

Comparative studies of photosynthesis in different parts of *Sargassum thunbergii**

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Photosynthetic and respiratory rates of different parts of the brown alga *Sargassum thunbergii* were measured with a differential gas-volumeter. It is clear that various parts of a *S. thunbergii* plant are differentiated with different photosynthetic properties. The light-saturated photosynthetic rates were highest in leaves, intermediate in vesicles and lowest in axes of main branches on any of dry weight and chlorophyll *a* bases. The axes of main branches showed similar chlorophyll content, but higher light-saturated photosynthetic rates in the apical compared with the basal portions. The leaves showed lower chlorophyll content but higher light-saturated photosynthetic rates (on dry weight basis) in the apical than in the basal portions. On the chlorophyll *a* basis, the light-saturated net photosynthetic rates of both leaves and vesicles were higher in the apical compared with the basal portions. It is also clear that the vesicles, in addition to supplying floatation, contribute significantly to the photosynthetic production of the plant.

Key Index Words: Chlorophyll content—differentiation—photosynthesis—light curve—*Sargassum thunbergii*.

Typical *Sargassum* plants consist of a holdfast, a stem from which main branches or main axes are formed, and lateral branches arising from the main axes which produce 'leaves', vesicles and, during the mature season, receptacles. Such thallus differentiation is presumably correlated with an appropriate functional specialization of different thallus parts and may partly be described in terms of biochemical and physiological properties. Such functional specialization has been reported in *Laminaria*, *Macrocystis*, and *Fucus*. Gradients of chemical composition (BLACK 1954) and long distance translocation of stored assimilation products (HELLEBUST and HAUG 1972; SCHMITZ and LOBBAN 1976) have been already reported for *Laminaria* species. Furthermore, WEIDNER and KÜPPERS (1973) reported a differential distribution of certain carboxylating enzymes within the thallus of

Laminaria hyperborea, and KÜPPERS and KREMER (1978) reported a longitudinal difference of carbon dioxide fixation capacities in three *Laminaria* and three *Fucus* species. WHEELER (1980) showed changes in photosynthetic rate and pigment content along the fronds of *Macrocystis pyrifera*. However, there are no reports of such specialization in *Sargassum*, a plant that has more complicated morphological differentiation.

Sargassum beds in Japan are important subtidal forests as typical as the communities of *Ecklonia* and *Eisenia*, being noticed as nursery grounds for fishes and shellfishes, and as biomass resources and sources of raw material for algin industries. A number of ecological investigations on *Sargassum* (YOSHIDA *et al.* 1963; NAKAMURA *et al.* 1970, 1971; CHAUHAN and KRISHNAMURTHY 1971; UMEZAKI 1974; TANIGUCHI and YAMADA 1978; KANE and CHAMBERLAIN 1979; UMEZAKI 1983, 1984, 1985, 1986) have been done.

From botanical and ecological perspectives,

* Dedicated to the memory of the late Dr. Munenao KUROGI (1921-1988), Professor Emeritus of Hokkaido University.

it is important to obtain a general knowledge of the photosynthesis of *Sargassum* plants. A better understanding of ecological characteristics of *Sargassum* must be based on the knowledge of photosynthesis and respiration. However, little knowledge has been accumulated on the photosynthesis of *Sargassum* (THOMAS and TREGUNNA 1968; YOKOHAMA 1977; GAO and UMEZAKI 1988). The present study on *Sargassum thunbergii* (MERTENS ex ROTH) O. KUNTZE aims to determine photosynthetic capacities of different parts correlated to thallus differentiation.

Materials and Methods

Sargassum thunbergii is a perennial species growing on rocks in the mid to low intertidal

zone. The species is distributed along the coasts of both the Sea of Japan and the Pacific Ocean throughout the Archipelago of Japan. The plant elongates by apical growth, and grows rapidly in the early summer season in Wakasa Bay facing the Sea of Japan (UMEZAKI 1974). The 'leaves' of *S. thunbergii* are filiform, up to 1 cm long and 1 to 2 mm wide, and cover the whole length of the main and lateral branches. The vesicles are fusiform, 3–5 mm long and 1–2 mm in diameter. Different parts of *S. thunbergii* are illustrated in Figure 1.

The experiments were carried out during the period from May to July 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 *Sargassum thunbergii* were collected at Nagahama, Maizuru Bay, where plants form a conspicuous zone at approximately -10 to $+15$ cm tide level and mature in July. The main branches fall off after maturation. Newly germinated plants or sprouts on main branches appear in September.

