

**ATOLL RESEARCH BULLETIN  
NO. 375**

**CHAPTER 11**

**LIGHT AND TEMPERATURE DEPENDENCE OF OXYGEN EXCHANGE,  
CARBON ASSIMILATION AND PRIMARY PRODUCTION IN  
*THALASSODENDRON CILIATUM* BLADES**

**BY**

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

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## CHAPTER 11

### LIGHT AND TEMPERATURE DEPENDENCE OF OXYGEN EXCHANGE, CARBON ASSIMILATION AND PRIMARY PRODUCTION IN *THALASSODENDRON CILIATUM* BLADES

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#### INTRODUCTION

Seagrasses play an important role in coastal ecosystems, serving as a food source and habitat for numerous animals as well as stabilizing sediments and forming biotopes (Stephes 1968, den Hartog 1970, Bjorndal 1980, Sheridan and Livingston 1983). Despite the low diversity of seagrasses in the world ocean (only 50 species, Lakshman 1985, Dawes 1987), they can be found in all geographical zones occupying depths from 0 to 40 m. Seagrasses are especially abundant near river estuaries and reef lagoons where they are often the dominant autotrophic producers. For example, the standing crop of *Thalassia testudinum* in Bear Cut produces 2750 g dry wt·m<sup>-2</sup> a year (Jones 1968) and *T. testudinum* from Boca Ciega Bay, Florida, 1198 g dry wt·m<sup>-2</sup> (Taylor and Saloman 1968).

*Thalassodendron ciliatum* (Försk) den Hartog also displays high productivity: up to 2 kg C·m<sup>-2</sup>·yr<sup>-1</sup> (Harves 1982, Aleem 1984, Thorhaug 1986). In favorable seasons, the growth rate of some species can be very high and the rate of blade elongation can reach 1 - 1.5 cm·day<sup>-1</sup> (Greenway 1974, Johnstone 1979). The blade growth of *Halodule wrightii* Ascherson from the Indian River, Florida, during the spring is 11% per day (Virnstein 1982).

Physiological studies have been widely conducted on the production capacities of separate plants, associations of seagrasses and their epiphytes and the effects of environmental factors on photosynthesis, growth and development (Backman and Barilotti 1976, McRoy and McMillan 1977, Weigert 1979, Harlin 1980, Montfrans et al. 1984, Dennison and Alberte 1982, 1985). *Zostera marina* and *Thalassia testudinum* are the most widely studied of all seagrasses. In a number of investigations, seagrasses were successfully cultivated (Lakshmanan 1985, Thorhaug 1986).

The goal of this work was to study the light dependence of oxygen evolution and carbon assimilation during photosynthesis, as well as the temperature dependence of oxygen exchange in *Thalassodendron ciliatum* blades from 0-33 m in depth. Using the data obtained, net primary production of the seagrass was calculated for both clear and turbid waters of the Seychelles Islands.

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## MATERIALS AND METHODS

The study was carried out during the expedition of the R/V Akademik A. Nesmeyanov to the Seychelles Islands during January - March 1989. The seagrass *Thalassodendron ciliatum* (Försk) den Hartog which grew in abundance on Cœtivy, Farquhar, Aldabra and Desroches Islands at depths of 0-37 m was chosen as the subject for study. Cœtivy Island was especially convenient for a comparative study since vast growths of *T. ciliatum* occurred there at all depths to 37 m, both on the inside of the lagoon and on the outer reef slope.

We studied young, mature and old blades of the leaf cluster. The leaf cluster of *Thalassodendron ciliatum* can be subdivided into two equal portions which are mirror images of each other. The young blades included the 1st and 2nd blades of every half of a given leaf cluster, the 3rd and 4th blades were referred to as mature blades, and the 5th blade was designated as an old blade.

Daily photosynthetic production was calculated on the basis of measurements of light and temperature dependence of oxygen exchange of *Thalassodendron ciliatum* blades and their comparison with values of habitat illumination and temperature at 0, 2, 15, and 33 m depths (Kinsey 1985). Light curves of O<sub>2</sub> evolution by fragments of *T. ciliatum* blades at different temperatures (from 10° to 40°C) were measured in the laboratory by an open platinum electrode (Leletkin 1978). A halogen lamp with a capacity of 1 kW was used as a light source. Photosynthetically active radiation was isolated by glass light filters. Required illumination was established with the help of neutral glass light filters. In order to evaluate illumination, produced by the halogen lamp in the PAR region in a quantum flux density, the ratio  $1 \text{ W}\cdot\text{m}^{-2} = 5 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  was used (McCree 1972).

The rate of oxygen evolution was measured as the difference between electrode records in the light and in the dark. The gross photosynthetic rate at saturation intensity of natural light was determined in those (and neighboring) blades in which the net photosynthesis ( $P_{\text{net}}$ ) and dark respiration (R) had been measured by the Winkler method (Propp et al. 1982, Littler and Arnold 1985). Gross photosynthesis was then calculated at any point of a light curve by the formula:

$$P_i = \frac{P_{\text{max}} A_i}{A_{\text{max}}}$$

where  $P_i$  is the gross photosynthetic rate, in ml O<sub>2</sub>·g dry wt<sup>-1</sup>·h<sup>-1</sup>;  $P_{\text{max}}$  is the gross photosynthesis rate at saturating light intensity determined by the Winkler method ( $P_{\text{net}}^{\text{max}} + R$ ), in ml O<sub>2</sub>·g dry wt<sup>-1</sup>·h<sup>-1</sup>;  $A_i$  is the gross photosynthetic rate, in  $\mu\text{A}$  of current; and  $A_{\text{max}}$  is the gross photosynthesis rate at saturating light intensity, in  $\mu\text{A}$  of current.

The radioactive method of measurement of light dependence of carbon assimilation is described in Chapter 9 of the present collection (Titlyanov et al. 1992). The radiocarbon method was used to measure the rate of net photosynthesis of macrophytes at different light intensities (Kolmakov and Tarankova 1978, Jensen et al. 1985).

## RESULTS

Light curves of net photosynthesis ( $P_s$  vs. I) of the 2nd and 5th blades of *Thalassodendron ciliatum* from different depths measured at various water temperatures are presented at Figures 1 and 2. The shape of the curves is characterized by the following parameters: light intensity

corresponding to compensating point of photosynthesis ( $I_c$ ), half-saturation ( $I_{1/2}$ ) and saturation of photosynthesis ( $I_k$ ), tangent of inclination of depths the initial section of the light curve ( $tg\alpha$ ), maximal rates of net photosynthesis ( $P_{net}/max$ ) and dark respiration ( $R$ ). *T. ciliatum* is characterized by low levels of  $I_k$  ( $30-50 \mu E \cdot m^{-2} \cdot s^{-1}$ ). And accordingly  $0.5 P_{max}$  level is also reached at relatively low densities of incident flow ( $I_{1/2}$  is from  $5$  to  $25 \mu E \cdot m^{-2} \cdot s^{-1}$ , whereas compensation of respiration ( $I_c$ ) requires less than  $5 \mu E \cdot m^{-2} \cdot s^{-1}$  of illumination. The steepness of the initial section ( $tg\alpha$ ) of the photosynthetic light curve is from  $30$  to  $65 \mu l O_2 \cdot g^{-1} \text{ fresh wt} \cdot h^{-1} \mu E^{-1} \cdot m^{-2} \cdot s^{-1}$  at *in situ* temperatures. Differences between young and old blades are displayed by an increase of the  $I_k$  level in the 5th blade for plants dwelling deeper than  $1$  m (Figs. 1 and 2). In old blades, the steepness of the initial section of a light curve ( $tg\alpha$ ) also decreases. Light intensity which corresponds to the compensation point does not depend upon blade age.

