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INTERTIDAL AND UPPER SUBTIDAL ZONES OF THE
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**E. A. TITLYANOV, K. Y. BIL', P. V. KOLMAKOV,
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PHOTOSYNTHESIS IN COMMON MACROPHYTE SPECIES IN THE INTERTIDAL AND UPPER SUBTIDAL ZONES OF THE SEYCHELLES ISLANDS

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E.A. Titlyanov^{*}, K.Y. Bil' ^{**}, P.V. Kolmakov^{*}, A.A. Lapshina^{*} and T.R. Pärnik^{***}

ABSTRACT

Photosynthetic capacity, light curves of CO₂ assimilation and the path of carbon in photosynthesis of common marine macroalgae and seagrasses of the Seychelles Islands were studied by the radiocarbon method. Intertidal and upper subtidal species of marine plants have similar photosynthetic capacities but the latter decrease considerably in species growing below 25 m when the photosynthetically active radiation (PAR) is less than 15% of incident surface PAR (PAR_s). All macrophytes studied exhibited daily variations in the photosynthetic light curves. Photosynthetic light saturation values (I_k) and the angle of the initial slopes (α) of light curves increase from morning to midday and decrease again towards evening. During the evening, photosynthesis in intertidal macroalgae and seagrass was inhibited considerably by PAR greater than 250 μE·m⁻²·s⁻¹. When tropical species of marine plants became adapted to lower light intensities at great depths or in shaded habitats, the chlorophyll and phycoerythrin contents increased as did the efficiency of the use of low light (<60 μE·m⁻²·s⁻¹). Some species increased their photosynthetic capacity when shaded. Tropical seagrasses exhibited the same adaptive reaction to light as seaweeds; however, the range of variation in the structure and function of their photosynthetic apparatus was narrower than in algae.

INTRODUCTION

Our knowledge of photosynthetic productivity of benthic seaweeds and seagrasses of the tropical zone lags significantly behind the knowledge for temperate waters (Lüning 1985). Recently, Mark and Diane Littler, with coworkers, published a series of reviews and experimental papers devoted to the study of primary production and factors that control it in macroalgae of subtropical and tropical latitudes, and thus accelerated knowledge in this field of research (Littler 1973a, b, 1980, Littler et al. 1983, 1986, 1988, Littler, Kauker 1984, Jensen et al. 1985, Lapointe et al. 1987). These authors standardized the procedure of measuring the primary production of macroalgae (Littler 1979, Littler and Arnold 1985) and used this parameter for analyzing numerous species and morphological forms of algae from a wide range of environments on subtropical and tropical shores, mainly on tropical reefs in the Atlantic Ocean (Littler et al. 1983, 1986, 1988, Littler and Littler 1984, 1988, Jensen et al. 1985, Lapointe et al. 1987) and the warm temperate Pacific Ocean (Littler and Arnold 1980, 1982, Littler and Littler 1980). These and other authors (Buesa 1977, Dawes et al. 1987, Bach 1979,

* Institute of Marine Biology, Far East Branch, USSR Academy of Sciences, Vladivostok, 690032, USSR

** Institute of Soil Sciences and Photosynthesis, USSR Academy of Sciences, Pushchino, Moscow Region, 142292, USSR

*** Institute of Experimental Biology, Estonian Academy of Sciences, Harku, 203051, Estonia

Duraco and Dawes 1980, Davis and Dawes 1981, de Ruyter van Steveninck and Breeman 1981, O'Neal and Prince 1982) demonstrated considerable fluctuations in the primary production of tropical macrophytes. The primary net production of individual macrophytes on a coral reef ranges from 0.03 to 14 mg C fixed·g dry wt⁻¹·h⁻¹, or 0.6 to 15 mg C fixed·g ash-free dry wt⁻¹·h⁻¹ (Littler and Kauker 1984, Jensen et al. 1985, Lapointe et al. 1987, Littler et al. 1988).

The net algal production in the tropics depends both on the internal conditions of the plants, which determine their productive capacity, and on external environmental factors. The most significant internal factors are seasonal variability of plants (algae have a 7-fold season-dependent difference in their production, Littler et al. 1979, Littler and Arnold 1980, O'Neal and Prince 1982), the age of thalli or their parts (Chapman 1962, Littler and Arnold 1980, Littler and Kauker 1984), reproductive status of thalli (Littler and Arnold 1980) and the existence of different growth forms (such as fine filamentous thalli, massive and crustose forms, Peterson 1972, Littler and Arnold 1980, Littler and Kauker 1984, Littler et al. 1988). Important external factors include high temperatures and desiccation of intertidal macroalgae (Littler and Arnold 1980, Mathieson and Dawes 1986), chemical characteristics of waters, (Lapointe et al. 1987, Littler et al. 1988), and irradiance (Peterson 1972, Littler and Arnold 1980).

The multidisciplinary Soviet-American expedition, aimed at the study of seaweeds and seagrasses of the Seychelles Islands, provided an opportunity to widen our knowledge of the productivity physiology of tropical macrophytes. We established two objectives:

1. To conduct research on mechanisms of adaptation of marine plants to light intensity in tropical conditions and to elucidate their dependence on the light factor and selected morpho-functional features of plants.
2. To determine the photosynthetic capacity of the most common macrophyte species and growth forms of the intertidal and upper subtidal zones of tropical island shelves.

STUDY AREAS

The capacity and photosynthetic function in marine plants inhabiting tropical environments was studied on islands of the Seychelles and Amirantes Groups: Cœtivy, Farquhar, Aldabra, Desroches, Providence, African Banks, Saint-Joseph, Cosmoledo, Astove and Praslin. Plant material was collected at depths of 0 to 50 m under different conditions of irradiance, temperature, water motion and sedimentation (Table 1).

Seaweeds and seagrasses of the intertidal zone of Aldabra, Cosmoledo and Cœtivy were subjected to stressful environments: e.g., growing mainly in intertidal pools or in dense mats on boulders and dead corals. Intertidal pools warmed to 35-37°C during the sunny midday period and algae on the mat surface received about 1200-1400 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PAR. Typical pools had somewhat increased salinity (to 34.9 ppt), the pH reached 8.75 ± 0.15 , the PO_4 content was 0.46 ± 0.05 ; P_{org} , 0.10 ± 0.03 ; NO_2^- , 0.34 ± 0.15 ; NH_4^+ , 1.64 ± 0.81 ; NO_3^- , 2.95 ± 1.76 ; N_{org} , 19.2 ± 3.33 μM (Novozhilov et al. 1989).

In the subtidal zone, the photon flux density (PFD) was less intensive. At the depth range of 30 to 40 m, PFD averaged 8-12% PAR_s, which in the middle of a sunny day ranged from 60-90 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Between depths of 2 to 12 m, we observed a considerable precipitation of coral sand and silt. Water temperature decreased gradually from 28°C at the surface to 26°C at 30 m deep. At a depth of 40 to 50 m, temperatures were lower (23-25°C) and only on Cœtivy did temperatures fall to 17-20°C at 40 m depth (Novozhilov et al. 1989). The content of dissolved nutrients in the bottom portion of

the upper subtidal zone (down to 30-40 m deep) differed little from that in the surface water layer, but values were much lower than in intertidal pools and had the following average values for all the islands: PO_4^{---} , 0.225 ± 0.119 ; P_{org} , 0.226 ± 0.178 ; NO_2^- , in traces; NH_4^+ , 0.35 ± 0.12 ; NO_3^- , 0.46 ± 0.37 ; N_{org} , $10.2 \pm 3.5 \mu\text{M}$. An increased content of inorganic phosphorus, PO_4^{---} , $0.45 \pm 0.08 \mu\text{M}$ was found near Cöetivy and Farquhar Is. deeper than 40 m (Novozhilov et al. 1989).

In the subtidal zone, above 20 m, macroalgae often grew among the seagrass *Thalassodendron ciliatum* and at the base of old corals. Sometimes they formed compact mats on dead corals. This means that at intermediate depths, as in the intertidal zone, marine plant communities experience a strong self-shading. At 35 m, some algae occurred as epiphytes on stalks and leaves of *T. ciliatum*, or attached to coral pebbles on sites devoid of seagrass. *T. ciliatum* did not form a continuous carpet at 33 m, but was scattered. Deeper than 35 m, seagrass beds were reduced or absent and algae colonized coral pebbles as sparse beds or individuals not shading each other.

METHODS AND MATERIALS

To analyze the productive capabilities of algae and to study their photosynthesis, we attempted to select samples not shaded by other plants. Algal shading or self-shading is shown in Table 1 in average PAR values, received by plants in their habitats. We collected plants irrespective of "life forms", Table 1 gives qualitative characteristics of the habits and the thickness of algal thalli.

When sampled from the bottom, the plants were placed (still underwater) in semi-transparent vessels and brought to the ship within 1-2 hours where they were transferred into aquaria with running seawater, biological filtering and intensive air bubbling (Butorin et al. 1980). The amount of the incident solar radiation was controlled by neutral filters made of white linen. The plants remained in the aquaria, until the next day when they were analyzed. Plants selected for analysis appeared healthy and pigmentation was typical of their natural habitat. Small plants (3-4 cm long) were measured whole, but only the middle part was taken from larger macrophytes. In *Thalassodendron ciliatum*, we analyzed mature leaves (the 2nd and the 3rd outward from the young central leaf). Prior to analysis, the plants, still underwater, were carefully freed of epiphytes under a dissection microscope and washed in fresh filtered seawater.

In situ measurements of photosynthetically active radiation.

For underwater measurements of PAR we used an autonomous irradiance meter with a photodiode of linear performance within a broad light range. In front of the photodiode a 300-740 μm -pass range compound light filter was installed to measure PAR. The limits of photon flux density measurement were within 0.24 to 3800 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. The extent of PAR attenuation within the water column was measured throughout the depth range (Titlyanov et al. 1988).

A surface irradiance meter (Yanishevsky's pyranometer) was used for daily continuous registration of the total solar radiation incident to the sea surface (PAR_s). The amount of PAR_s during the daytime was taken equal to 50% of the total solar radiation incident to the surface of the sea (Tooming and Gulyaev 1967) and corrected for reflection by the water surface: 3% in the midday, 20% during the first and the last hours of the light day and 10% at the second and penultimate hours of the day. Moreover, from the attenuation of the PAR by the water column in coral habitats and from the PAR_s values during a day, we calculated the underwater PAR at a given depth at any time of the day both in absolute values of photon flux density, $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, and in PAR_s percentage (Jerlov 1976). PAR measurements in algal growth were done with the same underwater photometer, mainly at 1000-1200 local time.

Determinations of pigment contents.

The plant material was ground in a porcelain mortar with glass sand and 90% acetone. Algal and seagrass chlorophylls were extracted with acetone. Chlorophyll content in acetone extracts was measured on a Shimadzu MPS-5000 spectrophotometer. The a and b chlorophyll contents in extracts were assessed using the Vernon formula (Vernon 1960), chlorophyll c_2 , by the formula of Jeffrey and Hamphrey (1975), chlorophyll a in red algae was determined by Lie's method (Lie 1978). Phycoerythrin was extracted from red algae with seawater (Lie 1978) and its concentration in the solution was determined as described in O'Carra (1965).

Radiocarbon determination of dependence of photosynthesis on light (P_s vs. I curves)

The radiocarbon method was used to measure the rate of net photosynthesis of macrophytes at different light intensities (Kolmakov and Tarankova 1978). The experiments were run in a thermostated chamber, 440 ml in volume, equipped with light filters of different light transmission. Water temperature in the chamber was maintained at 27-28°C. The algae were placed in a chamber filled with seawater onto special grids after which the chamber was closed with a set of neutral light filters and heat filter (0.2% solution of $CuSO_4$). A high-pressure luminescent lamp was used as the source of light. Under various light filters, in the chamber cells, PAR was equal to 8, 15, 60, 160, 250, 380 $\mu E \cdot m^{-2} \cdot s^{-1}$.

