

Seasonal variation of photosynthetic properties of *Ecklonia cava* (Laminariales, Phaeophyta) in Nabeta Bay, central Japan*

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Abstract: The research was carried out to quantify the photosynthetic rates of a perennial seaweed *Ecklonia cava* KJELLMAN (Laminariales, Phaeophyta) with monthly samplings from April 1986 to April 1987. Photosynthesis and respiration were measured by a differential gas-volumeter in several bladelets. The photosynthesis-light curves were different among bladelets almost every month; however, in winter, when all the bladelets were new, the curves were quite similar. On a frond area basis, the youngest bladelets showed higher net photosynthesis than the older ones, with highest P_{max} values ($44-49 \mu\text{IO}_2 \cdot \text{cm}^{-2} \cdot \text{h}^{-1}$) in early spring and lowest ($19-31 \mu\text{IO}_2 \cdot \text{cm}^{-2} \cdot \text{h}^{-1}$) in autumn, the reproductive period. On a dry weight basis, the P_{max} values showed a hierarchical order inversely related to the thickness of the bladelets, with a maximum in the 2nd bladelet and a minimum in the 11th. On a chlorophyll *a* basis, the hierarchical order was similar to that on a dry weight basis, but P_{max} did not show any big seasonal variation. The respiration rate of each bladelet was quite stable throughout the year, except for the 2nd bladelet with two high peaks in November and February, the formation periods of autumn and winter bladelets respectively. The photosynthetic response of *E. cava* blade is closely related to its growth process. The blade of this species apparently adjusts its pigment content to the prevailing light conditions in the surrounding water.

Introduction

As in terrestrial plants, light is the most important factor affecting the biology of seaweeds. Besides its primary importance in the photosynthesis, light is a signal for numerous photomorphogenetic responses such as reproduction, growth and distribution (LÜNING, 1980, 1981; NOVACZEK, 1984; LOBBAN *et al.*, 1985; MAEGAWA *et al.*, 1987). The photosynthetic rates of large seaweeds have scarcely been studied due to the difficulties encountered in handling these algae (DREW, 1973; JASBBY,

1978; KREMER, 1978; LITTLER and LITTLER, 1985). YOKOHAMA and ICHIMURA, (1969) devised a differential gas-volumeter for measuring O_2 consumption or evolution by aquatic organisms, and several papers have been published dealing with the photosynthetic characteristics of various seaweeds (YOKOHAMA, 1971, 1973a, b; MIZUSAWA *et al.*, 1978; OOHUSA, 1980; KATAYAMA *et al.*, 1985; MAEGAWA *et al.*, 1987). This manometric method has been improved allowing easier measurements for macrophytes or small marine animals (YOKOHAMA *et al.*, 1986; YOKOHAMA and MAEGAWA, 1988).

The sporophytes of *Ecklonia cava* KJELLMAN are widely distributed on rocky shores along the Pacific coast of central Japan. In previous papers (ARUGA, 1981; YOKOHAMA *et al.*, 1987) it was reported that the standing crop of *E. cava* communities attains a maximum in summer and a minimum in winter; this is mainly related to the seasonal variation of the blade growth process (HAROUN *et al.*, 1989). Recently, SAKANISHI *et al.* (1988) developed a suitable treatment of

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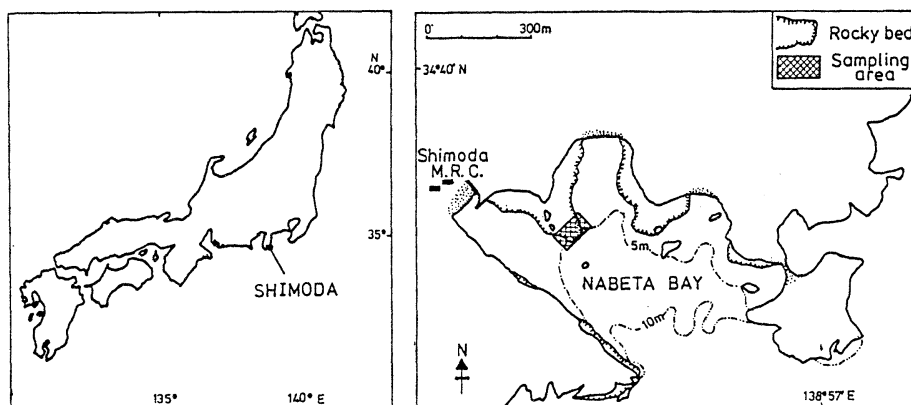


Fig. 1. Maps showing the sampling area in Nabeta Bay, Shimoda, central Japan.

tissue segments from the thalli of *Ecklonia* and *Eisenia* to measure the photosynthesis of these Laminariales species by the above-mentioned oxygen technique.