The shape of the light vs. photosynthesis curves depends upon water temperature. In the majority of the experiments, photosynthetic rates on both the plateau region ( $P_{max}$ ) and the linear section of the light curve ( $\alpha$ ) increase with the rise of water temperature from  $10$  to  $30^\circ C$ . Further increases in water temperature up to  $40^\circ C$  lead to a decrease of both these values. In plants collected from  $15$  to  $33$  m and incubated in  $40^\circ C$  water, photosynthesis was not saturated ( $I_k$ ) even at  $200 \mu E \cdot m^{-2} \cdot s^{-1}$ . Extremely low temperatures ( $10^\circ C$ ) caused irregular responses of the parameters  $I_k$  and  $I_c$ .

Maximal net photosynthesis and respiration at the natural temperature of a plant habitat ( $27-28^\circ C$ ) are shown in Table 1. Both in young and old blades, net photosynthesis gradually increases while moving from the surface to  $15$  m in depth ( $1.5$  and  $1.8$  times in the 2nd and 5th blades, respectively) and continuously decreases at further submergence down to  $33$  m (on the average by a factor of  $1.4$ ). The  $P_{net}/max$  level of young blades was at all depths  $1.5$  times higher than in old ones and at  $33$  m -  $1.2$  times higher. The respiration rates of the blades decrease with depth. The 5th blade has lower  $R$  values at all depths in comparison with the 2nd one ( $1.8$  times at the surface and only  $1.5$  times at  $33$  m). The ratio of net photosynthesis to respiration is typical for marine macroflora:  $2-4$  (Burriss 1977, Titlyanov 1983). This parameter nearly doubles during the first  $2$  m in depth and then does not change substantially.

Plants from  $15$  m in depth showed the greatest potential photosynthetic activity, but it is unknown if higher capacities of deep water plants are realized *in situ*.

Values of daily net production calculated at different depths, depending on water clarity, are presented in Figure 3. Production is calculated for a day with average PAR values ( $10-20 \mu E \cdot m^{-2} \cdot s^{-1}$  in the afternoon) in the period from  $15-30$  January 1989, near Coetivy and Farquhar Islands. Photon flux density at various depths was calculated proceeding from spectral curves of penetration of a  $1$  m deep layer of different clearness (I-III ocean and 3 coastal types of water, Jerlov 1976). Waters of type I do not occur in the region of the Seychelles, they are taken as a case of maximal possible photosynthetic activity of plants at great depths. To evaluate the intensity of  $O_2$  evolution, the ratio  $mg O_2 = 0.3 mg C$  was used (McRoy and McMillan 1977).

Net production of *Thalassodendron ciliatum* blades changes with depth in the following way (Fig. 3). In the intertidal zone, young and old blades can accumulate  $1.35$  and  $0.82 mg \cdot C \cdot g^{-1}$  fresh wt, respectively during  $24$  h. At  $1-2$  m in depth, the carbon assimilation capacity increases in young blades  $2.3$  times, in old blades -  $2.1$  times (Table 1). At the first several meters of depth, daily net production exactly follows the increase of  $P_{net}/max$ , which indicates that plants dwelling there reach their peak photosynthetic capacities. At  $15$  m in depth, in the clearest waters (type I ocean) production of a young blade is essentially the same as at  $2$  m ( $3.3 mg \cdot C \cdot g^{-1}$  fresh wt  $\cdot 24 h^{-1}$ ), but old blade production increases up to  $2.5 mg \cdot C \cdot g^{-1}$  fresh wt  $\cdot 24 h^{-1}$ . At  $33$  m in depth, production of both young and old blades drops to  $2.3$  and  $1.9 mg \cdot C \cdot g^{-1}$  fresh wt  $\cdot 24 h^{-1}$ , respectively, in accordance with

$P_{net}/max$  changes (Table 1). Thus, in the clearest waters, maximal photosynthetic capacities of *T. ciliatum* blades are reached at all depths and maximal production takes place at about 15 m. Even at 33 m in depth, the 24 h carbon balance is positive.

However, waters in the natural habitat show clarity values only between II ocean and 3 coastal types depending on meteorological conditions (Novozhilov et al. 1989). This means that a 10-fold drop of incident surface PAR occurs not at 100 m (as in the type I waters) but at 30, 15 and 8 m depths for waters of II, III ocean and 3 coastal types, respectively (Jerlov 1976). At depths of more than 2 m, production also changes depending on water type. In type II ocean waters, *Thalassodendron ciliatum* production at 15 m is lower than at shallower depths (Fig. 3). At 33 m in depth, production of the 2nd and 5th blades is approximately the same. In the most turbid waters of the 3 coastal type, production of young and old blades from 15 m in depth is only 33% and 50% of the maximum possible, and beginning from 26 m the carbon balance becomes negative. Thus, at 15 m in depth under natural conditions of illumination, the photosynthetic capacities of 1 g of young blade reaches 30-80% of the calculated maximal productivity, and 1 g of an old one - 20-70%. At 33 m in depth, these values for the 2nd and 5th blades range, respectively, from 0 to 80% and from 0 to 85%. The optimal depth for maximal primary production is about 2 m, where photosynthetic capacities of plants are actually reached. Positive 24 h balance of carbon determines the lower limit of *T. ciliatum* growth at 25-40 m which conforms to the ecological data obtained during our expedition (Ch. 5, Gutnik et al. 1992).

Temperature dependence of oxygen exchange in seagrass blades. Temperature is an important environmental factor affecting primary production of marine plants in tropical waters. On the islands studied, intertidal pools can be warmed up to 40°C and even higher during a day, and during rains they can be cooled to 20°C. On the other hand, deep water plants can be periodically cooled (to 20-15°C) due to up-welling (Novozhilov et al. 1989).

The temperature dependence of net photosynthesis for *Thalassodendron ciliatum* blades from various depths (Figs. 4 and 5) shows a maximum between 25-32°C and is not dependent on blade age or depth. Variations in the maximum levels were mainly correlated with the light intensity at which the temperature dependence was registered. For example, in plants from 15 m in depth exposed to low light ( $\alpha$  section of the light curve), the maximal rate of  $O_2$  evolution occurred at 28°C for young blades and at 25°C for old blades, whereas at light saturation, 32°C was required to reach the maximum. The greatest differences between plants were correlated with their sensitivity to temperature changes, which can be characterized by the coefficient  $Q_{10}^{-\Delta P \Delta T} P_{max}$ , where  $\Delta P$  = the change of net photosynthesis rate in the interval  $\Delta T = 10^\circ C$ ;  $P_{max}$  = net photosynthetic rate in the maximum of the temperature curve. Values of this parameter for  $O_2$  evolution rate at light saturation with reference to blade age and habitat depth are given in Table 2. A 10° C drop in temperature from optimal causes a similar decrease in the photosynthesis rate in both young and old blades, which is more pronounced (up to 60%) in plants from 2 and 33 m depths and minimal in plants from the surface (37%). A 10° temperature increase above optimal also causes a decrease of net photosynthesis, but differs between the 2nd and 5th blades and is minimal for shallow water plants. Variations of  $Q_{10}$  are interesting since they suggest a greater resistance of photosynthesis to temperature fluctuations in plants from the intertidal zone where such fluctuations are the most frequent.

The dark respiration rate increases up to 40°C, with growth in all the samples except plants from 2 m in depth (Figs. 4 and 5). Respiration of these plants is maximum at temperatures corresponding to the photosynthetic optimum. At the extremes of the temperature intervals, rates of  $O_2$  uptake differ as much as 4-6 times.

