

Comparative photosynthetic capacities of different parts of *Sargassum horneri* (Phaeophyta)*

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Net photosynthetic and dark respiratory rates measured with a differential gas-volumeter increased but chlorophyll content decreased with increasing leaf area ratio in leaves of *Sargassum horneri*. It was estimated that chlorophyll *a* increased 1.7–4.1%, while net photosynthetic and dark respiratory activities decreased 1.4–5.8% and 4.6–8.9%, respectively, as a leaf grew one day older. Vesicles were shown to possess high photosynthetic capacity in addition to supplying floatation. Photosynthetic activity was highest in leaves, intermediate in vesicles and lowest in the holdfast and primary laterals. It is shown that different parts of a *S. horneri* plant have different photosynthetic properties.

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

Studies of photosynthetic characteristics of *Sargassum* plants are fundamental to understanding their ecological properties. Diurnal photosynthetic performance was reported in *S. thunbergii* (Gao and Umezaki 1989a, b) and *S. horneri* (Gao 1990b) to show higher oxygen evolution rates in morning than in afternoon on fine days. Photosynthetic activity was reported to be higher in apical portion than in basal portion of *S. horneri*, *S. hemiphyllum* and *S. confusum* on a basis of chlorophyll *a* (Yokohama 1977). In studies on *S. horneri*, *S. serratifolium*, *S. autumnale*, *S. thunbergii* and *S. patens*, Gao and Umezaki (1988) reported that 'leaves' of the lower parts showed higher chlorophyll content but lower photosynthetic rate on a chlorophyll *a* basis, compared with the upper parts. Photosynthetic capacity of *S. thunbergii* was found to be obviously affected by nitrate and phosphate concentrations in seawater (Gao and Nakahara 1990). Diurnal photosynthetic rates were demonstrated to increase with PO_4^{3-} enrichment in pelagic *Sargassum* species, *S. natans* and *S. fluitans*

(Lapointe 1986). Gao (submitted) showed that photosynthetic rate increased with increasing water current speed in adult *S. thunbergii* plants. It was also reported that *S. muticum* assimilated bicarbonate ion in photosynthesis (Thomas and Tregunna 1968).

Gao and Umezaki (1989c) reported that various parts of a *S. thunbergii* plant were differentiated with different photosynthetic properties, being comparable to the findings in *Laminaria* (Weidner and Kupperts 1973, Kupperts and Kremer 1978), *Fucus* (Kupperts and Kremer 1978), *Macrocystis* (Wheeler 1980) and *Padina* (Yokohama 1977) plants. The present study gives different photosynthetic characteristics among various parts in *S. horneri*, which has been used as a food or a vegetable at some local places in Japan (Ikehara 1987). The seasonal variation of photosynthetic capacity of *S. horneri* was already reported (Gao 1990a) to show a similar pattern to that of growth as previously reported (Umezaki 1984).

Materials and Methods

A *Sargassum horneri* plant (Fig. 1) consists of

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a holdfast, a primary lateral from which leaves and lateral branches are formed. The lateral branches produce both 'leaves' and vesicles and, during the mature season, receptacles. The species is distributed, from 1 m upto 20 m deep, along the coast of both the Sea of Japan and the Pacific Ocean throughout the Archipelago of Japan.

The experiments were carried out during the period from August to November 1986 and 1987 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. Samples of *S. horneri* were collected at Nagahama, Maizuru Bay, where the plant forms flourishing community at 1-3 m depth during the period from November to April next year and matures in May; juveniles appear in July.

Photosynthesis and dark respiration were measured at 20°C in the laboratory in the same way as previously reported (Gao and Umezaki 1989c, Gao 1990a) with a differential gas-volumeter, 'Productmeter', devised by Yokohama and Ichimura (1969) and improved by Yokohama *et al.* (1986). Light was supplied with an incandescent lamp (National, 110 V 150 W), and photosynthetically active radiation (PAR, 400-700 nm) of the supplied light was measured with an underwater quantum sensor (LICOR, LI-192S) linked with a recorder (Toa Electronics Ltd., FBR-253A). Water temperature in the water bath was controlled by using a Taiyo Coolnit (CL-30).

Chlorophylls were determined by freezing samples at -20°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, 647 and 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).

Fresh weight of samples was measured after blotting water drops from the thallus with tissue paper. Dry weight was determined after drying the samples at 85°C for 20-24 hours.