The present investigation was done to measure the photosynthetic rates of the pinnate blade of *Ecklonia cava* during one-year period. Another objective in the study was to investigate the relationship between physiological activity and the phenology of the blade. Finally, we try to relate the annual pattern of photosynthetic response to some possible environmental factors.

Material and methods

Morphologically, the *E. cava* sporophyte can be divided into three parts: a holdfast, a long stipe (more than 50 cm long in adult plants) and a pinnate blade composed of lateral bladelets (HAYASHIDA, 1977; MAEGAWA and KIDA, 1984). As in other species of Laminariales, primary growth is concentrated in the transitional zone between stipe and blade. When growth is initiated, the primary blade moves upward, developing several bladelets in both sides (usually with lateral protuberances); while the sporophyte erodes from the distal ends of both primary blade and bladelets.

The research was carried out at Shimoda Marine Research Center (S.M.R.C.), University of Tsukuba, close to Nabeta Bay, Shimoda (Izu Peninsula), with monthly samplings from April 1986 to April 1987. Every month 4 adult plants were randomly sampled from a homogeneous population of *E. cava* at 5 m depth (Fig. 1). All

the plants were quickly transferred to S.M.R.C. and were kept in outdoor tanks supplied with flowing seawater before use. Special care was taken not to wound the frond and to protect them from direct sunlight. Pieces measuring 15 cm² were cut out from the central part of the 2nd, 5th, 8th and 11th bladelets longer than 10 cm as numbered starting from the proximal part of the blade. In January there were not 8th or 11th bladelets available due to the shortness of the blade. To avoid abnormal results caused by cutting, the pieces were kept in running seawater overnight in the laboratory (SAKANISHI *et al.*, 1988). At the same time, small discs (0.73 cm²) of the bladelets were taken and frozen for quantitative analyses of chlorophylls.

Photosynthesis and respiration were measured by a differential gas-volumeter adapted for large seaweed pieces, with four set of culture flasks of 250 ml capacity as the reaction and compensation vessels (YOKOHAMA and MAEGAWA, 1988). All the measurements were done at 20 °C and with an illuminance gradient of 0 to 20 klux (0-400 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) by using a slide projector with an incandescent lamp (Kondo, 100V 300W) as a light source. The illuminance was changed in a stepwise fashion with neutral density filters (Toshiba TND-50, -25 and -12.5). Illuminance and photon flux density were measured by a lux meter (Minolta T-1) and a quantum meter (LI-COR LI-185b/LI-192S).

The discs for the determination of chlorophyll content were ground with 90 % acetone and the absorbances of the extract were measured at 630 and 664 nm with a dual beam spectrophotometer

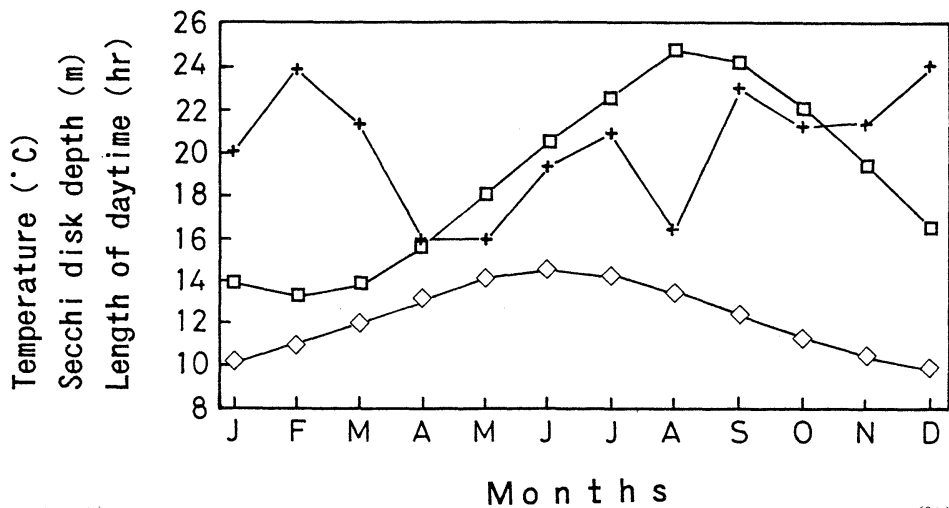


Fig. 2. Seasonal variation of environmental parameters studied. □ Temperature (°C), + Secchi disk depth (m) and ◇ Length of daytime (hr).

