

## Seasonal variation of photosynthetic capacity in *Sargassum horneri*\*

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Photosynthesis on a dry weight basis was measured with a differential gas-volumeter in *Sargassum horneri* to see its seasonal changes. Photosynthetic activity in leaves of *S. horneri* showed two peaks a year, one in November and the other in March. The seasonal pattern of photosynthesis was similar to that reported for growth of this species. Net photosynthetic rates of the upper leaves were higher than those of the lower leaves in all months except June, when the plants became mature. In June, net photosynthetic rate in the lower leaves was higher than that in the upper ones. An adaptive shift of net photosynthetic response to temperature was observed with a decline in seawater temperature from July to December. Besides temperature, growth stage and nutrient conditions in the sea also accounted for considerable seasonal photosynthetic variability.

*Key Index Words:* Phaeophyta—photosynthesis—respiration—*Sargassum horneri*.

*Sargassum* plants were reported to show different photosynthetic characteristics among different parts (GAO and UMEZAKI 1988a, b, 1989a). Diurnal photosynthesis of *S. thunbergii* and *S. horneri* was found to show higher morning rate and afternoon depression on fine days (GAO and UMEZAKI 1989b, c, GAO 1989). However, little is known about seasonal variation in photosynthesis of *Sargassum* plants (PRINCE 1980).

Rapid growth of several *Sargassum* species has been reported to occur primarily during periods of low water temperatures (TSUDA 1971, CARPENTER and COX 1974, DE WREEDE 1976, UMEZAKI 1984). It was suggested that optimal growth of tropical seaweeds should occur primarily in winter (MATHIESON and DAWES 1974). However, PRINCE and O'NEAL (1979) showed that growth of *S. pteropleuron* was rapid during the period of maximum water temperature in summer. PRINCE (1980) reported that a significant decline in photosynthetic rates of *S. pteropleuron* coincided with senescence of the annual axis and the declining water

temperatures of winter. KILAR and HANISAK (1988) reported seasonal patterns of morphological variability in *S. polyceratium*.

*S. horneri*, an annual species, is distributed on the coasts of both the Sea of Japan and the Pacific Ocean throughout the Archipelago of Japan, and is one of the most common species around Japan. It grows on rocks at low tide level or at depths of 1 to 5 m, and rarely 10 m. The thallus often reaches several meters in length. *S. horneri* matures in spring, and disintegrates after the maturation period; then juveniles germinated from fertilized eggs appear. It has been used as a food or a vegetable from old times, and even now harvested plants are sold in some local places in Japan (IKEHARA 1987).

Knowledge of seasonal photosynthetic variations is fundamental to understanding seasonal patterns of growth of photosynthetic plants and to explaining their ecological characteristics. The objective of this study was to determine the seasonal variation of photosynthesis in *S. horneri*. Further, I wished to confirm the differences in photosynthetic capacity between the upper and lower leaves of this species examined by GAO and UMEZAKI (1988a, b).

\* Dedicated to the memory of the late Dr. Boudewijn H. BRINKHUIS, who kindly read and edited the manuscript.

## Materials and Methods

Water and atmospheric temperatures were measured daily at 10 o'clock in the morning at the Fisheries Research Station of Kyoto University, which is located at the seaside of Maizuru Bay, one of the branch bays of Wakasa Bay by the Sea of Japan. Figure 1 shows mean monthly atmospheric and surface seawater temperatures. Experiments were carried out from 1987 to 1988 at the station. Samples of *Sargassum horneri* were collected at the seaside within the station.

*S. horneri* locally matures in May, and decays after maturation. Juveniles germinated from fertilized eggs appear (visible to the naked eye) in July. In July and August, plants were juvenile, about 1 to 3 cm long, and whole plants were used for photosynthetic and dark respiratory measurements. In other months, leaves of the apical and the basal portions were used for the measurements. The fifth to seventh leaves from the apex were designated as the upper (apical) leaves and the leaves (the nearest ones to the holdfast) from basal portion of the plant were designated as the lower (basal) leaves.