Light dependence of carbon assimilation in seagrass blades ( $P_s$  vs. I). The carbon

photoassimilation rate was studied with reference to light intensity in *Thalassodendron ciliatum* from various depths during different times of the day in order to determine the daily dynamics of photosynthesis in middle aged blades (3rd and 4th, Fig. 6). For these experiments, plants from various depths were put in aquaria shaded by white cloth to establish illumination conditions close to those in the natural habitats. During 1-3 days of adaptation, the light dependence of photosynthesis was determined during the morning, afternoon and evening hours.

Daily fluctuations in the carbon photoassimilation rate were approximately the same in plants from different depths. The photosynthetic rate at saturating light intensity ( $P_{\max}$ ) increased during the first half of the day and dropped during the afternoon. The maximal rate ( $P_{\max}$ ) was observed at 1300 in blades from 0-26 m in depth, with 7 to 8.5 mg CO<sub>2</sub>:g dry wt<sup>-1</sup>·h<sup>-1</sup>· $P_{\max}$  in plants from 33 m in depth was only half this value.

In plants from 0, 2-3 and 5 m depths, the initial slope of the light curve ( $\alpha$ ) decreased from morning to evening hours, i.e., the efficiency of utilization of low light declined. Clear day changes of this parameter were not recorded for plants from 11, 26 and 33 m depths. A light curve plateau was not found in all the experiments (1300 h, 2-3 m depth; 0800 h, 11 m depth). There were no clear patterns in the daily fluctuations of the light level at which photosynthetic light saturation ( $I_k$ ) occurred. In the majority of cases, light saturation of CO<sub>2</sub> assimilation occurred at relatively low PAR intensities: between 50 and 100  $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ . Photosynthetic inhibition by light fluxes of more than 240  $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  took place during morning hours in plants from 0, 5 and 33 m, in the afternoon - from 5 and 33 m and in the evening - from 0.5, 2-3, 11, 26 and 33 m. The middle-aged blades displayed daily variations in the carbon assimilation rate ( $P_{\max}$ ), as did young (2nd) and old (5th) blades of plants taken from both intertidal pools (0.5 m depth) and from the subtidal zone (2 m in depth).

The amplitude of daily fluctuations of  $P_{\max}$  was greater in intertidal plants than in plants from 2 m in depth. The greatest difference of  $P_{\max}$  between the afternoon and evening hours (4.5 mg CO<sub>2</sub>:g dry wt<sup>-1</sup>·h<sup>-1</sup>) was recorded in old blades of *Thalassodendron ciliatum* inhabiting intertidal pools.

On the basis of the light curves presented at Figure 6 and additional measurements, the potential net production per day for plants taken from all depths (0 to 33 m) was calculated (Fig. 7). Primary net production was calculated by the method of graphic summation (Nichiporovich 1956), i.e., potential photosynthetic production  $P_{\max}$  for each daylight hour (from 0800 to 1700 h) was summarized. The maximum potential net production occurs in plants from the middle depths (from 6 to 23 m), and the minimum one - to intertidal and deep water (33 m) plants.

## DISCUSSION

The light curves of net photosynthesis of *Thalassodendron ciliatum* blades are close in general shape to those of other seagrass species (Buesa 1974, Dennison 1985). However, *T. ciliatum* shows very early saturation of photosynthesis ( $I_k = 30\text{-}50 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) in comparison with *Zostera marina* (65-120  $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , Dennison and Alberte 1985) or *Thalassia testudinum* (about 170  $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , Buesa 1974, King and Schramm 1976).

The rates of  $P_{\text{net}}/\text{max}$  and R rates are close to those of other species of seagrasses (Jones 1968, Buesa 1974, Hefferman and Gibson 1983). Fluctuations of these parameters for *Thalassodendron ciliatum* are similar to those reported earlier for macrophytes (Ramus et al. 1976, 1977).

Light curves of carbon assimilation differ from those of oxygen evolution mostly due to the  $I_k$  index which is shifted towards greater light intensities in the light curves of carbon assimilation. This

shift can be explained by difference in the method of light curve determination. Changes of functional indices of light curves of O<sub>2</sub> evolution and CO<sub>2</sub> uptake connected with habitat depth are close to each other. These are stable and show a high level of P<sub>max</sub> for plants from middle depths (2-15 m for O<sub>2</sub> evolution and 6-23 m for CO<sub>2</sub> uptake) and also a drop in P<sub>max</sub> for intertidal and deep water plants. There are tendencies in the increase of the slope of the linear section of both light curves (O<sub>2</sub> and CO<sub>2</sub>) and adaptation to the decrease of light quantity with depth (from 0 to 26 m).

On the basis of the data, the depth distribution of *Thalassodendron ciliatum* primary production of blades is determined by light conditions which also limit the lower boundary of the species distribution. On the islands studied, maximal seagrass productivity was found at about 2 m in depth which is not exposed to air at low tide. Relatively high photosynthetic production at middle and lower depths is maintained due to physiological adaptation to light. This phenomenon is rather well studied in terrestrial plants and marine algae and is characterized specifically by the increase of photosynthetic capacities and the decrease of respiration with depth (Titlyanov 1983, Titlyanov et al. 1987).

Temperature curves of net photosynthesis of *Thalassodendron ciliatum* have the classical shape with well-expressed temperature optimum at 28-30°C. Measured temperature optimum of *T. ciliatum* photosynthesis is close to the temperature optimum of growth of tropical seagrass *Thalassia testudinum* from Biscayne Bay, Florida (near 30°C at salinity 30ppt., Zieman 1975).

The position of the temperature optimum is less dependent on depth which was shown for macroalgae (Kanwisher 1966, Yokohama 1972, Katayama et al. 1985).

The study of temperature effects on the primary production of *Thalassodendron ciliatum* revealed that a 10° temperature rise from optimal (28-30°C) for  $\Delta t$  interval during daylight hours at shallow depths leads to a drop of net production equal to  $Q_{10} \cdot P_{net}/max \cdot \Delta t$ , where  $P_{net}/max$  - net photosynthesis rate at the temperature optimum. In comparison with 24 h production, which on the shallows is determined by the product  $P_{net}/max \cdot L$ , where  $L$  - day length, the loss makes  $Q_{10} \cdot \Delta t \cdot L^{-1}$  percent. Thus, if temperature increases during the entire day, the loss of 24 h production is equal to  $Q_{10}$  percent, which does not exceed 30% for shallow plants. Similar considerations can be applied in the case of a temperature drop at shallow depths, where the loss of photosynthetic production can reach 60% at 20°C (Table 2).

As was shown for three species of seagrasses from Florida - *Thalassia testudinum*, *Syringodium filiforme* and *Halodule wrightii* (McMillan 1984) - tropical seagrass species have high heat tolerance and can survive temperatures of 36°C for 4 weeks and 39°C for up to 36 h.

Nighttime drops in temperature and the attendant decrease in respiration leads to an increase in the 24 h net production. To estimate the effects of  $R$  decreases the 24 h carbon balance, the following ratio was used:  $P_{net} \cdot 24h^{-1} = P_{net}/day - R_{night}$ , where  $P_{net}/24h$  and  $P_{net}/day$  - 24 h and daily net production,  $R_{night}$  - total night respiration. If the respiration rate during the night is  $K$  times less, then taking into account that  $P_{net}/max / R = N$  (Table 1) and using the equation of balance, it is easy to show that the 24 h production increases  $(N - 1/k)/(N-1)$  times. For shallow algae, for example, a nighttime water temperature of 20°C can cause an increase in 24 h production by 1.5 fold in comparison with the optimal temperature (28-30°C).