Leaf area was determined by making a shade on a film, weighing the shaded part, and multiplying by the ratio of area to weight of the film. Leaf area ratio (LAR), the ratio of leaf area to leaf dry weight, was determined.

Leaf formation rate per day was determined by measuring the number of leaves at the beginning and at the end of a period (8 days, Aug. 17-25 1987), during which the plants (about 4 cm long) were maintained in the sea at their natural depth (1 m).

Daily relative change rates (CP) of chlorophyll, photosynthesis and respiration in a leaf were determined by the following formula:

$$CP = \frac{\ln C_b - \ln C_a}{(L_b - L_a)/L_f} \times 100,$$

where C_b and C_a represent chlorophyll content, net photosynthetic or respiratory rates of basal (or older) and apical (or younger) leaves, respectively; L_b and L_a , leaf order number counted from the apex for the basal and the apical leaves, respectively; L_f , leaf formation rate (the number of leaves formed per day).

The correlations of photosynthesis, dark respiration and chlorophyll content to LAR were analyzed by computer with a regression analysis program.

Results

Light-saturated net photosynthesis and dark respiration of the leaves produced from primary lateral increased parabolically, but chlorophyll *a* content decreased hyperbolically with increasing LAR, which increased from basal portion to apical portion of a *Sargassum horneri* plant (Fig. 1).

Figure 2 shows photosynthesis-light curves of apical and basal leaves on a chlorophyll *a* basis (A), on a leaf area basis (B) and on a dry weight basis (C). Dark respiration rate and net photosynthetic rate at above 100 $\mu\text{E m}^{-2} \text{s}^{-1}$ was higher in the apical than in the basal leaves on any of the bases. Light compensation point was higher in the apical leaves compared to the basal leaves, with the former

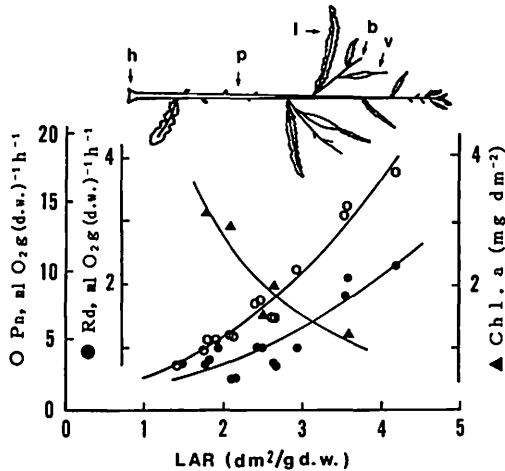


Fig. 1. Relationships of net photosynthesis (Pn), dark respiration (Rd) and chlorophyll (Chl. a) content to leaf area ratio (LAR) in a *Sargassum horneri* plant (h, holdfast; p, primary lateral; l, leaf; b, lateral branch; v, vesicle). Pn, Rd and Chl. a are expressed as functions of LAR (X) respectively as follows: $Pn = 1.45 + 0.94 X^2$ ($r^2 = 0.96$), $Rd = 0.26 + 0.12 X^2$ ($r^2 = 0.80$) and $Chl. a = 1.02 + 7.46/X$ ($r^2 = 0.84$). Chlorophyll a content was the mean for 4-6 samples.

being 30 and $27 \mu E m^{-2} s^{-1}$ and the latter 15 and $13 \mu E m^{-2} s^{-1}$ on a dry weight basis and on a leaf area basis, respectively. On a chlorophyll a basis (A), light compensation point of the apical leaves was similar to that of the basal ones. Net photosynthesis was saturated at about $300 \mu E m^{-2} s^{-1}$ in the basal leaves, but was not saturated until $600 \mu E m^{-2} s^{-1}$ in the apical leaves. Net photosynthetic rates at $600 \mu E m^{-2} s^{-1}$ of the apical leaves were 3.5, 1.5 and 2.9 times, and dark respiration rates of the apical leaves were 2.0, 2.5 and 3.3 times as high as those of the basal leaves on a chlorophyll a basis, on a leaf area basis and on a dry weight basis, respectively.