Photosynthesis and respiration were measured in the laboratory as reported by YOKOHAMA *et al.* (1986) with a differential gas-volumeter, "Productmeter" (Nikko Kagaku Ltd.), equipped with eight pairs of reaction and compensation vessels kept in a water bath fitted with a motor to shake the vessels. Photosynthetic and respiratory rates were determined from the volumes of oxygen evolved or consumed by the samples. For photosynthesis-light curves, various photon flux densities were attained in a stepwise fashion from the lowest to the highest by changing the number of white paper sheets. Light was supplied with halogen lamps of slide projectors (Cabin Industry, Twin Cabin Super). Dark respiration was measured by completely covering the reaction vessel with opaque plastic. Fresh weight of the samples was measured after blotting water drops from the thallus surface with tissue paper. Dry weight was determined after drying the samples at 85°C for 20–24 hours. The

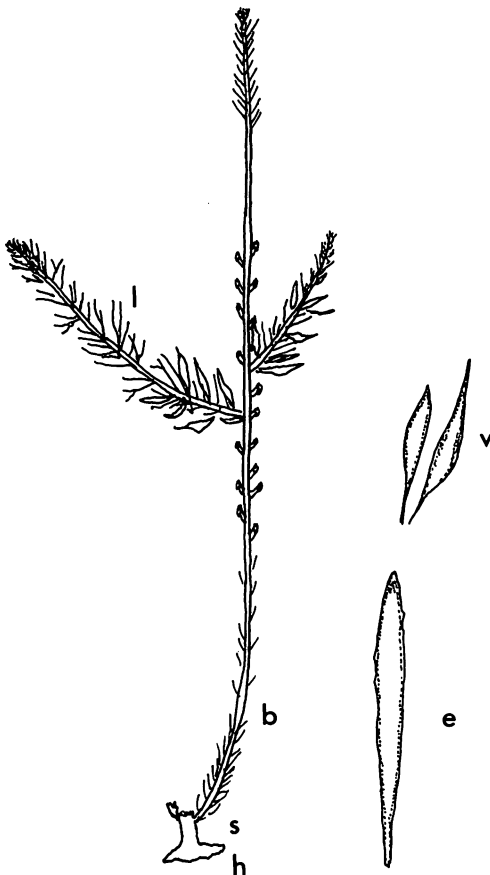


Fig. 1. *Sargassum thunbergii*. 'h', holdfast; 's', stem; 'b', main branch; 'l', lateral branch; 'v', vesicle; 'e', leaf.

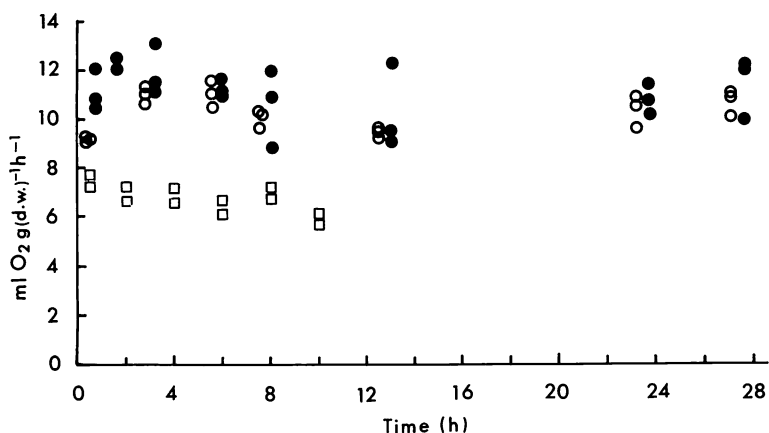


Fig. 2. Changes with time of net photosynthesis of a *Sargassum thunbergii* plant after cutting. ○, branches, and ●, leaves of the apical portion. □, leaves of the basal portion. Measured at $560 \mu\text{E m}^{-2} \text{s}^{-1}$ and 20°C .

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). The water temperature in the water bath was controlled by using a Taiyo Coolnit (CL-30). Photosynthesis and dark respiration were measured at 20°C . The water temperature in the sea varied from 18 to 23°C during the experimental period.

The photosynthetic and respiratory measurements for vesicles, receptacles and axes of main branches were carried out soon after cutting. The effect of cutting on net photosynthetic rate was investigated for the 'leaves' and lateral branches. Figure 2 shows the changes with time of the net photosynthesis of leaves and lateral branches after cutting. The net photosynthetic rate in 'leaves' of the basal portion showed the highest values soon after cutting and then declined slightly with time, while that of the apical portion was constant for about six hours after cutting. The net photosynthetic rate of the lateral branches of apical portion was lower soon after cutting and recovery occurred about three hours later. On the basis of these results, photosynthesis measurements were made soon after cutting for 'leaves' and after three hours' storage in flowing seawater for lateral branches.

Chlorophylls were extracted with 90% acetone and filtered through absorbent cotton, after being homogenized by grinding the samples frozen at -20°C in a mortar with quartz sand. 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).

Results

Net photosynthetic rates (dry weight basis) of the 'leaves' from the basal portion were much lower compared with those from apical portion (Fig. 3A). As shown in Figure 3, net photosynthetic rate of vesicles from the apical portion was slightly lower than the rate of leaves from the apical portion (A), and was lower than the rate of vesicles from the basal portion (B).