(Shimadzu UV-320). Chlorophyll *a* and *c* concentrations were calculated using the formulae of JEFFREY and HUMPHREY (1975).

All the procedures were repeated monthly at least with 3 replicates for each bladelet. Afterwards, a statistical analysis was applied and the average of all measurements for each bladelet was used as the monthly values for that bladelet.

As possible environmental control, the following parameters were studied: seawater temperature and Secchi disc depth as well as the length of daytime (Fig. 2). The seawater temperature at Nabeta Bay was daily obtained by the S.M.R.C. staff (Anon., 1981-1986). There is a minimum in mid-winter (February, 12.8 °C), and a maximum in late summer (August, 25 °C). As an indirect measure of light conditions in Nabeta Bay water, was used the Secchi disc depth measured in Sagami Bay off Shimoda (HOGETSU *et al.*, 1977). The maximal values were found in mid-winter (20-24m) and the minimal ones were recorded during the summer months (13-18m). The same trend was also observed in Nabeta Bay. The seasonal variation of the length of daytime at Shimoda was obtained from the National Meteorological Datum.

Results

Photosynthesis-light curves

Photosynthesis-light curves are illustrated in

Fig. 3 on a frond area bases, a dry weight basis and a chlorophyll *a* basis for the July, October, December and March samples. In all the cases, the photosynthetic rates increased with increase of illuminance within the range used in this study. The light-limited part of each curve was quite similar among the bladelets, but when the illuminance increased the response of each bladelet was different.

Seasonal variation of P_{max}

The net photosynthetic rates at 20 klux, henceforth considered as P_{max} , were maximal in winter-early spring ($44-49 \mu\text{O}_2 \cdot \text{cm}^{-2} \cdot \text{h}^{-1}$, $5.3-9.2 \mu\text{O}_2 \cdot \text{mg}^{-1} \cdot \text{h}^{-1}$ and $1.3-2.2 \mu\text{O}_2 \cdot \mu\text{g chl. } a^{-1} \cdot \text{h}^{-1}$) and minimal in early autumn ($19-30 \mu\text{O}_2 \cdot \text{cm}^{-2} \cdot \text{h}^{-1}$, $0.8-2.7 \mu\text{O}_2 \cdot \text{mg}^{-1} \cdot \text{h}^{-1}$ and $0.5-0.9 \mu\text{O}_2 \cdot \mu\text{g chl } a^{-1} \cdot \text{h}^{-1}$). The P_{max} on a dry weight basis began to increase as early as in November (in the 2nd bladelet), and reached maximal values in March, thereafter they gradually declined to the minimal values of September or October (Fig. 4). The decline of P_{max} from winter to late summer was more drastic on a dry weight basis than on a frond area basis or on a chlorophyll *a* basis. The dominant hierarchical order of P_{max} on a dry weight basis was 2nd, 5th, 8th and 11th bladelets from high to low performance; however, in mid-winter the P_{max} values were quite similar among the bladelets. From November to January, the bladelets formed in autumn