Photosynthetic and respiratory measurements were carried out with a differential gas-volumeter 'Productmeter' as reported by YOKOHAMA *et al.* (1986). Photosynthesis and respiration were measured at 20°C (near the yearly average water temperature in the sea). Photosynthesis and respiration versus temperature curves were deter-

mined from 7 to 39°C in July, October and December. Photosynthesis was measured at  $600 \mu\text{E m}^{-2}\text{s}^{-1}$ , at which it was almost saturated (GAO and UMEZAKI 1988b).

Chlorophylls were determined by freezing samples at  $-20^\circ\text{C}$ , grinding in a mortar with quartz sand, extracting with 90% acetone, and filtering through absorbent cotton with 90% acetone. The absorbances of the acetone extract were measured at 750, 664, 630 nm with a spectrophotometer (Hitachi Ltd., Model 100-2). The concentrations of chlorophylls *a* and *c* were calculated by the formulae of JEFFREY and HUMPHREY (1975). Data were analyzed using Student's t-test to ascertain statistical significance.

## Results

Net photosynthetic rate of juvenile *Sargassum horneri* was lower in August compared to July (Fig. 2A). Rates of the upper leaves increased to reach a maximum in November, showing highest values in October, November and December. Photosynthetic rates then decreased in January and February, being less than half the rate in November, again increased in March, and finally decreased from April to June. Net photosynthetic rates of the lower leaves were lower than those of the upper leaves in all months except in June when the plants became mature. In June, net photosynthetic rate was higher in the lower leaves than in the upper leaves. Net photosynthetic rates in the lower leaves were higher in November, February and March compared to the other months, and did not fluctuate as greatly as in the upper leaves (Fig. 2A).

Dark respiratory rates of the upper leaves reached a maximum in November, decreased until May, and then increased in June (Fig. 2B). Dark respiratory rates in the lower leaves were lower compared to those in the upper leaves in all the months except in May, when rates were similar in the upper and lower leaves. Dark respiratory rates of the lower leaves did not fluctuate as greatly as those of the upper leaves (Fig. 2B).

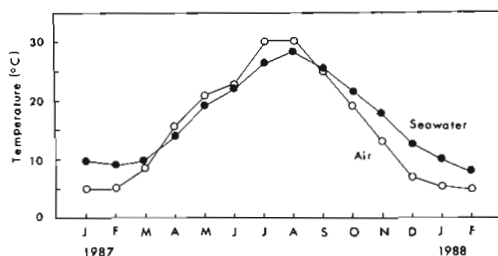


Fig. 1. Seasonal changes of monthly mean atmospheric and surface seawater temperature at the study locality (from Fisheries Research Station of Kyoto University).