Figure 4 shows the average photosynthesis-light curves on the basis of dry weight measured for the different parts of the plants. Net photosynthesis and dark respiration showed a little higher rate on the average for the lateral branches of the apical portion compared with the basal portion (Fig. 4A). Net photosynthesis was not saturated even at $560 \mu\text{E m}^{-2} \text{s}^{-1}$. The net photosynthetic and dark respiratory rates of 'leaves' from the apical

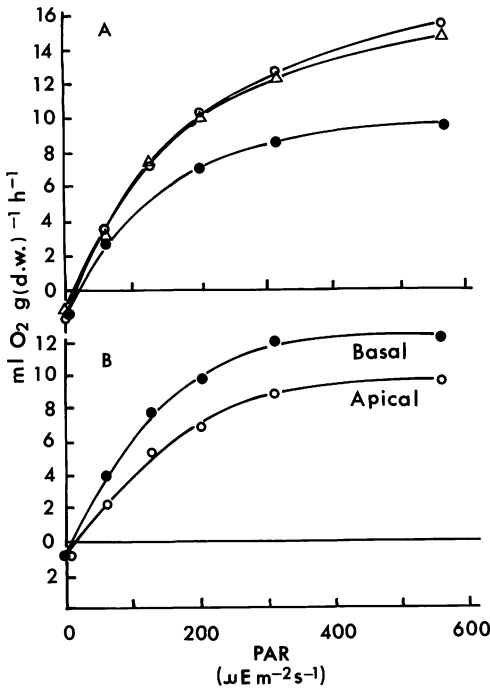


Fig. 3. Photosynthesis-light curves of *Sargassum thunbergii*. (A) \circ , leaves and Δ , vesicles of the apical portion; \bullet , leaves of the basal portion of a plant about 50 cm long. (B) \circ , vesicles of the apical portion; \bullet , vesicles of the basal portion of a plant about 70 cm long.

portion showed much higher values compared with those from the basal portion (Fig. 4B). Photosynthesis was saturated at about $300 \mu\text{E m}^{-2} \text{s}^{-1}$ in 'leaves' of basal portions but was not saturated until $560 \mu\text{E m}^{-2} \text{s}^{-1}$ (Fig. 4B) in leaves of apical portions. In the photosynthesis-light curves for the axes of main branches (Fig. 4C), both the photosynthetic and dark respiratory rates showed much higher values in the apical compared with the basal portions. Photosynthesis was saturated at about $200 \mu\text{E m}^{-2} \text{s}^{-1}$ for axes of the basal portion but was not saturated for those of the apical portion. Photosynthesis of receptacles was saturated at about $300 \mu\text{E m}^{-2} \text{s}^{-1}$ (Fig. 4D). Photosynthesis of vesicles from apical portions did not saturate until $560 \mu\text{E m}^{-2} \text{s}^{-1}$ (Fig. 4D).

Figure 5 shows the photosynthesis-light curves based on chlorophyll *a* for vesicles (A), 'leaves' (B) and axes of main branches (C).

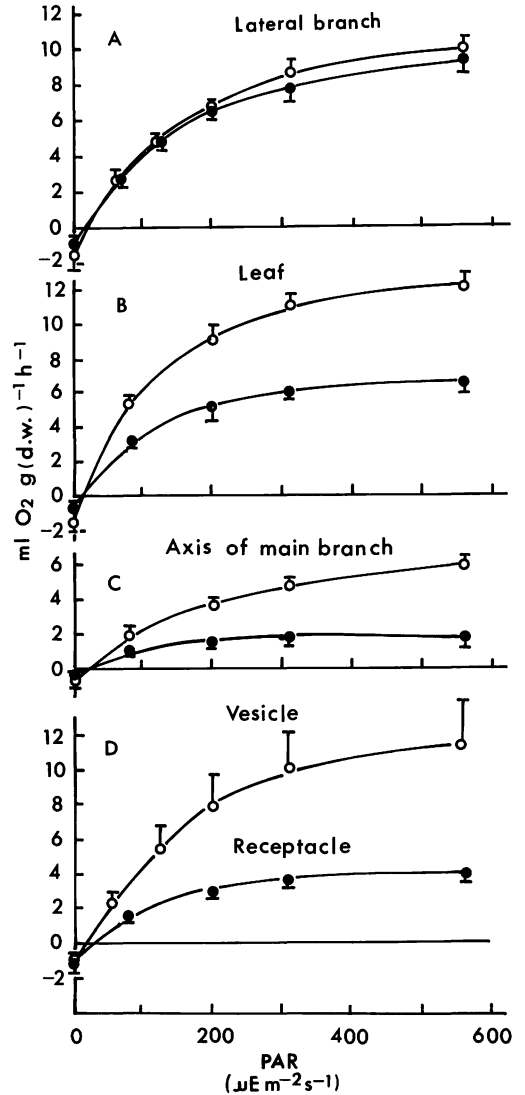


Fig. 4. Photosynthesis-light curves of *Sargassum thunbergii*. Values are the means \pm SD of three to five plants 50–80 cm long, measured at 20°C . (A, B, C) \circ , the apical portion; \bullet , the basal portion. (D) \circ , vesicles; \bullet , receptacles.