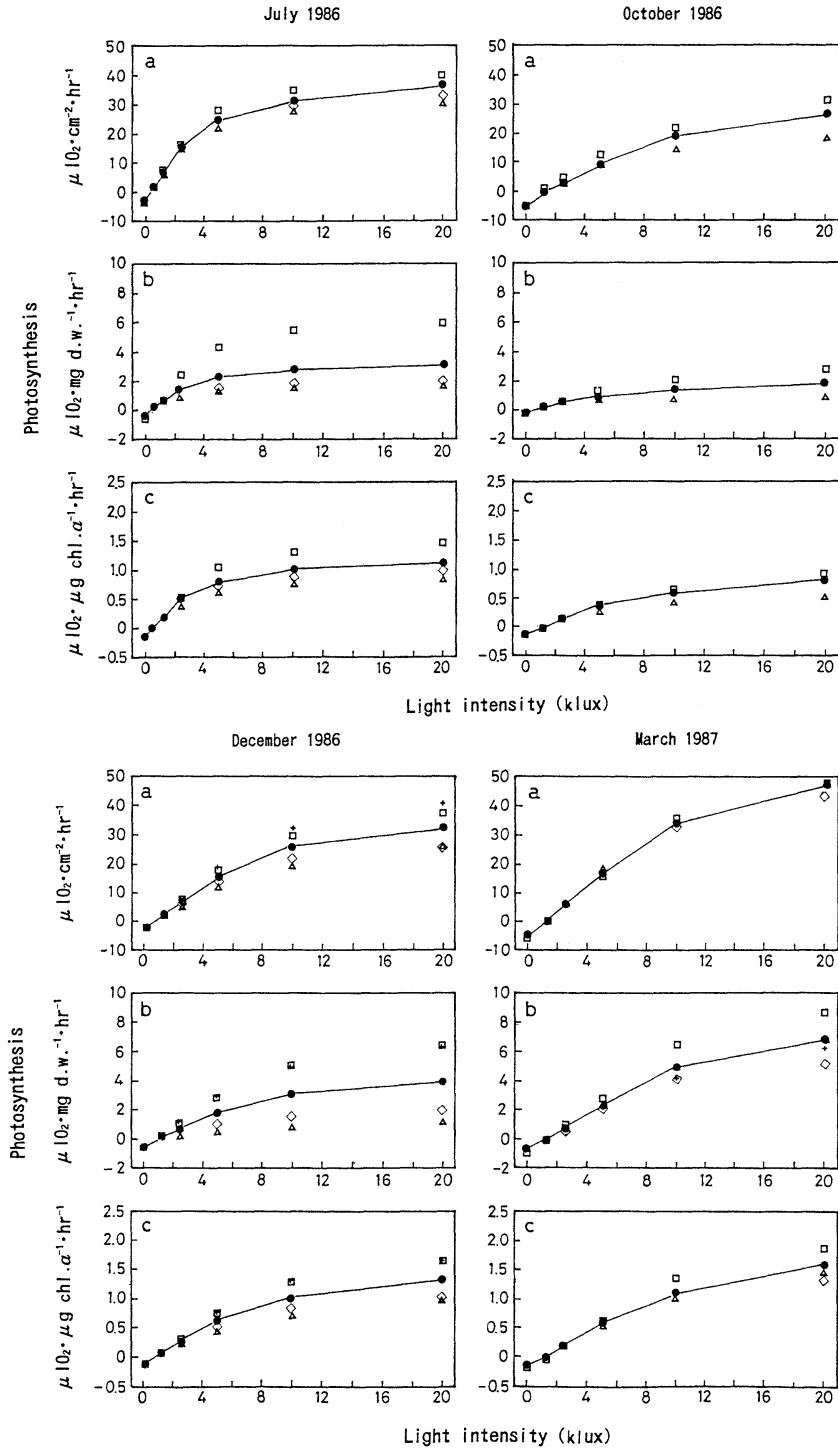


Fig. 3. Photosynthesis-light curves of each bladelet and the average of *Ecklonia cava* blade on a frond area, on a dryweight and on a chlorophyll *a* bases in selected months (July, October and December 1986, and March 1987). □ 2nd, + 5th, ◇ 8th, △ 11th and ● average.

