing stocks is determined more by physical and biological factors (wave action, desiccation and grazing; Berchez *et al.* 1989, Oliveira and Berchez 1993) than by intrinsic growth rates.

Estimated carbon production, normalized to substrate surface area, can be calculated for four of the five experimental seaweed species based on the measured productivities (Fig. 1) and biomasses (Table III), assuming PQ = 1.00. Estimated production was highest for *Sargassum cymosum* (about 1.32 g C m^{-2} h^{-1}), due to its high standing crop, and for *Ulva fasciata* (about 0.79 g C m^{-2} h^{-1}), due to its high photosynthetic rate. Estimated production was lower for *Pterocladia capillacea* (0.69 g C m^{-2} h^{-1}) and *Hypnea musciformis* (0.22 g C m^{-2} h^{-1}) which had intermediate productivities and biomasses. These production estimates do not take into account self-shading for seaweed species with high standing crops.

The net PQ values in the five seaweed species studied were generally less than unity and the range of measured means varied from 0.42 to 1.01 (Figs 2 and 3). The PQ did not differ significantly among seaweeds representing the three taxonomic divisions and three functional-form groups (Fig. 2, $P < 0.05$). In *Ulva fasciata* and *Pterocladia capillacea*, PQ decreased over a period of several days to two weeks (Fig. 3, $P < 0.05$); *Sargassum cymosum* did not show significant variation from one week to the next (Fig. 3, $P < 0.05$).

The effect of N- and P-nutrient enrichment on net photosynthesis (oxygen evolution) in three seaweeds is shown in Figure 4. Both *Ulva fasciata* and *Pterocladia capillacea* responded to nutrient enrichment by increasing the rate of net photosynthesis compared to the controls; photosynthesis in *Sargassum cymosum* was not affected by nutrient enrichment. The PQ values were unaffected by nutrient enrichment (Fig. 5). Although shade adaptation to 19% of the incident light increased net photosynthesis in *P. capillacea* from 131 ± 20 to 184 ± 24 μmol O_2 g dw^{-1} h^{-1} (mean ± SD, n = 3) when measured under full inci-

Table III. Standing stocks (biomass, as dry weight or fresh weight) of seaweeds from São Paulo State, Brazil, arranged according to functional-form group. All measurements were from the zone in which the species normally occurs. nd = dry weight : fresh weight conversion factor not specified.

Species	Biomass ($g\ m^{-2}$)		Reference
	fw	dw	
Sheet			
Dictyopteris delicatula Lamouroux	nd	21–135	Paula 1978
Rhodymenia sp.	40–116	nd	Johnscher-Fornasaro *et al.* 1984
Ulva sp.	6–1550	nd	Johnscher-Fornasaro *et al.* 1984
Filamentous			
Bryocladia sp.	29–790	nd	Johnscher-Fornasaro *et al.* 1984
Ceramium sp.	2–144	nd	Johnscher-Fornasaro *et al.* 1984
Chaetomorpha antennina (Bory) Kützing	31–60	nd	Johnscher-Fornasaro *et al.* 1984
Cladophora prolifera (Roth) Kützing	10–34	nd	Johnscher-Fornasaro *et al.* 1984
Enteromorpha sp.	4–270	nd	Johnscher-Fornasaro *et al.* 1984
Hincksia (= *Giffordia* sp.)	31–70	nd	Johnscher-Fornasaro *et al.* 1984
Hypnea musciformis (Wulfen) Lamouroux	81–1235	13–190	Schenkman 1989
Hypnea sp.	4–1000	nd	Johnscher-Fornasaro *et al.* 1984
Coarsely-branched			
Gigartina teedii (Roth) Lamouroux	nd	103–278	Braga 1985
Gracilaria ferox J. Agardh	60–351	nd	Paula 1978
Laurencia scoparia J. Agardh	92–488	nd	Paula 1978
Pterocladia capillacea (Gmelin) Bornet *et* Thuret	750–2500	nd	Oliveira Filho and Sazima 1973
P. capillacea	1613–4500	215–600	Berchez 1985, Oliveira and Berchez 1993
Pterocladia sp.	2–420	nd	Johnscher-Fornasaro *et al.* 1984
Thick-leathery			
Sargassum cymosum C. Agardh	nd	200–802	Schenkman 1989
S. cymosum var. *cymosum*	2070–4511	391–853	Paula 1978, Oliveira Filho and Paula 1979
S. cymosum var. *nanum* Paula *et* Oliveira	1109–2531	210–478	Paula 1978, Oliveira Filho and Paula 1979
Sargassum vulgare C. Agardh	91–132	nd	Johnscher-Fornasaro *et al.* 1984
Jointed-calcareous			
Jania sp.	2–1580	nd	Johnscher-Fornasaro *et al.* 1984

dent sunlight ($P < 0.05$), it had no effect on the value of PQ. The PQ for shade-adapted *P. capillacea* (0.52 ± 0.10; mean ± SD, n = 3) was not significantly different from the PQ for control thalli (0.42 ± 0.11).