Both net photosynthesis and dark respiration of 'leaves', vesicles and axes showed higher values in the apical portion compared with those in the basal portion. Little difference was found in the initial slopes of the photosynthesis-light curves for vesicles between the basal and the apical portions compared with those for 'leaves' and axes of main branches.

For clear comparisons among the different

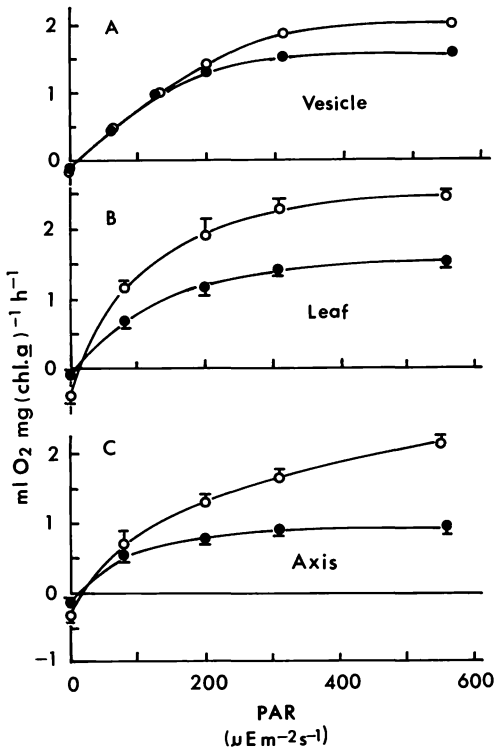


Fig. 5. Photosynthesis-light curves of *Sargassum thunbergii* at 20°C. (A) A single plant about 70 cm long. (B, C) Means \pm SD of five plants 60–70 cm long. \circ , the apical portion; \bullet , the basal portion.

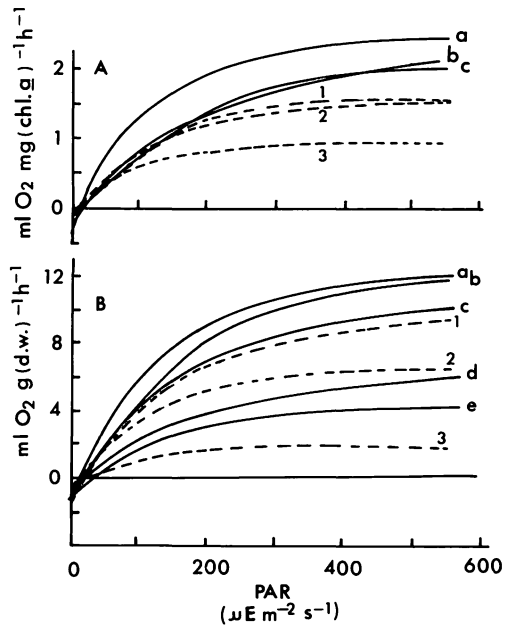


Fig. 6. Comparisons of photosynthesis-light curves of different parts of *Sargassum thunbergii* (replotted from Figs. 4 and 5). (A) 'a' leaves; 'b', axes of main branches; and 'c', vesicles; of apical portion: '1', vesicles; '2', leaves; and '3', axes of main branches; of basal portion. (B) 'a', leaves; 'b', vesicles; 'c', lateral branches; 'd', axes of main branches; and 'e', receptacles; of the apical portion: '1', lateral branches; '2', leaves; and '3', axes of main branches; of the basal portion.

parts, photosynthesis-light curves in Figures 4 and 5 were replotted in Figure 6. On a dry weight basis (B), the average net photosynthetic rates at $560 \mu\text{E m}^{-2} \text{s}^{-1}$ were 12.0, 11.5, 10.0, 6.0 and 4.0 $\text{ml O}_2 \text{g (d.w.)}^{-1} \text{h}^{-1}$, and the average respiratory rates were 1.7, 1.2, 1.6, 0.8 and 1.3 $\text{ml O}_2 \text{g (d.w.)}^{-1} \text{h}^{-1}$ for 'leaf', vesicle, lateral branch, axis of main branch and receptacle, respectively. The 'leaves' showed the highest values in both photosynthesis and respiration. The light compensation points were about 25, 20, 20, 18 and 13 $\mu\text{E m}^{-2} \text{s}^{-1}$ for receptacles, lateral branches, axes of main branches, vesicles and 'leaves' of the apical portion, respectively. They were higher in the apical than in the basal portions for 'leaves', lateral branches and axes of main branches except for vesicles. A considerable difference was also found in the photosynthesis-light curves based

on chlorophyll *a* among the different parts (A). The leaves from apical portion showed the highest values and the axes of main branches from basal portion gave the lowest.

Segments from base to apex of a *Sargassum thunbergii* plant were cut without separating the 'leaves', vesicles and lateral branches. Photosynthesis and dark respiration were measured for these segments to determine their changes. Both net photosynthetic and dark respiratory rates based on dry weight were found to increase from the base to the apex of the plant. Subsequently, gross photosynthetic rate also increased from the base to the apex of the plant. Relationships of the relative gross photosynthesis and the dry weight to fresh weight (d.w./f.w.) ratio to the height of the segment of a plant are shown in Figure 7. The gross photosynthesis increased logarithmically and the d.w./f.w.