Chlorophyll contents were compared among the leaves of different positions (Table 1). Data for the basal leaves obtained in 1986 (1987) were about 0.72 (0.76) times higher in chlorophyll a content and 1.13 (1.12) times higher in chlorophyll c content on a fresh weight basis, and were 1.12 (1.40) times higher in chlorophyll a content and 1.62 (1.91) times higher in chlorophyll c content on a leaf area basis, compared with those for the

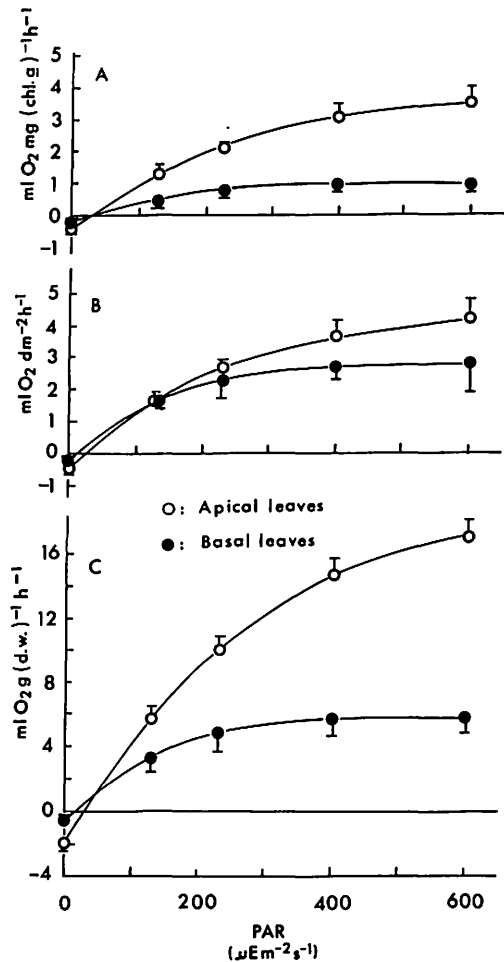


Fig. 2. Photosynthesis-light curves of the apical (○) and the basal (●) leaves of *Sargassum horneri* on a chlorophyll a basis (A), on a leaf area basis (B) and on a dry weight basis (C). The mean \pm S.E. for 5 plants (about 10 cm long) measured at 20°C in October 1987.

apical leaves. Chlorophyll c to a ratio was also higher in the basal than in the apical leaves. Chlorophylls a and c contents and chlorophyll c to a ratio of middle leaves were lower than those of basal leaves but higher than those of apical ones (Table 1, 1987). LAR of apical leaves was about 34% and 70% higher compared to middle leaves and basal leaves, respectively (Table 1).

Figure 3 compares a photosynthesis-light curve of vesicles with those of the basal and apical leaves in November. Net photosynthesis

Table 1. Comparisons of chlorophyll (Chl.) contents and leaf area ratio (LAR) among the apical, middle and basal leaves of *Sargassum horneri*.
Date: October 7, 1986

Leaf position	Chl. a	Chl. c	Chl. a	Chl. c	Chl. c/a	LAR (dm ² d.w.g ⁻¹)	Samples (n)
	(mg f.w.g ⁻¹)		(mg dm ⁻²)				
Apical	0.812±0.014	0.112±0.001	1.472±0.104	0.203±0.012	0.138±0.002	2.446±0.437	6
Basal	1.396±0.096 (1.719)*	0.238±0.017 (2.125)	3.125±0.205 (2.123)	0.532±0.033 (2.621)	0.170±0.004 (1.232)	1.785±0.414 (0.730)	6

Date: October 10, 1987

Leaf position	Chl. a	Chl. c	Chl. a	Chl. c	Chl. c/a	LAR (dm ² d.w.g ⁻¹)	Samples (n)
	(mg f.w.g ⁻¹)		(mg dm ⁻²)				
Apical	0.724±0.061	0.095±0.008	1.209±0.109	0.157±0.015	0.132±0.002	3.532±0.964	6
Middle	1.088±0.062 (1.503)	0.161±0.009 (1.695)	1.953±0.162 (1.6159)	0.288±0.024 (1.834)	0.148±0.001 (1.121)	2.630±0.234 (0.745)	4
Basal	1.275±0.056 (1.761)	0.201±0.006 (2.116)	2.899±0.378 (2.398)	0.457±0.052 (2.911)	0.158±0.002 (1.197)	2.075±0.272 (0.587)	4

* Figures in parentheses are values relative to those of apical leaves.

of vesicles was saturated at about 400 $\mu\text{E m}^{-2} \text{s}^{-1}$. Light-saturated net photosynthetic rate and dark respiration rate of vesicles were much lower compared to those of apical leaves but higher compared to those of basal ones.