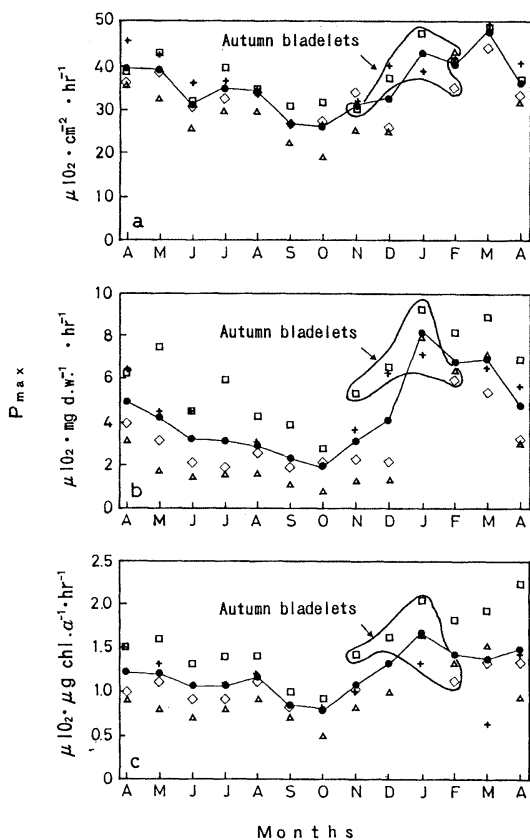


Fig. 4. Relationship between the seasonal variation of P_{max} on a frond area, on a dry weight and on a chlorophyll *a* bases of each bladelet and the phenological state of *Ecklonia cava* blade (April 1986 - April 1987). □ 2nd, + 5th, ◇ 8th, △ 11th and ● average.

showed specifically high photosynthetic rates.

Seasonal variation of respiration rates

Both on a frond area basis and on a chlorophyll *a* basis, the monthly average of respiration rate did not show any big variation, 2.7-4.8 $\mu\text{O}_2 \cdot \text{cm}^{-2} \cdot \text{h}^{-1}$ and 0.1-0.2 $\mu\text{O}_2 \cdot \mu\text{g chl. a}^{-1} \cdot \text{h}^{-1}$, during the period of study with relatively low values in December and March. On the other hand, the variations were bigger on a dry weight basis, 0.2-0.8 $\mu\text{O}_2 \cdot \text{mg}^{-1} \cdot \text{h}^{-1}$ (Fig. 5).

Comparing the monthly variation of the respiration rate of each bladelet, it is possible to get some suggesting trends. In any of the bases considered, the respiration rate of the 2nd

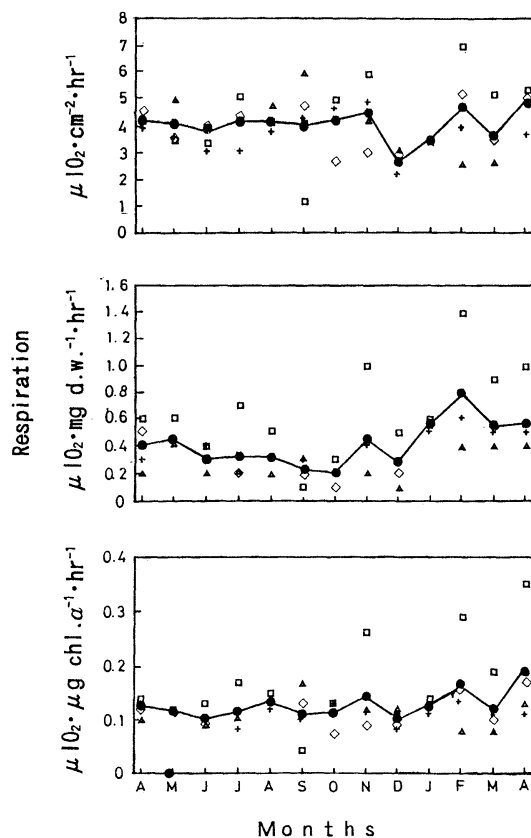


Fig. 5. Seasonal variation of respiration rate of each bladelet and the average of *Ecklonia cava* blade on a frond area, on a dry weight and on a chlorophyll *a* bases (April 1986 - April 1987). □ 2nd, + 5th, ◇ 8th, △ 11th and ● average.

bladelet showed a greater oscillation than those of the other bladelets, with a minimal values in September and two maximal values in November and in February. The high respiration rate on a chlorophyll *a* basis in April 1987 of the 2nd bladelet was due to the abnormally low content of chlorophyll *a* in the replicate samples used; there is no good explanation for this result.

Seasonal variations of compensation point (I_c) and saturation onset parameter (I_k)

Both parameters were calculated from the photosynthesis-light curves. As the values were quite similar among the curves irrespective of the different bases, only the values on a frond area basis are used in this paper (Fig. 6).