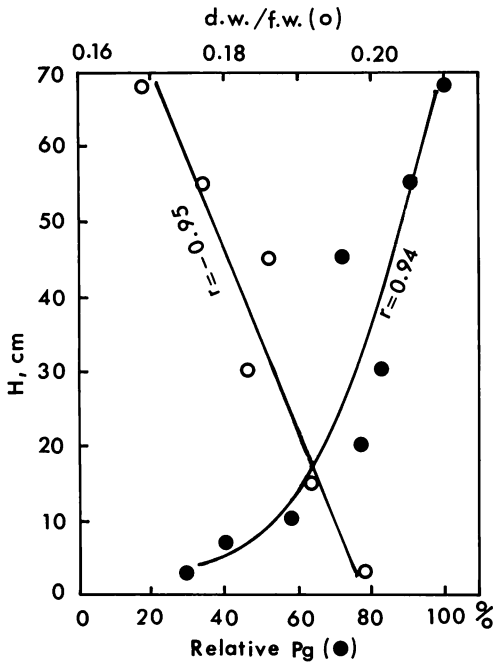


Fig. 7. Relationships of relative gross photosynthesis (P_g) at $560 \mu E m^{-2} s^{-1}$ and $20^\circ C$ and dry weight to fresh weight (d.w./f.w.) ratio (Y) to the height (H , vertical position from the holdfast) of a *Sargassum thunbergii* plant. The relationships are expressed by $P_g = 4.66 + 21.50 \ln H$ and $Y = 0.200 - 4.255 \times 10^{-4} H$. 'r', the regression coefficient.

ratio decreased linearly from the base to the apex of the plant. As indicated by the regression coefficient, both the relative gross photosynthesis and the d.w./f.w. ratio were

closely related to the height of the segment.

Figure 8 illustrates the amounts in fresh weight and the chlorophyll *a* content on a fresh weight basis of different parts of a *Sargassum thunbergii* plant. As clearly shown, vesicles account for a considerable part, about 55%, of the plant, while 'leaves', axes of lateral branches and main branches account for 12, 24 and 9% of the whole plant, respectively. The chlorophyll *a* content decreased in vesicles but increased in axes of lateral branches from the basal to the apical portions.

The basal portion showed higher chlorophylls *a* and *c* contents in 'leaves' and vesicles, but not in axes of main branches, compared with the apical portion (Table 1). Chlorophyll *a* in vesicles was highest in both apical and basal portions. The content of chlorophyll *c* was highest in vesicles and in 'leaves' for the apical and basal portions, respectively. Chlorophyll *c* to *a* ratios of leaves and axes were higher in the basal than in the apical portions. There was no significant difference in chlorophyll *c* to *a* ratio between the apical and the basal portions for vesicles. The d.w./f.w. ratio was higher in the basal portion compared with the apical portion, and was highest in axes.

Based on the data in Table 1, chlorophylls *a* and *c* were 36% and 68% higher in the basal than in the apical portions for 'leaves', and 17% and 15% higher for vesicles, and 4%

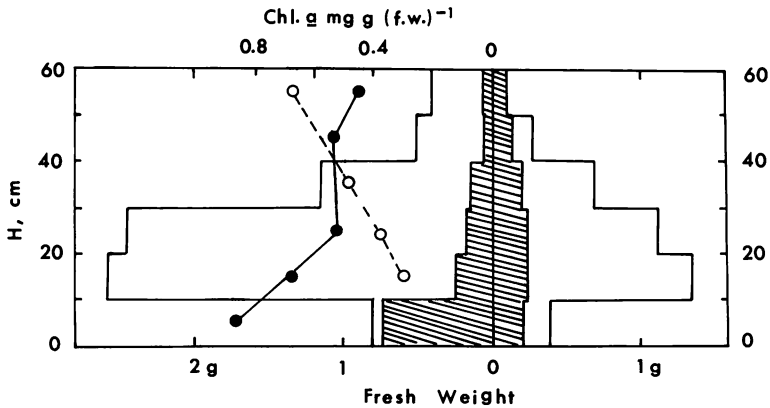


Fig. 8. Diagram showing the vertical distributions of different parts of a *Sargassum thunbergii* plant. Left-hand side is for leaves (hatched area) and vesicles (open area). Right-hand side is for axes of lateral branches (open area) and main branch (hatched area). Chlorophyll *a* contents of vesicles (●) and axes of lateral branches (○) are also indicated.

Table 1. Chlorophyll contents [mg g (f.w.)^{-1}] and dry weight to fresh weight ratio (d.w./f.w.) of leaves, vesicles and axes of main branches of the apical and basal portions of *Sargassum thunbergii*. Each datum indicates the mean \pm SD of five sample.