Figure 4 compares a photosynthesis-light curve of primary laterals with that of leaves of

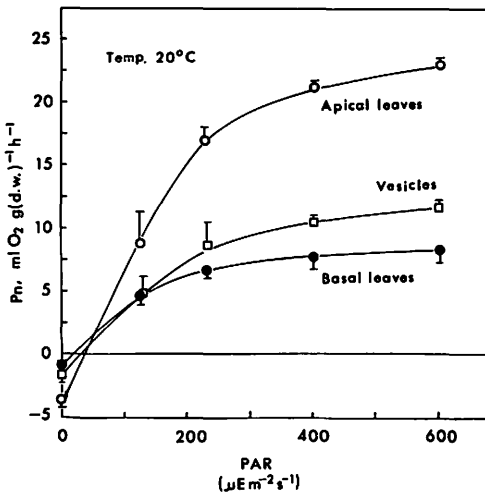


Fig. 3. Photosynthesis-light curve of vesicles compared to those of apical and basal leaves in *Sargassum horneri*. The mean±S.E. for 5 plants (about 25 cm long) measured in November 1987.

juvenile plants. Dark respiratory and net photosynthetic rates were much higher in leaves than in primary laterals. Photosynthesis of primary laterals was saturated at about 250 $\mu\text{E m}^{-2} \text{s}^{-1}$. Light-saturated net photosynthetic rate and dark respiratory rate of leaves were respectively about 4 and 2 times as high as those of primary laterals.

Figure 5 illustrates relationships of pho-

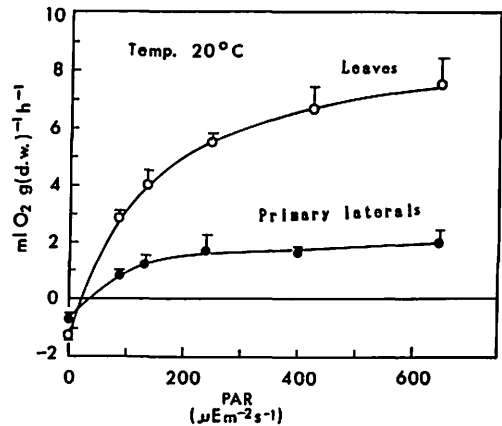


Fig. 4. Photosynthesis-light curve of primary laterals compared to that of leaves of juvenile plants of *Sargassum horneri*. The mean±S.E. for 12 plants (about 2.5 cm long) measured in August 1987.

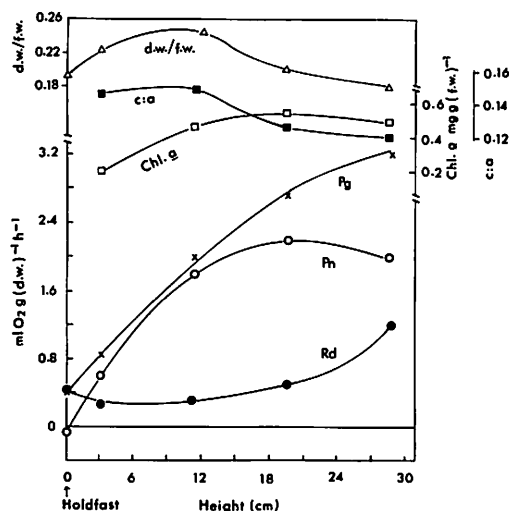


Fig. 5. Relationships of gross photosynthesis (Pg), net photosynthesis (Pn), dark respiration (Rd), chlorophyll *a* content (Chl. *a*), chlorophyll *c* to *a* ratio (*c* : *a*) and dry weight to fresh weight ratio (*d.w./f.w.*) to the height of primary laterals of *Sargassum horneri*. Primary laterals of 4 plants were used. Measured at 20°C in November 1987.

tosynthesis, dark respiration, chlorophyll content and dry weight/fresh weight ratio to the height of primary laterals. Dark respiration showed a little higher values in holdfast compared to the basal part of primary laterals, and increased to show higher values in the apical part. It was clear that the holdfast also showed photosynthetic activity. Net photosynthesis increased from the holdfast to reach a maximum and then decreased owing to much higher dark respiration in the apical

portion. Gross photosynthesis increased from the holdfast to the apex of primary lateral. Chlorophyll *a* content increased from the base to the apex of primary laterals, and chlorophyll *c* to *a* ratio was higher in the basal than in the apical portions of primary laterals. Ratio of dry weight to fresh weight increased from the holdfast to reach a maximum in the basal portion and then decreased until the apex of primary laterals.