Based purely on stoichiometric and theoretical considerations (Williams *et al.* 1979, Williams and Robertson 1991), PQ values of less than unity were unexpected. Simultaneous measurements of oxygen exchange and CO_2 uptake are not usually conducted on marine macroalgae. Measurements of oxygen evolution and ^{14}C uptake in young sporophytes of *Eisenia arborea* Areschoug yielded PQs ranging from 0.96 to 1.32 (Arnold 1980). Similar methods used to measure PQs in five species of brown seaweeds endemic to the Antarctic gave PQs that ranged from 1.1 to 2.7 (Thomas and Wiencke 1991). The use of constant-pressure manometry for oxygen evolution and ^{14}C uptake yielded PQs that ranged from 1.2 to 1.3 for *Gracilaria verrucosa* (Hudson) Papenfuss and from 1.2 to 1.4 for *Bostrychia binderi* Harvey (Hoffman and Dawes 1980). Constant-volume manometric measurements of PQs in fourteen species of seaweeds (Buesa 1980) resulted in an average PQ of 1.19 (range: 1.00 to 1.37) in nine species of green algae. In two brown algae, the average PQs were 1.38 and 1.26; in three red algae, the average PQs ranged from 1.15 to 1.46.

There are also reports of PQs of less than unity. An oxygen electrode and a pH-stat have been used to measure oxygen evolution and CO_2 removal at constant pH and alkalinity by four freshwater macrophytes (Pokorný *et al.* 1989). The PQs ranged from 0.48 to 1.18 (average: 0.77) in *Cabomba caroliniana* A. Gray and from 0.12 to 0.90 (average: 0.50) in the charophyte *Nitella* sp. For three other species of vascular plants, the PQs ranged from 0.93 to 1.32 in *My-*

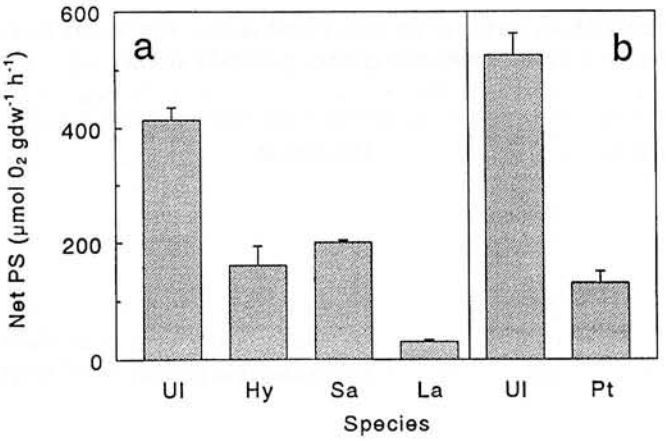

Fig. 1. (a) Net photosynthesis (oxygen evolution) for several seaweed species on cloudy days (average PAR about 350 to 650 µmol quanta m^{-2} s^{-1}). Mean ± SD (n = 3). The species are arranged from left to right according to functional-form group: sheet-like (Ul = *Ulva fasciata*), filamentous (Hy = *Hypnea musciformis*), coarsely-branched (La = *Laurencia papillosa*, Pt = *Pterocladia capillacea*), and thick-leathery (Sa = *Sargassum cymosum*). (b) Net photosynthesis on sunny days (average PAR during incubation about 970 to 1260 µmol quanta m^{-2} s^{-1}).

riophyllum salsugineum Orchard, from 0.11 to 1.82 in *Lagarosiphon major* (Ridley) Moss, and from 1.04 to 2.24 in *Egeria densa* Planchon. In the kelp *Laminaria longicruris* de la Pylaie, PQs varied from 0.77 to 1.57 over an annual cycle (Hatcher *et al.* 1977). At high oxygen concentrations, the PQs in the marine phytoplankton species *Pavlova lutheri* (Droop) Green and *Glenodinium* sp. ranged from 0.1 to 1.0 (Burris 1981).

