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Seasonal changes in photosynthetic capacity of *Laminaria longissima* MIYABE (Phaeophyta)*

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Photosynthesis and dark respiration of blade discs of *Laminaria longissima* were measured once a month for a year. Light-saturation of photosynthesis at *in situ* temperature occurred at 200–400 $\mu E\ m^{-2}\ s^{-1}$. No photoinhibition of photosynthesis was observed within the light intensity range investigated (max. 1000 $\mu E\ m^{-2}\ s^{-1}$). The light-saturated net photosynthetic rate at *in situ* temperature reached its maximum in September and its minimum in December. The respiratory rate at *in situ* temperature was low from winter to spring. The light-saturated net photosynthetic rate at a constant temperature (10°C) was higher in the colder season and reached its maximum in January.

Key Index Words: blade discs—Laminaria longissima—*Phaeophyta—photosynthesis—respiration—seasonal change.*

Laminaria longissima MIYABE is one of the most important seaweeds in Japan from both the ecological and economic points of view. It is the largest species of *Laminaria* in Japan, with blades usually reaching 8 m long or more (TOKIDA *et al.* 1980), and sometimes 20 m. This species forms kelp beds in depths from the low water mark to the subtidal zone and plays an important role as a primary producer in rocky shore ecosystems of the eastern Pacific coast of Hokkaido. Plants of this species have been used as human food like some other members of the genus *Laminaria* and closely related genera, which are called *kombu* in Japan (KAWASHIMA 1984).

Ecophysiological studies concerning photosynthesis and productivity have been intensively made on two species of Laminariales, *Ecklonia cava* and *Eisenia bicyclis*, that form marine forests in central Japan (YOSHIDA 1970, YOKOHAMA 1977, TANAKA *et al.* 1983, YOKOHAMA *et al.* 1987, MAEGAWA and KIDA 1987, MAEGAWA *et al.* 1987, 1988, SAKANISHI *et al.* 1988, 1989). However, only a few studies have been made on photosynthesis of *Laminaria* species growing in the northern part of Japan (NIIHARA 1975, MATSUYAMA 1985). No ecophysiological study concerning photosynthesis has been made on *L. longissima*. The present study was carried out to clarify the photosynthesis-light relationship and seasonal changes in photosynthetic activity which influence the seasonal growth of *L. longissima* plants.

Material and Methods

Photosynthesis and respiration of *Laminaria longissima* were measured monthly from September 1987 to August 1988 with plants growing in the upper subtidal zone at Katsurakoi, Kushiro, Hokkaido (Fig. 1). It

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is estimated from the stage of development of the zoosporangial sori on the blade (cf. SASAKI 1969, 1973, KAWASHIMA 1983) that most of the samples collected from September 1987 to January 1988 were plants younger than one year old, and those from February to August 1988 were at least one year old.

Collected sample plants were brought to the Hokkaido Regional Fisheries Research Laboratory and kept in an indoor tank supplied with running seawater before use. Discs of 3.1 cm^2 were cut out of the peripheral portion in the middle part of each plant, and they were kept in running seawater overnight (for ca. 12 hr) in the laboratory before measuring photosynthesis or respiration in order to avoid unreliable results associated with the trauma of cutting (SAKANISHI *et al.* 1988). Approximately half of the discs obtained had zoosporangial sori from September 1987 to January 1988 while from February to August 1988 all the discs lacked the sori, since the middle part of a plant was occupied by the old blade with the sori in the former period while the new blade formed beneath the old blade occupied the middle part in the latter period.

Measurements of photosynthesis and respiration were carried out with blade discs by the light-and-dark bottle method. A blade disc was incubated in a D.O. bottle of about 100 m*l* for 30 min in photosynthesis measurement, and for 45 min in respiration measurement. The bottles were shaken at 120 rpm during incubation since YOKOHAMA and ICHIMURA (1969) reported that shaking markedly increased the photosynthetic rate of discs of *Padina arborescens* in bottoles. The oxygen concentration in seawater was determined by the Winkler titration method before and after the incubation. For determining the photosynthesis-light relationship, photosynthesis was measured at *in situ* temperatures (monthly averaged water temperatures) under various photon flux densities. Photosynthesis and respiration measurements were also carried out under constant temperature and light conditions of 10°C and 400 $\mu E\,m^{-2}\,s^{-1}$ or in darkness. Photoreflector lamps (National 100 V 500 W) were used for photosynthesis measurements. Photon flux densities were measured with a quantum meter (LI-COR LI-1000/LI-192S).