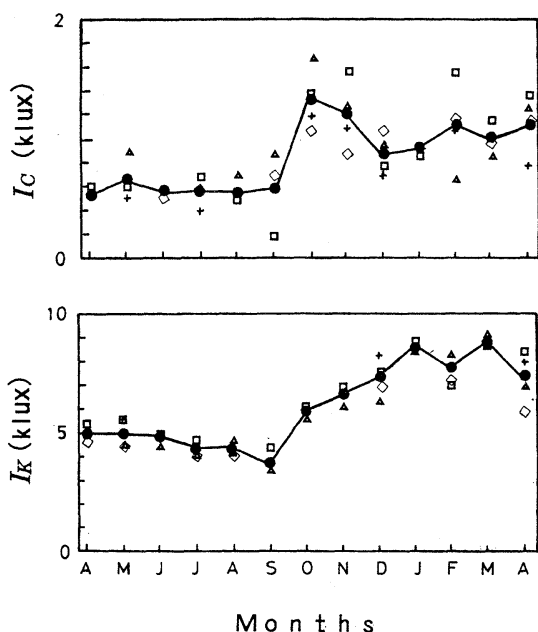


Fig. 6. Seasonal variation of I_c and I_k of each bladelet and the average of *Ecklonia cava* blade on a frond area basis (April 1986–April 1987). \square 2nd, + 5th, \diamond 8th, \triangle 11th and \bullet average.

In the case of I_c (Fig. 6A), lower values were found during the spring-summer period, 0.2–0.9 klux (3.3 – $16.6 \mu E \cdot m^{-2} \cdot s^{-1}$), while higher values were obtained from autumn to the next spring, 0.7–1.7 klux (11.5 – $31.6 \mu E \cdot m^{-2} \cdot s^{-1}$), with the highest average value in October.

The saturation onset parameter I_k (Talling, 1957; Kirk, 1983) was higher than 3 klux ($60 \mu E \cdot m^{-2} \cdot s^{-1}$). The trend of the seasonal variation of I_k was similar to that of I_c with lower values in spring-summer and higher values in autumn-winter.

Seasonal variation of chlorophyll content and dry weight

Figure 7 shows the variations of chlorophyll *a* and *c* contents per unit area of the bladelet. In all the bladelets, the chlorophyll *a* content was minimal from November to January, wherefrom it started to increase (Fig. 7A). The chlorophyll *a* content was always lower in the 2nd bladelet and almost always highest in the 11th bladelet. During the winter months all

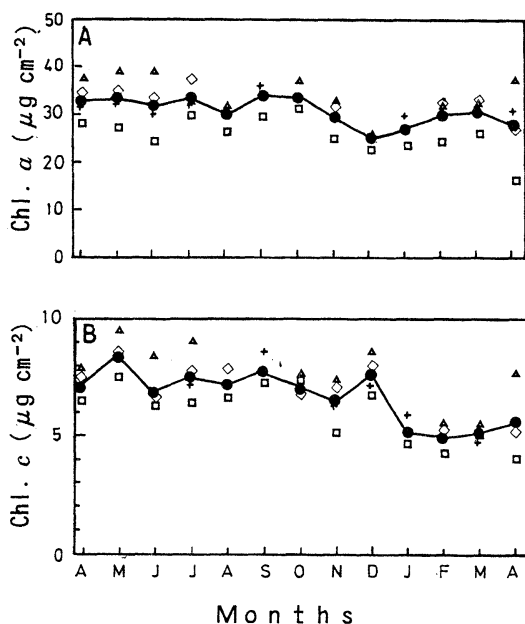


Fig. 7. Seasonal variation of chlorophyll *a* and *c* contents of each bladelet and the average of *Ecklonia cava* blade (April 1986–April 1987). \square 2nd, + 5th, \diamond 8th, \triangle 11th and \bullet average.

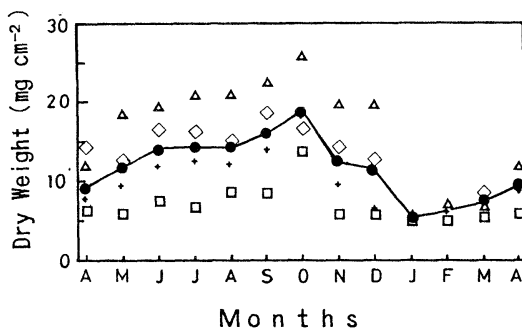


Fig. 8. Seasonal variation of dry weight of each bladelet and the average of *Ecklonia cava* blade (April 1986–April 1987). \square 2nd, + 5th, \diamond 8th, \triangle 11th and \bullet average.

bladelets showed lower values than during spring-early summer period, except for big differences in April 1987.