At the beginning of the experiment the plants were kept in running seawater for 20 min under the light filters. This period was sufficient to obtain a stabilization of physiological processes in the plants transferred into experimental conditions (Titlyanov 1978). The water was then substituted for radioactive carbonate dissolved in seawater (2.5 mM, the initial concentration of HCO_3^- in seawater was 2.0-2.3 mM), specific radioactivity of 100 MBk·ml⁻¹. After a 20 min exposure to light and continuous stirring of water in the chamber on a laboratory shaker, the samples were taken out, washed thoroughly with seawater for 15 min, fixed at 105°C, and dried to constant weight at 60-70°C. The material was not treated with acid to remove radioactive inorganic carbon, assuming that the amount left in the thalli was about equal to the amount of non-radioactive carbon assimilated during the first minutes of exposure. The samples were dried to a constant weight, weighed, ground on a micro-mill and stuffed into cells. The final preparation was a cylindrical tablet 2 mm thick and 0.5 cm² in area. The radioactivity in these tablets (in a layer of full radioabsorption) was determined by the end-type counter T-25-BFL on a recounting instrument with 5% measuring efficiency. The rate of net photosynthesis was calculated in mg CO₂·g dry wt⁻¹·h⁻¹ by the following formula:

$$P = \frac{N_r}{K_r \cdot a_c \cdot t}, \text{ where}$$

N_r , was the radioactivity of the material, emissions·min⁻¹;

a_c , the specific radioactivity of the introduced carbonic acid MBk·mg CO₂⁻¹;

t , the exposure time, h;

K_r , coefficient, accounting for the physical properties of the tablet of material and for the specific features of the counter (Bykov and Koshkin 1969).

The coefficient K_r was determined experimentally. For this purpose, we took a weighed amount of algae (in g) with a certain amount of radioactive carbon (A, MBk). In tablets with the layer of full radioabsorption the obtained radioactive material was counted in emissions·min⁻¹. Then, according

to the formula,

$$K_r = \frac{N_r \cdot m}{A}$$

the coefficient rate was found for the specific plant material, calculated on the recounting instrument. In our experiments, depending on the properties of the material, the K_r coefficient varied from 43.1 to 51.0 emissions·g⁻¹·min⁻¹·MBk⁻¹. The experiments were conducted in triplicate, with double determinations of sample radioactivity.

Analysis of photosynthetic products

The plant samples were placed into an exposure chamber filled with filtered seawater containing radioactive bicarbonate with the specific radioactivity of 550 MBk/mmol H¹⁴CO₃⁻. The algae were exposed with H¹⁴CO₃⁻ to PAR of 300 μE·m⁻²·s⁻¹ for 15, 60 or 300 s. After exposure, the samples were immediately fixed with boiling 80% ethanol and acidified with 5% formic acid. The samples were ground and subjected to full extraction of the alcohol-water-soluble organic fraction, where the extent of radioactivity was determined as emissions·min⁻¹ on a standard counting device (see above). The photosynthetic rate was calculated by the formula:

$$P = \frac{n_1 \cdot V/v + n_2 \cdot M/m}{a_c \cdot t \cdot W \cdot S}, \text{ where}$$

P is the rate of photosynthesis, μmol CO₂·g dry wt⁻¹·h⁻¹;

n_1 , radioactivity of the volume (v , cm³) of a sample of the alcohol-water-soluble fraction, emissions·s⁻¹;

V, the total volume of alcohol-water-soluble fraction, cm³;

M, the total weight of insoluble residual, g;

S, counting efficiency of the radiometric instrument, imp·s⁻¹·MBk⁻¹;

a_c , the specific radioactivity, MBk·mmol CO₂⁻¹;

t, the time of exposure, h;

W, the weight of tested material, g dry wt;

n_2 , radioactivity of the weight (g) of a sample of insoluble residual in emissions·s⁻¹.

The composition of metabolic products was determined by two-dimensional ascending chromatography in the solvent systems described earlier (Bil' et al. 1981). The amount of individual radioactive products, determined chromatographically, was expressed in % of the total.

Adaptation of algae to light and dissolved inorganic nutrients

Seaweeds sampled from the reef-flat intertidal zone, i.e. *Thalassodendron ciliatum* and its epiphytes *Ulva rigida* and *Geldiopsis* sp., were placed in an aquarium with about 30-20% PAR, and in two aquaria with artificial illumination having PAR of 240 and 90 μE·m⁻²·s⁻¹, respectively. The plants were evenly illuminated and did not shade each other in the aquaria; the water temperature was maintained at 28°C with a photoperiod of 12 hours. After acclimation of the plants for 10 days, the chlorophyll and phycoerythrin contents were determined for one group of plants and light dependence of photosynthesis was analyzed. Another group of plants was fertilized with dissolved inorganic nutrients for two hours under the above light conditions. The final concentrations of salts were 10 mM for NH₄Cl and 1 mM for KH₂PO₄. Then the plants were placed back in the aquaria and kept there for another three days in the same light regimen before analysis of the pigment

content and determination of the rate of photosynthesis.

RESULTS

Pigment content of macrophytes in relation to depth and light

Table 2 shows the results of analyses for pigment content in algal thalli and leaves of seagrasses of the Seychelles Islands sampled from depths from 0 to 50 m on non-shaded sites. In plant associations at shallow depths, it is difficult to find a single plant that is not self-shaded or shaded by other plants in thick growths. Since precise determinations of light absorption by algal associations present technical difficulties, light was measured only approximately (Tables 1, 2, 3). As depth increased from 0 to 37 m, the chlorophyll contents of mature leaves of the seagrass *Thalassodendron ciliatum* increased by 20-30% (Table 2). At a depth of 2-3 m, the chlorophyll content of *Thalassia hemprichii* is 15-20% higher than in material from the intertidal zone. At a depth of 10 m, the content of chlorophyll a in the green alga *Caulerpa cupressoides* showed a 30% increase over intertidal levels. At its maximal depth, about 50 m, *Caulerpa sp.* showed a 50%-decrease in the chlorophyll content compared with material from 25 m.

Table 2 also compares the pigment contents in groups of algae growing at different depths and united by their taxonomic affinity and "life form" (Littler et al. 1983). Laminar and filamentous forms of green algae from the intertidal zone had 50% more pigments than material from depths of 2-4 m, but at 25-30 m, the pigment content was 3.7 times higher than in intertidal forms. Red algae with filamentous branched thalli are also capable of concentrating chlorophyll and phycoerythrin in deep waters; e.g., *Wrangelia argus* from 30 m contained 3.5 times more chlorophyll a and 1.8 times more phycoerythrin than five other shallow-water species of Rhodophyta. It is interesting to examine the distribution of pigments within thalli of *Sargassum cristaefolium* sampled from algal thickets. Here, as a result of intraspecific-shading, the illumination of phyllodes decreased from the top to the base from 100% to 5% PAR_s, whereas the pigment content in phyllodes increased 2.5 times. With shading, the chlorophyll concentration increased also in the pneumatocysts of *Sargassum* plants. Calculating the average content of the sum total of chlorophylls a and b in seagrasses in mg·g wet wt⁻¹, we obtain the following depth-dependent distribution: 1.4±0.8 for 0 m, 1.6±1.2 for 0.5-2m, 1.7±1.0 for 10-25 m, and 1.8±1.2 mg·g dry wt⁻¹ for 30-50 m. Thus, from 0 to 30-50 m deep, all algal and seagrass species showed a mean 36% increase in chlorophyll content.

Light dependence of photosynthesis during light hours

Variations in the dependence of net photosynthesis on light (P_s vs. I curve) during the day were studied in 13 species at 0700-0900, 1000-1300, and 1600-1800 local time. To compare patterns of photosynthetic dependence on light for all of the species examined, the rates were recalculated in relative units; i.e., 100% corresponded to the maximal rate of photosynthesis obtained during the day in plants of each species investigated at a particular depth. All plants were divided into three groups: those from shallow depths of 0-2 m, from medium depths of 10-15 m and from maximal depths of 25-50 m. For each plant group, the average light curves of photosynthesis were plotted in relative units for the morning, midday and evening (Fig. 1). A majority of the plants showed changes in P_s vs. I curves during the day. From morning to midday hours, photosynthetic light saturation values (I_k) and the initial slope α of each P_s vs. I curve or the efficiency of the use of weak light increased. The first half of the day showed a considerable increase (50-70%) in photosynthetic capacity. During the evening hours, the opposite patterns were observed: the level of photosynthesis on the light curve plateau decreased again to the morning rates, or lower in most cases, and the angle of the initial slope of P_s vs. I curve also diminished. Plants inhabiting different depths have different kinds of

daily changes of their P_s vs. I curves. For example, in the evening hours, a photon flux density of $250 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ inhibits the photosynthesis of deep-water plants, and at $380 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, the rate of photosynthesis is nearly half of the maximal rate at these hours. In plants from the intertidal zone, the initial linear slope of the light curve (α) decreases less than in deep-water plants.

The variations described above in light-dependence of photosynthesis were also observed in the phyllodes of *Sargassum cristaefolium*, taken from differently illuminated parts of the plant (Fig. 2). Here, as with depth dependence, a decrease in phyllodes illumination entails the loss of photosynthetic resistance to increased light intensity in the evening. In the shaded parts of plants, the change in the slope of α is greater during the day.

Fig. 3 depicts changing photosynthetic efficiencies in the use of incident light of different intensities during the day for deep-water samples of the seagrass *Thalassodendron ciliatum* and two green algae. All plants exhibited the same patterns. The photosynthetic efficiency of the use of weak light ($15 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) increased from 0700 to 1100-1300 by 60-70%. Following 1100 to 1300, the efficiency of weak light use was at its greatest. The midday light of $15 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ was sufficient for deep-water plants to reach 70-80% of their maximum photosynthetic rates. After 1700, the efficiency of the use of weak light dropped to that equivalent to 0700-0800. The efficiency of using light bright enough to achieve photosynthetic saturation ($150 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) increased gradually to 1300 and then decreased considerably towards the evening, however always remaining higher than the morning rates. Inhibition of photosynthesis in deep-water plants by high levels of photon flux density ($\text{PAR} > 380 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) may begin as early as 1300, by evening (1700) photo-inhibition was significant in *Halimeda gracilis* and especially in *Caulerpa* sp.

Capacity of photosynthesis in tropical marine plants at different depths

Measurement of the light dependence of photosynthesis during the day showed that tropical marine plants reach their highest capacities at midday (1200-1300). Plants of the intertidal zone did not differ significantly in the levels of maximum primary production, whereas subtidal plants exhibited considerable differences in the maximum rate of photosynthesis (Fig. 4). The highest photosynthetic capacities were observed in marine plants down to depths of 20-25 m, i.e., to 10% PAR_s . The highest production rates were $17.9 \text{ mg CO}_2\cdot\text{g dry wt}^{-1}\cdot\text{h}^{-1}$ for *Valonia fastigiata* at a depth of 25 m; $12.0 \text{ mg CO}_2\cdot\text{g dry wt}^{-1}\cdot\text{h}^{-1}$ for the upper thallus of *Sargassum cristaefolium*; $9.3 \text{ mg CO}_2\cdot\text{g dry wt}^{-1}\cdot\text{h}^{-1}$ for *Laurencia corymbosa* at a depth of 10 m and $9.1 \text{ mg CO}_2\cdot\text{g dry wt}^{-1}\cdot\text{h}^{-1}$ for *Thalassodendron ciliatum* at a depth of 23 m. The lowest productive capabilities, i.e., 2.0 to 3.0 $\text{mg C}\cdot\text{g dry wt}^{-1}\cdot\text{h}^{-1}$, were found in *Codium tomentosum*, *Caulerpa brachypus*, *Halimeda opunta* and *Hypnea spinella*.

Variations in photosynthetic light curves P_s vs. I and productive capabilities as a function of depth

Four species of marine plants were compared growing at depths between 0 and 50 m (Fig. 5). Considerable differences in the form of the P_s vs. I curve and productive capabilities of photosynthesis were found in mature leaves of the seagrass *Thalassodendron ciliatum*. The photosynthetic capacity increased with depth up to 25-30 m, but decreased at the maximum depth (33-37 m) and accounted only for 30% that of shallow sites. With increasing depth, the initial slope of the P_s vs. I curve (α) more than doubled when PAR diminished from 90 to 10% PAR_s and was lower at greater depths. In specimens of *T. ciliatum* inhabiting the greatest depths, photosynthetic inhibition by light exceeding $250 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. *Laurencia corymbosa* also showed higher photosynthetic capacity and a steeper initial slope of the P_s vs. I curve when PAR decreased from 90 to 30% PAR_s with depth. A similar depth-dependent decrease in PAR caused negligible but

opposite changes in the light dependence of photosynthesis in the green alga *Caulerpa cupressoides*. In habitats with less than 5% PAR_s, *Caulerpa sp.*, growing abundantly at depths of 40-50 m near Astove island, loses its net photosynthetic abilities.