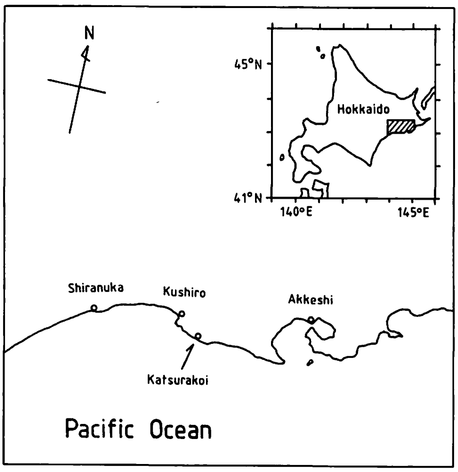

Fig. 1. The site of this study.

Results

Photosynthesis-light curves of *Laminaria longissima* plants on a frond area basis at *in situ* temperatures are presented in Fig. 2. The light-saturation of photosynthesis occurred at 200–400 $\mu E\,m^{-2}\,s^{-1}$. The saturating light level was low from spring to early summer. The photosynthetic rate completely saturated within the light levels investigated except for in December and April. The compensation light levels ranged from 1 to 8 $\mu E\,m^{-2}\,s^{-1}$, being high from autumn to early winter and low from late winter to spring, with some exceptions.

Figure 3 shows the seasonal changes of the light-saturated net photosynthetic and respiratory rates at *in situ* water temperatures. The photosynthetic rate reached a maximum of 55 $\mu l\,O_2\,cm^{-2}\,h^{-1}$ in September, thereafter declined, and reached a minimum of 31 $\mu l\,O_2\,cm^{-2}\,h^{-1}$ in December and January. The net photosynthetic rate then increased gradually toward August. The respiratory rate at *in situ* temperature ranged from 1 to 6 $\mu l\,O_2\,cm^{-2}\,h^{-1}$, being generally high in summer and low in winter.

In Fig. 3, almost parallel trends can be seen between the changes in light-saturated net photosynthetic rate and the *in situ* temperature except during the colder season. The net photosynthetic rate at *in situ* temperature decreased with temperature from September to December, but it increased from December

