

## Comparative Photosynthetic Capacities of the Leaves of Upper and Lower Parts of *Sargassum* Plants

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(Accepted 27 February 1988)

### Abstract

Photosynthesis-light curves of the leaves of upper and lower parts of five species of *Sargassum* plants were measured with a Nikko-Tron Productmeter. The saturated net photosynthetic rates of the leaves of upper parts were higher in *S. thunbergii* and *S. serratifolium* and lower in *S. horneri*, *S. autumnale* and *S. patens* on the basis of dry weight, and were higher for each species on the basis of chlorophyll *a* than those of the leaves of lower parts. Respiration rates were found to be reduced in the leaves of lower parts compared to the upper parts. Respiration rates were also reduced in species from deeper habitats compared to those from shallower habitats. Chlorophyll contents were found to be higher in the leaves of lower parts compared to those of upper parts, with the former having a 1.36 to 8.74 times greater chlorophyll *a* concentration. Chlorophyll *c* to *a* ratios of the leaves of upper parts were higher compared to the leaves of lower parts. It is concluded that these results are due to ontogenetic differentiation in the photosynthetic unit (PSU), which gives rise to a different photosynthetic performance between the leaves of upper and lower parts of *Sargassum* plants.

### Introduction

*Sargassum*, the largest genus in the Phaeophyta, is distributed throughout the tropical to temperate regions of the world. Along the coasts of the Japan Sea and the Pacific Ocean in Japan, the genus constitutes an important part of the marine flora. Many species of *Sargassum* usually have such large plants that the localities where the alga grows luxuriantly are called *Sargassum*-beds or garamoba in Japanese. More and more attention has been focussed on *Sargassum* not only from the standpoint of its fishery importance as nursery grounds for fish spawning but also as a biomass resource and algin-containing seaweed.

A number of ecological investigations on *Sargassum* (Yoshida *et al.* 1963, Chauhan and Krishnamurthy 1971, Umezaki 1974, Taniguchi and Yamada 1978, Kane and Chamberlain 1979, Umezaki 1983, 1984, 1985, 1986) have been reported. However, there are few studies of photosynthesis and respiration of *Sargassum* (Thomas and Tregunna 1968, Yokohama

1977). An understanding of the ecological characteristics of *Sargassum* must be based on a knowledge of photosynthesis and respiration. Moreover, it is necessary to investigate the photosynthesis of *Sargassum* for an estimation of its primary productivity.

A plant of *Sargassum* has a holdfast, a 'stem' from which main 'branches' (or main axes) are formed, which give rise to 'leaves', lateral 'branches', vesicles and receptacles. In perennial species, the stem annually produces several main branches which fall off after reaching maturity. The 'leaves' of the lower part of a main branch in a larger *Sargassum* plant standing in the sea are positioned at the bottom of the community, while those of the upper part are positioned on or near the sea surface. Leaves of *Sargassum* plants growing at different depths are also exposed to different *in situ* light conditions. The present study examines the leaves of lower and upper parts of *Sargassum* plants to determine whether there are any differences in their photosynthetic responses to light.

## Material and Methods

Samples of *Sargassum horneri* (Turner) C. Agardh, *S. serratifolium* C. Agardh, *S. patens* C. Agardh and *S. autumnale* Yoshida were collected from Takahama, Wakasa Bay which is located in the middle of Honshu, facing the Japan Sea. *Sargassum thunbergii* (Mertens ex Roth) O. Kuntze was collected at Nagahama, Maizuru Bay, a branch bay of Wakasa Bay. *Sargassum horneri* is an annual species and the others are perennial.

*Sargassum thunbergii* forms a conspicuous zone at approximately -10 to +15 cm tidal level and matures in July. *Sargassum serratifolium* and *S. patens* form communities at a depth of 1.5 to 3 meters and mature from May to June. *Sargassum horneri* and *S. autumnale* form communities at about 1 m depth and mature in April and September, respectively.