Experiments designed to simulate a diurnal incubation, in which the incident photon flux density was increased and decreased stepwise, have been used to investigate the diurnal course of variation in the PQ in *Ulva* sp. (Kenney 1985). Using pH and oxygen electrodes, the PQs were measured hourly and ranged from 0.5 to 1.5. In this study, the oxygen production rate was found to decrease as a function of ambient oxygen concentration over a range between 25% and 250% of saturation. This oxygen-sensitive decrease in oxygen production rate was associated with PQ values of less than unity. Similar methods yielded PQs ranging from 0.93 to 3.13 (mean = 1.57) for eight species of marine macrophytes, including *Ulva californica* Wille, the seagrass *Phyllospadix torreyi* Watson, and six species of articulated coralline algae (Kindig and Littler 1980). When these macrophytes were exposed to sewage effluent, PQs varied from 0.60 to 2.61 (average = 1.33; Kindig and Littler 1980). During the recovery from sewage exposure, the PQs ranged from 0.26 to 1.99 (average = 1.24). Values of PQ less than unity were associated with the more sewage-tolerant species (Kindig and Littler 1980).

The decrease in photosynthetic oxygen evolution, relative to CO_2 uptake, that occurs when algal thalli [the green alga *Ulva lobata* (Kützing) Setchell *et* Gardner and the brown alga *Colpomenia sinuosa* (Roth) Derbès *et* Solier] are held in small vessels was noted by Littler (1979) and related to increased ambient oxygen levels. An inhibitory effect of high oxygen concentration on photosynthetic oxygen evolution has also been found in several species of seaweeds from New Zealand (Dromgoole 1978) and in the red macroalga *Chondrus crispus* Stackhouse (Brechignac and André 1985). A possible explanation for oxygen sensitivity of photosynthesis and PQ less than unity would be photorespiration (glycolate production) as a result of the oxygenase activity of RuBP carboxylase at high ambient oxygen concentrations. Even in this case, the complete metabolism of glycolate via the photorespiratory carbon oxidation cycle (if present) to produce CO_2 and, ultimately, carbohydrate would cause the overall PQ to approach unity. The extent to which photorespiration occurs in marine macroalgae remains controversial (Lobban and Har-

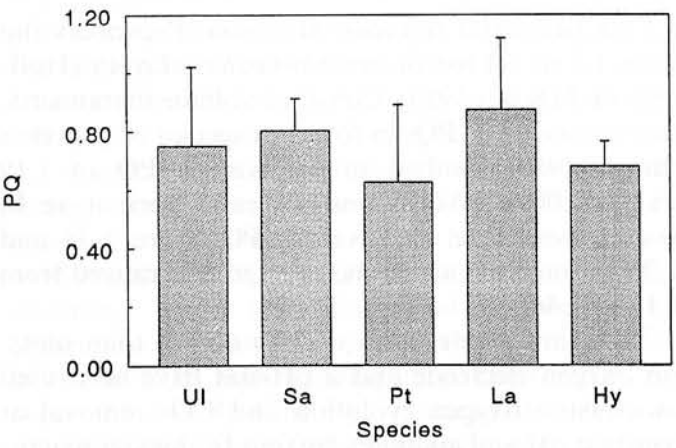

Fig. 2. Photosynthetic quotients (PQ = molar ratio of O_2 release to CO_2 uptake) for five seaweed species. Species as in Figure 1. Pooled data from experiments on four days. Mean ± SD ($3 \leq n \leq 9$).

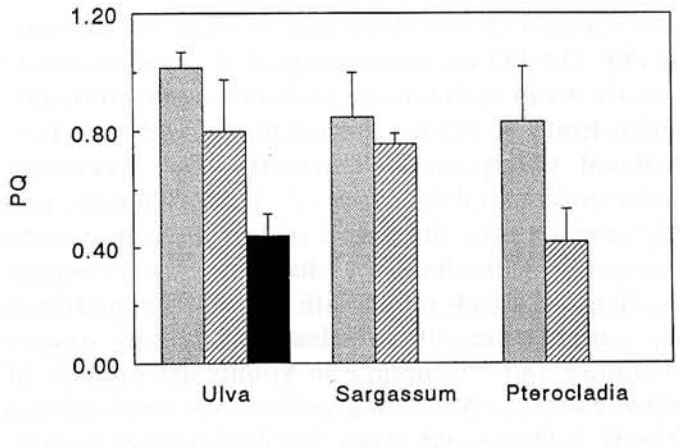

Fig. 3. Week-to-week variation in PQ for three seaweed species (Ulva = *U. fasciata*, Sargassum = *S. cymosum*, Pterocladia = *P. capillacea*). Stippled, crosshatched, and solid bars represent successive weekly measurements. Mean ± SD (n = 3).