The chlorophyll *c* content was also low during winter time in the new bladelets, which were formed from November to January, but it was high in other seasons (Fig. 7B). Moreover, the pigment content was usually lower in the

younger bladelets (2nd and 5th) than in the older ones (8th and 11th).

In the dry weight per unit area of the bladelet (Fig. 8), there was a clear seasonal variation. A progressive thickening in all bladelets was observed from spring to early autumn, thereafter a quick decrease was measured to reach the minimal values of mid-winter. Usually the oldest bladelets showed higher values than the youngest ones; but in mid-winter the dry weight of the four bladelets considered was quite similar.

Discussion

In general, the photosynthetic response of algae can be characterized by the parameters P_{max} , I_k , I_c and dark respiration, allowing easy comparison among the published data (STEEMANN NIELSEN, 1975 + DRING, 1982). In this study photosynthesis-light curves were monthly obtained with four different bladelets of *E. cava*. The photosynthetic response of each bladelet was distinct with the position in the blade and with seasons. These results are related to the specific developmental stages monthly encountered on each bladelet. The saturating irradiation recorded in this study is in the range described by LÜNING (1981) for mid-sublittoral species, i.e. $150-250 \mu E \cdot m^{-2} \cdot s^{-1}$ (7-12 klux). In a recent paper (MAEGAWA *et al.*, 1987), it was reported that the level of light saturation for photosynthesis in young sporophytes of *E. cava* was lower (3-4.8 klux) as a consequence of their understory life and the lower amount of non-photosynthetic tissues (holdfast, stipe and medullary layer); the same trend was found in other Laminariales species (KAIN, 1979; NOVACZEK, 1984). SMITH (1981) also reported much lower I_k (about 2.5 klux) in a brown alga, *Lobophora variegata*, which forms thick rippled sheets in sublittoral waters, probably due to its higher surface/volume ratio. In several species of *Sargassum* from the shallow sublittoral zone of the Japan Sea their I_k values were quite similar to those of *E. cava*, while I_k was higher in *S. thunbergii* (MERTENS ex ROTH) O. KUNTZE which inhabits the intertidal zone (GAO and UMEZAKI, 1988) than in *E. cava* of this study.

The shift of low I_k and P_{max} values in summer months to high values of winter months in *E.*

cava is possibly related to the different thickness of the bladelets as suggested by the results of LÜNING and DRING (1985) about light transmittance through algal thalli and also by the results of MAEGAWA *et al.* (1987) who compared photosynthesis when the blade of young *E. cava* sporophytes was illuminated from one side and from both sides. Thin bladelets and high transparency of seawater reported in this study together with low leaf area index (LAI) (YOKOHAMA *et al.*, 1987) allow high photosynthesis efficiency in mid-winter, but in summer with thick bladelets, low transparency and mutual shading of the canopy (high LAI; see YOKOHAMA *et al.*, 1987) the efficiency of photosynthesis becomes lower. In addition, water temperature is an important factor in the regulation of photosynthetic metabolism by controlling pigment concentration and/or activities of the Calvin cycle enzymes (DAVISON, 1987; DAVISON and DAVISON, 1987). In *E. cava* blade, the slowdown of the growth rate from July, when the seawater temperature goes up higher than $22^\circ C$, was inversely correlated with the reproductive activity (HAROUN *et al.*, 1989). The low P_{max} values in June is probably related to an endogenous shift of metabolism from the production of new bladelets to the formation of sori and the reserve of photoassimilates in the summer bladelets.

WHEELER (1980) working with *Macrocystis pyrifera* (L.) C. AG. described that the photosynthesis capacity on a frond area basis of selected fronds increased from the apical to the median blade and then decreased towards the basal sporophylls. ARUGA (1983) recorded the highest P_{max} in subproximal bladelets of *E. cava* which approximately correspond to the 5th bladelet of this study. MATSUYAMA (1983) obtained the highest P_{max} in the longest lobe of *Undaria pinnatifida* SURINGER f. *distans* MIYABE et OKAMURA, with a drastic reduction of photosynthesis capacity towards the eroding apical part of the blade.