Acclimation of tropical marine plants to PAR under experimental conditions

Three plant species were used in this experiment, the seagrass *Thalassodendron ciliatum*, occurring on the reef flat in the intertidal zone and two of its epiphytes, *Ulva rigida* and *Gelidiopsis* sp. We tested the effect of lowered light intensities on the photosynthetic pigment content and photosynthesis in the above species (Table 3). Compared with the initial levels, the content of chlorophylls and phycoerythrin increased in plants during a 10-day experiment with considerably lowered PAR, $90 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. After fertilization with dissolved inorganic nutrients (3 h) and subsequent retention of the plants for three days under the same lowered intensity in water without nutrients, the chlorophyll content in *U. rigida* increased again by 30%, but only when the photon flux density was $90 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Only under these experimental conditions did *Gelidiopsis* sp. show considerably elevated chlorophyll a and phycoerythrin contents. The chlorophyll content in leaves of *T. ciliatum* changed insignificantly and without apparent pattern in all conditions of the nutrient-enrichment experiment.

The dependence of net photosynthesis on light also was analyzed (Fig. 6). Although the results are not presented in this article, we did not detect any significant differences in the character of the P_s vs. I curves under different conditions of the experiment in the seagrass *Thalassodendron ciliatum*. The decrease in light intensity to $90 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ reduced the photosynthetic capacity of *Ulva rigida* by 50% compared to that at $240 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and also more than doubled the angle of initial slope of the photosynthetic light curve α . When fertilized with N and P, *U. rigida* did not change its photosynthetic capacity but α increased.

In the red alga *Gelidiopsis* sp., at $90 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, the light curve of photosynthesis had a steeper initial slope than at $240 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, but showed a lower photosynthetic light saturation value. Fertilization increased the photosynthetic capacity and α of *Gelidiopsis* sp. under both light conditions, especially when the photosynthetic light saturation value was 2.4 times as high as in algae without nutrients.

The path of carbon in photosynthesis

Table 4 gives the composition of primary products of photosynthesis in two species of seagrasses and six seaweeds occurring in stressful conditions of intertidal pools and in the upper subtidal at shallow depths. Our analysis revealed that in all species of marine plants studied, 3-phosphoglyceric acid was the first stable product of photosynthesis, accounting for 100-50% of all labeled primary photosynthetic products in plants after 15 s of exposure to light with $\text{H}^{14}\text{CO}_3^-$. With longer exposures, e.g. 300 s, labeled carbon transforms uniformly from 3-phosphoglyceric acid into non-phosphoralated sugars. Environmental conditions do not change the distribution and redistribution patterns of the label in the intermediate and definitive products of photosynthesis. Only in one case, in the seagrass *Thalassia hemprichii* growing in the intertidal zone, 28% of the radioactive carbon of primary products was found in asparaginic acid during the first 15 s of exposure. However, the character of redistribution of the label does not permit a conclusion on the primary synthesis of aspartate.

DISCUSSION

Adaptation of tropical seaweeds and seagrasses to different light intensities

It was shown earlier that most species of temperate macroalgae have the *Ulva*-type of adaptation, that is, a considerable variety of responses enabling them to acclimate to a wide range of light intensities; for most species from 100-80% to 5-3% PAR_s and for some, up to 0.1 or even 0.05% PAR_s (Titlyanov 1983, Titlyanov et al. 1987). The following are, in our view, most common responses of the *Ulva*-type marine plants to reduced light intensities: 1) accumulation of photosynthetic pigments in chloroplasts and increasing the size of photosynthetic units (Lie and Titlyanov 1978, Leletkin 1981); 2) increasing the efficiency of the use of absorbed light (Titlyanov et al. 1987); 3) increasing the content of photosynthetic units per weight of tissue and the area of thallus surface (Leletkin 1981, Titlyanov et al. 1987); 4) increasing the size of chloroplasts and the number of photosynthetic membranes in chloroplasts (Titlyanov et al. 1974); 5) increasing photosynthetic capacity (Titlyanov et al. 1987).

How do tropical marine plants adapt themselves to light? Scarce data (O'Neal and Prince 1982, Titlyanov et al. 1983, Littler et al. 1988) and general theoretical speculations (Littler and Littler 1988) lead us to believe that tropical and temperate species of seaweeds and seagrasses have similar mechanisms and reactions of adaptation to light. However, tropical macrophytes are subjected to environmental effects that differ considerably from those in temperate zones. Examples are extremely high temperatures in the intertidal zone, a weak temperature stratification of the water column and a low content of dissolved inorganic nutrients. Species composition of tropical waters differs greatly from that of the temperate zone. Calcareous green and red algae are dominant and vast expanses are covered by seagrasses (Littler and Littler 1988). Crustose and massive forms are numerous among the growth forms and epiphytism is widespread (Littler and Littler 1988).

Our investigations on 27 species of seaweeds and seagrasses have shown that the basic adaptive reactions mentioned above do manifest themselves in the tropics. Still, in spite of a wide range of changing light intensities, the range of variations of the physiological characters of photosynthesis is much narrower than in plants of the temperate zone. For example, the photosynthetic pigment content in plants of the temperate zone may change 6-7 fold, depending on habitat illumination (Lie and Titlyanov 1978), whereas in the tropics we recorded only 3.5-fold changes. There is a general low level of chlorophyll content and especially phycoerythrin in marine tropical plants. The highest content of these pigments occurred in deep-water species: chlorophyll a in *Avrainvillea amadelpha* = 0.52 mg·g wet wt⁻¹ and phycoerythrin in *Wrangelia argus* = 0.89 mg·g wet wt⁻¹. In the temperate zone, contents such as 1.2-0.8 mg·g wet wt⁻¹ for chlorophyll a and 4-2 mg·g wet wt⁻¹ for phycoerythrin are not rare (Lie and Titlyanov 1978). What are the causes of these differences? Perhaps they are reflective of a shortage of dissolved inorganic nutrients, especially nitrogen, in tropical waters. Our experiments on algal adaptation to low light intensity against the background of fertilization with inorganic nutrients support this speculation. Tropical algal species also have less capability to increase the efficient use of weak light. Lower photosynthetic light saturation is one mechanism of adaptation of tropical algae and especially seagrasses to the use of solar radiation over a wide range. In most species investigated, irrespective of the place of growth, photosynthesis was saturated even at 40-90 μE·m⁻²·s⁻¹. Such a low light saturation level is also typical of algae of temperate latitudes, but particularly those growing under extreme low light conditions (Titlyanov et al. 1987).

The seagrass *Thalassodendron ciliatum* is a special case which, like a majority of algal species investigated, exhibits the above adaptive reactions but to a far lesser extent than macroalgae. Adaptation of *T. ciliatum* to a wide range of illumination intensities, from 100 to 8% PAR_s, is mainly due to an extremely low light saturation, a high content of chlorophylls, 1-2 mg·g wet wt⁻¹ and a great photosynthetic capacity at saturating light intensities (7-9 mg CO₂·g dry wt⁻¹·h⁻¹).

Diurnal changes in light dependence of algal photosynthesis

It was shown earlier that light dependence of algal photosynthesis is variable throughout the day (Titlyanov et al. 1978), but until recently little attention has been given both to the study of mechanisms responsible for daily photosynthetic changes and to calculations of primary production. All species of marine plants investigated here showed variations in the pattern of photosynthetic light curves during the day. These changes were as follows: the photosynthetic capacity rose from the morning to midday hours and decreased towards the evening. These changes were considerable and the potential photosynthetic activity of algae at midday was 1.5-2 times higher than in the morning, which is comparable to similar algal reactions in temperate latitudes (Titlyanov et al. 1978). Along with the increased photosynthetic capacity, the efficiency of the use of weak light also increased toward midday; i.e., the initial slope of the P_s vs. I curve steepened. This pattern reversed during the second half of the day. Photosynthesis is inhibited by a photon flux density above $250 \mu E \cdot m^{-2} \cdot s^{-1}$. PAR in excess of $380 \mu E \cdot m^{-2} \cdot s^{-1}$ reduces the photosynthetic rate of deep-water algae as early as 1300. These PAR intensities never inhibited photosynthesis in algae and seagrasses during the morning. The observed daily changes in the functioning of the photosynthetic apparatus of algae and seagrasses needs further elucidation.

Productive capacities of tropical marine plants

This study shows that tropical algae and seagrasses maintain a constant level of productive capabilities within a rather wide range of illumination intensities, i.e. from 100 to 15% PAR_s , and only deep-water species, which receive no more than 10-8% PAR_s , reduce their photosynthetic capacity 2.5-3 fold. Stressful conditions of the intertidal zone do not significantly lower photosynthesis of algae and seagrasses. Maximal rates of net photosynthesis ranged from 18 to 2 mg $CO_2 \cdot g \text{ dry wt}^{-1} \cdot h^{-1}$ in different algal and seagrass species. The highest rate of photosynthesis was in *Sargassum* (10-12) mg $CO_2 \cdot g \text{ dry wt}^{-1} \cdot h^{-1}$, green laminar algae (7-18); red algae with filamentous highly branched thalli (7-9) and seagrasses (7-10). The lowest capacity of net photosynthesis was in algae of the genus *Halimeda* (2-3) mg $CO_2 \cdot g \text{ dry wt}^{-1} \cdot h^{-1}$. Our data on the maximum net production of algae and seagrasses obtained with the use of the radiocarbon method approximate those obtained in the expedition by I. I. Cherbadiji who used the oxygen technique. According to his unpublished data, the maximum daily net photosynthesis, evaluated as mg $CO_2 \cdot g \text{ dry wt}^{-1} \cdot h^{-1}$, was for *Enteromorpha* sp.: 20; *Thalassodendron ciliatum* (whole plant with the stalk and roots): 3-4; *Sargassum* sp. (whole plant): 6; *Padina* sp.: 8; *Caulerpa cupressoides*: 4; *Halimeda* sp. (whole plant): 0.7 mg $CO_2 \cdot g \text{ dry wt}^{-1} \cdot h^{-1}$. Other data show that the net photosynthesis of the genus *Halimeda* from deep waters of the Bahamas fluctuated from 1.3 to 4.8 mg $CO_2 \cdot g \text{ dry wt}^{-1} \cdot h^{-1}$ (Jensen et al. 1985). The net photosynthesis of *Caulerpa paspaloides* in Florida fluctuates, depending on season, from 0.8 to 6 mg $CO_2 \cdot g \text{ dry wt}^{-1} \cdot h^{-1}$ (O'Neal and Prince 1982). The highest rates of net photosynthesis in algae of the Belize Barrier Reef were as follows: *Acanthophora spicifera*, 15; *Dictyota divaricata*, 21; *Halimeda opuntia*, 7 mg $CO_2 \cdot g \text{ dry wt}^{-1} \cdot h^{-1}$ (Lapointe et al. 1987). According to many authors, different species of *Halimeda* have rates of net photosynthesis varying from 2.1 to 6.7 mg $CO_2 \cdot g \text{ dry wt}^{-1} \cdot h^{-1}$ (Littler et al. 1988). Thus, the data on the maximum net production of macrophytes in the Seychelles Islands are similar to those obtained from other tropical regions of the world.

The path of carbon in photosynthesis of macrophytes

The data we obtained on the path of carbon in photosynthesis of tropical species of algae and seagrasses provide additional support of the earlier idea (Titlyanov 1983) that there are no species among marine multicellular algae with photosynthesis on the C_4 - path. In certain situations; e.g., in very low light (Yadykin and Titlyanov 1980), during the sporogenetic stage (Kolmakov et al. 1985),

large amounts of amino-acids such as aspartate and alanine emerge in the early products of photosynthesis to suggest the outflow of 3-phosphoglyceric acid from the Calvin cycle into alternative paths and active β -carboxylation. Such changes in the orientation of photosynthetic carbon metabolism have been noted in the tropical seagrasses *Thalassia hemprichii*.

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Table 1. Marine plants and their habitats.