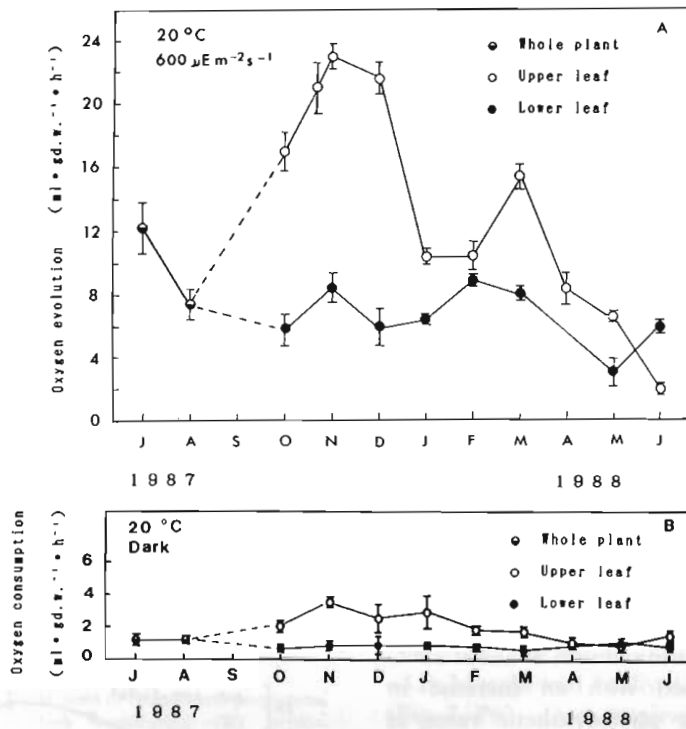


Fig. 2. Seasonal variations of net photosynthesis (A) and dark respiration (B) in the upper and lower leaves of *S. horneri*. The data are the means  $\pm$  S.E. of 3 to 12 samples.

Dry weight to fresh weight (d.w./f.w.) ratio of the upper leaves was lowest in October, November and December, when net photosynthetic and dark respiratory rates were highest. The ratio was significantly higher ( $P < 0.01$ ) in the lower leaves than in the upper leaves in all the months (Fig. 3).

Comparing the seasonal variations of photosynthesis and dark respiration of the upper leaves, it is easy to see that higher

photosynthetic rates coincided with higher dark respiratory rates. As indicated in Figure 4, net photosynthesis increased linearly with increase in dark respiration. Such a linear relationship was statistically significant ( $P < 0.001$ ).

Figure 5 shows net photosynthesis and dark respiration versus temperature curves of *S. horneri* obtained in July (A), October (B) and December (C). Net photosynthesis in July,

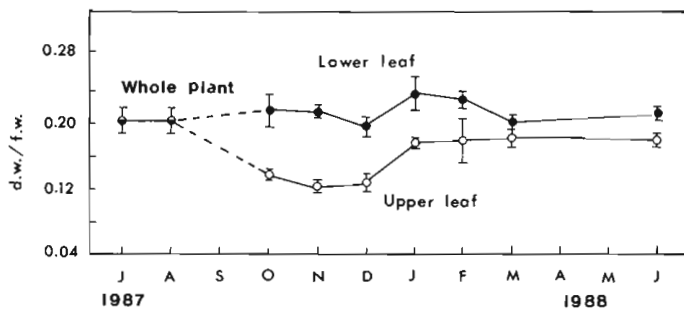


Fig. 3. Seasonal variations of dry weight to fresh weight ratios (d.w./f.w.) of the upper and lower leaves of *S. horneri*. The data are the means  $\pm$  S.E. of 3 to 12 samples.

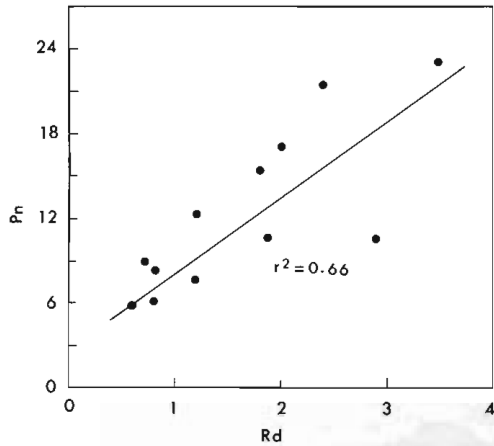


Fig. 4. Relationship between net photosynthesis ( $P_n$ , at  $600 \mu\text{E m}^{-2} \text{s}^{-1}$ ) and dark respiration ( $R_d$ ) of the upper leaves of *S. horneri*. Photosynthetic or respiratory rates are expressed in  $\text{ml O}_2 (\text{d.w.})^{-1} \text{h}^{-1}$ , measured at  $20^\circ\text{C}$ .