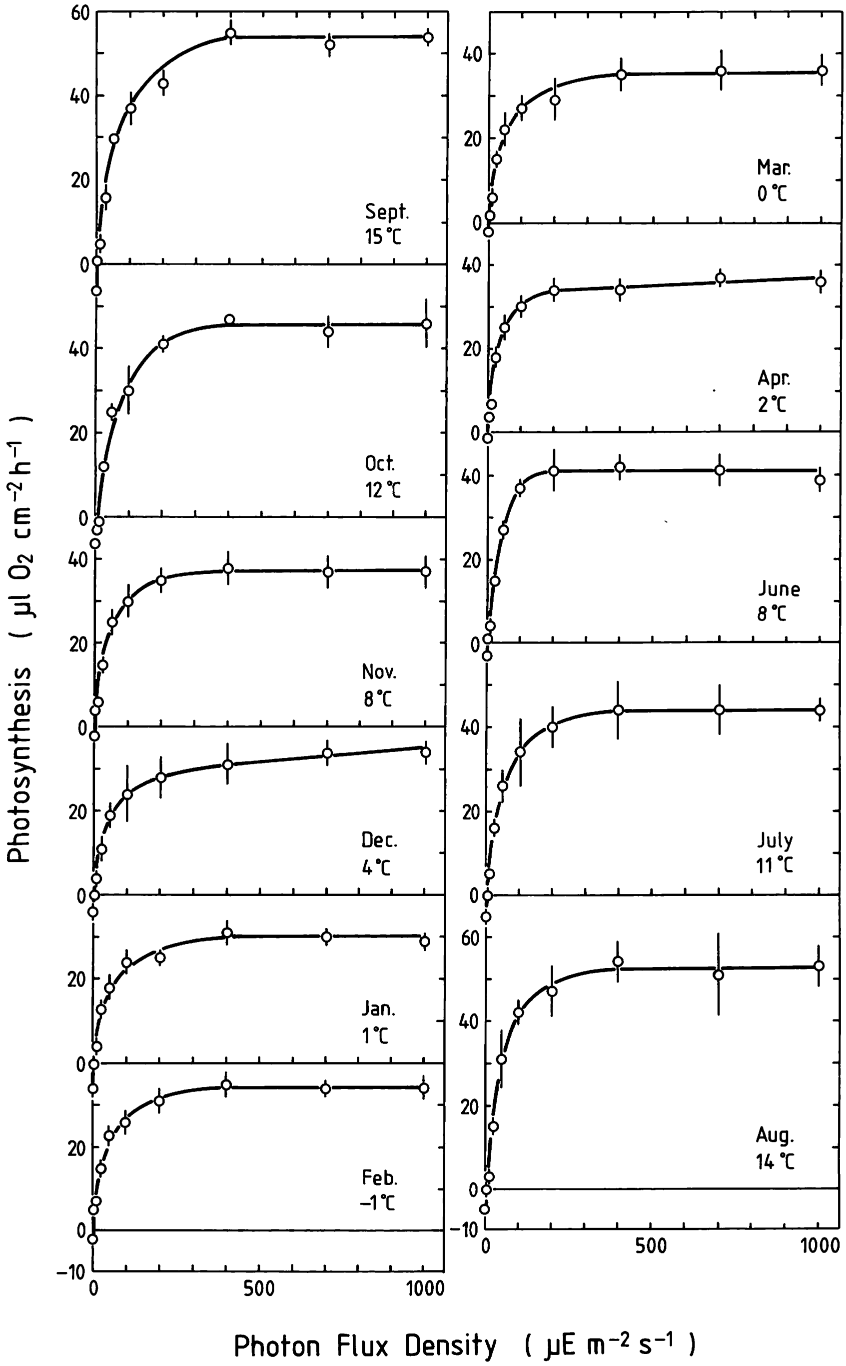

Fig. 2. *Laminaria longissima*. Photosynthesis-light curves at *in situ* water temperatures from September 1987 to August 1988. Mean ± SD for 5–6 replicates.

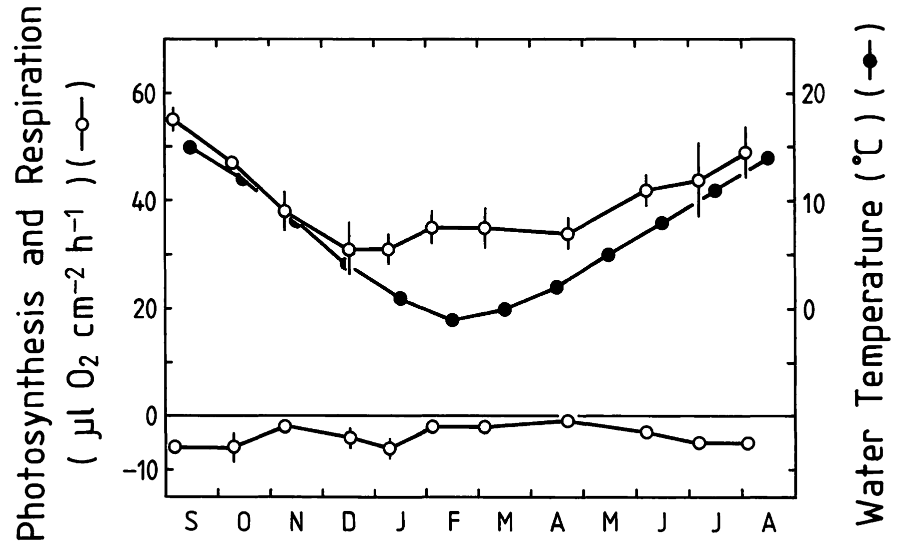

Fig. 3. *Laminaria longissima*. Seasonal changes in the light-saturated net photosynthetic and the respiratory rates (open circles) deduced from the photosynthesis-light curves in Fig. 2 and *in situ* water temperature (solid circle).

to February in spite of a continued temperature decline, while it did not increase from February to April in spite of a temperature increase. From April to August it increased with temperature.

Seasonal changes of the light-saturated net photosynthetic and the respiratory rates under constant conditions (10°C) are presented in Fig. 4. The photosynthetic rate was low in September–November, increased in December and reached a maximum of 61 $\mu l\,O_2\,cm^{-2}\,h^{-1}$ in January. It declined in spring to reach a lower level in summer. A minimum of 30 $\mu l\,O_2\,cm^{-2}\,h^{-1}$ was obtained