Plant species Growth form	Habitat, conditions	Depth, m	Illumination, % PAR _s
Angiospermae			
1. <i>Thalassodendron ciliatum</i> (Forskål) den Hartog	Islands of Cöetivy, Farquhar, Aldabra, intertidal pools	0	80-100
	Farquhar, Desroches, upper subtidal	0.5	50-90
	Cöetivy, Farquhar, Providence, upper, subtidal, high sedimentation, dense growth	2	40-70
	Cöetivy, dense growth	11	30-50
	Desroches, dense growth	13	30-50
	Aldabra, single patches on sand	15	10-20
	African Banks, on coral debris, dense growth	17	10-15
	Providence, dense growth on coral debris	20	10-15
	Cöetivy, growth on coral debris	23	12-16
	African Banks, dense growth	25	5-10
	Cöetivy, Providence, from sparse growths to single plants	33	8-10
African Banks, sparse growths	37	8-10	
2. <i>Thalassia hemprichii</i> (Ehrenb.) Aschers	Farquhar, intertidal pools	0	100

Table 1. Continued.

Chlorophyta			
3. <i>Avrainvillea amadelpa</i> Gepp, large leathery lamellae	Saint Joseph, single plants on coral pebble	30	10-12
4. <i>Boodlea struveoides</i> Howe filamentous, assembled in "pads"	Aldabra, intertidal pools single "pad" assemblages	0	100
5. <i>Caulerpa cupressoides</i> (West) Ag. massive filaments	Cosmoledo, intertidal drained pools, single plants	0	100
	upper subtidal, among corals, partly covered by sand	7-10	50-60
6. <i>Caulerpa brachypus</i> leathery laminated phyllodes	Cosmoledo, intertidal drained pools	0	50-60
	Astove, upper subtidal opposite to the passage to lagoon	0.5	60-90
7. <i>Caulerpa</i> sp. thick watery phyllodes	Aldabra, upper subtidal single plants	25	10-13
8. <i>Codium tomentosum</i> (Huds.) Stackh. thick branched thallus	Saint-Joseph, upper subtidal, single plants on coral debris	30	10-12
9. <i>Dictyosphaeria cavernosa</i> (Forskål) Boerg laminated thallus	Farquhar, deep intertidal pools, single plants	0.5	80-90
10. <i>Enteromorpha kylinii</i> Bliding thin, filamentous	Aldabra, intertidal pool, epiphytes on <i>Thalassodendron ciliatum</i>	0	60-100
11. <i>Enteromorpha</i> sp. filamentous, thin	Providence, upper subtidal and intertidal, among sand on coral fragments	0-0.5	90-100

Table 1. Continued.

12. <i>Halimeda gracilis</i> Harv. et Ag. calcareous, thin	Aldabra, upper subtidal,	25	10-13
13. <i>Halimeda micronesica</i>	Aldabra, intertidal pools, dense pads among other algae	0	60-100
14. <i>Halimeda opuntia</i> (Linn.) Lam calcareous, thick	Saint Joseph, upper subtidal single plants	30	10-12
15. <i>Halimeda tuna</i> (Ell. and Sol) Lam calcareous, thick	Saint Joseph, upper subtidal single plants	30	10-12
16. <i>Udotea orientalis</i> A et E Gepp laminated thalli	Saint Joseph, upper subtidal tidal, single plants	30	10-12
17. <i>Ulva rigida</i> C. Ag. laminated thallus	Aldabra, deep intertidal pools, strong current, epiphytes of <i>Thalassodendron ciliatum</i> stalks	0.5	60-90
18. <i>Valonia aegagropila</i> (Roth) Ag. thick watery crust	Aldabra, upper subtidal, single plants	25	10-13
Phaeophyta			
19. <i>Dictyopteris delicatula</i> Lam. laminated, thin	Saint Joseph, upper subtidal, single plants on coral debris	30	10-12
20. <i>Sargassum cristaefolium</i> C. Ag. laminated leathery phylloids	Praslin, upper subtidal, dense growths, heavy self-shading	30	10-12
21. <i>Turbinaria ornata</i> (Turn) J. Ag. massive thalli	Aldabra, intertidal pools, single plants	0	80-100
Rhodophyta			
22. <i>Acanthophora spicifera</i> (Vahl) Boer thin branched	Astove, lagoon, intertidal and upper subtidal growths over the <i>Thalassia hemprichii</i>	0-0.5	50-100

Table 1. Continued.

23. <i>Gelidiopsis</i> sp. thin branched	Aldabra, upper subtidal, strong current, epiphytic on <i>Thalassodendron</i> <i>ciliatum</i> stalks	0.5	60-90
24. <i>Hypnea spinella</i> (C. Ag.) Kütz. filamentous, branched	Cosmoledo, intertidal pools sometimes drained	0	100
25. <i>Laurencea corymbosa</i> J. Ag., thin branched	Cosmoledo, intertidal pools	0	100
26. <i>Laurencia</i> sp. thin, branched	Aldabra, intertidal pools, sometimes drained		
27. <i>Wrangelia argus</i> (Mont.) Mont. thin, filamentous	Saint Joseph, upper subtidal, single thalli	30	10-12

Table 2. Content of photosynthetic pigments in marine plants. Chl.a = chlorophyll a; Chl.b = chlorophyll b (Green algae); Chl.c₂ = chlorophyll c₂(Brown algae); P = Phycoerythrin (Red algae); * = mean arithmetic values from 3-5 experiments; \pm = standard deviation; ** = mean arithmetical value of two parallel measurements.

Species	Habitat, (m), depth % PAR _s	Chl. a mg·g wet wt ⁻¹	Chl. b mg·g dry wt ⁻¹	Chl. c ₂ mg·g wet wt ⁻¹	P mg·g dry wt ⁻¹
In samples of one species from different depths					
<i>Thalassodendron ciliatum</i> (seagrass)					
	Cöetivy, Farquhar, Aldabra, intertidal zone, 0, 100	0.72±0.06	2.4±0.2	0.43±0.1	1.4±0.3
	Cöetivy, Farquhar, Providence, 2, 80	0.63±0.06	1.98±0.3	0.32±0.1	1.08±.3
	Cöetivy, Desroches, Aldabra, African Banks, 11-17;40-20	0.81±0.1	2.75±0.2	0.45±0.1	1.54±0.4
	Cöetivy, Providence, African Banks, 33-37; 10-8	0.89±0.2	2.8±0.6	0.49±0.2	1.68±0.8
<i>Thalassia hemprichii</i> (seagrass)					
	Farquhar intertidal zone, 0,100	0.57**	1.7	0.27	0.81
	Farquhar, 2,60	0.67	2.0	0.27	0.81
<i>Caulerpa cupressoides</i> (green alga with massive thallus)					
	Cosmoledo intertidal zone 0,100	0.10	0.6	0.06	0.36
	Cosmoledo, 10,30	0.13	0.78	0.06	0.36
<i>Caulerpa</i> sp. (green alga with massive thallus)					
	Aldabra 25, 10	0.17	1.0	0.09	0.54
	Astove 50, 5	0.11	0.66	0.06	0.36

Table 2. Continued.

Species	Habitat, (m), depth % PAR _s	Chl. a mg·g wet wt ⁻¹	Chl. b mg·g dry wt ⁻¹	Chl. c ₂ mg·g wet wt ⁻¹	P mg·g dry wt ⁻¹
In differently illuminated plant parts					
<i>Sargassum cristaefolium</i>					
	Praslin, upper thallus 0, 5, 90				
	phyllodes	0.18	0.4	0.03	0.07
	pneumatocysts	0.12	0.27	0.02	0.04
	middle thallus 1,30				
	phyllodes	0.45	0.62	0.05	0.11
	pneumatocysts	0.21	0.46	0.04	0.09
	lower thallus 1.5, 5				
	phyllodes	0.45	1.0	0.07	0.15
	pneumatocysts	0.20	0.4	0.04	0.09
In filamentous and laminated green algae					
<i>Boodlea struveoides</i>					
	Aldabra, intertidal zone, 0, 100	0.15	0.97	0.07	0.46
<i>Enteromorpha kylinii</i>					
	Aldabra, intertidal zone, 0, 100	0.19	1.1	0.07	0.40
<i>Ulva rigida</i>					
	Aldabra, intertidal zone, 0, 100	0.15	1.0	0.07	0.48
<i>Dictyosphaeria cavernosa</i>					
	Cosmoledo intertidal zone, 0, 100	0.05	0.39	0.02	0.16
<u>Average of the four species</u>		<u>0.14±0.05</u>	<u>0.86±0.32</u>	<u>0.06±0.02</u>	<u>0.37±0.12</u>

Table 2. Continued.

Species	Habitat, (m), depth % PAR _s	Chl. a mg·g wet wt ⁻¹	Chl. b mg·g dry wt ⁻¹	Chl. c ₂ mg·g wet wt ⁻¹	P mg·g dry wt ⁻¹
<i>Microdictyon montagnei</i> Providence, 2, 80		0.14	0.77	0.08	0.44
<i>Enteromorpha</i> sp. Providence, 2, 80		0.09	0.3	0.05	0.17
<u>Average of the two species</u>		<u>0.11±0.03</u>	<u>0.53±0.23</u>	<u>0.07±0.02</u>	<u>0.3±0.1</u>
<i>Avrainvillea amadelpha</i> St. Joseph, 30, 10		0.58	1.16	0.37	0.74
<i>Udotea orientalis</i> St. Joseph, 30, 10		0.46	0.92	0.19	0.38
<u>Average of the two species</u>		<u>0.52±0.08</u>	<u>1.04±0.12</u>	<u>0.28±0.12</u>	<u>0.56±0.18</u>
<i>Laurencia</i> sp. Aldabra intertidal zone, 0, 100		0.10	0.67	0.67	4.49
<i>Gelidiopsis</i> sp. Aldabra intertidal zone, 0, 100		0.06	0.3	0.86	3.7
<i>Laurencia corymbosa</i> Cosmoledo intertidal zone, 0, 100		0.06	0.4	0.27	1.8
<i>Hypnea spinella</i> Cosmoledo intertidal zone, 0, 100		0.05	0.33	0.22	1.43
<i>Acanthophora spicifera</i> Astove intertidal zone, 0, 100		0.05	0.35	0.36	2.52
<u>Average of the five species</u>		<u>0.06±0.02</u>	<u>0.41±0.07</u>	<u>0.48±0.2</u>	<u>3.0±0.4</u>

Table 2. Continued.

Species	Habitat, (m), depth % PAR _s	Chl. a mg·g wet wt ⁻¹	Chl. b mg·g dry wt ⁻¹	Chl. c ₂ mg·g wet wt ⁻¹	P mg·g dry wt ⁻¹
<i>Wrangelia argus</i> St. Joseph, 30, 10		0.21	1.7	0.89	6.9
Other algae studied					
<i>Halimeda micronesica</i> (green alga, calcified) Aldabra intertidal zone, 0, 100		0.20	0.44	0.21	0.46
<i>Turbinaria ornata</i> (brown alga, massive thallus) Aldabra intertidal zone, 0, 100		0.22	0.53	0.12	0.29
<i>Calulterpa brachypus</i> (green alga, massive thallus) Cosmoledo littoral zone, 0, 100		0.19	1.1	0.09	0.54
<i>Valonea aegagropila</i> (green alga, massive thallus) Cœtivy, 23, 16		0.05	0.43	0.02	0.26
<i>Halimeda gracilis</i> (green alga, calcified) Aldabra 25, 10		0.09	0.54	0.04	0.24
<i>Codium tomentosum</i> (green alga, massive thallus) St. Joseph, 30, 10		0.07	0.32	0.05	0.23
<i>Halimeda tuna</i> (green alga, calcified) St. Joseph, 30, 10		0.13	0.29	0.08	0.18
<i>Dictyopteris delicatula</i> (brown alga, laminated) St. Joseph, 30, 10		0.17	0.77	0.08	0.36

Table 3. Variations in photosynthetic pigment contents of marine plants during the course of adaptation to different light intensities and under fertilization with mineral nitrogen and phosphorus (concentrations: N - 10 mM; N source - NH_4Cl ; P-1mM; source - KH_2PO_4). Pigment values presented with the value for $\text{mg}\cdot\text{g wet wt}^{-1}$ listed above $\text{mg}\cdot\text{g dry wt}^{-1}$.

