

Studies on diurnal photosynthetic performance of *Sargassum thunbergii* I. Changes in photosynthesis under natural sunlight

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A flow-through system was established to carry out photosynthetic measurements of macroalgae under natural sunlight. Changes in photosynthesis of *Sargassum thunbergii* with changes in solar radiation under different weather conditions were measured with the flow-through system. It was found that photosynthetic rate was higher in the morning than in the afternoon on fine days and showed little difference between the morning and the afternoon on a rainy day. Midday, or afternoon, photosynthetic depression observed on fine days could not be accounted for by an increase in dark respiration. Despite midday or afternoon photosynthetic depression, daily net and gross productions were found to increase linearly with an increase of daily photosynthetically active solar radiation.

Key Index Words: Photosynthesis—dark respiration—PAR—*Sargassum thunbergii*.

In coastal areas, seaweeds play an important role as primary producers. Estimations of the primary production of seaweeds often rely on photosynthesis-light and solar radiation curves. Seaweeds are usually subjected to dramatic changes of solar radiation throughout a day. Are the changes in photosynthesis with the solar radiation independent of light histories? Is the estimated photosynthetic production close to the actual diurnal production? It is possible that P_{max} and initial slope of a photosynthesis-light curve differ when a seaweed has been exposed to different light histories, or at different times of day under natural sunlight. Diurnal photosynthesis has been found to show higher morning photosynthetic rates and afternoon depression in tropical grasses (ITO *et al.* 1973), freshwater submerged angiosperms (GOULDER 1970, HOUGH 1974) and phytoplankton (DOTY and OGURI 1957, YENTSCH and RYTHER 1957, HARRIS 1973, SOURNIA

1974, MARRA 1978). But there are few reports on the diurnal photosynthesis of seaweeds. RAMUS and ROSENBERG (1980) measured the diurnal photosynthesis of seaweeds and reported that photosynthesis-light curves measured in the laboratory showed a great difference from natural diurnal photosynthesis. However, SMITH (1981) reported no depression of diurnal photosynthetic pattern in *Codium carolinianum* and *Lodophora variegata* calculated from an *in situ* study. MAEGAWA and ARUGA (1983), studying on a cultivated *Monostroma latissimum* population, also reported that no midday or afternoon depression of photosynthesis was observed, even on fine days. Therefore, it is important to follow photosynthetic changes under natural sunlight to make clear whether seaweeds exhibit a pattern of diurnal photosynthetic variation similar to higher plants and phytoplankton, or not.

Sargassum, a genus in the Phaeophyceae, constitutes an important part of the marine flora, forming an extensive vegetation in the coastal areas of Japan and playing an impor-

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tant role in the coastal ecosystem. *Sargassum thunbergii* is a perennial species growing on rocks at middle to lower level in the intertidal zone, forming a conspicuous belt in places not exposed to strong wave action, and is distributed on the coasts of both the Sea of Japan and the Pacific Ocean throughout the Archipelago of Japan. The knowledge of photosynthesis is important for the estimation of productivity of *Sargassum*. Although there are several reports on photosynthesis in *Sargassum* up to now (THOMAS and TREGUNNA 1968, YOKOHAMA 1977, MIZUSAWA *et al.* 1978, GAO and UMEZAKI 1988), nothing has been reported on diurnal photosynthesis and daily photosynthetic production of plants in this genus. In the present study it was intended to follow the photosynthetic changes of *Sargassum thunbergii* under natural sunlight to make clear its diurnal photosynthesis pattern.

Materials and Methods

The present study was carried out at the Fisheries Research Station of Kyoto University situated at the head of Maizuru Bay, one of the branch bays of Wakasa Bay facing the Sea of Japan. Here, *S. thunbergii* forms a conspicuous zone at approximately -10 to $+15$ cm tide level and matures in July. After

maturation, the main branches decay away and newly germinated main branches and juveniles appear about two months later.

The measurements of diurnal photosynthesis were carried out in October and December 1986. Whole juveniles or young plants derived from naturally-occurring germlings were collected and cleaned of obvious epiphytes before use. Samples used for measurements of diurnal photosynthesis or dark respiration were about 1.5 and 3 cm long in October and December, respectively. Five to ten samples were used for each measurement of diurnal photosynthesis or dark respiration.

