Photosynthetic Performances of Temperate Sargassum and Kelp Species Growing in the Same Habitat

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Characteristics of photosynthesis-light and photosynthesis-temperature relationships were seasonally compared among 4 species, two temperate Sargassum (S. ringgoldianum and S. spathulophyllum) and two temperate kelp (Ecklonia cava and Eisenia bicyclis), growing in the same habitat in Oura Bay, Shimoda, central Japan. The photosynthesis-irradiance (P-I) curve of each species at the in situ temperature and the photosynthesis-temperature (P-T) curve at near saturation irradiance (400 μmol·m⁻²·s⁻¹) were determined by using differential gas-volumeters. Maximum photosynthetic rates (Pmax) for P-I curves of the two Sargassum species were higher from summer to autumn than from winter to spring, while those of the two kelp species showed little difference among seasons. Net photosynthetic rates (Pn) at 100-400 μmol·m⁻²·s⁻¹ of the Sargassum species were higher than those of the kelp species in autumn, spring and summer, while in winter the rates were about the same between the Sargassum and kelp species. Among seasons, the light saturation index (Ik) values, dark respiration rates and light compensation points of Sargassum species differed more than those of kelp species. Optimum temperature for P-T curves of Sargassum species was 29°C and that of kelp species was 27°C in summer, while in winter the former was 27°C and the latter was 25°C. Pn at 400 μmol·m⁻²·s⁻¹ at 10-33°C of Sargassum species were considerably higher than those of kelp species from spring to summer, while from autumn to winter the rates at 5-27°C were about the same between the two. At supra-optimum temperatures, Pn of kelp species decreased more sharply than those of Sargassum species in each season. These facts indicate that the two temperate Sargassum species have a higher potential photosynthetic performance under warmer conditions than the two temperate kelp species even though they grow in the same habitat.

Key Words: Ecklonia cava, Eisenia bicyclis, Fucales, Laminariales, photosynthesis, Sargassum ringgoldianum, Sargassum spathulophyllum

INTRODUCTION

Sargassum species (Sargassaceae, Fucales) and kelp species (Alariaceae and Laminariaceae, Laminariales) are ecologically and economically important brown algae in some East Asian countries (Tokuda et al. 1987; Critchley and Ohno 1998). Fifty-eight species of Sargassum were reported in Japan (Yoshida et al. 2000), which are sometimes divided into “temperate Sargassum” and “tropical Sargassum” with respect to their distribution (Tanaka 1997). On the other hand, 36 species (12 genera) of kelp species are reported in Japan (Yoshida et al. 2000), many of which are known to be distributed in cooler waters around Hokkaido and the Tohoku district, northern Japan, but some of which are distributed in central to southern Japan and called “temperate kelp” (Kawashima 1993). In temperate waters both “temperate Sargassum” and “temperate kelp” are dominant seaweeds, often forming extensive seaweeds beds (e.g. Environmental Agency of Japan 1994) with a high productivity (Yoshida 1970; Yokohama et al. 1987; Murase et al. 2000).

Many studies have been conducted on the photosynthesis of “temperate Sargassum” (Yokohama 1973; Mizusawa et al. 1978; Gao and Umezaki 1988, 1989; Honda and Okuda 1989, 1990; Gao 1990) or “temperate kelp” (Maegawa et al. 1988; Sakanishi et al. 1988, 1989;
Aruga et al. 1990, 1997; Haroun et al. 1992; Kurashima et al. 1996; Serisawa et al. 2001a, b) in Japan. However, comparisons of photosynthesis-temperature relationships between “temperate Sargassum” and “temperate kelp” growing in the same habitat by using a unified method or technique have not been sufficient yet and only a few preliminary studies have been compared between the two (e.g. Yokohama 1973).

Photosynthetic rates of temperate Sargassum or temperate kelp have been reported to differ depending on their habitats (Mizusawa et al. 1978; Peckol and Ramus 1985; Serisawa et al. 2001b) and to change by season (Yokohama 1973; Honda and Okuda 1989, 1990; Sakanishi et al. 1989; Gao 1990; Serisawa et al. 2001a, b).

In the present study, we seasonally compared the characteristics of photosynthesis between temperate Sargassum (S. ringgoldianum Harvey and S. spathulophyllum J. Tanaka et Murakami) and temperate kelp (Ecklonia cava Kjellman and Eisenia bicylis (Kjellman) Setchell) growing in the same habitat at Shimoda, central Japan using a unified method (differential gas-volumeter). Furthermore, S. spathulophyllum has been recently described by Murakami et al. (1999) and its physiological information remains limited.