Species, habitat, depth (m), % PAR_s	Pigments:	Experimental variants					
		Initial variant	Natural light 20% PAR_s	without N and P		with N and P	
				Artificial light ($\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) : % PAR_s		240:20	90:8
<i>Ulva rigida</i> Aldabra, inter- tidal zone 0; 60-20	Chl. a Chl. b	0.15 0.9 0.07 0.42	0.16 0.96 0.09 0.54	0.15 0.6 0.07 0.42	0.21 1.26 0.11 0.66	0.15 0.6 0.07 0.42	0.27 1.62 0.13 0.78
<i>Gelidiopsis</i> sp. Aldabra, inter- tidal zone 0; 60-20	Chl. a P	0.06 0.32 - -	0.05 0.27 0.49 2.6	0.05 0.27 0.37 1.96	0.07 0.37 0.60 3.18	0.05 0.27 0.41 2.17	0.12 0.64 0.70 3.7
<i>Thalassodendron</i> <i>ciliatum</i> Aldabra inter- tidal zone; 0; 100-80	Chl. a Chl. b	0.64 2.18 0.27 0.92	0.61 2.07 0.28 0.95	0.62 2.1 0.29 0.98	0.62 2.1 0.29 0.95	0.40 1.36 0.18 0.61	0.54 1.84 0.28 0.95

Table 4. Composition of primary products of photosynthesis in marine plants collected from intertidal pools and the upper subtidal zone of Aldabra Atoll. * = phosphoric ethers of sugars, PhES; 3-PhGA, 3-phosphoglyceric acid; ** - "Sugars" indicates the sum of saccharose, glucose, fructose etc.

Species	Time of exposure on bight with C ¹⁴ , s	Radioactivity of alcohol-water-soluble fraction. % of total							
		3-PhGA + PhES*	** Sugars	Aspartate	Glutamate	Alanine	Serine+ Glycine	Malate	Unidentified
<i>Thalassodendron ciliatum</i>	15	76.3	8.3	6.5	-	1.1	1.1	-	6.1
	60	39.1	37.7	6.1	5.4	3.3	2.5	3.1	2.8
	300	5.1	73.2	4.3	0.7	3.3	9.8	-	3.6
<i>Thalassia hemprichii</i>	15	55.7	4.4	27.9	-	4.2	7.9	-	-
	60	13.6	54.3	17.0	-	2.1	7.9	2.1	3.0
	300	6.7	55.3	7.4	0.3	3.0	23.1	-	4.2
<i>Enteromorpha kylinii</i>	15	93.6	1.1	-	-	1.8	-	-	3.5
	60	87.2	1.9	3.5	1.0	5.0	-	-	1.4
	300	61.5	16.5	5.6	4.2	10.2	-	-	1.8
<i>Ulva rigida</i>	15	94.6	1.7	0.3	-	2.8	0.7	-	-
	60	89.1	2.9	3.1	-	2.8	-	-	2.1
	300	59.1	13.7	7.6	2.2	8.7	2.4	5.1	1.0
<i>Boodlea struveoides</i>	15	83.4	-	1.1	3.2	9.1	0.6	-	6.6
	60	28.5	-	2.8	1.3	11.5	-	-	1.9
	300	33.9	33.2	4.4	9.4	9.3	9.9	-	-
<i>Turbinaria ornata</i>	15	58.7	36.5	3.0	-	1.8	-	-	-
	60	18.8	74.9	3.0	-	3.3	-	-	-
	300	12.8	72.1	5.0	0.8	5.0	2.3	-	2.0
<i>Laurencia</i> sp.	15	100.0	-	-	-	-	-	-	-
	60	85.2	13.1	-	0.9	0.8	-	-	-
	300	52.2	18.2	6.1	1.4	3.7	18.4	-	-
Plants of the upper subtidal zone, depth 0.5 m, 90 - 60 % PAR_s									
<i>Thalassodendron ciliatum</i>	60	50.9	37.2	1.8	2.3	1.4	2.3	2.8	1.3
<i>Ulva rigida</i>	60	93.7	3.0	1.6	-	1.5	-	-	0.2
<i>Gelidiopsis</i> sp.	15	81.4	-	-	-	-	-	-	18.6
	60	86.7	4.2	1.5	-	1.1	6.5	-	-
	300	14.9	62.0	1.6	-	-	21.4	-	-

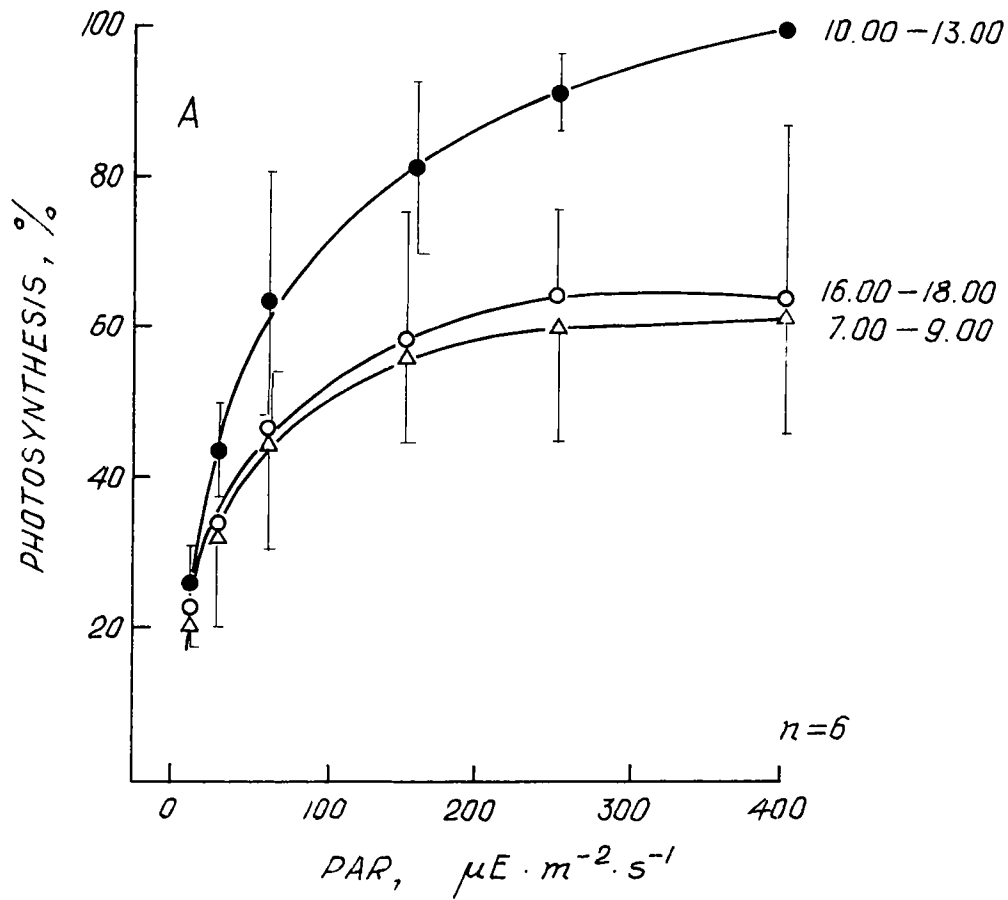


Figure 1 (A). Daily variations in light dependence of marine plant photosynthesis (P_s vs. I curve). A, shallow water plants, 0 - 0.5 m depth, 100 - 90 % PAR_s (*Dictyosphaeria cavernosa*, *Caulerpa cupressoides*, *Hypnea spinella*, *Sargassum cristaefolium*). B, plants of medium depth, 10 - 15 m, 30 - 15 % PAR_s (*Caulerpa* sp., *Codium tomentosum*, *Halimeda tuna*, *Avrainvillea amadelpha*, *Halimeda gracilis*).

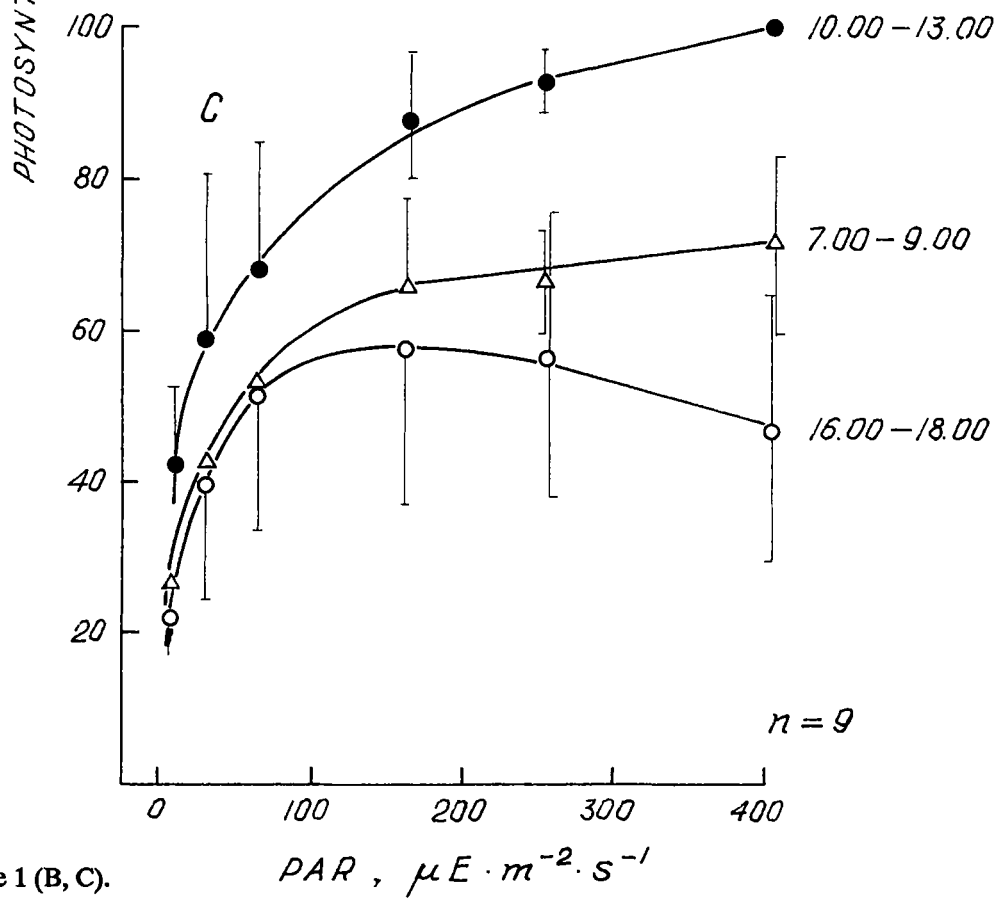
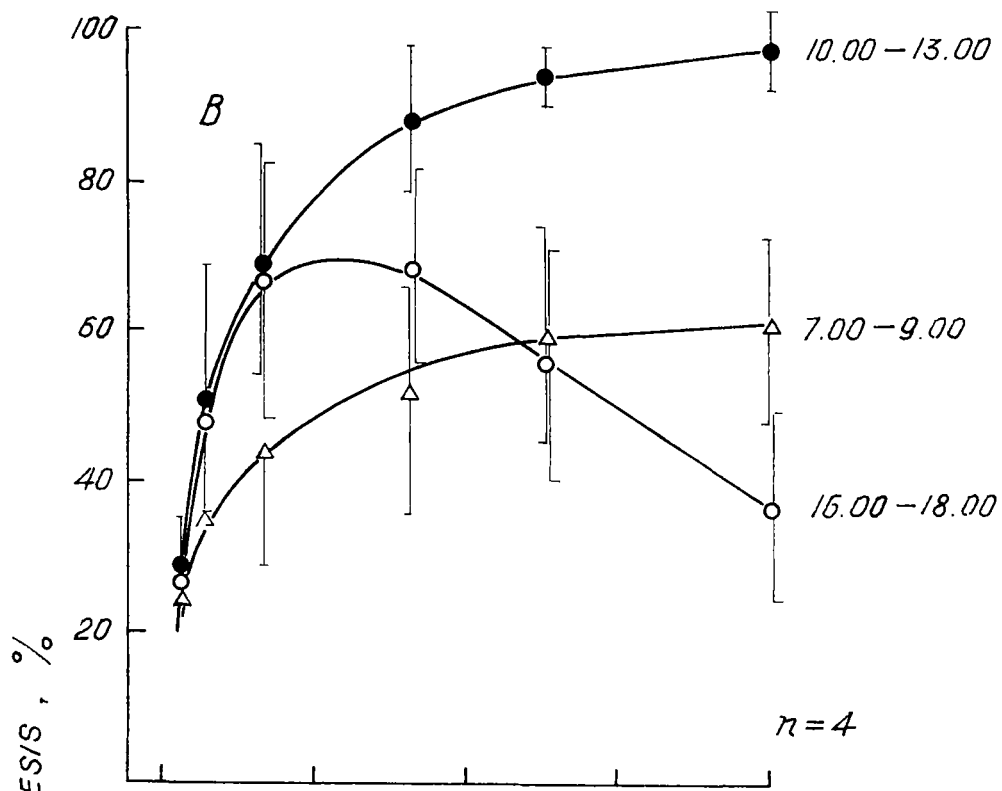


Figure 1 (B, C).