Figure 1 shows the flow-through system for measuring photosynthesis and respiration. The ends of the pipe are cone-shaped, which gives a uniform water flow through the pipe (P). Transparent and opaque pipes, 70 cm long and 3 cm in inner diameter, were used for measurements of photosynthesis and dark respiration, respectively. Samples (Th) were fixed by inserting their holdfasts into a cord and kept erect in the pipe. Water flow through the pipe was tested with uranine dye. The flow rate of the filtered seawater (filtered through sand and coal particles) was controlled with a flow meter (Kojima, RK 1200).

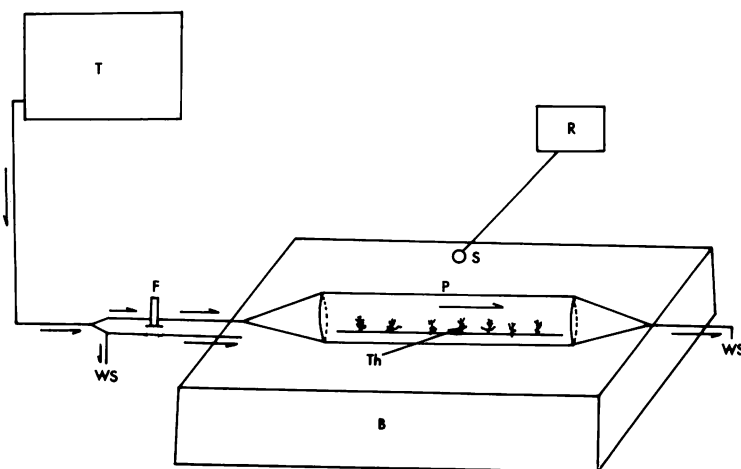


Fig. 1. Outline of the system for measuring diurnal photosynthesis and dark respiration. T, water tank for supplying filtered seawater; F, flow meter; P, assimilation pipe; Th, thallus; S, underwater quantum sensor; R, recorder; WS, water sampling tube; B, water box.

Inflowing and outflowing seawater were sampled almost simultaneously in D. O. bottles of about 100 ml in duplicate each time. Water sampling was made once every hour or every two hours for photosynthetic or respiratory measurements, respectively. The dissolved oxygen concentration of seawater was determined by the Winkler titration technique. The titration was made within 3 to 4 hours after water sampling. Photosynthesis (P) or respiration (R) rate [$\text{ml O}_2 \text{g(d.w.)}^{-1}\text{h}^{-1}$] was calculated by the following equation:

$$P \text{ or } R = (A - B) \times F \times 60 \times 1/W,$$

where A and B represent D. O. concentrations (ml l^{-1} , 0°C and 760 mmHg) of outflowing and inflowing seawater, respectively; F, flow rate (l min^{-1}) of filtered seawater supplied into the pipe; W, dry weight (g) of samples determined after drying at 85°C for 20 hours. Different samples were used for the measurements of photosynthesis and dark respiration. During the daytime, dark respiration was measured by placing samples in an opaque pipe for about 20 minutes. After the dark respiration measurement, samples were taken out of the pipe and exposed to solar radiation under the same conditions as those for photosynthetic measurements.

Photosynthetically active radiation (PAR, 400–700 nm) of incident solar light was measured continuously from sunrise to sunset with an underwater quantum sensor (LICOR, LI-192S) linked with a recorder (TOA Electronics Ltd., FBR-253A). Water temperature in the pipe, which was maintained in a water tank, was in harmony with that in the sea. Water temperature was in ranges of $21\text{--}23^\circ\text{C}$ and $13\text{--}14^\circ\text{C}$ during the experiment periods in October and December, respectively.

In order to value diurnal photosynthesis measured under different temperatures in October and December, it was necessary to know the relationships of photosynthesis and respiration to temperature. Photosynthesis and respiration versus temperature curves

were obtained in March and September in the laboratory with a differential gas-volumeter, "Productmeter" (Nikko Kagaku Ltd.), devised by YOKOHAMA and ICHIMURA (1969) and improved by YOKOHAMA *et al.* (1986). Light was supplied by incandescent "high beam bulbs" (National, 110V 150W). The water temperature was controlled by using a Taiyo Coolnit (CL-30). Dark respiration was measured by covering the reaction vessel completely with opaque plastic.