	Chl. <i>a</i>	Chl. <i>c</i>	Chl. <i>c/a</i>	d.w./f.w.
Apical portion				
Leaf	0.665 \pm 0.009	0.074 \pm 0.001	0.111 \pm 0.048	0.139 \pm 0.013
Vesicle	0.821 \pm 0.004	0.094 \pm 0.002	0.113 \pm 0.002	0.161 \pm 0.012
Axis	0.534 \pm 0.001	0.060 \pm 0.002	0.110 \pm 0.004	0.194 \pm 0.004
Basal portion				
Leaf	0.902 \pm 0.048	0.124 \pm 0.009	0.137 \pm 0.003	0.181 \pm 0.028
Vesicle	0.958 \pm 0.027	0.108 \pm 0.002	0.112 \pm 0.001	0.167 \pm 0.027
Axis	0.514 \pm 0.003	0.064 \pm 0.005	0.124 \pm 0.009	0.261 \pm 0.003

lower and 7% higher for axes of main branches. However, net photosynthetic rate (at $560 \mu\text{E m}^{-2} \text{s}^{-1}$) on a dry weight basis was about 21% lower for vesicles (Fig. 3B), and 100% and 200% higher for 'leaves' and axes of main branches (Fig. 4B, C), respectively, in the apical compared with the basal portions. On a chlorophyll *a* basis, net photosynthetic rate was about 33%, 66% and 150% higher in the apical compared with the basal portions for vesicles, 'leaves' and axes of main branches, respectively (Fig. 5). The cause of increased chlorophyll content but decreased photosynthesis in the basal portion

will be discussed later.

Photosynthetic rates were measured at $560 \mu\text{E m}^{-2} \text{s}^{-1}$ for different parts and were plotted as a function of the d.w./f.w. ratios (Fig. 9). As indicated, the gross photosynthesis of *Sargassum thunbergii* is closely correlated with the d.w./f.w. ratio, expressed as linear (A) and exponential (B) functions on chlorophyll *a* and dry weight bases, respectively. Gross photosynthesis decreased with increasing d.w./f.w. ratio.

Discussion

The difference in photosynthesis-light curves between 'leaves' and vesicles was much larger on a chlorophyll *a* basis than on a dry weight basis for the apical portion (Fig. 6). This could be caused by higher chlorophyll contents in vesicles than in 'leaves' (Table 1). Photosynthetic responses of vesicles to light showed values about twice that of axes of main branches on a dry weight basis (Fig. 6B), but showed little difference on a chlorophyll *a* basis (Fig. 6A). This was due to the much higher chlorophyll content of the former (Table 1).

In this study, vesicles accounted for more than 50% of the fresh weight of *Sargassum thunbergii* (Fig. 8) and were photosynthetically very active (Fig. 3B and 4D). On the basis of the photosynthesis-light curves (Fig. 4) and the dry weight [obtained from fresh weight (Fig. 8) by taking account of the d.w./f.w.

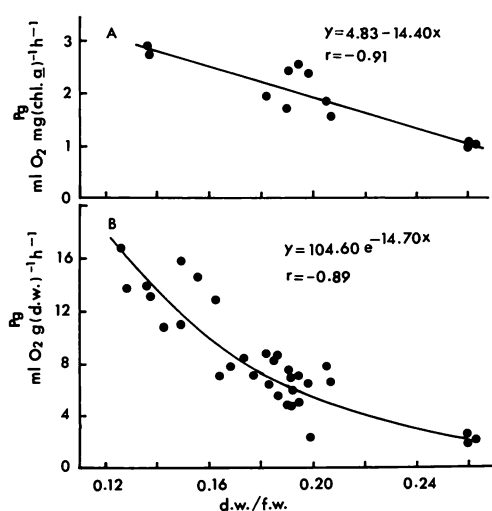


Fig. 9. Relationships between gross photosynthesis and the d.w./f.w. ratio of various parts of *Sargassum thunbergii*.

ratios], it was estimated that more than 60% of the photosynthetic production per hour of the plant under saturating solar radiation depended on vesicles, only 14% on 'leaves', and the rest on axes of main and lateral branches. After maturation, main branches of the plant fall off, and new main branches appear from the stem in September. These newly sprouted main branches and small young plants germinated from fertilized eggs have no vesicles. Vesicles gradually appear and their number increases with age. It is reasonable to assume that the photosynthetic production of *S. thunbergii* is almost entirely by 'leaves' when plants are small or young, with the contribution from vesicles increasing as plants grow larger. It is clear that vesicles of this plant contribute remarkably to the photosynthetic production in addition to supplying floatation.

Photosynthetic activity was already reported to be higher in the apical than in the basal portions for *Sargassum horneri*, *S. hemiphyllosum* and *S. confusum* on the basis of chlorophyll *a* (YOKOHAMA 1977). In studies on *Sargassum horneri*, *S. serratifolium*, *S. autumnale*, *S. thunbergii* and *S. patens*, GAO and UMEZAKI (1988) also reported that 'leaves' of the lower part showed higher chlorophyll content but lower photosynthetic rates on a chlorophyll *a* basis. Photosynthetic activity of *Padina arborescens* becomes lower toward the base of the plant where the chlorophyll content is higher (YOKOHAMA 1977). These results are similar to those of the present study. Possible reasons for increased chlorophyll content but decreased photosynthetic capacities in the basal portion of *S. thunbergii* are discussed below.