It is interesting to note that production increases due to a drop in the respiration level can be reached also by a change of salinity. Thus, for the seagrass *Ruppia maritima* from Tampa Bay, Florida (Dawes 1974), a salinity rise at the same illumination level leads to a drop in the dark respiration without change of photosynthesis.

Changes of potential photosynthetic capacities ( $\text{CO}_2$  assimilation) within a day for the seagrass *Thalassodendron ciliatum* are the same as for temperate and tropical macroalgae (Titlyanov et al. 1991). They are expressed in the increase of  $P_{\text{max}}$  rate towards the afternoon and in its drop toward evening. This feature was found in blades of all ages. The decrease in slope of the linear section of the light curve of  $\text{CO}_2$  assimilation from morning to evening hours is probably connected with the drop of chlorophyll concentration in *T. ciliatum* blades, as was shown for *Ulva fenestrata* thalli (Titlyanov et al. 1978).

High stable levels of potential photosynthetic capacities of *Thalassodendron ciliatum* blades which are maintained down to 23-26 m in depth is very important for the distribution of this seagrass into great depths. As revealed by our calculations, high potential photosynthetic capacities can be realized with high efficiency over a wide illumination range which leads to a stable high productivity throughout the depth range from 2 to 33 m, both in clear and turbid waters of the Seychelles (Fig. 3).

Stable levels of primary production of benthic autotrophs over a wide range of illumination was reported earlier for reef-building corals (Titlyanov et al. 1988) and for tropical macroalgae (Titlyanov et al. 1992, Ch. 9, this volume).

High production over a wide illumination range is a result of adaptation of benthic macrophytes to the natural habitat illumination. This is attained via a number of adaptive reactions which are not the same for different groups of aquatic plants (Titlyanov et al. 1987). For *Thalassodendron ciliatum*, adaptation to low light intensities in deeper waters leads to lower light saturation of photosynthesis, accumulation of photosynthetic pigments, an increase in the slope of the linear section of the light curve and a greater photosynthetic level at light saturation (Titlyanov et al. 1992, Ch. 9, this volume).

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Table 1. Rates of net photosynthesis at light saturation (P net/max) and dark respiration (R) at 27-28°C for young and old blades of *Thalassodendron ciliatum* from different depths. "\*" maximal deviation from average value at n=4.

| Depth<br>m | Blade<br>net/max<br>No. | $\mu\text{l O}_2\text{g fresh wt}^{-1}\cdot\text{h}^{-1}$ |             | P<br>R  |
|------------|-------------------------|---|-------------|---------|
|            |                         | P net/max   | R           |         |
| 0          | 2                       | 0.671±0.146   | 0.335±0.055 | 2.0±0.9 |
|            | 5                       | 0.411±0.016   | 0.191±0.015 | 2.1±0.3 |
| 2          | 2                       | 0.895±0.044   | 0.193±0.032 | 4.6±1.2 |
|            | 5                       | 0.569±0.1   | 0.147±0.051 | 3.9±3.0 |
| 15         | 2                       | 0.983±0.024   | 0.250±0.05  | 3.9±1.1 |
|            | 5                       | 0.753±0.022   | 0.178±0.046 | 4.2±1.6 |
| 33         | 2                       | 0.680±0.02  | 0.175±0.005 | 3.9±0.2 |
|            | 5                       | 0.580±0.02  | 0.160±0.02  | 3.6±0.6 |

Table 2. Values of  $Q_{10}$  coefficient for the 2<sup>nd</sup> and 5<sup>th</sup> blades of *Thalassodendron ciliatum* from different depths at temperatures lower and higher than 30°C.

| Depth, m  | $Q_{10}$ at Temp. 20-30°C |    | $Q_{10}$ at Temp. 30-40°C |     |
|-----------|---------------------------|----|---------------------------|-----|
|           | 2                         | 5  | 2                         | 5   |
| 0         | 37                        | 33 | -20                       | -12 |
| 2         | 62                        | 58 | -30                       | -14 |
| 15        | 45                        | 47 | -23                       | -36 |
| 33        | 60                        | 50 | -20                       | -20 |
| Blade No. | 2                         | 5  | 2                         | 5   |

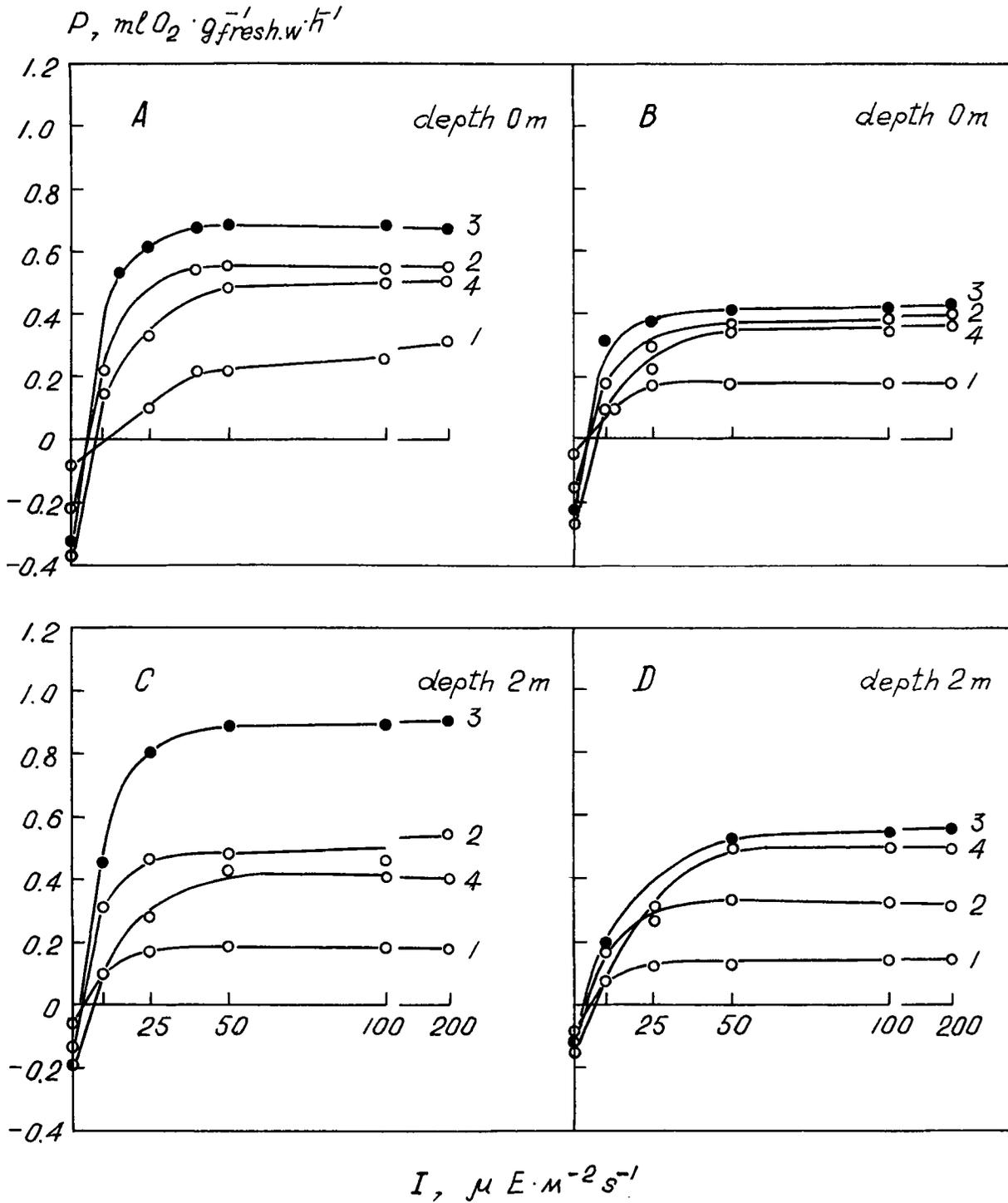


Figure 1. Light curves of photosynthesis of the 2<sup>nd</sup> (A,C) and 5<sup>th</sup> (B,D) leaves of *Thalassodendron ciliatum* from 0 and 2 m in depth at different temperatures (1=10°, 2=25°, 3=30°, 4=40°C).