MATERIALS AND METHODS

Kelp beds at Shimoda, central Japan are mainly composed of Eisenia bicylis in the subtidal water from the low-watermark to 3-7 m depth and Ecklonia cava in deeper subtidal water down to 20-30 m depth (Iwahashi et al. 1979; Hayashida 1983; Serisawa et al. 2003). These two kelp species are perennial palm-like Lamnariaceae algae, having many dark brown, flat and coriaceous bladelets. These two species were chosen as typical “temperate kelp”. However, it was difficult to choose the representative of “temperate Sargassum”, because in Oura Bay more than twenty species of Sargassum grow in intertidal to subtidal zone, that mature in different seasons and have different longevities. Furthermore, the leaves of Sargassum species vary in color, shape and thickness among species (Yoshida 1983). Taking into account these points, we selected two perennial “temperate Sargassum”, S. ringgoldianum and S. spathulophyllum, and sampled them from the same habitat as Ec. cava and Ei. bicylis. These two Sargassum species mature in summer and have many dark brown, flat and coriaceous leaves (Yoshida 1983; Murakami et al. 1999), which is similar to the two kelp species.

Eight individuals of Ec. cava, Ei. bicylis, S. ringgoldianum and S. spathulophyllum were collected by diving at Shidagaura (34°40’N 138°57’E) in Oura Bay, Shimoda, central Japan (Fig. 1). They were collected at 1 m depth (Ei. bicylis and S. spathulophyllum) and at 5 m depth (Ec. cava and S. ringgoldianum) and brought to the Shimoda Marine Research Center, University of Tsukuba within 20 minutes after collection. Samplings were carried out in the middle of November 1995 (autumn), in the middle of February (winter), in the beginning of May (spring) and in the end of July 1996 (summer).

Plant lengths of Ec. cava and Ei. bicylis used in the present experiment were 70-90 cm. Discs of 3.5 cm² were cut out from the bladelets located at third to fifth position from the base of a primary blade of Ec. cava or arm-like branch of Ei. bicylis by using a cork borer (Sakanishi et al. 1988). As photosynthetic activities of bladelets with zoosporangial sori are considerably lower (Aruga et al. 1990), the central parts of bladelets without zoosporangial sori were chosen. The sampled pieces of bladelets were kept in running seawater in the laboratory overnight before the measurement of photosynthesis to reduce unreliable results due to cutting (Sakanishi et al. 1988).

Thallus length of S. ringgoldianum and S. spathulophyllum used in this experiment were about 20 cm and 10 cm in autumn, 30 cm and 15 cm in winter, 40 cm and 20 cm in spring, and 80 cm and 50 cm in summer, respectively. In some Sargassum species, photosynthetic activities of the leaves have been reported to differ among their locations (Gao and Umezaki 1988). The leaves located on the middle or lower parts of thalli in both S. ringgoldianum and S. spathulophyllum were chosen and 3-5 cm² squares or discs were cut out from the central part of the leaves. The sampled pieces of leaves were also kept in running seawater in the laboratory until the measurement of photosynthesis. Each piece of the leaf was digitally scanned after measurement of photosynthesis and the surface area calculated by using the public domain NIH Image program (developed at the U.S. National Institutes of Health and available from the Internet).

For measurements of photosynthesis and dark respiration of the pieces of bladelets or leaves, 8 sets of differential gas-volumeter, “Productmeter” (Nikkou-Kagaku, Tokyo, Japan) were used (Yokohama and Ichimura 1969; Yokohama et al. 1986). Vessels used for
photosynthesis measurement were flasks of 35 mL in capacity. One piece of bladelet or leaf was placed in a reaction vessel with 10 mL of filtered seawater while into a compensation vessel was poured 10 mL of filtered seawater only. The reaction and compensation vessels were attached to a Productmeter, and immersed in a water bath (30 x 70 x 30 cm), which were controlled at a constant water temperature by a thermostat (Taitec CL-150F, Koshigaya, Japan), being shaken by means of a motor drive. The reaction vessels were illuminated from below by projector lamps reflected with mirrors placed under the water bath. As the light source, photo slide projectors (Elmo S-300, Nagoya, Japan) with incandescent lamps (Philips KP-10s 100 V, 300 W, Tokyo, Japan) were used. Irradiances (400, 200, 100, 50, 25 μmol·m⁻²·s⁻¹) were regulated using neutral density glass filters (Toshiba TND-50, 25, 12.5, Tokyo, Japan) and measured with a quantum photon meter and underwater sensor (LI-COR LI-192S & UWQ 2805, Nebraska, USA).