The experiments were carried out during May to July in the Fisheries Research Station of Kyoto University situated at the head of Maizuru Bay. Samples collected at Takahama were transported to the station within an hour of collection and maintained in flowing sea water, exposed to solar radiation, for 2 to 3 days until the completion of experiments. Samples of *Sargassum thunbergii* collected at Nagahama were used immediately for the photosynthesis and respiration measurements. The samples used for the photosynthesis or respiration measurements were 50 to 70 cm long in *S. thunbergii*, 80 to 90 cm long in *S. horneri* and *S. autumnale*, 120 to 150 cm long in *S. serratifolium* and *S. patens*, respectively.

Photosynthesis and respiration measurements were carried out in the laboratory with a Nikko-Tron Productmeter (Nikko Kagaku Ltd.), which has eight pairs of reaction and compensation vessels in a water bath equipped with a motor to shake the vessels. Photosynthesis and respiration were measured in the way described by Yokohama *et al.* (1986). 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 the white paper filters. Light was supplied from the halogen lamps of slide projectors (Cabin Industry, Twin Cabin Super). Dark respiration was determined by covering the reaction vessel completely with light-proof plastic. The photosynthetically active radiation (PAR) of the supplied light was measured with an underwater quantum sensor (Meiwa Ltd., 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). Photo-

synthesis-light curves were obtained at 20 °C for all five species. The temperature in the sea varied from 18 to 23 °C during the experimental period.

Chlorophylls were extracted from fresh tissues with 90% acetone. The absorbances of the acetone extract were measured at 750, 664, 630 nm with a spectrophotometer (Hitachi Ltd., Model 100-2) and the concentrations of chlorophyll *a* and *c* were calculated using the formulae of Jeffrey and Humphrey (1975).

## Results

Figure 1 shows the photosynthesis-light curves of the leaves of lower and upper parts of *Sargassum thunbergii*, *S. horneri*, *S. serratifolium*, *S. patens* and *S. autumnale*. The Net Photosynthetic rate of the leaves of upper parts, based on dry weight, was higher in *S. thunbergii* and *S. serratifolium* and lower in the other three species compared to that of the lower parts at high PAR. Dark respiration was greater in the leaves of upper parts compared to that of the lower parts in all of the species. The light compensation point was higher in the leaves of upper parts compared to that of the lower parts in all species except *S. serratifolium*. Saturation PAR ( $I_k$ ) was about 300 and 200  $\mu\text{E m}^{-2} \text{s}^{-1}$  in *S. thunbergii*, 200 and 180  $\mu\text{E m}^{-2} \text{s}^{-1}$  in *S. horneri*, 160 and 170  $\mu\text{E m}^{-2} \text{s}^{-1}$  in *S. serratifolium*, 250 and 220  $\mu\text{E m}^{-2} \text{s}^{-1}$  in *S. patens* and 180 and 200  $\mu\text{E m}^{-2} \text{s}^{-1}$  in *S. autumnale* (Fig. 1), for the leaves of the upper and lower parts respectively. Comparing the photosynthesis-light curves of the different species (Fig. 1), it can be clearly seen that the light-saturated net photosynthetic rates based on dry weight were in the following order from the highest to the lowest: *S. thunbergii*, *S. autumnale*, *S. serratifolium*, *S. horneri* and *S. patens* for the leaves of upper parts, and, *S. thunbergii*, *S. horneri*, *S. autumnale*, *S. serratifolium* and *S. patens*, for the leaves of lower parts.

Table I shows the chlorophyll contents of the leaves of the five species. Both the chlorophyll *a* and *c* contents were higher in the leaves of lower parts than in that of upper parts of all species. The content of chlorophyll *a* in the leaves of the lower parts were 1.36, 2.56, 3.06, 3.75 and 8.74 times that in the leaves of the upper parts in *Sargassum thunbergii*, *S. serratifolium*, *S. autumnale*, *S. horneri* and *S. patens*, respectively. The chlorophyll *c* to *a* ratio was higher in the leaves of upper parts compared to that of the lower parts for all species except *S. thunbergii*. The difference in the photosynthetic rate based on dry weight (Fig. 1) therefore appears to be greatly related to the chlorophyll content (Table I), and this will be discussed later.