Results

The system for measuring photosynthesis and respiration in the present study kept samples erect in flowing seawater, and this made it possible to measure photosynthesis or respiration under conditions close to those in the sea. However, the time lag for detecting oxygen evolved or consumed by samples kept in the pipe, which may be related to the flow rate, the inner diameter and length of the pipe, should be considered. In preliminary experiments, changes of D. O. concentration of outflowing seawater were measured in the laboratory under constant light and temperature conditions at different flow rates after samples had been put into the pipe. As shown in Figure 2, it took about 8, 6, 5 and 2

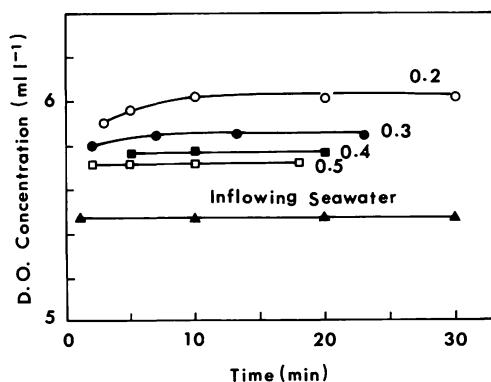


Fig. 2. Time courses of D. O. concentrations in the outflowing seawater at different flow rates (0.2, 0.3, 0.4 and 0.5 l min^{-1}) after 8 individuals of *S. thunbergii* were put into the transparent assimilation pipe at $1000 \mu\text{E m}^{-2}\text{s}^{-1}$ and 16°C in the laboratory. Solid triangles show D. O. concentrations in the inflowing seawater.

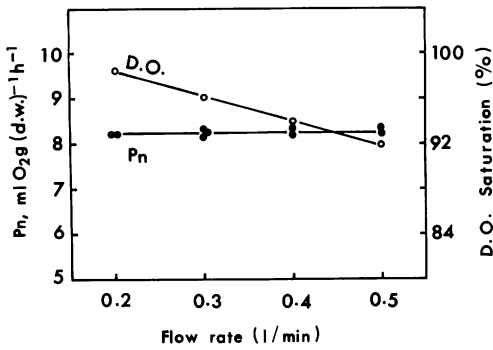


Fig. 3. Relationships of net photosynthesis (P_n) of *S. thunbergii* and D. O. saturation of outflowing seawater to flow rates. Calculated from Fig. 2.

minutes for D. O. concentrations to level off at flow rate of 0.2, 0.3, 0.4 and 0.5 $l\ min^{-1}$, respectively. The D. O. concentration was levelled in a shorter time as flow rate increased. Photosynthetic rates at different flow rates were calculated from data of Figure 2. As indicated in Figure 3, photosynthetic rate was not influenced by flow rate although the D. O. saturation decreased as flow rate increased within the range investigated. Fresh weight and dry weight of the samples used for these measurements were 5.394 and 0.794 g, respectively. Influences of flow rate on photosynthetic rate might have occurred if more samples were used at any one time.

A relationship of dry weight of samples to relative net photosynthesis is shown in Figure 4. Relative net photosynthesis showed constant values till 0.9 g as the dry weight of samples increased, and was reduced at 1.6 g dry weight of samples, while D. O. saturation increased with an increase of weight of samples.

Based on the results of Figures 2-4, the diurnal photosynthesis and dark respiration measurements of *S. thunbergii* were carried out on condition that the weight of samples was 4-5 g fresh weight (0.59-0.74 g dry weight) and the flow rate was 0.2 $l\ min^{-1}$ for respiratory measurement and within a range of 0.2-0.4 $l\ min^{-1}$ for photosynthetic measurement.