Each measurement of oxygen evolution or consumption was begun after 10-30 minutes for temperature equilibration, and continued for 20-40 minutes. In order to prevent the lowering of photosynthetic activity at the first measurement, reaction vessels with samples were put into a water bath and were shaken for 45 minutes at a high irradiance (400 μmol·m⁻²·s⁻¹).

Photosynthesis-irradiance (P-I) curves were determined at gradually decreasing irradiance (400, 200, 100, 50, 25 μmol·m⁻²·s⁻¹ and dark) at approximately the same as the in situ water temperature when the samples were collected; at 17°C in autumn, at 12°C in winter, at 17°C in spring, and at 23°C in summer. The measurements were conducted from 8:00 to 12:00 during 4 days in each season. Photosynthesis-temperature (P-T) curves were determined at progressively increasing temperature (5, 10, 15, 20, 25, 27, 29, 31 and 33°C) at near saturation irradiance (400 μmol·m⁻²·s⁻¹). The measurements were conducted from 13:00 to 21:00 during 4 days in each season.

Net photosynthetic rate (Pn) and dark respiration rate (Rd) were determined for each irradiance and temperature per unit area. Parameters of P-I curves were Pmax (the maximum Pn), Rd, IS (the initial slope, the slope of the straight line connected with Rd and Pn at 25 μmol·m⁻²·s⁻¹), Ic (the light compensation point, the irradiance at which the straight line connected with Rd and Pn at 25 μmol·m⁻²·s⁻¹ and x axis intersect), Ik (the light-saturation index, the irradiance at which extrapolation of the straight line connected with Rd and Pn at 25 μmol·m⁻²·s⁻¹ and the light-saturated rate of the P-I curve intersect). These values were statistically compared among the 4 species in each season and
among seasons in each species by ANOVA and Fisher's post-hoc test.

RESULTS

Light saturation on P-I curves occurred at slightly over 400 \( \mu \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \) in autumn and at 200-400 \( \mu \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \) in other seasons in \textit{S. ringgoldianum}, at 200-400 \( \mu \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \) in spring and at slightly over 400 \( \mu \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \) in other seasons in \textit{S. spatulophyllum} and at 200-400 \( \mu \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \) in each season in \textit{E. cava} and \textit{E. bicyclis} (Fig. 2). The net photosynthetic rates \( (P_n) \) at 100-400 \( \mu \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \) of the two \textit{Sargassum} species were mostly higher than those of the two kelp species in autumn, spring and summer \( (p < 0.05, \text{not significant in autumn at } 100 \mu \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}) \), while in winter at 0-400 \( \mu \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \) the rates were about the same among the 4 species.

The \( P_{max} \) values of two \textit{Sargassum} species were higher in autumn and summer \( (\text{highest in summer } 50-52 \mu \text{L} \ O_2 \ \text{cm}^{-2} \cdot \text{h}^{-1} \ \text{in both species}) \) and lower from winter to spring \( (\text{lowest in winter } 31-36 \mu \text{L} \ O_2 \ \text{cm}^{-2} \cdot \text{h}^{-1} \ \text{in both species}) \) \( (p < 0.05) \) (Fig. 3). The \( P_{max} \) values of two kelp species showed no significant differences among seasons \( (24-30 \mu \text{L} \ O_2 \ \text{cm}^{-2} \cdot \text{h}^{-1} \) \( p > 0.05 \)). The \( P_{max} \) values were higher in \textit{Sargassum} species than in kelp species in each season \( (p < 0.05) \). The \( R_d \) and \( I_c \) values of \textit{Sargassum} species were different among seasons \( (p < 0.05) \), ranging \( 6.3-10.3 \mu \text{L} \ O_2 \ \text{cm}^{-2} \cdot \text{h}^{-1} \) and 11-16 \( \mu \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \) in \textit{S. ringgoldianum} and 2.6-7.6 \( \mu \text{L} \ O_2 \ \text{cm}^{-2} \cdot \text{h}^{-1} \) and 6-10 \( \mu \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \) in \textit{S. spatulophyllum}. Conversely, the \( R_d \) and \( I_c \) values of two kelp species showed no significant differences among seasons \( (5.8-6.8 \mu \text{L} \ O_2 \ \text{cm}^{-2} \cdot \text{h}^{-1} \) and 11-12 \( \mu \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \) in both species) \( (p > 0.05) \). The \( I_k \) values of \textit{Sargassum} and kelp species differed significantly among seasons \( (p < 0.05) \), although the differences of kelp species were smaller than those of \textit{Sargassum} species. The \( I_k \) values of \textit{Sargassum} species were 44-84 \( \mu \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \), larger than those of kelp species \( (29-45 \mu \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}) \) each season \( (p < 0.05) \). The \( I_S \) values of \textit{Sargassum} and kelp species were 0.40-0.83 and 0.47-0.63, respectively and also differed significantly among seasons \( (p < 0.05) \). The differences of \( I_S \) values of kelp species were smaller than those of \textit{Sargassum} species.