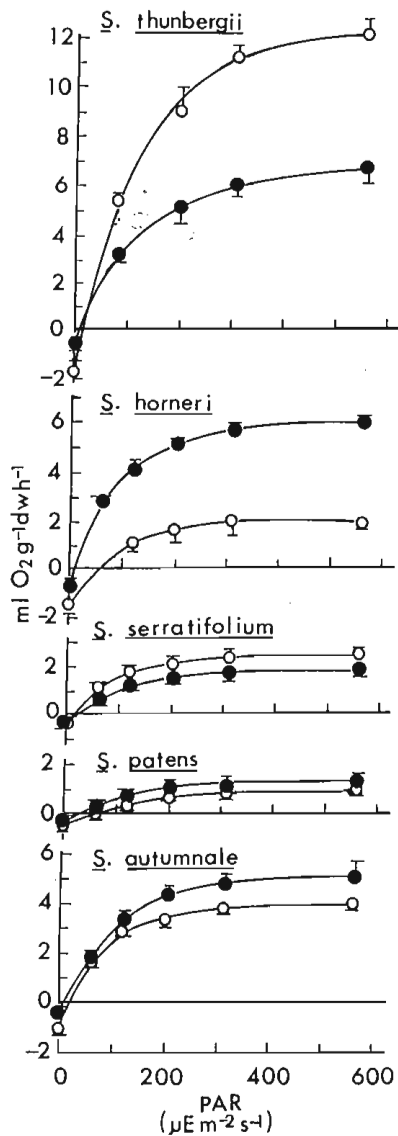


Fig. 1. Photosynthesis-light curves of the leaves of upper (open circles) and lower parts (filled circles) for five species of *Sargassum*, measured at 20 °C on the basis of dry weight. Net photosynthesis or respiration values are the means of three to six samples  $\pm$  standard deviation.

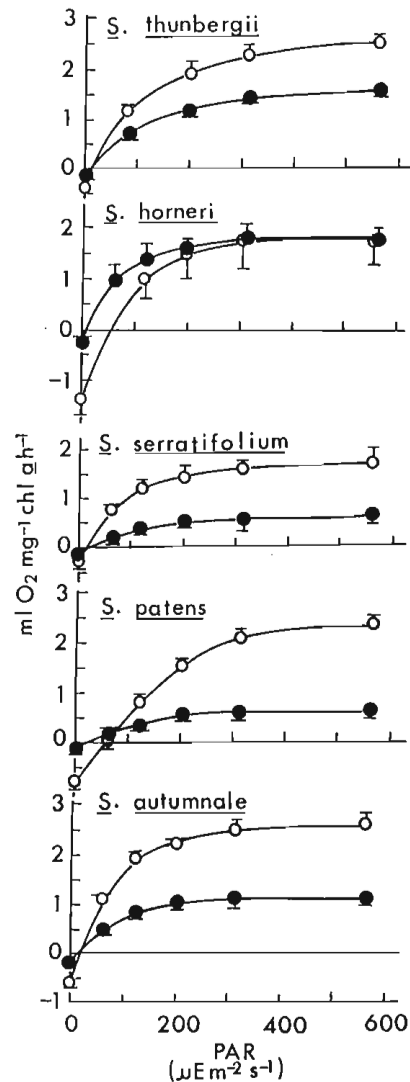


Fig. 2. Photosynthesis-light curves of the leaves of upper (open circles) and lower parts (filled circles) for five species of *Sargassum*, measured at 20 °C on the basis of chlorophyll *a*. Net photosynthesis or respiration values are the means of three to six samples  $\pm$  standard deviation.