As indicated in Table 2, a new leaf was formed every two days; i.e. neighbouring leaves were different in age by two days. The 4th to the 6th leaves and the 15th to the 17th leaves numbered from the apex were respectively considered as the apical and the basal leaves in October in the present study. Consequently, the difference in age between apical leaves and basal leaves was about 20 days. As chlorophyll contents increased (Table 1), but net photosynthesis and dark respiration decreased in leaves from the apical portion to the basal portion (Fig. 1), the daily relative chlorophyll increase rate, and the daily net photosynthesis and respiration decrease rates in a leaf were estimated in different positions of primary laterals (Table 3). Irrespective of bases, as a leaf grew one day older, chlorophylls *a* and *c* increased respectively 1.7–4.1% and 2.7–5.1%, and net photosynthetic capacity and dark respiratory activity decreased respectively 1.4–5.8% and 4.6–8.9%.

Table 2. Daily leaf formation rate (*R*, number day⁻¹) of *Sargassum horneri* in the sea.

Sample No.	1	2	3	4	5	6	7	8	9	10	Average ± S.E.
<i>R</i>	0.5	0.5	0.4	0.5	0.4	0.4	0.3	0.8	0.5	0.3	0.5 ± 1.1

Table 3. Estimated daily relative chlorophyll increase rate (RCIR), net photosynthesis decrease rate (RPDR) and dark respiration decrease rate (RRDR) in a leaf of *Sargassum horneri*.

	Leaf area basis		Dry weight basis		Chlorophyll <i>a</i> basis
	Chl. <i>a</i>	Chl. <i>c</i>	Chl. <i>a</i>	Chl. <i>c</i>	
RCIR (% day ⁻¹)	4.1	5.1	1.7	2.7	
RPDR (% day ⁻¹)		1.4		4.1	5.8
RRDR (% day ⁻¹)		4.6		7.2	8.9

Discussion

It is clear that light-saturated net photosynthetic rates and dark respiratory rates of leaves decreased on any of a dry weight, a leaf area and a chlorophyll bases, while chlorophyll content increased, from the apex to the base of a *Sargassum horneri* plant; i.e. the highest chlorophyll contents were confined in older leaves, but the highest photosynthetic activity was confined in younger leaves. However, light-saturated net photosynthetic rates of the apical leaves of *S. horneri* were lower (on a dry weight basis) or similar (on a chlorophyll basis) in June compared with those of the basal leaves as previously reported (Gao and Umezaki 1988). The difference may be related to the periods the photosynthetic measurements were carried out. In June, when *S. horneri* matured and then decayed away, net photosynthesis was much reduced while dark respiration was much increased in the apical leaves as demonstrated by Gao (1990a) in his seasonal studies of photosynthetic capacity of the species. Küppers and Kremer (1978), in their studies on *Laminaria digitata*, *L. hyperborea*, *L. saccharina*, *Fucus spiralis*, *F. vesiculosus* and *F. serratus*, showed that less pigments were contained in younger regions compared to older ones. Wheeler (1980) also showed that the meristem of *Macrocystis pyrifera* contained less pigments. *S. horneri* elongates apically, and its apical portion is younger than its basal portion. The results of the present study that chlorophyll contents were higher in older leaves than in younger leaves agree with those reported by the above authors.

There are several reports (Ramus *et al.* 1976a, b, 1977; Wheeler 1980; Wassman and Ramus 1973; Perez-Bermudez *et al.* 1981) to show that photosynthetic pigments in seaweeds increased with water depth or the degree of shading. Basal leaves of *Sargassum* plants, near the bottom of the sea, get more or less reduced light because of light absorption by water column and shading by the upper parts of themselves. *S. horneri*, *S. thunbergii*, *S. serratifolium*, *S. patens* and *S. autumnale* were reported to show higher chlorophyll contents

in basal leaves than in apical leaves (Gao and Umezaki 1988). Gao and Umezaki (1989c) also reported that chlorophyll contents of leaves and vesicles were higher in the basal portion than in the apical portion. Similar results were obtained in *S. horneri* in the present study. Increased chlorophyll contents in the basal leaves of *Sargassum* plants can be considered partially to be caused by an adaptation to the reduced light conditions. However, as demonstrated in the present study, chlorophyll contents increased as LAR decreased with aging of a leaf; and chlorophyll *a* content was estimated to increase 1.7–4.1% as a leaf grew one day older. In October *S. horneri* plants were about 10 cm long, and the differences of light reduction around leaves of different positions could be negligible. Therefore, it is reasonable to consider that light condition contributed little to the differences in photosynthetic pigment content among leaves of *S. horneri* during the experiment period.