The \( P_n \) gradually increased with increased temperature up to the optimum temperature and decreased with increased temperature in supra-optimum temperatures in each species in each season (Fig. 4). The

![Fig. 2. Photosynthesis-irradiance curves of \textit{Sargassum ringgoldianum} (solid triangles), \textit{Sargassum spatulophyllum} (solid squares), \textit{Ecklonia cava} (open triangles) and \textit{Eisenia bicyclis} (open squares). Data are expressed as the mean ± SD \((n=8)\).](image-url)
temperatures of kelp species decreased more sharply than those of Sargassum species in each season. The \( Pn \) at 33°C of kelp species were considerably lower irrespective of the seasons, while those of Sargassum species kept higher activity. The \( Pn \) of Sargassum species at higher temperature range of 25°C and over were larger in summer than in winter (\( p < 0.05 \), not significant in S. spathulophyllum at 25 and 27°C) (Fig. 5). On the other hand, \( Pn \) of kelp species at 5-29°C were larger in winter than in summer (\( p < 0.05 \), not significant in E. cava at 29°C). The shift of optimum temperature for photosynthesis was 2°C from winter to summer in each species. The \( Pn \) at supra-optimum temperatures of the kelp species decreased sharper in winter than in summer.

**DISCUSSION**

Measuring the photosynthetic rate at the *in situ* water temperature provides basic information about the physiological activity of the seaweed under conditions similar to the field. The two Sargassum species (S. ringgoldianum and S. spathulophyllum) showed distinct seasonal variations in P-I curves at the *in situ* temperatures (Fig. 2), with the change of \( P_{\text{max}}, R_d, I_c, I_k \) and \( I_S \) (Fig. 3). The same trend was reported in some temperate Sargassum species (S. horneri and S. micrancanthum) (Honda and Okuda 1989, 1990) and tropical Sargassum species (S. pteropleuron) (Prince 1980). Kilar et al. (1989) studied the relationships between the growth phase and photosynthesis of *S. polyceratium* (tropical Sargassum) growing in Florida and found that light-saturated photosynthetic rate was highest in autumn (active growth phase), lowest in summer (stasis phase) and medium in spring (senescence phase) and in winter (reproductive phase). Conversely, \( P_{\text{max}} \) values of temperate Sargassum species (S. horneri and S. micrancanthum) were higher in summer and autumn than in spring (Honda and Okuda 1989, 1990) irrespective of their ecotype of spring-mature-type or autumn-mature-type. Seasonal growth phase of *S. ringgoldianum* and *S. spathulophyllum* studied in the present experiment, has

*Fig. 3.* Seasonal variations of the parameters of the photosynthesis-irradiance (P-I) curves; \( P_{\text{max}} \) (maximum photosynthetic rate; A), \( R_d \) (dark respiration rate; B), \( I_c \) (light compensation point; C), \( I_k \) (light-saturation index; D) and \( I_S \) (initial slope; E) for Sargassum ringgoldianum (solid triangles), Sargassum spathulophyllum (solid squares), *Ecklonia cava* (open triangles) and *Eisenia bicyclis* (open squares). Data are expressed as the mean ± SD (n = 8).
been reported in detail; adult plants begin to grow rapidly in spring, attain a maximum length and weight from late spring to early summer, mainly mature in summer, gradually the old branches and leaves fall off prior to the production of new branches and leaves from before winter (Yoshida 1983; Terawaki and Goto 1986; Murakami et al. 1999). Pmax values of the two Sargassum species were lowest in winter during the stasis growth phase, low in spring during the active growth phase and high in summer (during reproduction phase) and in autumn (new branch and leaf producing phase) (Fig. 3). Therefore, the higher photosynthetic performance in summer and autumn irrespective of the maturation period is possibly a characteristic of temperate Sargassum species.