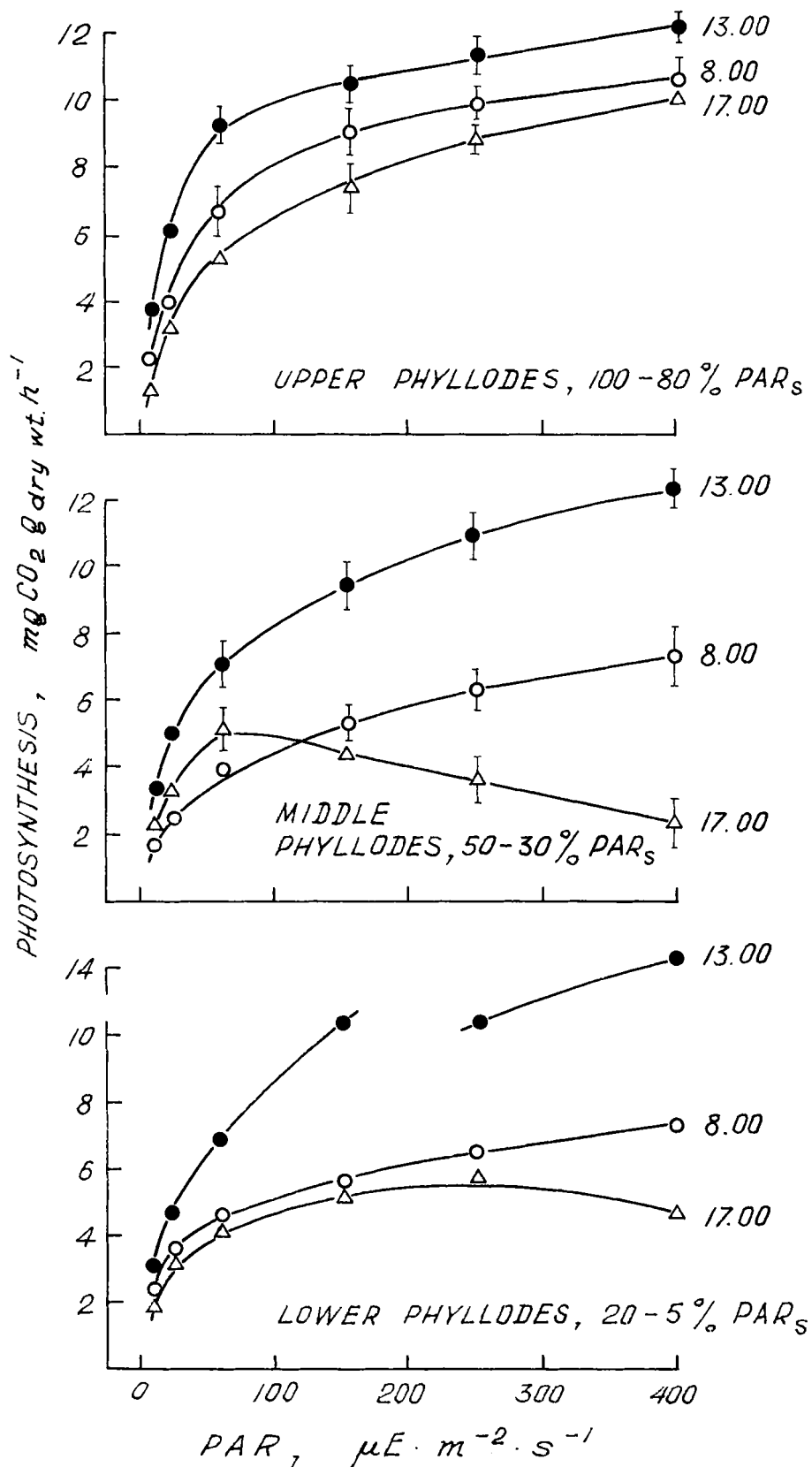


Figure 2. Light dependence of net photosynthesis (P_s vs. I curve) in phylloides of *Sargassum cristaefolium*.

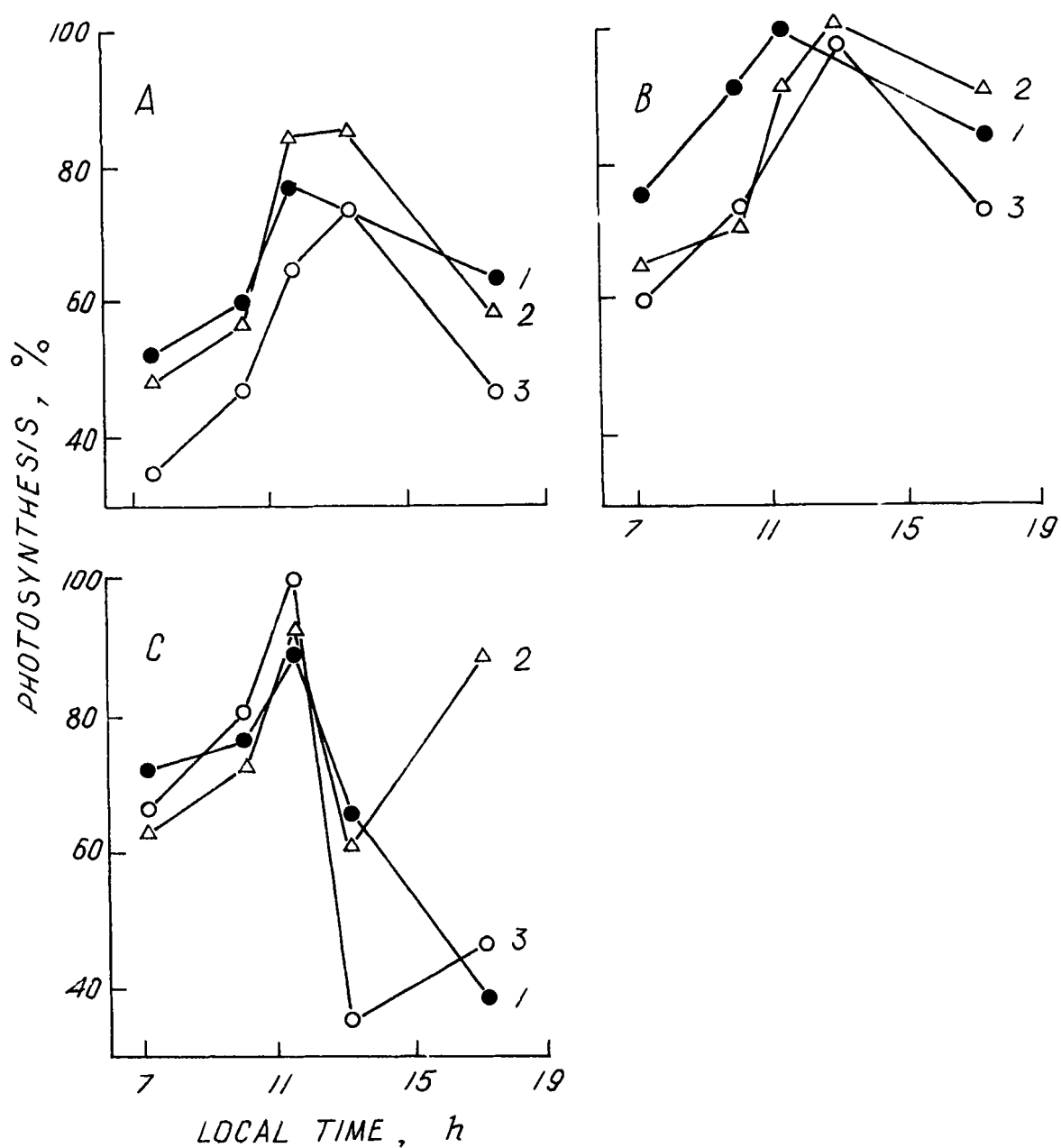


Figure 3. Daily variations of photosynthesis in marine plants. A, measurements at PAR 15 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; B, same at 160 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; C, PAR 380 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. 1, *Thalassodendron ciliatum*, depth 15 m; 2, *Caulerpa* sp., depth 25 m; 3, *Halimeda gracilis*, depth 25 m.

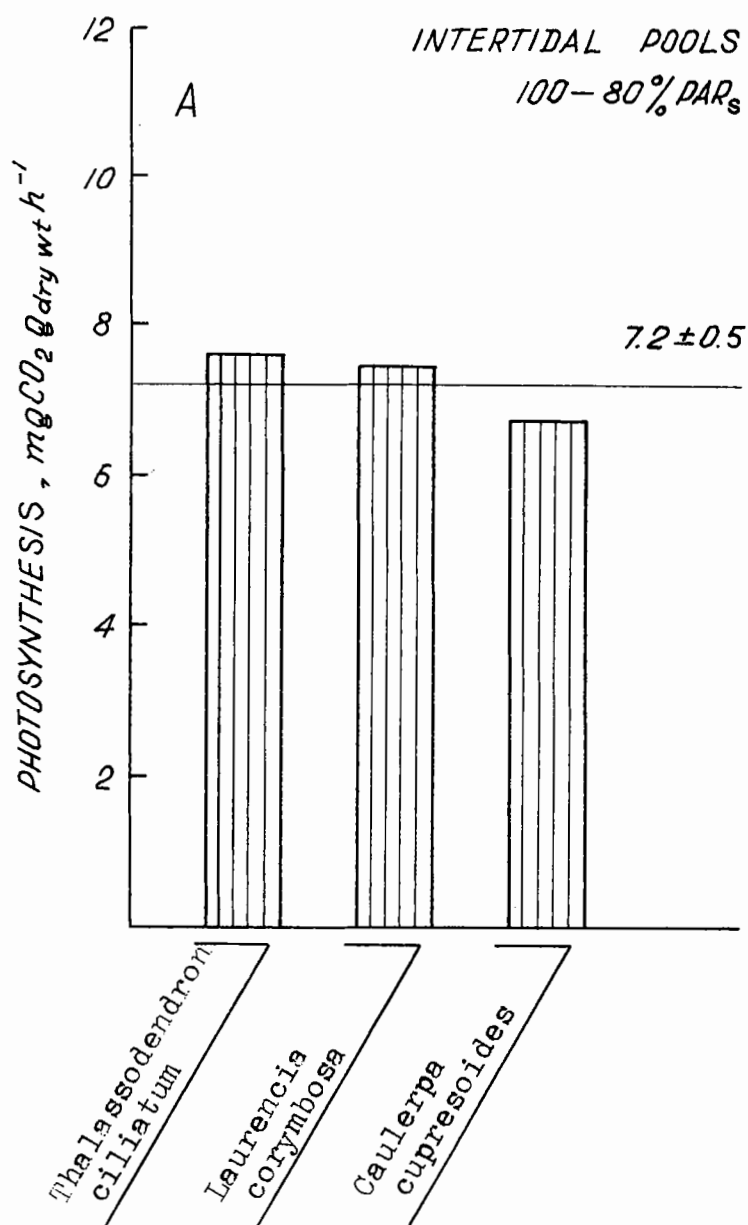


Figure 4 (A). Photosynthetic capacity of marine plants growing at different depths, net photosynthetic light saturation (I_k) in the middle of a sunny day. A - intertidal pools, B, - depth 0.5 - 2 m, C - depth 10 - 15 m, D - depth 20 - 25 m, E - depth 30 - 50 m.