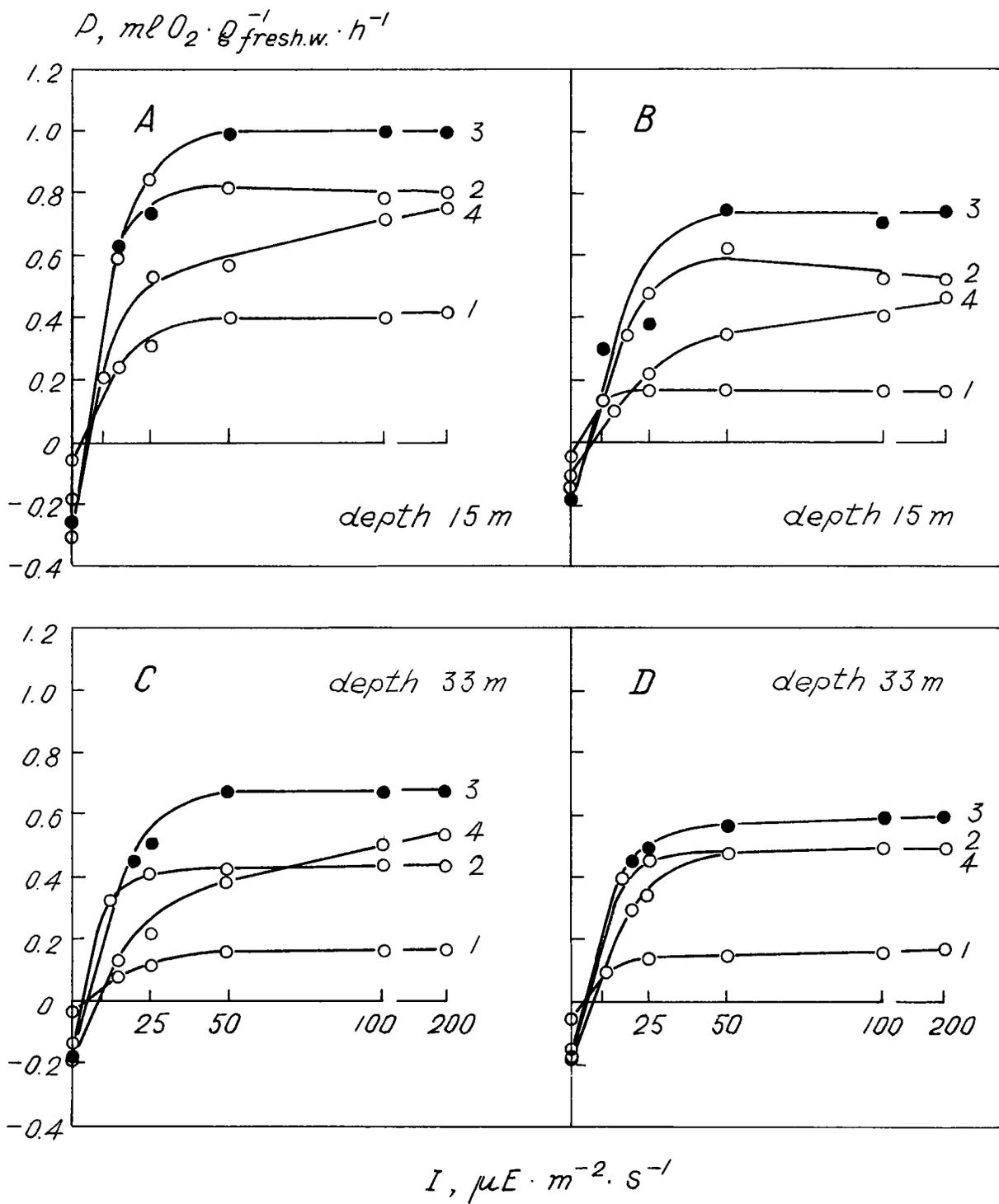


Figure 2. Light curves of photosynthesis of the 2<sup>nd</sup> (A,C) and 5<sup>th</sup> (B,D) leaves of *Thalassodendron ciliatum* from 15 and 33 m in depth at different temperatures (1=10°, 2=25°, 3=30°, 4=40°C).

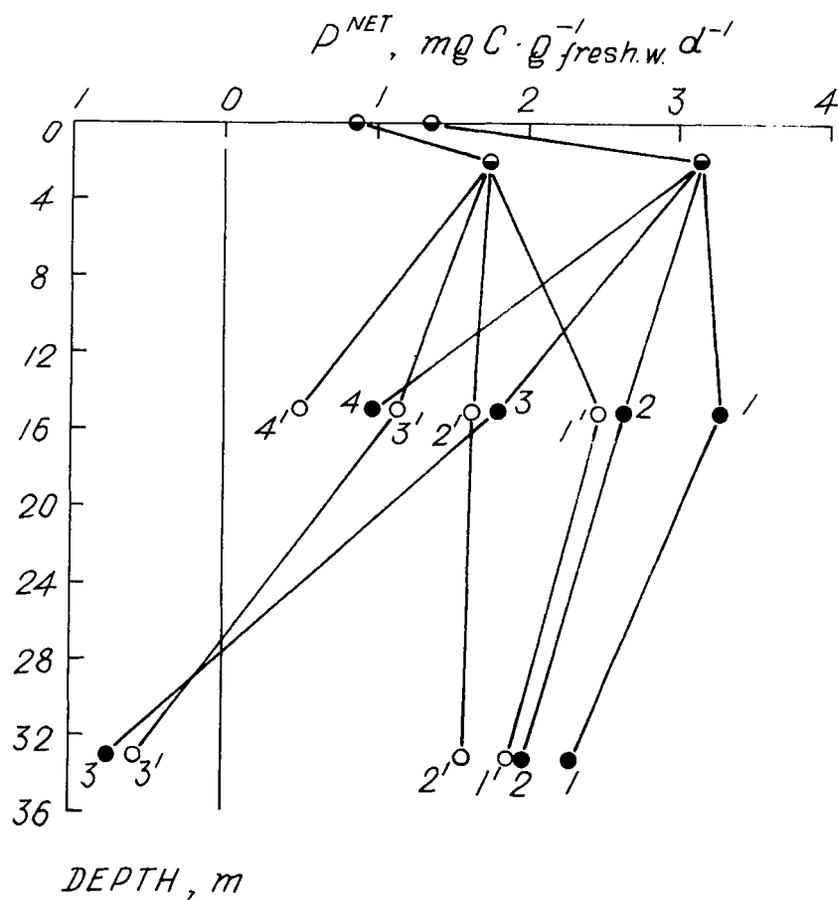


Figure 3. Daily net photosynthetic production ( $P^{net}$ ) as a function of depth in the 2<sup>nd</sup> (1-4) and 5<sup>th</sup> (1'-4') leaves of *Thalassodendron ciliatum* in waters of different transparency: 1 - Type I, 2 - Type II and 3 - Type III oceanic waters, 4 - Type III coastal waters (Jerlov 1980).