Figure 5 shows the diurnal net photosynthetic performance and the daily dark respira-

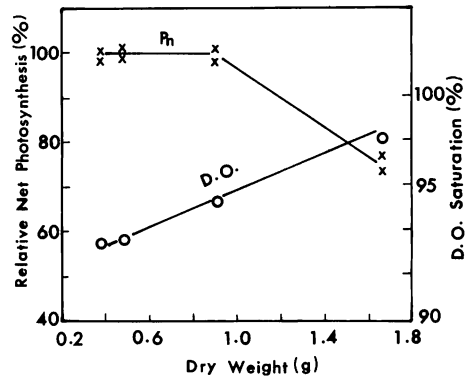


Fig. 4. Relationships of relative net photosynthesis (P_n) in *S. thunbergii* and D. O. saturation to dry weight of samples. Measured at $1000\ \mu E\ m^{-2}\ s^{-1}$ and $10^\circ C$ with a flow rate of 0.3 $l\ min^{-1}$.

tion of *S. thunbergii* juveniles on a fine day in October (A), and a fine day (B), a cloudy day (D) and a rainy day (C) in December. As indicated in Figure 5(A), net photosynthesis increased in early morning to reach a maximum at about 8 o'clock, decreased in late morning as solar radiation increased, increased again at noon and finally declined as solar radiation decreased in late afternoon. Dark respiration, which was measured with different samples kept under almost the same conditions as those for photosynthetic measurement, was found to be higher in daytime than at night, with the former about twice the latter on average. Daytime dark respiration was lower in morning and highest near midday when photosynthetic depression occurred (Fig. 5A). On a fine day in December (Fig. 5B), net photosynthesis increased to reach a maximum at about 10 o'clock in morning as solar radiation increased, and decreased in late afternoon as solar radiation decreased. Maximum of net photosynthesis was maintained for about 4 hours from late morning to early afternoon. Little difference in dark respiration was found between morning and afternoon. On a cloudy day (Fig. 5D), net photosynthesis increased with an increase in solar radiation in morning and decreased with a decrease in solar radiation in afternoon despite fluctuations in solar radiation. Dark respiration measured in early morning was