increased to reach a maximum at about  $29^\circ\text{C}$  and then decreased with an increase in temperature. Net photosynthetic rates at  $39^\circ\text{C}$  were negative. Dark respiration increased almost linearly with an increase in temperature to  $33^\circ\text{C}$  and then increased abruptly at  $39^\circ\text{C}$ . Net photosynthesis in October increased to reach a maximum at about  $27^\circ\text{C}$  and then decreased rapidly with an increase in temperature. Dark respiration increased linearly from  $7$  to  $27^\circ\text{C}$  and showed abrupt increases at  $33$  and  $39^\circ\text{C}$ . Net photosynthesis in December increased to reach a maximum at about  $25^\circ\text{C}$  and then decreased with increase in temperature. Net photosynthesis of the lower leaves showed trend similar to that of the upper leaves, only with a photosynthetic maximum at a higher temperature,  $27^\circ\text{C}$ . Dark respiration of the upper and the lower leaves increased almost linearly with an increase in temperature to  $33^\circ\text{C}$  and increased abruptly at  $39^\circ\text{C}$ . Net photosynthetic rates of the upper leaves were much higher than those of the lower leaves at all the temperature levels investigated except at  $39^\circ\text{C}$ . Net photosynthetic rates were higher in the lower leaves than in the upper leaves at  $39^\circ\text{C}$ . Dark respiratory rates of the lower leaves were lower compared with those

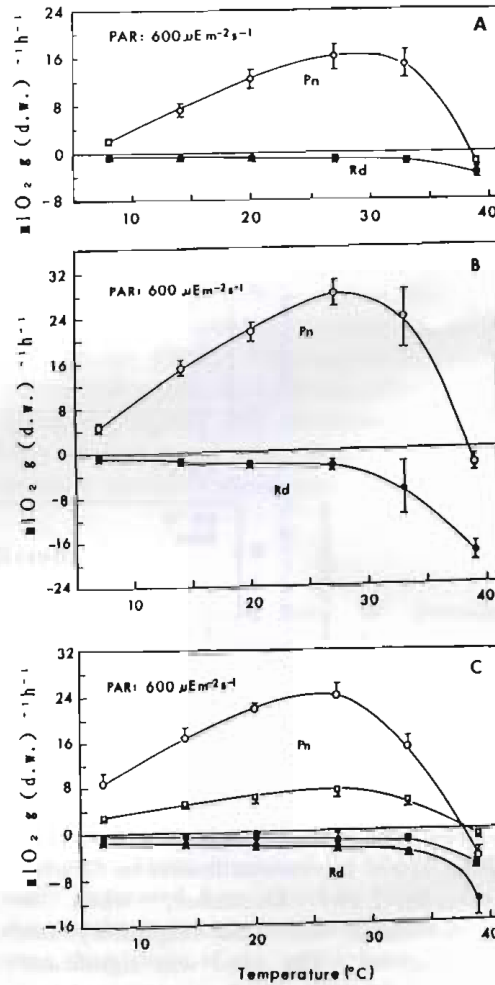


Fig. 5. Net photosynthesis ( $P_n$ ) and dark respiration ( $R_d$ ) versus temperature curves of the upper ( $\circ$ ,  $\bullet$ ) and lower ( $\square$ ,  $\blacksquare$ ) leaves of *S. horneri* in July (A), October (B) and December (C). The data are the means  $\pm$  S.E. of 5 to 16 samples.

of the upper leaves at all of the investigated temperatures.

Relative (taking maximum as 100) net photosynthesis and dark respiration versus temperature curves were compared among different months (Fig. 6). Net photosynthetic response to temperature showed higher values in the order of July, October and December at suboptimal temperature range ( $7$ – $25^\circ\text{C}$ ) (Fig. 6A). That is, net photosynthesis was reduced at lower temperatures in warmer months, while photosynthetic rate in colder