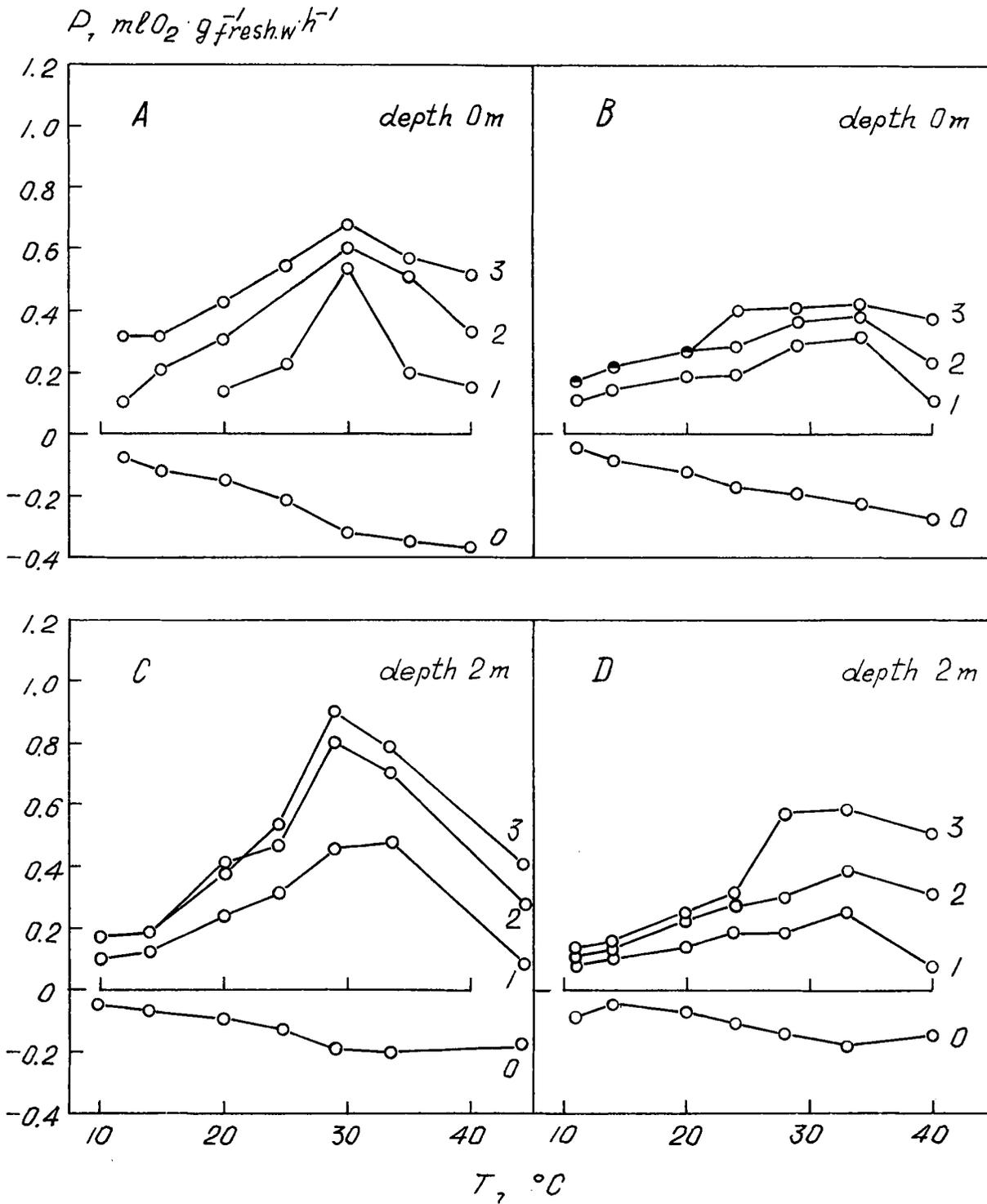


Figure 4. Temperature dependence of photosynthesis and dark respiration in the 2<sup>nd</sup> (A,C) and 5<sup>th</sup> (B,D) leaves of *Thalassodendron ciliatum* from 0 (A,B) and 2 (C,D) m in depth at different intensities of photosynthetic flow density: 0 - dark respiration; 1, 2, 3 for 10, 25 and 200  $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , correspondingly.

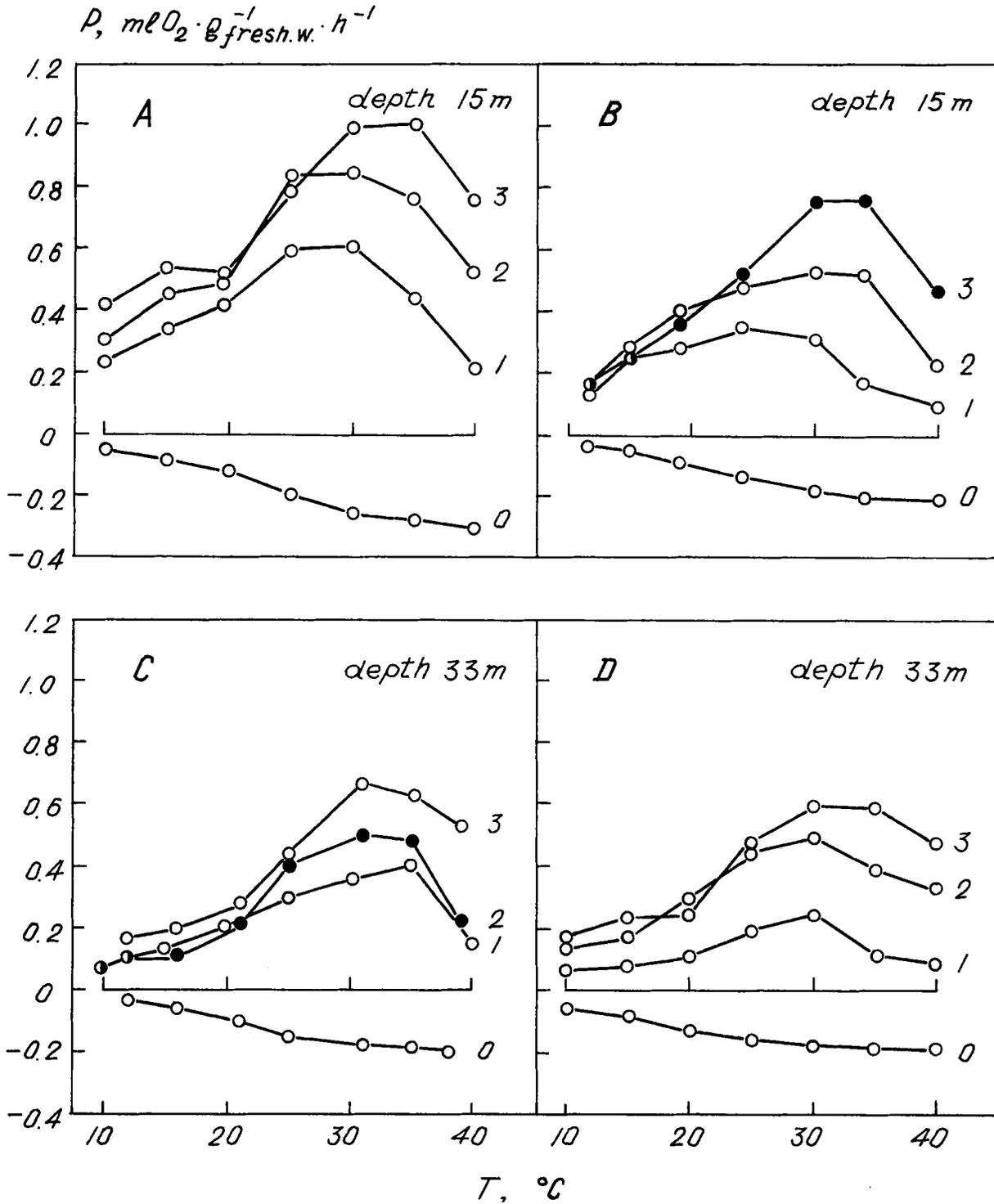


Figure 5. Temperature dependence of photosynthesis and dark respiration in the 2<sup>nd</sup> (A,B) and 5<sup>th</sup> (C,D) leaves of *Thalassodendron ciliatum* from 15 (A,B) and 33 (C,D) m in depth at different intensities of photosynthetic flow density: 0 - dark respiration, 1, 2, 3 for 10, 25, and 200  $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , correspondingly.