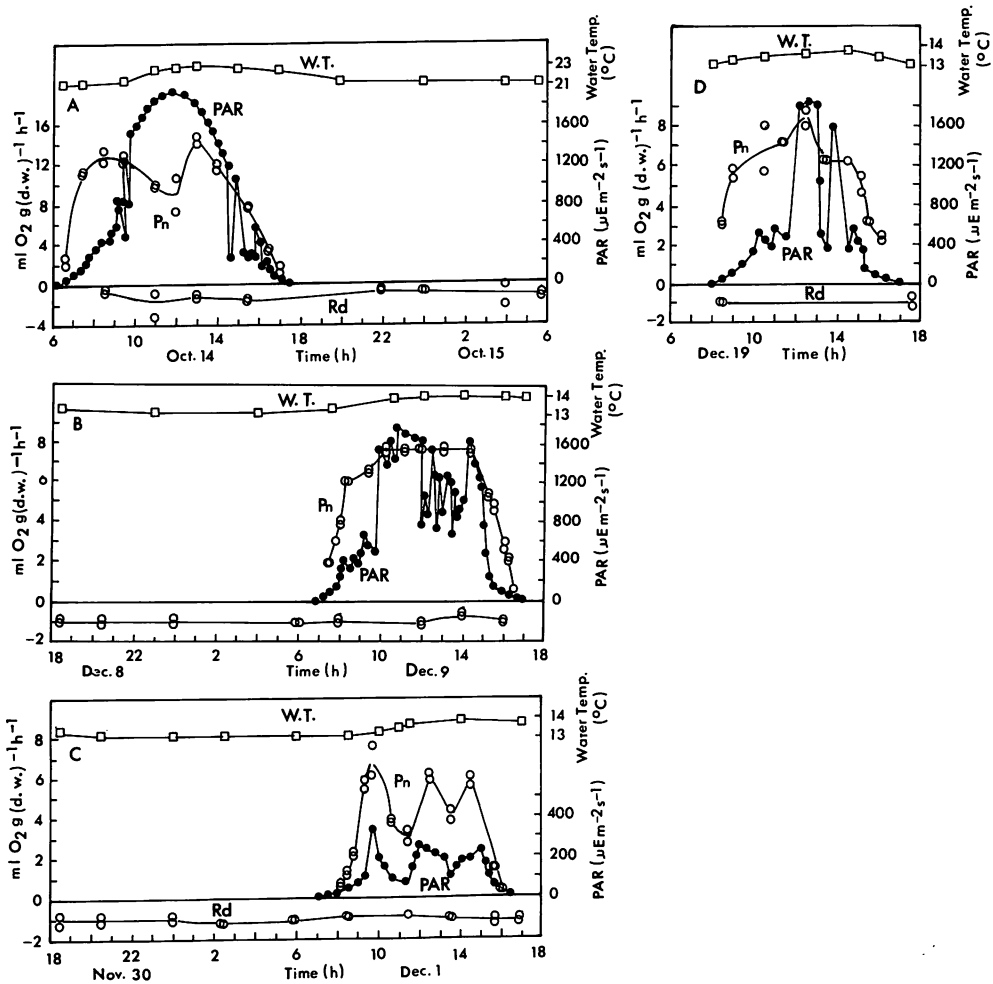


Fig. 5. Diurnal changes in net photosynthetic rate (P_n) and dark respiration rate (R_d) of *S. thunbergii* on a fine day in October (A) and December (B), and on a rainy day (C) and on a cloudy day (D) in December. Solid circles are photosynthetically active solar radiation (PAR) measured with a sensor set close to the assimilation pipe. W.T. is water temperature in the pipe.

almost the same as that in evening. This is in agreement with that on a fine day (Fig. 5B). On a rainy day in December (Fig. 5C), net photosynthesis varied with solar radiation. Dark respiration varied little throughout the day, which was in accordance with those on a fine day (Fig. 5B) and a cloudy day (Fig. 5D).

For detailed analysis of the diurnal photosynthesis of *S. thunbergii*, photosynthesis-light curves were derived from the data in Figure 5. PAR for constructing photosynthesis-light curves were determined from averaged values for 8, 6 and 5 minutes at flow rates of 0.2, 0.3 and 0.4 $l\ min^{-1}$, respectively,

taking into account time lags for detecting evolved oxygen in outflowing seawater (Fig. 2). Dark respiration rates measured in early morning after sunrise and in late afternoon before sunset were used for construction of photosynthesis-light curves. As indicated in Figure 6, two photosynthesis-light curves resulted from each curve of diurnal photosynthesis; one for increasing solar radiation preceding local noon and the other for decreasing solar radiation after noon. Net photosynthesis was higher in morning than in afternoon, even for the same photosynthetically active solar radiation (PAR), on fine or cloudy-

fine days in December. Net photosynthesis increased, saturated at about $300 \mu\text{E m}^{-2}\text{s}^{-1}$ and then decreased as the solar radiation increased in the morning on a fine day in October (Fig. 6A). Soon after noon, a recovery from the midday photosynthetic depression was observed. A considerable difference was found in the initial slopes of the curves derived from morning and afternoon photosynthesis, with slope much higher in morning than in afternoon. On a fine day in December (Fig. 6B), net photosynthesis in-

creased as solar radiation increased and saturated at irradiances above $600 \mu\text{E m}^{-2}\text{s}^{-1}$ in the morning, with the rate in morning higher compared with that in afternoon. On a cloudy-fine day in December (Fig. 6C), net photosynthesis was saturated at almost the same PAR as that on the fine day (Fig. 6B). Similarly, net photosynthetic rate was higher in the morning than in the afternoon. However, net photosynthesis was not saturated on the rainy day because of the much lower solar radiation, and little difference was found between morning and afternoon (Fig. 6D). Initial slope equations and P_{max} values for the curves of Figure 6 are shown in Table 1. Light compensation points of morning and afternoon curves were respectively 8 and $34 \mu\text{E m}^{-2}\text{s}^{-1}$ on October 14, 21 and $22 \mu\text{E m}^{-2}\text{s}^{-1}$ on December 1, 22 and $29 \mu\text{E m}^{-2}\text{s}^{-1}$ on December 9, and 14 and $23 \mu\text{E m}^{-2}\text{s}^{-1}$ on December 19. When