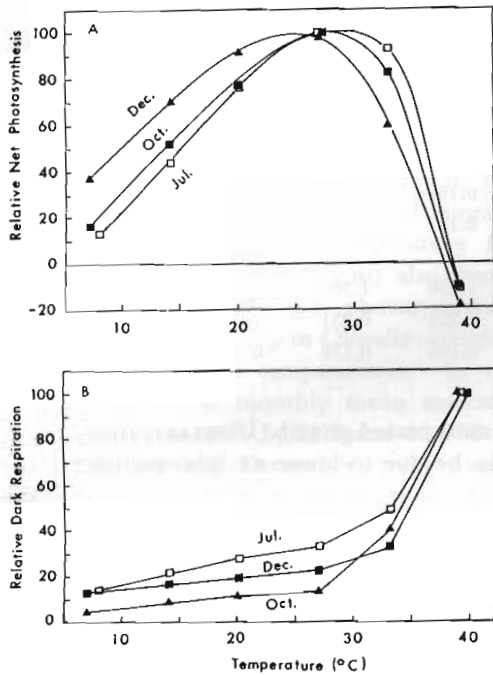


Fig. 6. Comparisons of relative net photosynthesis (A) and dark respiration (B) versus temperature curves of the upper leaves of *S. horneri* in different months.

months was higher at lower temperatures. Optimum temperatures for photosynthesis were at 29°C in July, 27°C in October and 25°C in December, indicating a shift with declining seawater temperature. At higher

temperatures above the optimum, photosynthesis was reduced faster in December, intermediate in October and slower in July. That is, net photosynthesis was reduced faster in colder months and slower in warmer months at higher temperatures. Relative dark respiration rates were higher in July compared to those in October and December, and higher in December than in October below 30°C (Fig. 6B).  $Q_{10}$  was about 1.8 in July and October, and 1.4 in December.

Net photosynthetic and dark respiratory rates at monthly mean seawater temperatures of *S. horneri* were estimated by conversion of the rates at 20°C to the rates at monthly mean seawater temperatures (Fig. 1) by taking into account the relative photosynthesis and respiration versus temperature curves (Fig. 6). Estimated net photosynthetic rates of *S. horneri* reached a maximum in October and November, decreased until February, increased in March, and finally decreased until June (Fig. 7, Pn). Dark respiratory rates of the upper leaves were also highest in November and were lower in April and May than in other months (Fig. 7, Rd). In June, when plants were decaying, dark respiratory rate increased to be equivalent to net photosynthetic rates. Net photosynthetic rates of the lower leaves were highest in November, decreased from December to May, and then

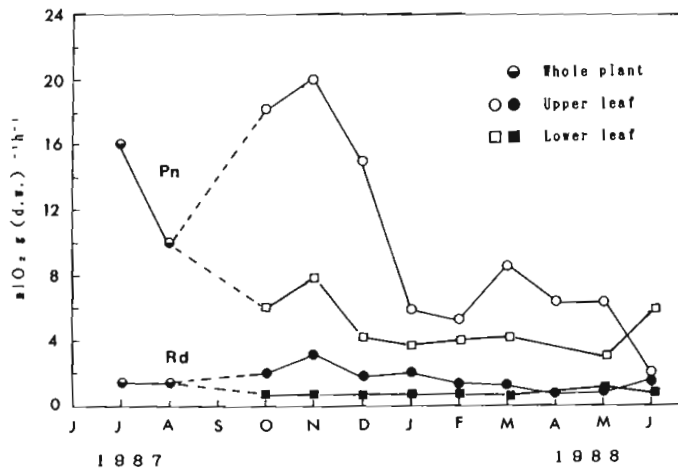


Fig. 7. Seasonal variations of net photosynthesis (Pn) and dark respiration (Rd) of the upper and lower leaves of *S. horneri* at monthly mean seawater temperature.

Table 1. Chlorophyll contents (mg/g f.w.) and *c/a* ratio of the upper and the lower leaves of *Sargassum horneri* in different months. Means of 1 to 3 measurements.