Photosynthesis-light curves measured on the basis of chlorophyll *a* (Fig. 2) differed from those determined on the basis of dry weight (Fig. 1). As shown in Figure 2, the light-saturated net photosynthetic rates were higher in the leaves of the upper parts compared to the lower parts for all species except *Sargassum horneri*. The light-saturated net photosynthesis of the leaves of *S. horneri* showed similar values for the lower and upper parts. The dark respiration rates of the leaves of upper parts were greater than those of the lower parts for all species. As well as this, the initial slopes of the photosynthesis-light curves were steeper, and the gross photosynthetic rate was higher, for the leaves of upper parts compared to those of the lower parts for all five species.

The initial slopes of the photosynthesis-light curves of the leaves of lower parts of the five *Sargassum* species were magnified and replotted from Figures 1 and 2 in Figure 3 for clear comparisons. As shown, the initial slopes, which can represent the apparent efficiency of photosynthetic apparatus, showed values from the highest to the lowest: *Sargassum horneri*, *S. thunbergii*, *S. autumnale*, *S. serratifolium* and *S. patens* on both the dry weight and chlorophyll *a* bases. *Sargassum serratifolium* and *S. patens* from deeper habitats showed smaller values of dark respiration but greater light compensation points compared to the other three species from shallower habitats. The light compensation points are about  $30 \mu\text{E m}^{-2} \text{s}^{-1}$  for *S. serratifolium* and *S. patens*, about  $10 \mu\text{E m}^{-2}$

Table I. Chlorophyll contents of the leaves of lower and upper parts of *Sargassum* plants for five species. Each value represents the mean  $\pm$  standard deviation for 5 samples.

Species and leaf position	Chlorophyll a (mg g <sup>-1</sup> fresh weight)	Chlorophyll c	Chlorophyll c: Chlorophyll a
<i>S. thunbergii</i>			
Lower	0.902 $\pm$ 0.048	0.124 $\pm$ 0.009	0.137 $\pm$ 0.003
Upper	0.665 $\pm$ 0.009	0.074 $\pm$ 0.001	0.111 $\pm$ 0.001
<i>S. horneri</i>			
Lower	0.746 $\pm$ 0.095	0.123 $\pm$ 0.018	0.165 $\pm$ 0.006
Upper	0.199 $\pm$ 0.035	0.044 $\pm$ 0.004	0.223 $\pm$ 0.018
<i>S. autumnum</i>			
Lower	0.887 $\pm$ 0.054	0.135 $\pm$ 0.015	0.152 $\pm$ 0.002
Upper	0.290 $\pm$ 0.063	0.055 $\pm$ 0.006	0.190 $\pm$ 0.006
<i>S. serratifolium</i>			
Lower	0.870 $\pm$ 0.072	0.171 $\pm$ 0.017	0.197 $\pm$ 0.004
Upper	0.340 $\pm$ 0.096	0.090 $\pm$ 0.007	0.265 $\pm$ 0.011
<i>S. patens</i>			
Lower	0.568 $\pm$ 0.083	0.087 $\pm$ 0.020	0.153 $\pm$ 0.007
Upper	0.065 $\pm$ 0.016	0.012 $\pm$ 0.001	0.185 $\pm$ 0.005

s<sup>-1</sup> for *S. horneri* and *S. thunbergii*, and about 15  $\mu\text{E m}^{-2} \text{s}^{-1}$  for *S. autumnale*.