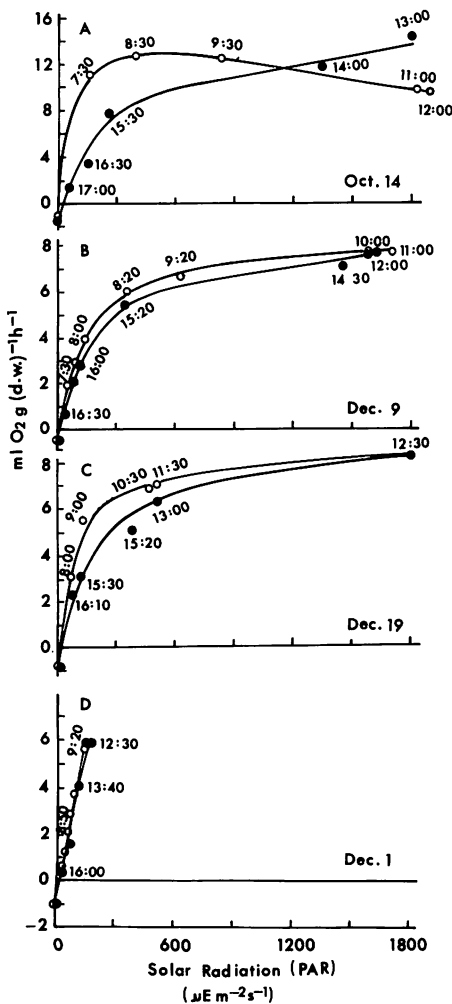


Fig. 6. Photosynthesis vs. solar radiation (PAR) curves of *S. thunbergii* obtained from Fig. 5. Open circles are for data before noon and filled circles are for data after noon. Numbers along the lines indicate the time of the day.

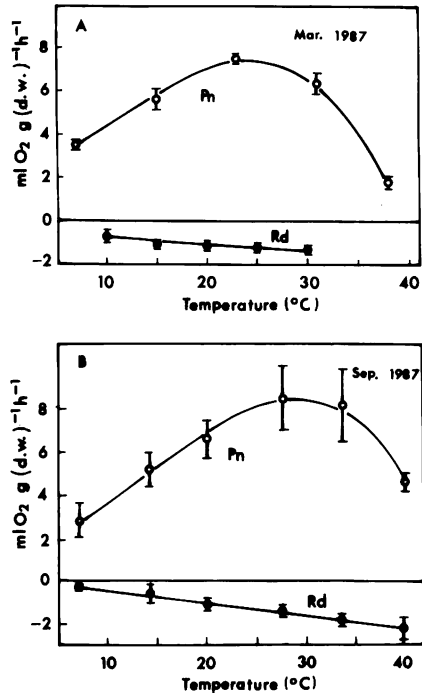


Fig. 7. Photosynthesis-temperature curves at $600 \mu\text{E m}^{-2}\text{s}^{-1}$ and respiration-temperature curves in dark of *S. thunbergii*. Measurements were made with four young plants about 3 cm long (A) and with six young plants 1–2 cm long (B). Mean of three measurements with SD.

Table 1. Initial slope equations and P_{\max} for photosynthesis-light curves in Figure 6. P in $\text{ml O}_2 \text{ g(d.w.)}^{-1}\text{h}^{-1}$ and I in $\mu \text{E m}^{-2}\text{s}^{-1}$.

Date	Initial slope equation		P_{\max}
	Morning	Afternoon	$\text{ml O}_2 \text{ g(d.w.)}^{-1}\text{h}^{-1}$
Oct. 14	$P=0.116I-0.93$	$P=0.043I-1.48$	12.6
Dec. 1	$P=0.045I-1.03$	$P=0.043I-1.01$	—
Dec. 9	$P=0.045I-1.00$	$P=0.035I-1.00$	7.8
Dec. 19	$P=0.069I-0.97$	$P=0.043I-0.97$	8.3

afternoon photosynthetic depressions were observed, light compensation point of morning curves was higher than that of afternoon ones.

Daily gross and net production of *S. thunbergii* were calculated from diurnal net photosynthesis and dark respiration in daytime and nighttime, as summarized in Table 2. Daytime net photosynthesis, gross and net production and respiration expressed in ml O_2 were converted to those in dry weight as $1 \text{ mg O}_2 (0.7 \text{ ml O}_2)$ is equivalent to $0.84 \text{ mg dry matter}$ (IKUSIMA 1967). Although PAR values were similar (36.6 and $33.2 \text{ E m}^{-2} \text{ day}^{-1}$) on October 14 and December 9, daytime net photosynthesis, daily net production and daily gross production on the former day were 1.8, 1.7 and 2.1 times the values on the latter, respectively.