RAMUS *et al.* (1977) found that chlorophylls *a* and *c* and fucoxanthin in *Ascophyllum nodosum* and *Fucus vesiculosus* increased with the water depth or more shade. WHEELER (1980) reported that transplanted juvenile plants of *Macrocystis pyrifera* showed higher pigment concentrations in deeper habitats than in shallower ones. Similar results have been obtained from other marine algae such as *Codium fragile*, *Udotea petiolata*, *Porphyra um-*

bilicalis, *Chondrus crispus* and *Dictyota dichotoma* (WASSMAN and RAMUS 1973; RAMUS *et al.* 1976a, b; PEREZ-BERMEDEZ *et al.* 1981). At Nagahama in Maizuru Bay, *Sargassum thunbergii* forms a conspicuous algal zone, so that their basal portions are usually shaded by upper parts, especially during the period when the plants grow larger. Increased chlorophyll content in leaves and vesicles of the basal portion of *S. thunbergii* (Table 1) can be considered partially to be caused by an adaptation to the reduced light conditions. In addition to light adaptation, aging and thallus differentiation can produce differences in pigment concentration or photosynthetic capacity. Consequently, the lower chlorophyll content in axes of branches may result from their differentiation. KÜPPERS and KREMER (1978), in 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. As mentioned earlier, *S. thunbergii* elongates apically, and the apical portions are younger than the basal portions. The results of the present study agree with those reported by KÜPPERS and KREMER (1978) for the *Laminaria* and *Fucus* species and by WHEELER (1980) for *Macrocystis pyrifera*; aging can be accompanied with increase of chlorophylls. The d.w./f.w. ratio, which usually increases with age, can be considered as a parameter engendering an aging effect on the photosynthetic capacity in *S. thunbergii* (Fig. 7). When the d.w./f.w. ratio increases and water content decreases, 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. This supports our suggestion, provided that the enzymatic activity could be depressed with an increase in the d.w./f.w. ratio.