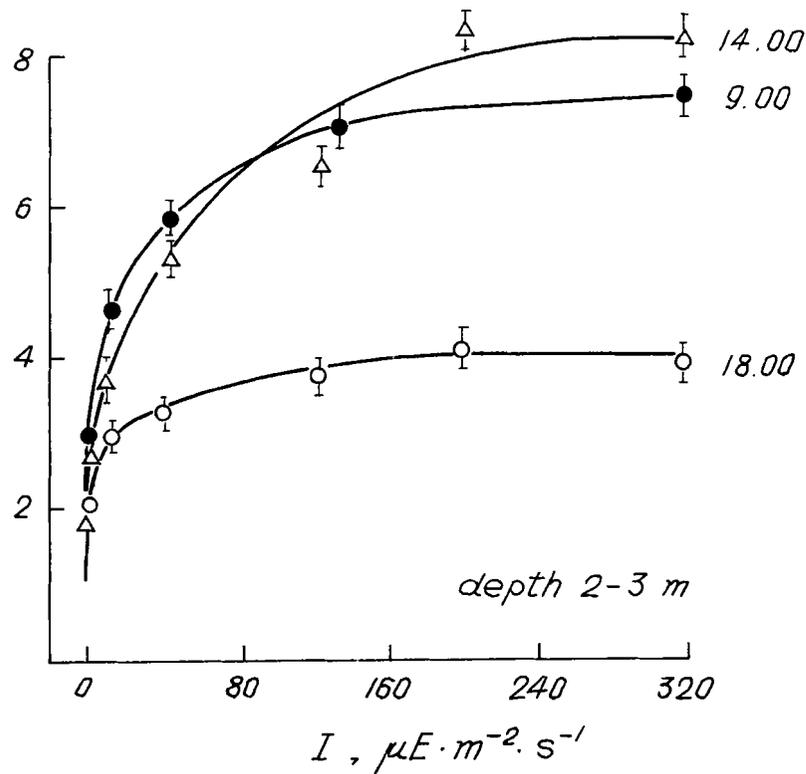
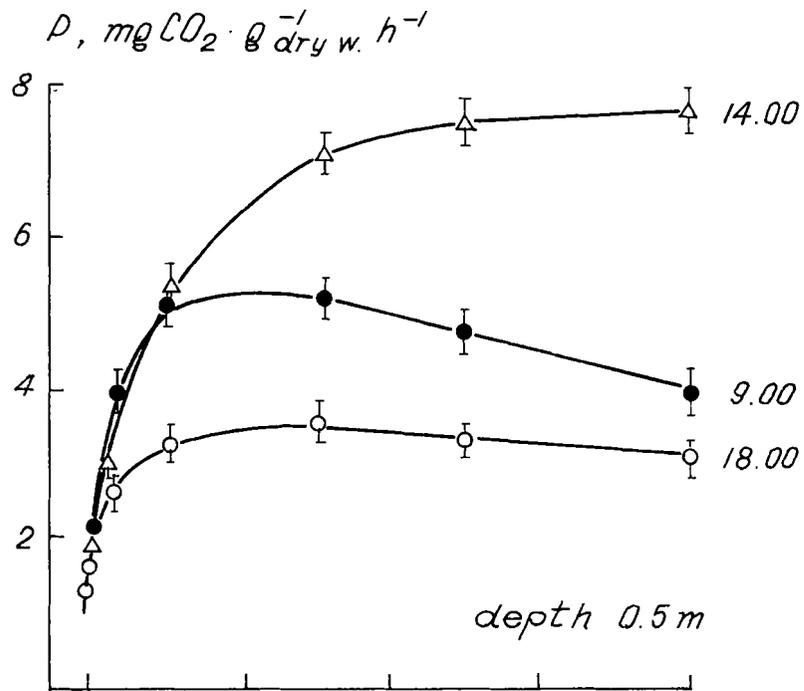


Figure 6 (A). Light dependence of photosynthesis in *Thalassodendron ciliatum* at various times of the day for a given depth.

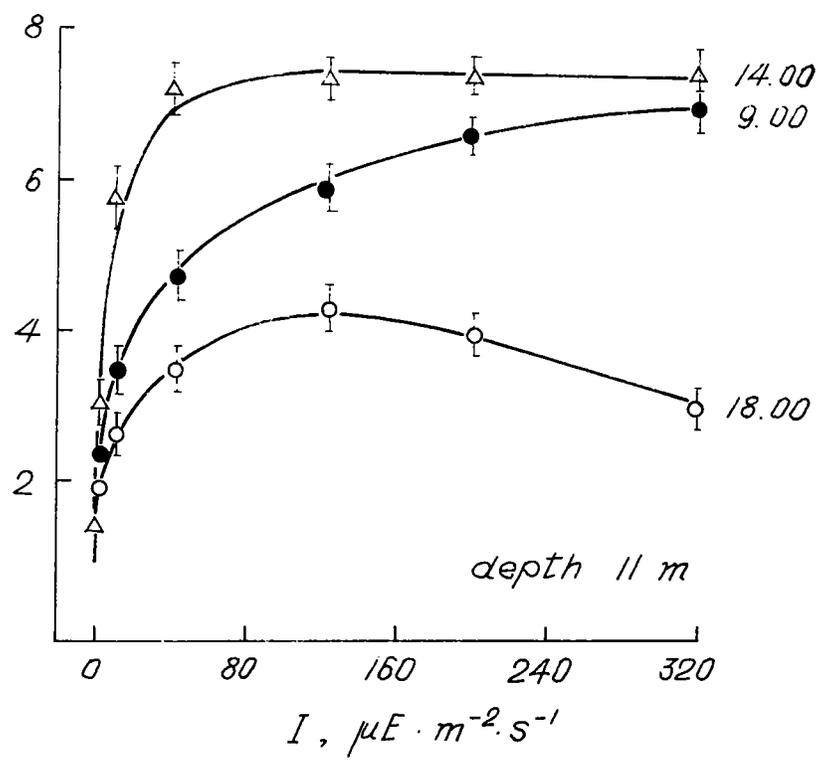
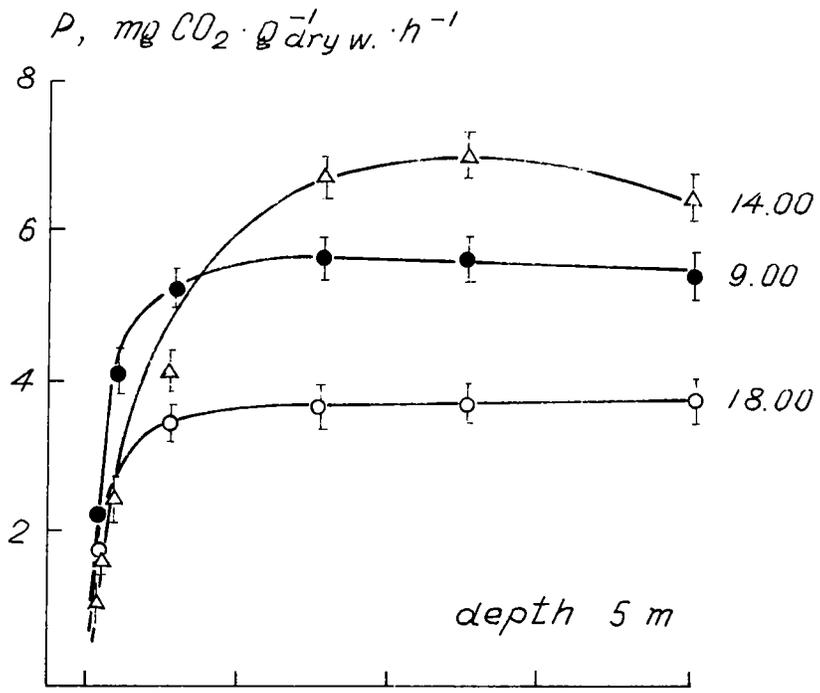


Figure 6 (B).