Photosynthesis-temperature curves were determined to see how photosynthesis of *S. thunbergii* was influenced by temperature. Light-saturated net photosynthesis for the young plants in March (Fig. 7A) increased to reach a maximum near 25°C and decreased

at higher temperatures. Photosynthesis in juveniles with primary leaves in September (Fig. 7B) increased to reach a maximum near 28°C and decreased at higher temperatures as well. Net photosynthesis at 22°C was 1.39 and 1.46 times that at 14°C in March and September, respectively. Light-saturated net photosynthetic rate in the morning on October 14 was about 1.64 times that on December 9; it is a little higher than the rate in Figure 7. Dark respiration increased linearly with an increase in temperature in both months. Q_{10} was about 1.42 and 1.67 in March and September, respectively.

The great difference in daytime net photosynthesis, daily net production and daily gross production between October 14 and December 9 might be attributed to the differences of temperature and growth stage. Juvenile plants used for photosynthesis and respiration measurements had primary leaves in October but only filiform ones in December. Total daily dark respiration on October 14 was about 5–10% higher compared with those on days in December (Table

Table 2. Daytime net photosynthesis (P_{nd}), daytime dark respiration (R_{dd}), nighttime respiration (R_{dn}), daily gross production (P_{g}) and daily net production (P_{n}) of *S. thunbergii*, with temperature and PAR.

Date	Temp. ($^\circ\text{C}$)	PAR ($\text{E m}^{-2}\text{day}^{-1}$)	[$\text{mg(d.w.) g(d.w.)}^{-1}$]				
			P_{nd}	R_{dd}	R_{dn}	P_{g}	P_{n}
Oct 14.	22	36.6	125.3 (87.6)*	14.8 (11.2)*	14.9 (11.3)*	140.1 (98.8)*	110.4 (76.3)*
Dec. 1	14	4.2	38.8	10.1	17.3	48.9	21.5
Dec. 9	14	33.2	69.7	11.6	16.8	81.3	52.9
Dec. 19	14	17.9	57.6	9.7	16.2	67.3	41.4

* Estimated values at 14°C in consideration of a temperature factor on the basis of the curves in Fig. 7.

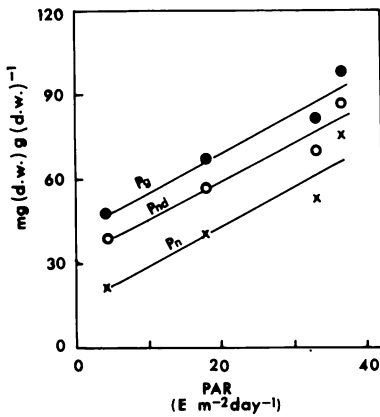


Fig. 8. Relationships of daytime net photosynthesis (P_{nd}), daily net production (P_n) and daily gross production (P_g) to PAR in *S. thunbergii* at 14°C.

2), and this must be due to higher temperature on the former than on the latter (Fig. 7). Daytime photosynthesis, daily net production and daily gross production on October 14 at 22°C were converted to those at 14°C by averaged factors (1.43 for net photosynthesis and 1.32 for respiration) from the photosynthesis-temperature and respiration-temperature curves determined in March (Fig. 7A) and September (Fig. 7B). Converted values for October 14 are higher in daytime net photosynthesis, daily gross and net production but lower in daytime and nighttime respiration compared to data for December 9. Disregarding the differences in growth stage, daytime net photosynthesis, daily net production and daily gross production were plotted as functions of PAR in Figure 8. As shown, these all increased almost linearly with increases in PAR during the period of investigation.