The leaves of lower parts of the *Sargassum* species from deeper habitats, near the bottom of the sea, get

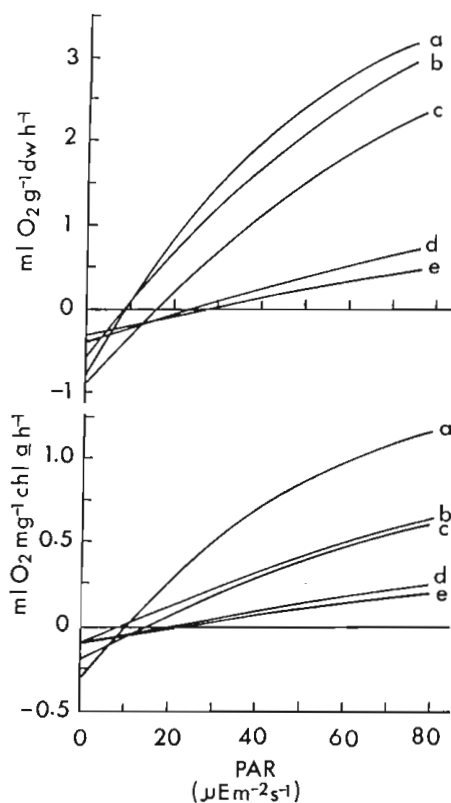


Fig. 3. Comparison of the magnified initial slopes of the photosynthesis-light curves of Figures 1 and 2 by the leaves of lower parts for the five species. a, b, c, d and e represent *Sargassum horneri*, *S. thunbergii*, *S. autumnale*, *S. serratifolium* and *S. patens*, respectively.

much reduced PAR compared to the upper parts near the sea surface. A relationship of relative PAR to depth in and out of *Sargassum serratifolium* community is illustrated in Figure 4. The PAR was decreased with depth to be less than 10% within the community and about 40% outside the community at the bottom of the sea compared to the PAR of the sea surface.

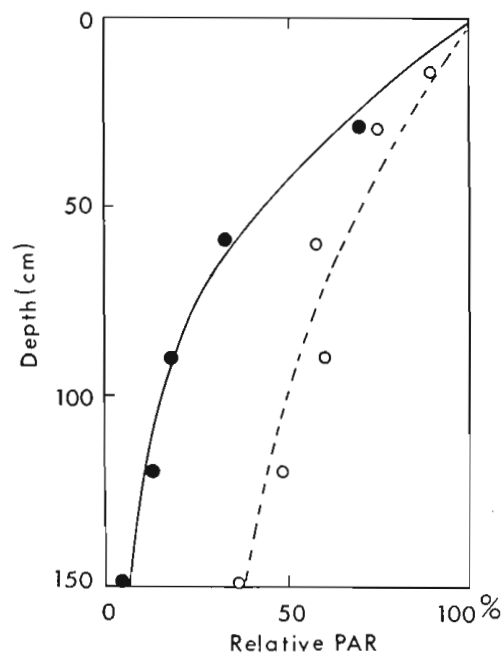


Fig. 4. Relationship between the relative solar radiation (PAR) and the depth, within the community (solid lines) and outside the community (broken line) of *Sargassum serratifolium*.



## Discussion

*Sargassum* plants are morphologically and histologically of relatively high structural complexity, in some regards implicating direct analogies to the equivalent features of the cormophytes. *Sargassum* plants grow from apical meristems, and the leaves of lower parts are older compared to the upper parts.

Several works have shown that the thallus differentiation of brown algal species can be described in terms of biochemical and physiological properties (Black 1954, Hellebust and Haug 1972, Schmitz and Lobban 1976, Küppers and Kremer 1978, Wheeler 1980). The data of the present study indicate the same conclusion.