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	June
Upper leaves							
Chl. <i>a</i>	0.812	0.816	0.844	1.271	1.201	1.388	0.199
Chl. <i>c</i>	0.112	0.114	0.116	0.162	0.143	0.142	0.044
Chl. <i>c/a</i>	0.138	0.140	0.137	0.127	0.119	0.102	0.221
Lower leaves							
Chl. <i>a</i>	1.396	1.448	1.270	1.350	1.589	1.570	0.746
Chl. <i>c</i>	0.238	0.239	0.206	0.224	0.251	0.247	0.123
Chl. <i>c/a</i>	0.170	0.165	0.162	0.166	0.158	0.157	0.165

increased in June (Fig. 7, Pn). Dark respiration showed higher values in May and June, during and after maturation period (Fig. 7, Rd). Both net photosynthesis and dark respiration of the upper leaves at ambient temperatures in the sea were higher than those of the lower leaves in all the months except in June, when net photosynthetic rate of the lower leaves exceeded that of the upper leaves.

Table 1 indicates chlorophyll contents of the upper and the lower leaves of *S. horneri* in different months. Chlorophylls *a* and *c* contents of the upper leaves were highest in January, February and March. Chlorophyll contents of both the lower and the upper leaves were lowest in June. Chlorophylls *a* and *c* contents, and *c* to *a* ratios were higher in the lower leaves than in the upper leaves in all the months.

### Discussion

Photosynthetic activity of leaves of *Sargassum horneri* showed two peaks in a year, one in November and the other in March. UMEZAKI (1984) reported that the daily increase in dry weight and in length of main axis showed two peaks, one in December to January and the other in February to March. Thus, the peaks for photosynthetic activity in the present study almost corresponded to the peaks for growth reported by UMEZAKI (1984). PRINCE (1980) reported that seasonal pattern of photosynthesis was similar to that for growth in *S. pteropleuron*. After becoming mature, *S. horneri* plants

almost ceased growth (UMEZAKI, 1984). This can be due to lower net photosynthetic rate and higher dark respiratory rate at this period, as shown in the present study.

GAO and UMEZAKI (1989a) reported that photosynthesis increased with a decrease in d.w./f.w. ratio in *S. thunbergii*. In the present study, net photosynthetic rate of the upper leaves of *S. horneri* decreased while d.w./f.w. ratio increased from December to January and February. Net photosynthetic rate was higher in the upper leaves than in the lower leaves, with d.w./f.w. ratio lower in the former than in the latter. The decline in photosynthesis in the leaves of *S. horneri* coincided with senescence of the leaves, as previously reported (UMEZAKI and GAO 1988b).

Receptacles accounted for nearly 70% fresh weight of a *S. horneri* plant, and showed much lower light-saturated net photosynthesis in June (GAO 1989). In the present study, light-saturated net photosynthetic rate of the upper leaves was equivalent to dark respiratory rate in June. Thus, daily net production of an individual plant of this species might approach zero or become negative in this month. Reduced photosynthetic rate was correlated with reduced chlorophyll contents of the species in June (GAO and UMEZAKI 1988a). In the present study, chlorophyll contents decreased faster in the upper than in the lower leaves when the plant became mature, so that net photosynthetic rate on a dry weight basis of the lower leaves exceeded that of the upper leaves in June.

Seasonal variability of the photosynthesis-temperature relationship was studied by ARUGA (1965a) in natural freshwater phytoplankton communities. He reported that the optimum temperature for photosynthesis adjusted in an adaptive fashion; the higher the temperature of the environment, the higher the optimum temperature for photosynthesis. ARUGA (1965b) also found an adaptive shift in the photosynthesis-temperature relationship in *Chlorella ellipsoidea* cultured at different temperatures. In the present study, the monthly mean seawater temperatures were 26.5, 21.5 and 12.5°C in July, October and December, respectively, when the photosynthesis-temperature curves were determined. Optimum temperature for photosynthesis in *S. horneri* was 29, 27 and 25°C in July, October and December, respectively. Net photosynthetic rate was higher at lower temperatures and was lower at higher temperatures in colder months as compared with warmer months. These results of *S. horneri* in the present study are similar to those reported by ARUGA (1965a, b) for phytoplankton. In studies on 4 species of green algae, 7 species of brown algae and 4 species of red algae, YOKOHAMA (1973) reported that the optimum temperature for photosynthesis was higher in summer than in winter. This is also similar to the results of the present study. Such an adaptive shift in optimum temperature through a year has been also shown in gametophyte development, growth and reproduction in *Laminaria saccharina* (LEE and BRINKHUIS 1988).