Discussion

Diurnal photosynthetic performance of *S. thunbergii* showed asymmetrical variation: that is, diurnal photosynthesis was found to show higher values in the morning and reduced rates in the afternoon, even for the same PAR on fine or cloudy-fine days (Fig. 6A, B & C). This is similar to patterns which were found in higher land plants (*Paspalum dilatatum* and

P. notatum) in summer (ITO *et al.* 1973), freshwater submerged angiosperms (GOULDER 1970, HOUGH 1974) and phytoplankton populations (HARRIS and LOTT 1973, JASSBY 1978, MARRA, 1978). However, MARRA (1978) showed in the laboratory with three different light regimes (constant, simulated diurnal variation, and fluctuating) that the afternoon depression can be largely removed by superimposing a light fluctuation on the diurnal regime, and suggested that purported endogenous rhythms can not be solely responsible for the afternoon photosynthetic depression. In the present study, the magnitude of the increase in dark respiration was not great enough to account for the photosynthetic depression. This is similar to the results reported for phytoplankton by LORENZEN (1963) and HARRIS (1973). Furthermore, afternoon depressions in net photosynthesis of *S. thunbergii* were found in December on moderately bright days (Fig. 6B & C), but the dark respiration showed almost no change (Fig. 5B & D). Therefore, the afternoon photosynthetic depression of *S. thunbergii* can not be due to an increase in dark respiration.

In the present study, when light saturation did not occur on a rainy day, little difference in the photosynthetic response to light was found between morning and afternoon (Fig. 6D). RAMUS and ROSENBERG (1980) reported that diurnal photosynthesis of two green algae, *Ulva curvata* and *Codium decortatum*, a brown alga, *Dictyota dichotoma*, and a red alga, *Gracilaria foliifera*, showed asymmetrical variation on fine days but symmetrical variation on a cloudy day. This is in agreement with results for *S. thunbergii* in the present study. However, the midday or afternoon photosynthetic depression was much smaller in the present study compared with that reported by RAMUS and ROSENBERG (1980). On October 14 the increase in the dark respiration in midday can be considered as being stimulated by the build-up of photosynthates as suggested by JASSBY (1978). Dark respiration of *S. thunbergii* maintained almost constant values in the day and night even on bright days in

December (Fig. 5B & D), although an afternoon photosynthetic depression was observed (Fig. 6B & C). This could be caused by the lower solar radiation and lower water temperature in December compared to October. Therefore, midday or afternoon photosynthetic depressions do not always coincide with increases in dark respiration.

MAEGAWA (1980) and MAEGAWA and ARUGA (1983) reported that *Monostroma latissimum* population photosynthesis showed no midday or afternoon depression even on fine days. In a natural population of seaweed, shading effects must be considered. In the community of *Sargassum thunbergii*, where plants shade each other, light conditions within the population will determine the diurnal photosynthesis of the plant. In the present study, plants maintained in the pipe were not shaded.

Estimation of daily primary production of seaweeds often depends on integration of photosynthesis-light curves determined in the laboratory with records of ambient solar radiation (e.g. BRINKHUIS 1977). However, data estimated in such a way may give rise to significant errors because of midday or afternoon photosynthetic depression. Whether photosynthesis-light curves determined in the laboratory at different times in a day are different or not, and to what degree daytime photosynthesis measured under natural sunlight is different from that estimated by the photosynthesis-light curves determined in the laboratory, should be considered in order to establish accurate estimates of primary production by seaweeds.

In the present study, differences in photosynthetic performance of *S. thunbergii* between morning and afternoon were confirmed on fine or cloudy-fine days. Such different diurnal photosynthetic performance patterns in *S. thunbergii* are difficult to explain without further investigations.

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高 坤山・梅崎 勇：ウミトラノオの光合成に関する研究 I. 太陽光下での光合成の日変化

大型海藻の光合成を流水中で測定する流水測定法を検討し、ウミトラノオの光合成が日射の変化に伴いどのように変化するかを、同一藻体群を用いて継続的に測定した。ウミトラノオの光合成は晴天下では同じ強さの日射に対して、午前は高い速度を示し、午後は低下を示した。しかし、雨の日にはこのような差が認められなかった。晴天下に認められた午後の光合成の低下は、暗呼吸の増加によるものではない。午後の低下にもかかわらず、ウミトラノオの日生産力は日射量の増加とともに直線的に増加した。(606 京都市左京区北白川追分町 京都大学大学院農学研究科熱帯農学専攻水産資源学研究室)