Photosynthetic rates on a dry weight or on a leaf area bases decreased but contents of chlorophylls increased in the leaves as LAR decreased from the apex to the base of a *S. horneri* plant. Because LAR decreased with increasing d.w./f.w. ratio (Fig. 6), photosynthesis which increased with increasing LAR

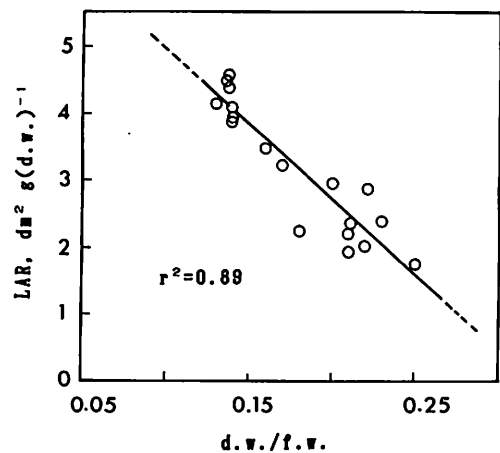


Fig. 6. Relationship between leaf area ratio (LAR) and dry weight to fresh weight ratio (d.w./f.w.) of leaves of *Sargassum horneri*. Measured in October 1987.

should decrease with increasing d.w./f.w. ratio in *S. horneri*. Photosynthesis of *S. thunbergii* was already reported to decrease with increasing d.w./f.w. ratio (Gao and Umezaki 1989c). The d.w./f.w. ratio (or LAR), which usually increases (or decreases) with aging, can be considered as a parameter engendering an aging effect on photosynthetic capacity in *S. horneri*. When the d.w./f.w. ratio increases or when LAR decreases, water content decreases, thereby the photolysis of water in photosynthesis can be slowed down, or the activities of some enzymes which directly or indirectly affect photosynthetic rate can be inhibited. For example, Küppers and Kremer (1978) demonstrated that the lower photosynthetic capacities in the older parts of *Fucus spiralis*, *F. serratus* and *F. vesiculosus* resulted from reduced activity of RuBP (ribulose-1,5-biphosphate) carboxylase.

S. thunbergii was shown to possess high photosynthetic capacity in vesicles, which contributed significantly to about 6% of the photosynthetic production of an adult plant from May to June (Gao and Umezaki 1989c). Vesicles of *S. horneri* were demonstrated to have high photosynthetic capacity in the present study. It was shown that vesicles occupied more and more percent in fresh weight as a plant grew larger, and it was estimated that photosynthetic production by vesicles in November and March accounted for 4% and 59%, respectively, while that by leaves about 90% and 34% of the hourly net photosynthetic production of a *S. horneri* plant under saturating solar radiation (Gao 1989). It is clear that vesicles of both *S. thunbergii* and *S. horneri* contribute considerably to their photosynthetic production in addition to supplying floatation. Photosynthetic production of a *Sargassum* plant seems to be done almost by leaves when it is young, and is contributed more and more by vesicles as it grows larger until maturation period.

Although the holdfast of *S. horneri* showed photosynthetic activity, its net photosynthetic rate (at $600 \mu\text{E m}^{-2} \text{s}^{-1}$) was almost zero, which means that it contribute little to the growth. It is a problem to be studied whether

there is any transpiration of photosynthates from leaves to holdfast in *S. horneri*. Photosynthetic capacities were lowest in holdfast and primary lateral, intermediate in vesicles and highest in leaves in *S. horneri*. It can be concluded that *S. horneri* is also differentiated with differed photosynthetic properties in various parts as in *S. thunbergii* (Gao and Umezaki 1989c).

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高 坤山：褐藻アカモクの藻体部位別の光合成能

アカモク (*Sargassum horneri*) の葉、気胞、主枝、固着器の光合成と暗呼吸を差動式検容器を用いて測定した。葉では葉面積比の増加に伴い、純光合成と暗呼吸速度は増加したが、クロロフィル含量は減少した。葉が1日加齢するにつれてクロロフィル含量は1.7~4.1%増加し、純光合成および暗呼吸はそれぞれ1.4~5.8%、4.6~8.9%減少すると推定された。気胞は浮力を提供すると同時に高い光合成能をもつことが示された。光合成活性は葉、気胞、主枝、固着器の順で低下した。アカモク藻体の形態的分化は光合成特性の違いを伴っていることが明らかになった。(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)