The quantitative light adaptation of some marine algae has been reported to be the results of either a uniform change in the size of the photosynthetic unit (PSU) and/or changes in the number of photosynthetic units (Beale and Appleman 1971, Sheridan 1972, Prézelin 1976, Ramus *et al.* 1976 a, b, 1977, Mishkind and Mauzerall 1980, Wheeler 1980). If the photosynthetic unit number were changing, oxygen output should increase on a biomass basis, and should not change on a chlorophyll *a* basis, the amount of oxygen produced being proportional to the amount of chlorophyll *a* (Prézelin 1976). On the other hand, if the size of the unit was changing, oxygen output should not change on the biomass basis and the same output based on chlorophyll *a* should decrease (Prézelin 1976). The photosynthetic rates of the leaves of lower parts of the *Sargassum* species based on chlorophyll *a* decreased (Fig. 2), it therefore appears that the size of the photosynthetic unit is larger in the leaves of lower parts, that is, more chlorophyll *a* is needed to produce the same amount of oxygen, compared to the leaves of the upper parts. However, the difference of the photosynthetic rates based on dry weight between the leaves of the upper and lower parts (Fig. 1) appears at odds with the analysis of the PSU discussed above. The observed changes can not be explained by changes in the PSU alone. This is probably due to the lowered activity of RubP (ribulose-1,5-bisphosphate) carboxylase of the leaves of lower parts, as has been shown by Küppers and Kremer (1978) for three species of *Fucus*. The older parts of *Fucus serratus* L., *F. spiralis* L. and *F. vesiculosus* L. showed higher pigment concentrations, lowered activity of RubP carboxylase which resulted in lower photosynthetic rates, compared to the younger parts (Küppers and Kremer 1978).

The adaptation of the algal pigments to reduced light environments has been well documented. Ramus *et al.* (1977) has shown with both *Ascophyllum nodosum* (L.) Le Jol. and *Fucus vesiculosus* that chlorophylls *a* and *c* and fucoxanthin increased with depth or more shade. Wheeler (1980) reported that transplanted juvenile plants of *Macrocystis pyrifera* (L.) C. Ag. showed higher pigment concentrations in deeper habitats compared to shallower ones. Similar results have been obtained with other marine algae (Wassman and Ramus 1973, Ramus *et al.* 1976 a, b, Perez-Bermudez 1981). The leaves of the lower parts of the *Sargassum* species are exposed to much lower light conditions (Fig. 4), and showed much higher chlorophyll *a* and *c* concentrations, with the proportions of the lower to the upper parts higher in the species from deeper habitats (Table I). This indicates the effects of adaptations of the leaves of lower parts to the reduced light conditions. However, the chlorophyll *c* to *a* ratios of the *Sargassum* species differed significantly between the leaves of lower and upper parts (Table I). This disagrees with the results reported by Ramus *et al.* (1977) for *Ascophyllum nodosum* and *Fucus vesiculosus*, by Wheeler (1980) for *Macrocystis pyrifera* and by Perez-Bermudez (1981) for *Dictyota dichotoma* (Huds.) Lamour. For the comparison between the leaves of the lower and upper parts of the *Sargassum* species of the present study, the leaf age effects must be considered as well as the light adaptation. Küppers and Kremer (1978) showed that less pigments were contained in the younger regions of *Laminaria digitata* (Huds.) Lamour., *L. hyperborea* (Gunn.) Fosl. and *L. saccharina* (L.) Lamour., and *Fucus spiralis*, *F. vesiculosus* and *F. serratus*, compared to the older regions. Wheeler (1980) also showed that the meristem of *Macrocystis pyrifera* contained less pigments. This is similar to the data of the present study. Subsequently, the increased chlorophyll concentrations and decreased chlorophyll *c* to *a* ratios (except *S. thunbergii*) of the leaves of lower parts of the *Sargassum* species can be considered to be the results of light and age adaptations.

The photosynthetic and respiratory rates of the leaves of upper parts of *Sargassum horneri* showed much lower and higher values than those reported by Yokohama (1977). This may be due to the period of the measurements of the present study, during which the *S. horneri* matured and then decayed away.

The *Sargassum* species from deeper habitats showed lower dark respiration rates (Fig. 3) and lower saturation PAR (Figs. 1 and 2), compared to the other

species from the shallower habitats. This can be considered to be the result of species adaptation to reduced light environment, in order to maintain relatively high productivity with smaller quantities of light.

It is concluded that ontogenetic differentiations in photosynthetic unit or/and in the activities of enzymatic proteins resulted in the different photosynthetic performance between the leaves of upper and lower parts of *Sargassum* plants.

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