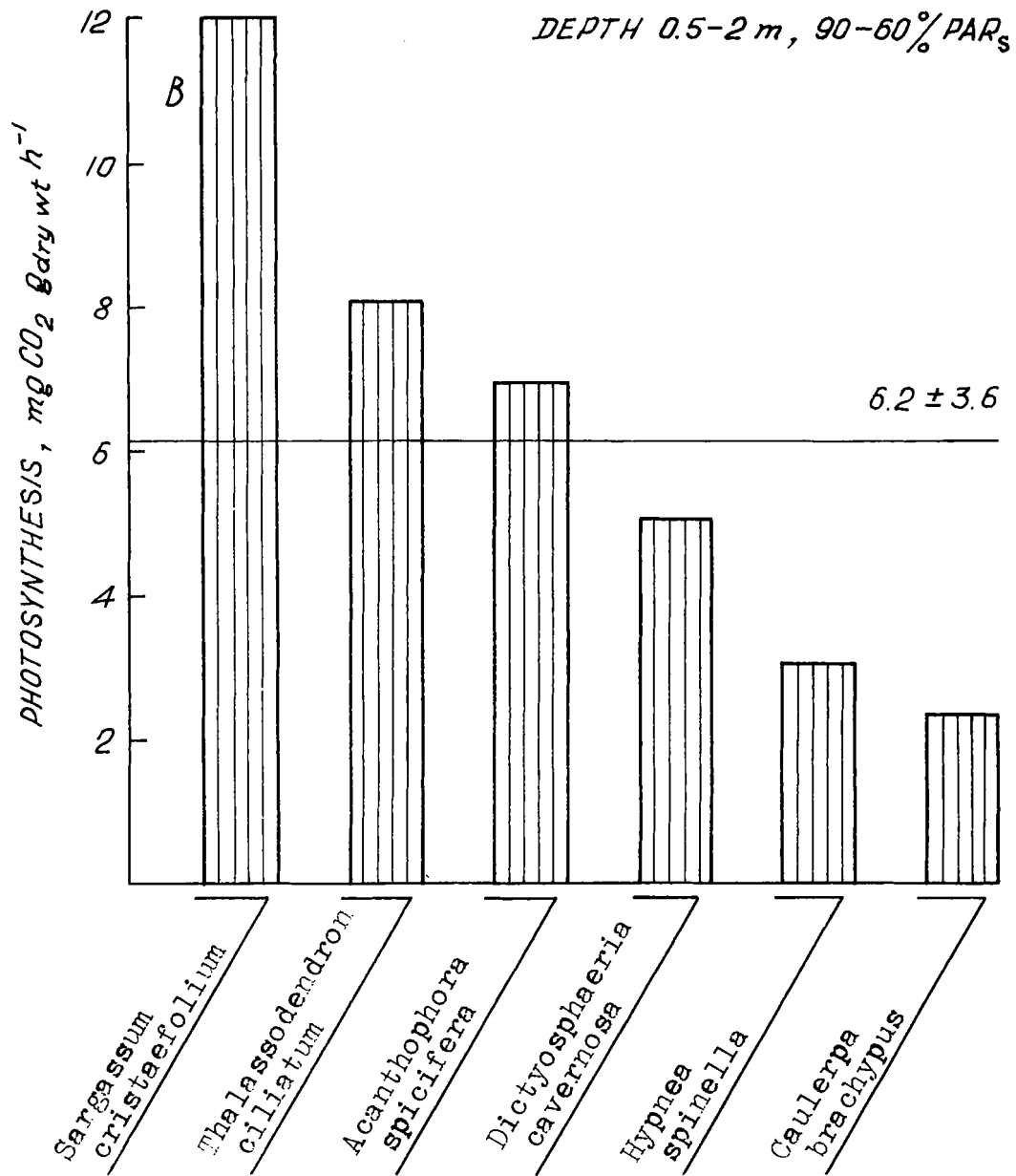


Figure 4 (B).

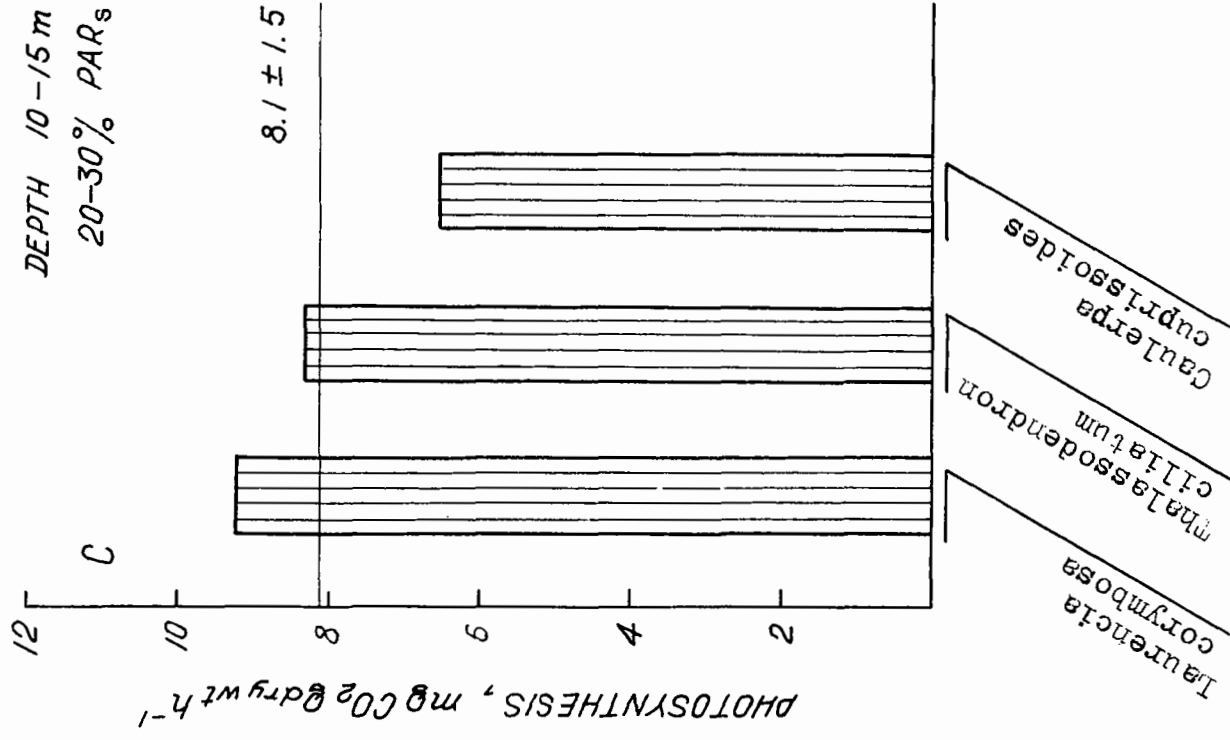


Figure 4 (C).

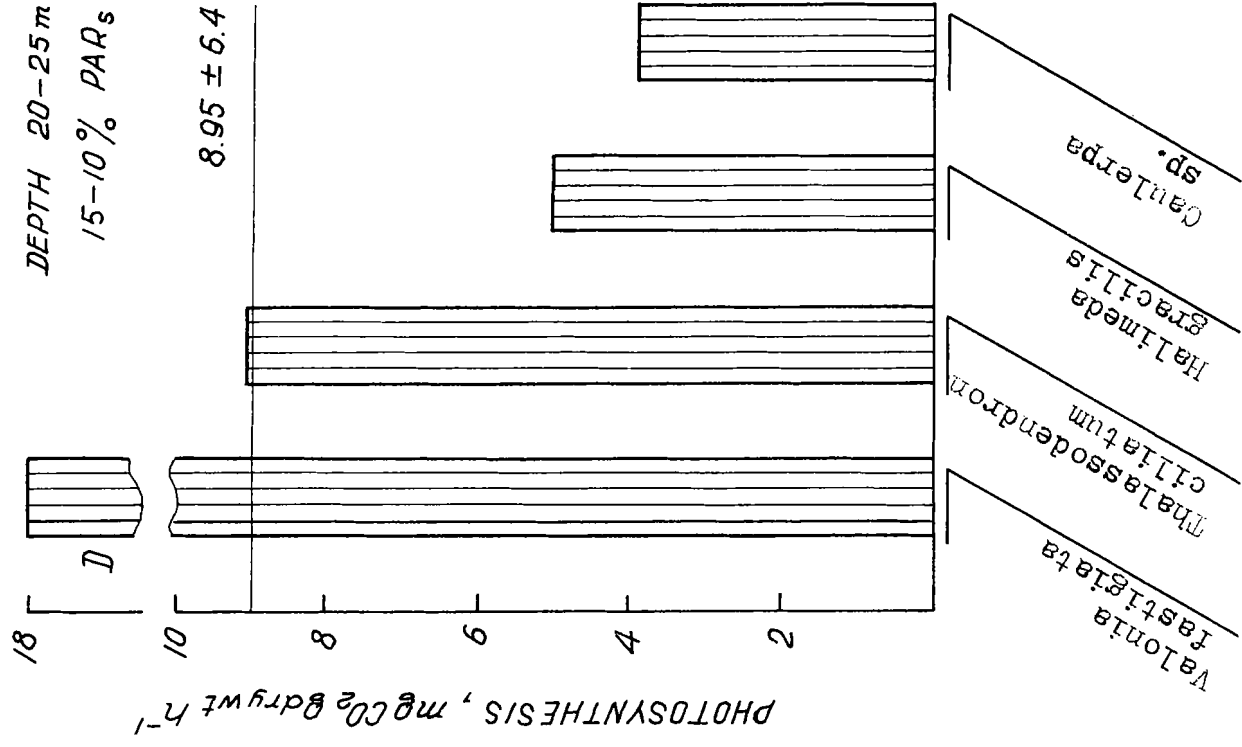


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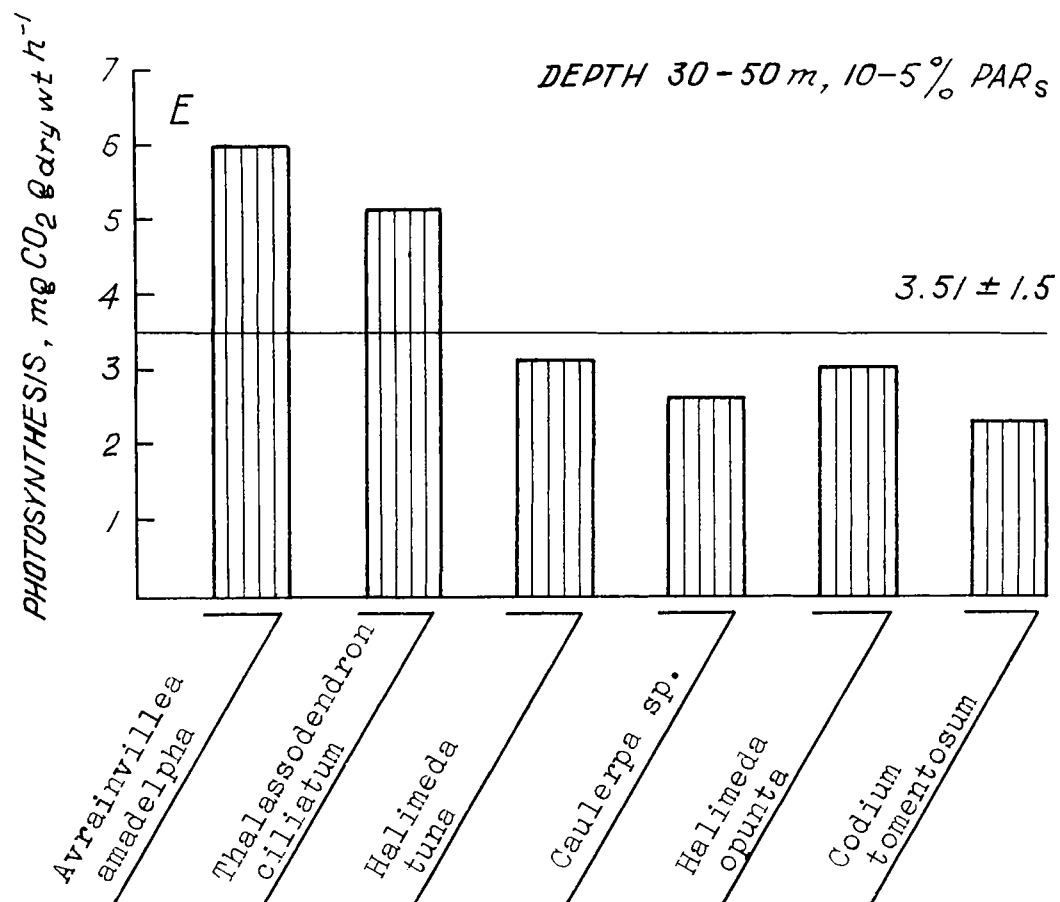