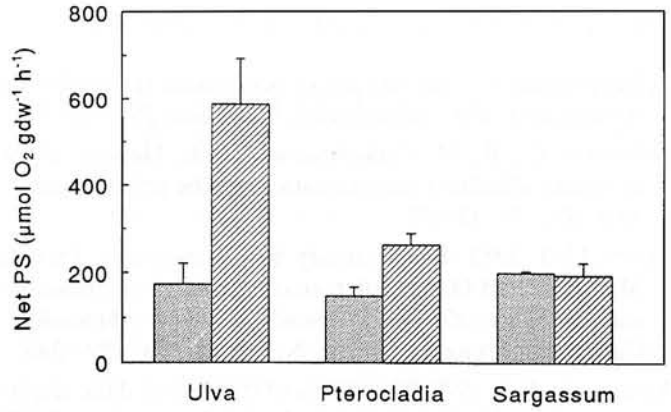

Fig. 4. Net photosynthesis (oxygen evolution) for three seaweed species in response to nutrient (nitrate + phosphate) enrichment. Crosshatched bars: enriched thalli; stippled bars: control. Mean ± SD (n = 3). Species as in Figure 3.

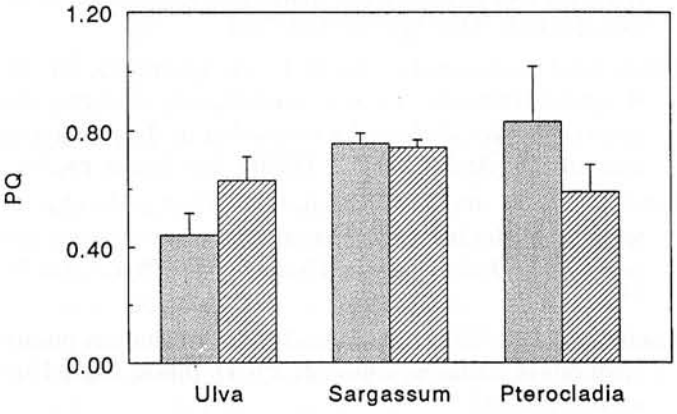

Fig. 5. Effect of N- and P-nutrient enrichment on PQ in three seaweed species. Crosshatched bars: enriched thalli; stippled bars: control. Species as in Figure 3. Mean ± SD (n = 3).

rison 1994, Reiskind *et al.* 1989). In the natural environment, while the plants are submerged, environmental conditions (fairly constant oxygen and total inorganic C concentrations) would not favor photorespiration. Oxygen concentration did not affect photosynthesis in the brown rockweed *Ascophyllum nodosum* (Linnaeus) Le Jolis (Johnston and Raven 1987) and similar results were reported for the red alga *Palmaria palmata* (Linnaeus) Stackhouse (Cook and Colman 1987). Significantly, both of these species showed evidence of a CO_2 concentrating mechanism.

Determination of the PQ may be sensitive to the techniques used to measure photosynthesis. During measurement, it is desirable to minimize environmental changes surrounding the algal thallus. Constant-pressure manometric techniques (*e. g.* Hoffman and Dawes 1980) allow photosynthesis (oxygen evolution) to be measured while the concentrations of O_2 and CO_2 in the low-volume liquid phase of the reaction flask remain fairly constant. Excess dissolved oxygen enters the gas phase and constant carbon dioxide is maintained via a chemical reaction in a side-arm flask (Dawes 1985). Under these conditions, sustained oxygen production would give PQ values ≥ unity, in agreement with theoretical predictions (Williams *et al.* 1979, Williams and Robertson 1991). When photosynthesis is measured in sealed vessels without a gas phase, using oxygen/pH electrodes or pH-stats (*e. g.* this study, Pokorný *et al.* 1989), conditions in the incubation medium (particularly oxygen concentration) are continuously changing and the resulting PQ values are often less than unity. Measurements of ^{14}C assimilation yield values that are probably between gross and net photosynthesis (Peterson 1980). The PQs based on the ^{14}C technique depend on whether gross or net oxygen production is used for the calculation.

Conclusion

The functional-form model provides a useful conceptual framework for predicting rates of photosynthesis and growth in seaweed communities in many different marine environments. Rates of production, normalized to biomass and to area of substrate, are now becoming available for inclusion in ecological models. The fact that maximum standing stocks of Brazilian seaweeds did not correspond to the growth potential determined from measurements of photosynthesis and growth suggests the importance of physical and biological interactions in structuring these seaweed communities.

Although the value of PQ is based on measurements of primary productivity, there was no correlation between PQ and the functional-form or taxonomic group to which a species belongs. Regardless of the measurement technique used, PQ values seem to show considerable variation. In this study, they were usually below the theoretically expected values of 1.0 to 1.3. A survey of the limited number of PQ determinations in the literature yielded values that ranged both above and below the expected values. Under the circumstances, whenever direct measurements of CO_2 uptake are not available, we recommend the continued use of PQ = 1.00 to facilitate interconvertibility in comparisons between studies of primary production by seaweeds.

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