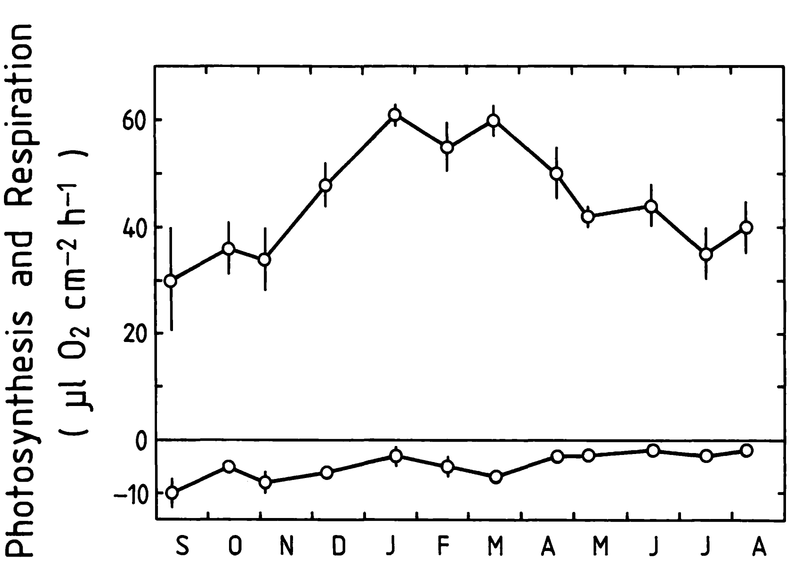

Fig. 4. *Laminaria longissima*. Seasonal changes in the light-saturated net photosynthetic and the respiratory rates at 10°C. Mean±SD for 3 replicates.

in September. The respiratory rate varied from 2 to 10 $\mu l\ O_2\ cm^{-2}\ h^{-1}$, being generally higher from September to March and lower from April to August.

Discussion

The saturating light level for photosynthesis in *Laminaria longissima* varies from 200 to 400 $\mu E\ m^{-2}\ s^{-1}$, and is comparable to that given for other Laminariales plants by King and Schramm (1976), Willenbrink *et al.* (1979), Lüning (1981), Gerard (1986), Maegawa *et al.* (1987) and Sakanishi *et al.* (1988, 1989). The seasonal change in the saturating light level for photosynthesis in *L. longissima* seems not to be attributable to the sun and shade adaptation as observed in natural phytoplankton (Aruga 1965) and macroalgae (King and Schramm 1976). Although the sun adaptation generally involves a higher saturation light level for photosynthesis and a lower initial slope (Boardman 1977), *L. longissima* does not show a higher saturation light level and a lower initial slope in spring and early summer when it may often be exposed to high photon flux density and sun adaptation can occur. The lower saturating light level for photosynthesis may be attributable to the fact that the blades of this species are thin in spring and early summer. The blade weight/area ratio as an index of thickness is low from April to July in this species. Lüning (1979) pointed out that in *Laminaria* spp. with thick thalli the photosynthetic rate gradually approached saturation with increasing light level due to the gradual increase in light penetrating through to the photosynthetic layer of the shade side of a thallus under unilateral illumination.

Photosynthesis-light curves at -1 and 0°C, which have scarcely been reported for seaweeds, were obtained in February and March in the present study (Fig. 2). Those curves were characterized by high P : R ratio and low compensation light level. These characteristics of *L. longissima* in winter could be advantageous for organic matter production.

Seasonal changes in the net photosynthetic rate of *L. longissima* at *in situ* temperatures (Fig. 3) suggest that photosynthetic capacity reaches a maximum in mid-winter. The seasonal changes at a constant temperature of 10°C (Fig. 4) show that photosynthetic activity is much higher in mid-winter than in other seasons. These results clearly indicate that the photosynthetic capacity of *L. longissima* reaches its maximum in mid-winter, which accounts for the observed increase in net photosynthetic rate with decreasing temperature from December to February (Fig. 3).

The seasonal changes in net photosynthetic rate of *L. longissima* at a constant temperature (10°C) in the present study are almost like those of *Ecklonia cava* at 20°C reported by Sakanishi *et al.* (1989). Although the photosynthetic capacity was high in winter when the blade tissue was younger and low in summer when the blade tissue was older in *E. cava*, seasonal changes in photosynthetic capacity of *L. longissima* cannot be attributed to aging in blade tissue, since the blade tissue used in January, showing the highest photosynthetic capacity, was not younger than the blade tissues used at other times of the year. In *L. longissima*, photosynthetic capacity seems to be affected by seasonal changes in physiological state rather than aging of blade tissue (Sakanishi *et al.* in preparation).

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坂西芳彦*・横浜康継**・有賀祐勝***：褐藻ナガコンブの光合成活性の季節変化

北海道釧路市桂恋地先の漸深帯上部に生育する褐藻ナガコンブを用いて，1年にわたり種々の温度・光条件で光合成を測定し，光合成-光特性と光合成活性の季節変化を明らかにした。現場水温における光合成は 200–400 μE m^{-2} s^{-1} で光飽和に達し，また 1000 μE m^{-2} s^{-1} までの範囲では強光阻害は認められなかった。現場水温における光飽和純光合成速度は，秋季に低下し，初冬に極小となり，その後厳冬期に緩やかなピークを示しながら夏季にかけて徐々に増大した。厳冬期に見られた緩やかなピークは，この時期に光合成能力が高まっていることを示している。（*085 北海道釧路市桂恋116 水産庁北海道区水産研究所，**415 静岡県下田市5-10-1 筑波大学下田臨海実験センター，***108 東京都港区港南4-5-7 東京水産大学藻類学研究室）