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References

- BLACK, W. 1954. Concentration gradients and their significance in *Laminaria saccharina* (L.) LAMOUR. J. Mar. Biol. Assoc. UK. **33**: 49–60.
- CHAUHAN, V. D. and KRISHNAMURTHY, V. 1971. Ecology and seasonal succession of *Sargassum swartzii* (TURN.) C. AG. in Indian waters. Phycos **10**: 1–11.
- GAO, K. and UMEZAKI, I. 1988. Comparative photosynthetic capacities of the leaves of upper and lower parts of *Sargassum* plants. Bot. Mar. **31**: 231–236.
- HELLEBUST, J. A. and HAUG, A. 1972. Photosynthesis, translocation, and alginic acid synthesis in *Laminaria digitata* and *Laminaria hyperborea*. Can. J. Bot. **50**: 169–176.
- JEFFREY, S. W. and HUMPHREY, G. F. 1975. New spectrophotometric equations for determining chlorophylls *a*, *b*, *c*₁ and *c*₂ in higher plants, algae and natural phytoplankton. Biochem. Physiol. Pfl. **167**: 191–194.
- KANE, D. F. and CHAMBERLAIN, A. H. K. 1979. Laboratory growth studies on *Sargassum muticum* (YENDO) FENSHOLT. Bot. Mar. **22**: 1–9.
- KÜPPERS, U. and KREMER, B. P. 1978. Longitudinal profiles of carbon dioxide fixation capacities in marine macroalgae. Plant Physiol. **62**: 49–53.
- NAKAMURA, Y., TATEWAKI, M., NAKAHARA, H., SAITO, S., NAGATA, K. and MASUDA, M. 1970. On the productivity of marine algal communities. Interim Rep. of the Kuroshio Littoral Region Research Group for JIBP-PM., p. 7–9. (in Japanese)
- NAKAMURA, Y., TATEWAKI, M., NAKAHARA, H., SAITO, S., NAGATA, K. and MASUDA, M. 1971. The seasonal variations of standing crops of *Sargassum thunbergii*. Interim Rep. of the Kuroshio Littoral Region Research Group for JIBP-PM., p. 15–17. (in Japanese)
- PEREZ-BERMEDEZ, P., GARCIA-CARRASCOSA, M., CORNEJO, M. J. and SEGURA, J. 1981. Water-depth effects in photosynthetic pigment of the benthic algae *Dictyota dichotoma* and *Udotea petiolata*. Aquatic Bot. **11**: 373–377.
- RAMUS, J., BEALE, S. I. and MAUZERALL, D. 1976a. Correlation of changes in pigment content with photosynthetic capacity of seaweeds as a function of water depth. Mar. Biol. **37**: 231–238.
- RAMUS, J., BEALE, S. I., MAUZERALL, D. and HOWARD, K. L. 1976b. Changes in photosynthetic pigment concentration in seaweeds as a function of water depth. Mar. Biol. **37**: 223–229.
- RAMUS, J., LEMONS, F. and ZIMMERMAN, C. 1977. Adaptation of light-harvesting pigments to downwelling light and the consequent photosynthetic performance of the eulittoral rockweeds *Ascophyllum nodosum* and *Fucus vesiculosus*. Mar. Biol. **42**: 293–303.
- SCHMITZ, K. and LOBBAN, C. S. 1976. A survey of translocation in Laminariales (Phaeophyceae). Mar. Biol. **36**: 207–216.
- TANIGUCHI, K. and YAMADA, Y. 1978. Ecological study on *Sargassum patens* C. AGARDH and *S. serratifolium* C. AGARDH in the sublittoral zone at Iida Bay of Noto Peninsula in the Japan Sea. Bull. Japan Sea Reg. Fish. Res. Lab. **29**: 239–253. (in Japanese with English summary)
- THOMAS, E. A. and TREGUNNA, E. B. 1968. Bicarbonate ion assimilation in photosynthesis by *Sargassum muticum*. Can. J. Bot. **46**: 411–415.
- UMEZAKI, I. 1974. Ecological studies of *Sargassum thunbergii* (Mertens) O. Kuntze in Maizuru Bay, Japan Sea. Bot. Mag. Tokyo **87**: 285–292.
- UMEZAKI, I. 1983. Ecological studies of *Sargassum miyabei* YENDO in Maizuru Bay, Japan Sea. Bull. Japan. Soc. Sci. Fish. **49**: 1825–1834.
- UMEZAKI, I. 1984. Ecological studies of *Sargassum horneri* (TURNER) C. AGARDH in Obama Bay, Japan Sea. Bull. Japan. Soc. Sci. Fish. **50**: 1193–1200.
- UMEZAKI, I. 1985. Growth of the stem in *Sargassum ringgoldianum* HARV. subsp. *coreanum* (J. AG.) YOSHIDA in Obama Bay, Japan Sea. Bull. Japan. Soc. Sci. Fish. **51**: 1441–1445.
- UMEZAKI, I. 1986. Growth of the primary laterals in *Sargassum ringgoldianum* HARV. subsp. *coreanum* (J. AG.) YOSHIDA in Obama Bay, Japan Sea. Bull. Japan. Soc. Sci. Fish. **52**: 957–963.
- WASSMAN, E. R. and RAMUS, J. 1973. Primary production measurements for the green seaweed *Codium fragile* in Long Island Sound. Mar. Biol. **21**: 289–297.
- WEIDNER, M. und KÜPPERS, U. 1973. Phosphoenolpyruvat-Carboxykinase und Ribulose-1,5-Diphosphat-Carboxylase von *Laminaria hyperborea* (GUNN.) FOSL.: das Verteilungsmuster der Enzymaktivitäten im Thallus. Planta **114**: 365–372.
- WHEELER, W. N. 1980. Pigment content and photosynthetic rate of the fronds of *Macrocystis pyrifera*. Mar. Biol. **56**: 97–102.
- YOKOHAMA, Y. 1977. Productivity of seaweeds. p. 119–127. In K. HOGETSU, M. HATANAKA, T. HANAOKA and T. KAWAMURA [ed.], Productivity of Biocenoses in Coastal Regions of Japan. Univ. of Tokyo Press, Tokyo.
- YOKOHAMA, Y., KATAYAMA, N. and FURUYA, K. 1986. An improved type of 'Productmeter', a differential gas-volumeter, and its application to measuring photosynthesis of seaweeds. Jap. J. Phycol. **24**: 37–

42. (in Japanese with English summary)
 YOSHIDA, T., SAWADA, T. and HIGAKI, M. 1963.
Sargassum vegetation growing in the sea around

Tsuyazaki, north Kyushu, Japan. Pac. Sci. 17:
 135-144.

高 坤山・梅崎 勇：ウミトラノオの藻体部位別の光合成活性に関する比較研究

褐藻ウミトラノオの藻体の部位別の光合成活性を差動式検容計（プロダクトメーター）を用いて調べ、葉、気胞、主枝などのような分化が光合成特性の違いを伴っていることを明らかにした。ウミトラノオの光飽和光合成速度は、乾重量当たりでもクロロフィル量当たりでも、葉、気胞、主枝の順で低下した。主枝では、クロロフィル含量はかわらないが、光飽和光合成速度は乾重量当たりでもクロロフィル量当たりでも上部のほうが下部より高かった。葉では、クロロフィル含量は下部のもののほうが上部のものより高かったが、光飽和光合成速度は乾重量当たりでもクロロフィル量当たりでも下部のものほうが上部のものより低かった。気胞では、クロロフィル含量は上部のものより下部のものが高く、光飽和光合成速度は乾重量当たりでは下部のものが高かったが、クロロフィル量当たりでは上部のものが高かった。また、光合成速度が光飽和に達するような光条件下では、ウミトラノオ藻体の光合成生産の約60%が気胞によって行われていると推算された。（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研究室）