In contrast to the Sargassum species, the two kelp species treated in the present study showed little seasonal variation in P-I curves at the in situ temperatures (Fig. 2), with little change of Pmax, Rd, Ic, Ik and IS (Fig. 3). This trend agrees with the Sakainishi et al. (1989) for Ec. cava. These kelp species mature from summer to autumn (Maegawa 1990; Taniguchi et al. 1991; Aruga et al. 1997; Serisawa et al. 2001c) and the growth rate of the stipe is highest in winter (Serisawa et al. 2002), the productivity of bladelets is higher from winter to spring (Yoshida 1970; Yokohama et al. 1987) and the

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**Fig. 4.** Photosynthesis-temperature curves of *Sargassum ringgoldianum* (solid triangles), *Sargassum spatulophyllum* (solid squares), *Ecklonia cava* (open triangles) and *Eisenia bicyclus* (open squares). Data are expressed as the mean ± SD (n = 8).
standing crop is highest in summer (Yoshida 1970; Yokohama et al. 1987; Serisawa et al. 2001c). Therefore, it can be said that the photosynthetic performance at in situ temperatures of the two kelp species are stable irrespective of the seasonal growth phase and the seasonal changes of environmental factors.

Davison (1987) reported that the $P_n$ for P-T curve of Laminaria saccharina at sub-optimum temperatures were larger in sporophytes incubated at low temperatures. In the present study, the $P_n$ for P-T curve of the kelp species at sub-optimum temperatures were apparently larger in winter than in summer (Fig. 5), a trend which has also been presented in previous reports (Hata and Yokohama 1976; Sakanishi et al. 1989; Serisawa et al. 2001b). These results might indicate that the photosynthetic performance of kelp species at sub-optimum temperatures is affected by the in situ water temperature or incubated temperature at a certain period. On the other hand, $P_n$ of the two Sargassum species at sub-optimum temperatures were about the same or slightly larger in summer than in winter (Fig. 5), which indicates that the photosynthetic performance of the two Sargassum species at sub-optimum temperatures is mostly not affected by in situ water temperatures.

The $P_n$ at around the optimum temperature for P-T curve of the two Sargassum species increased in summer (Figs 4, 5), a trend recognized not only in some other Sargassum species (Yokohama 1973; Hata and Yokohama
1976; Gao and Umezaki 1989) but also in some other Fucales species in cooler waters; *Ascophyllum nodosum* (Chock and Mathieson 1979) and *Pelvetia wrightii* (Saitoh et al. 1986). In contrast, *Pn* at around the optimum temperature for P-T curve of the two kelp species increased in winter (Figs 4, 5), a trend which was also presented in previous reports of *E. cava* and *Ei. bicyclis* (Sakanishi et al. 1989; Serisawa et al. 2001b) and of some other kelp species (Hata and Yokohama 1976; Saitoh et al. 1986). These facts indicate that some *Sargassum* and some other Fucales species have a greater *Pn* in warmer environmental conditions, while some kelp species show higher *Pn* in cooler environmental conditions.

In the present study, the two kelp species showed a considerable decrease of *Pn* at 30°C and over, irrespective of the seasons (Fig. 4), a trend which was presented in some other kelp species (Yokohama 1973; Niihara 1975; Hata and Yokohama 1976; Fain and Murray 1982; Saitoh et al. 1986; Davison 1987). On the other hand, some *Sargassum* species and some other fucoide species were reported to maintain higher *Pn* at 30°C and over (Healey 1972; Yokohama 1973; Brinkhuis et al. 1976; Hata and Yokohama 1976; Niemeck and Mathieson 1978; Chock and Mathieson 1979; Saitoh et al. 1986; Gao and Umezaki 1989; Gao 1990), which agree with the present results. Therefore, it can be said that Fucales species have higher photosynthetic performance at 30°C and over than kelp species.

Yokohama (1981) compared P-T curves among *Fucus* sp. (Arctic fucoide), *S. fusiforme* (temperate *Sargassum*), *S. ringgoldianum* (temperate *Sargassum*) and Undaria *pinnatifida* (temperate kelp) and suggested that fucoide species have a higher optimum temperature for photosynthesis than kelp species even they grow under colder habitat conditions. Yokohama (1973) also showed that *S. fusiforme* had a higher photosynthetic performance than *U. pinnatifida* at higher temperatures even though they grow in the same habitat. Saito et al. (1986) also found a similar trend between *Pelvetia wrightii* (cool temperate fucoide) and *Laminaria religiosa* (cool temperate kelp) growing in same habitat. In the present study, in spite of they grow under same habitat, photosynthetic performance under warmer condition was actually higher in the two temperate *Sargassum* than in the two temperate kelp species, as mentioned above. Generally, the origin of fucoide species (Fucales) is considered to be the warmer region of the Southern Hemisphere, while that of kelp species (Laminariales) is regarded as the colder region of the Northern Hemisphere (Clayton 1984; Lüning 1990). The differences of photosynthesis-temperature relationships between the two taxa growing under the same habitat conditions are probably related to the respective environmental conditions experienced during their respective evolutionary development.

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