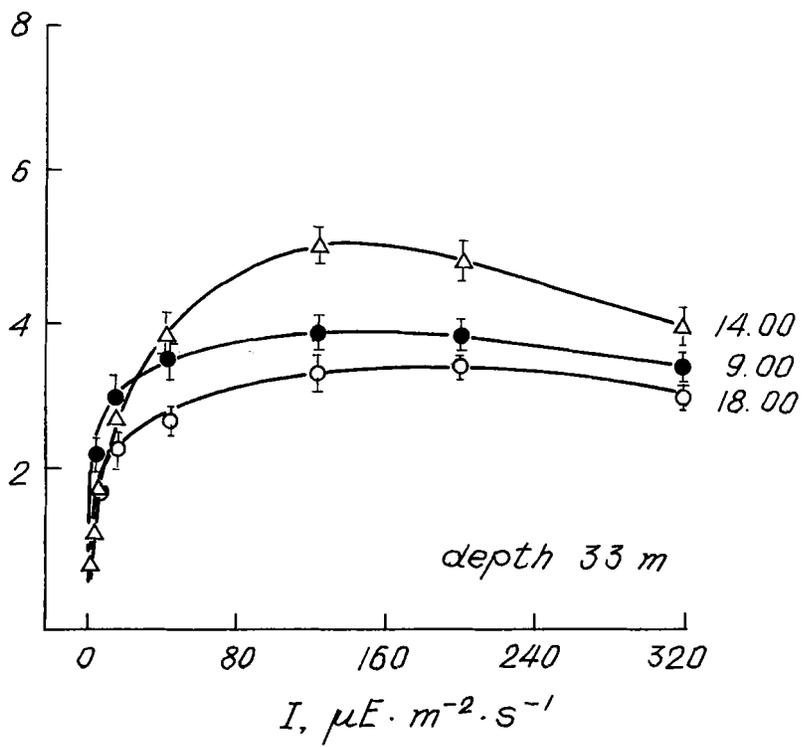
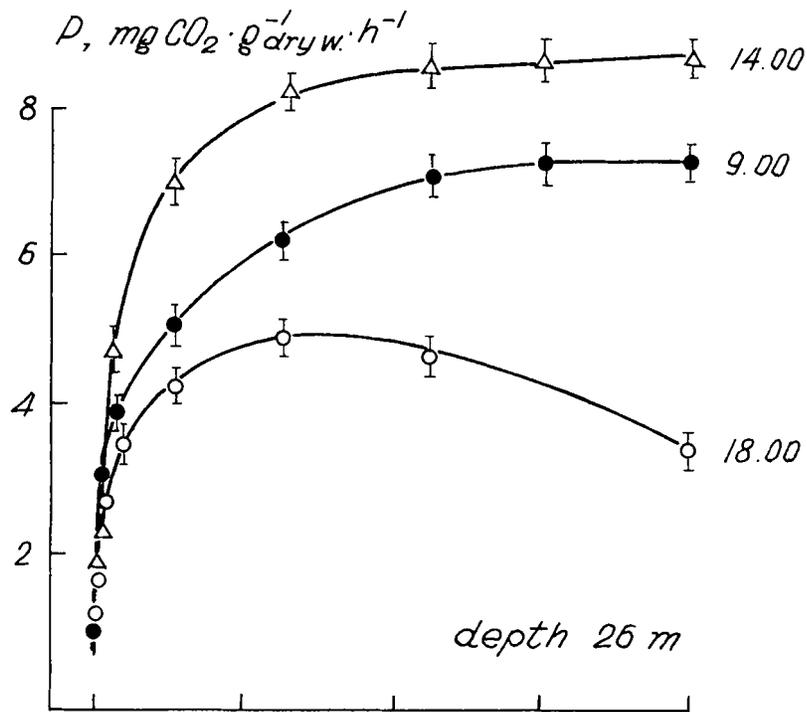


Figure 6 (C).

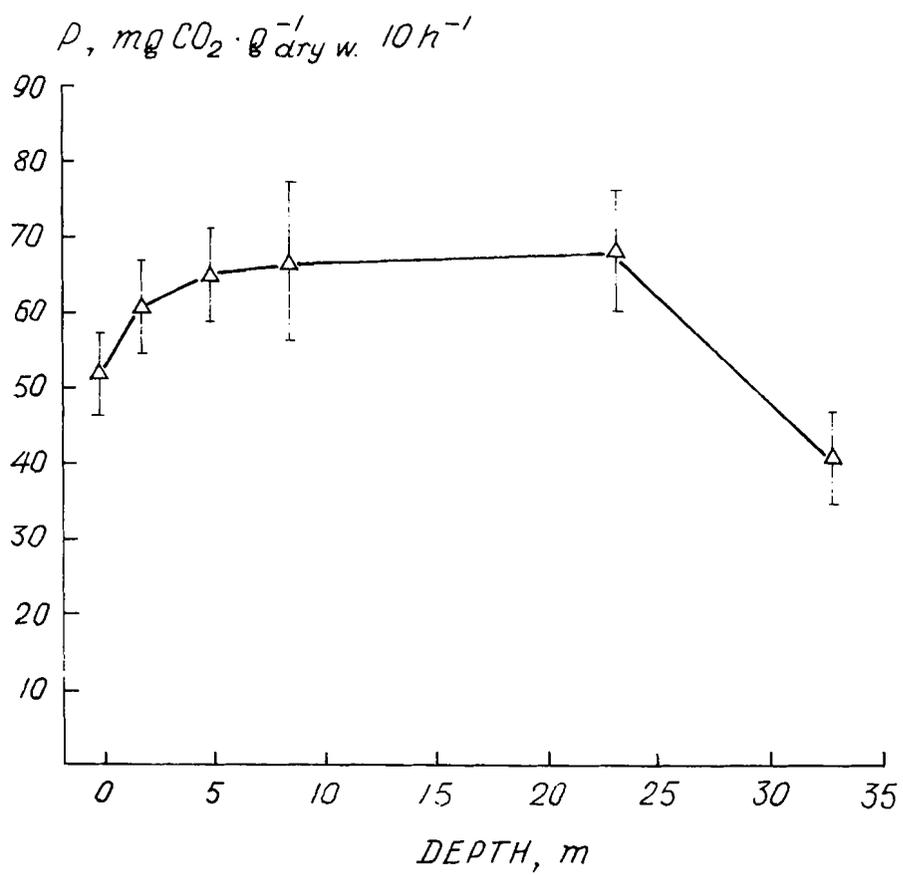


Figure 7. Daily potential production of middle-aged leaves of *Thalassodendron ciliatum* with reference to habitat depth.