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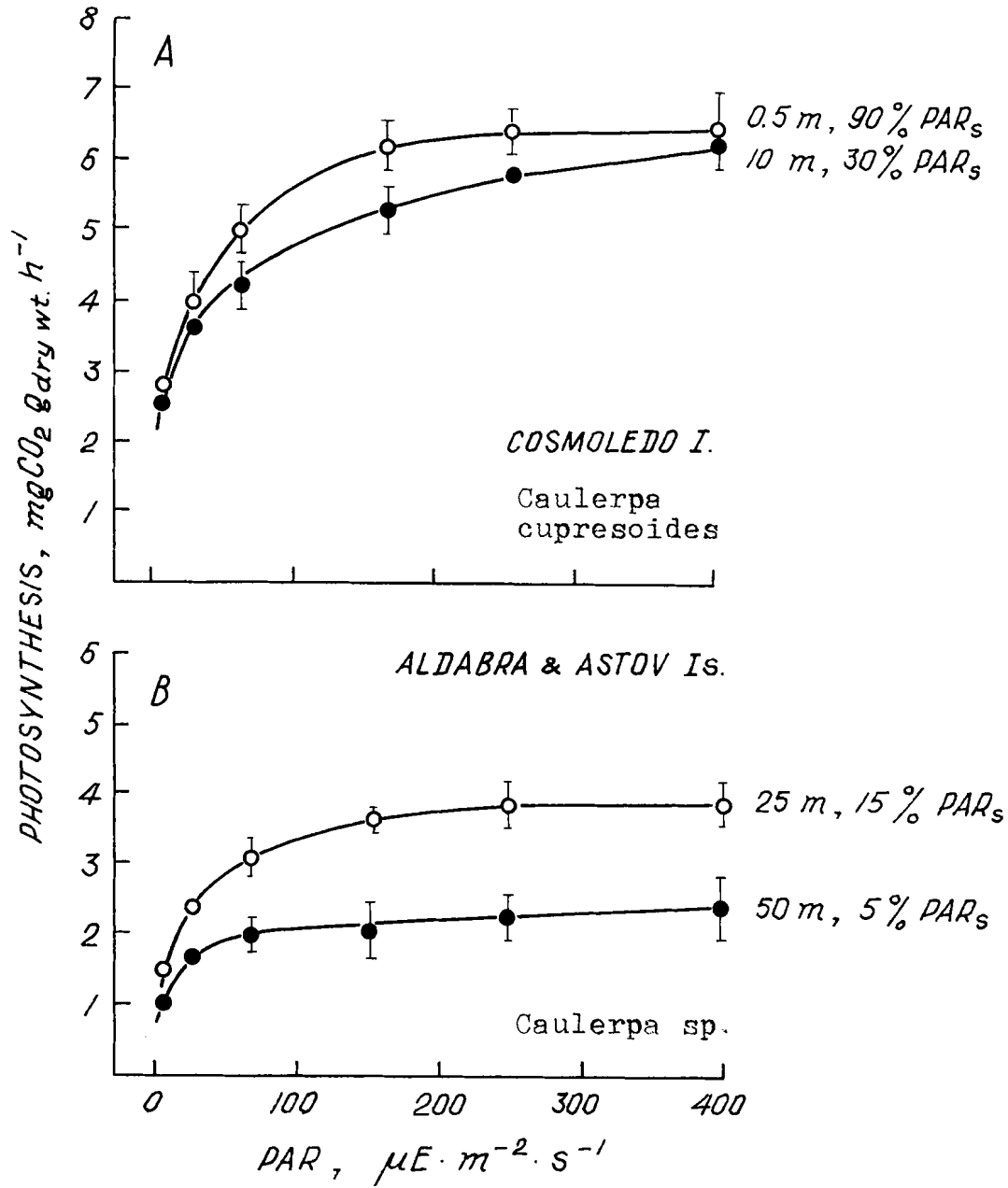


Figure 5 (A, B). Depth-dependence of net photosynthesis in marine plants at 1400 at different depths. A - *Caulerpa cupressoides*, B - *Caulerpa sp.*, C - *Thalassodendron ciliatum*, D - *Laurencia corymbosa*.

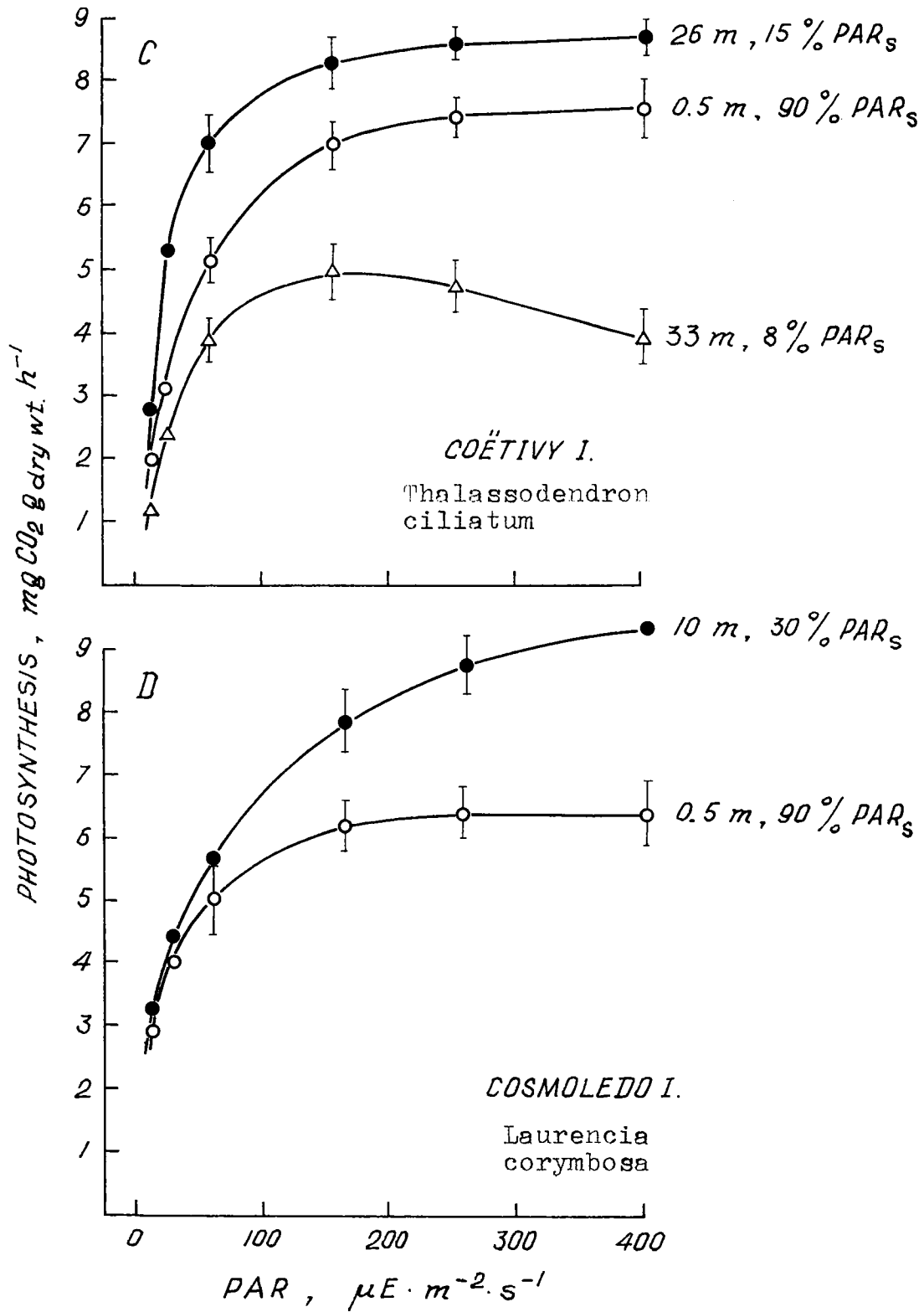


Figure 5 (C, D).

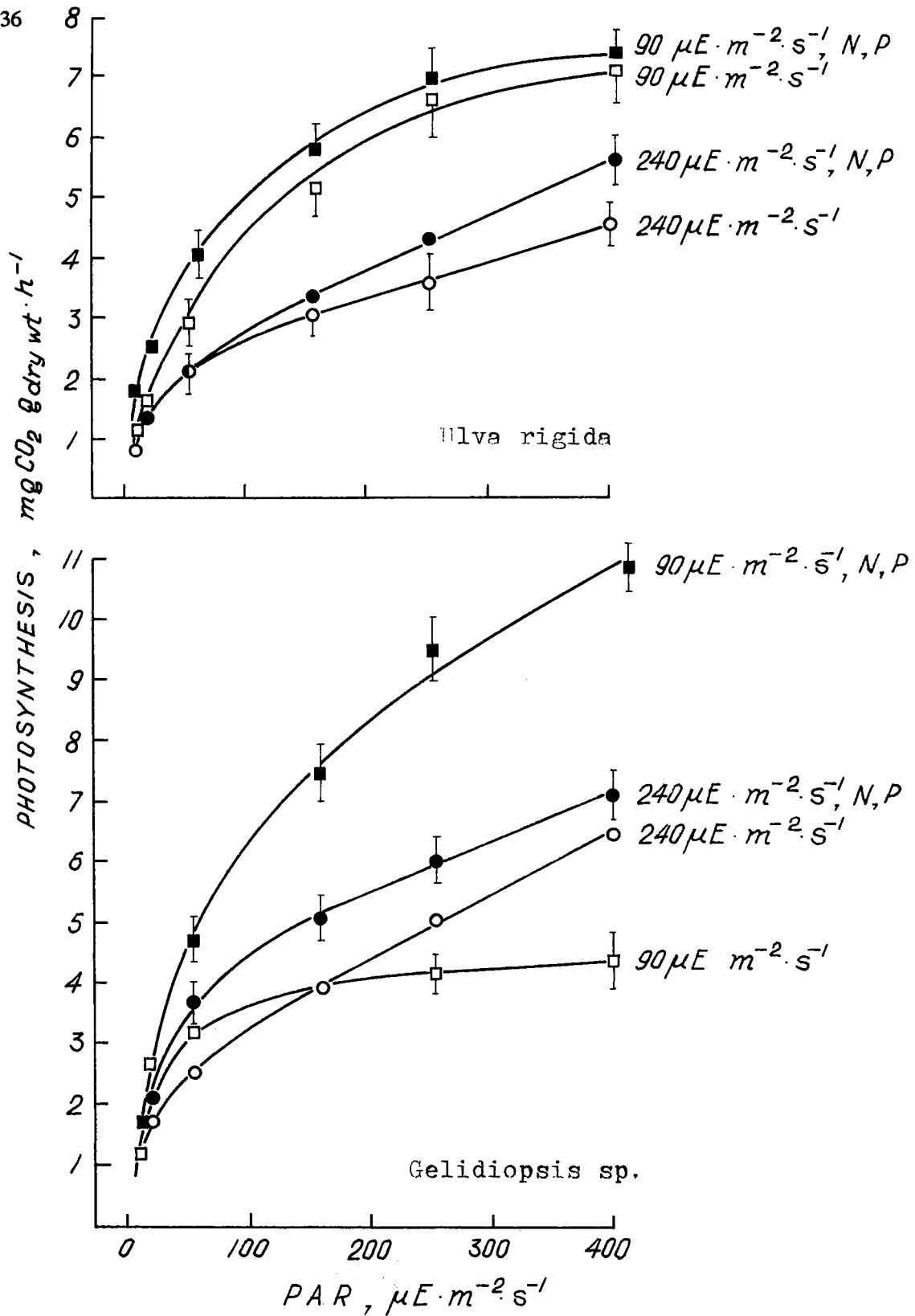


Figure 6. Light dependence of photosynthesis in the experiment on algal adaptation to low light intensity with, or without, addition of dissolved inorganic nutrients. N - 10 mM NH_4Cl ; P - 1 mM KH_2PO_4 .