HONDA and OKUDA (1989) reported that the upper leaves of both vernal and autumnal *S. horneri* showed highest light-saturated photosynthetic rates in autumn. The present study gave the results of vernal *S. horneri* similar to those reported by the above authors. The possible reasons for the seasonal variation of photosynthetic capacity in this species are conclusively discussed as follows.

Seasonal changes in temperature may greatly contribute to seasonal changes in photosynthesis of *S. horneri*. However, lower photosyn-

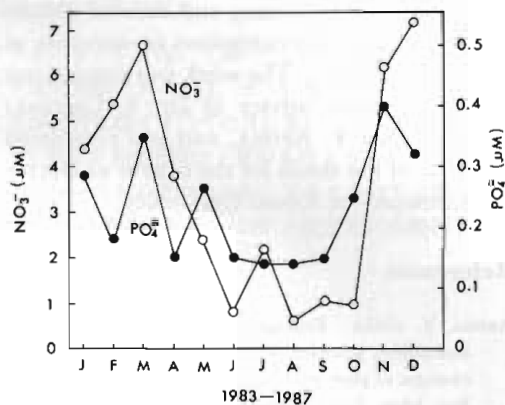


Fig. 8. Seasonal variations of mean nitrate and phosphate concentrations in seawater at Nagahama, Maizuru Bay (data by Dr. H. NAKAHARA).

thetic rates were found in juvenile plants in August and in plants after becoming mature in June, so that different growth stages seem to have different photosynthetic rates. KILAR and HANISAK (1988) reported that patterns of leaf development, senescence and loss caused pronounced seasonal changes in leaf length-width ratios in *S. polyceratium*. Seasonal changes in morphological characteristics of the leaves of *S. horneri* may give differences in photosynthesis. On the other hand, seasonal changes in nutrient conditions in the sea may also influence photosynthetic variability in a year. It was found that photosynthetic activity and chlorophyll contents of *S. thunbergii* depended significantly on nutrient conditions in the sea (GAO and NAKAHARA, in press). LAPOINTE (1986) demonstrated that diurnal photosynthetic rates in pelagic *Sargassum* species, *S. natans* and *S. fluitans* increased with PO<sub>4</sub><sup>3-</sup> enrichment. At the present locality, nitrate and phosphate concentrations were highest in November and March (Fig. 8), when the photosynthetic rate of *S. horneri* was highest. Therefore, nutrient conditions in the sea can also be an important parameter in consideration of the seasonal variability in photosynthesis of *S. horneri*.

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### 高 坤山：アカモクの光合成の季節変動

アカモクの光合成の季節変動を差動式検容計（プロダクトメーター）を用いて調べた。乾燥重量当りの光飽和光合成速度は10月と3月にピークを示した。このような光合成の季節パターンは、すでに報告されているアカモクの生長の季節パターンとほぼ一致した。光飽和光合成速度は6月を除くすべての月において上部の葉の方が下部のものより高かった。藻体が成熟した6月には下部の葉の光飽和光合成速度は上部のものより高かった。また、7月から12月にかけて水温変化に対応した光合成反応の適応的なシフトが認められた。アカモクの光合成の季節変動は温度以外に生育段階及び海水の栄養塩条件にも影響されると考えられる。（530 大阪市北区中崎西2丁目3番39号 関西総合環境センター）