The seasonal variation of P_{max} values is closely related with the physiological stages of the bladelets and the annual growth cycle of the blade (HAROUN *et al.*, 1989). From late spring to early autumn the blade thickened and entered the reproductive period and, at the same time,

P_{\max} decreased in overall bladelets; from November, however, with the onset of new blade formation there was a clear change in the photosynthetic response of the bladelets. In mid-winter the bladelets are all fresh and thin, with a high photosynthetic performance. The observed lowering of P_{\max} can be explained by the concurrent thickening of the blade from spring to autumn (Fig. 8), which usually starts from the upper bladelets. In November, the measurements of the 2nd bladelet were carried out on newly developed bladelets with very thin laminae. In general the youngest bladelets showed lower content of chlorophylls compared with the oldest bladelets. WHEELER (1980) with *M. pyrifera* fronds and GAO and UMEZAKI (1988) with *Sargassum* spp. also found less pigments in the youngest parts of the thalli. Another remarkable fact is that the chlorophyll *a* content of the autumn bladelets, which appeared from November to January, showed minimal values, and from that time on a slow increase was measured for all bladelets (Fig. 7). Thus, the difference in photosynthetic responses can be explained by the rapid increase in dry weight of the bladelets from April to October compared with the slow filling in of chlorophylls. As algae can modify and optimize their photosynthetic systems in an adaptative fashion according to their seasonal light climate (RAMUS *et al.*, 1976; KIRK, 1983; LOBBAN *et al.*, 1985), the blade of *E. cava* seems to shift its pigment content in relation to the prevailing light conditions.

The big oscillation in the respiration rate of the 2nd bladelet can be explained by the different developmental stages of that bladelet. In September, there was almost no growth in the 2nd bladelet, while in November the autumnal 2nd bladelet was growing very actively, and the new 2nd bladelet of February was also growing very fast. Respiration rates were also greater in the young, upper part leaves of *Sargassum* spp. compared with the older leaves from lower parts (GAO and UMEZAKI, 1988).

KING and SCHRAMM (1976) described the variation of P_{\max} in two Baltic Sea algae, *Fucus vesiculosus* and *Laminaria digitata*, using different thallus portions. In their study, P_{\max} values on a frond area basis were not very distinct

among the segments, but on a dry weight basis the subterminal portion showed a higher value compared to the basal portion. In this research we found a positive relationship between the bladelet position and their dry weight per unit area. Following the above-mentioned trend, in *E. cava* there is a negative relationship between the photosynthesis capacity on a dry weight basis and the bladelet position; the respiration rate was also higher in the youngest bladelet compared with others.

Taking into consideration other studies on *E. cava* (ARUGA, 1981, 1982, 1983; YOKOHAMA *et al.*, 1987) and the previously described annual growth cycle (HAROUN *et al.*, 1989) it is possible to define the blade of this species as a "conveyer belt" that would renew its biomass 3 times per year. One blade appears in autumn, with short and thin bladelets having low chlorophyll content. This blade would live until early winter when it is substituted by the winter blade having longer but still thin bladelets with higher content of chlorophylls. Finally, during the summer the blade biomass is composed of long and thick bladelets with a progressive decrease in pigments. In late autumn, large pieces of the blade are broken off and the resultant organic matter will eventually participate in the detrital trophic chains of coastal waters.

The photosynthetic responses of *E. cava* blade is closely related to its annual growth cycle. The distinct photosynthetic performance of the bladelets is a consequence of their ontogenetic differentiation. Growth and photosynthesis metabolisms seem to be mainly controlled by seawater temperature and light conditions.

Acknowledgments

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References

- Anonymous (1981-1986): Report of Coastal Observations. Shimoda Mar. Res. Center, Univ. Tsukuba, 31-36, 1-7.

- ARUGA, Y. (1981): Physiological characteristics of *Eisenia bicyclis* and *Ecklonia cava*. Marine Ranching Program 1980, 29-34 (in Japanese).
- ARUGA, Y. (1982): Physiological characteristics of *Eisenia bicyclis* and *Ecklonia cava*. Marine Ranching Program 1981, 19-24 (in Japanese).
- ARUGA, Y. (1983): Physiological characteristics of *Eisenia bicyclis* and *Ecklonia cava*. Marine Ranching Program 1982, 19-27 (in Japanese).
- DAVISON, I. (1987): Adaptation of photosynthesis in *Laminaria saccharina* (Phaeophyta) to changes in growth temperature. *J. Phycol.*, **23**, 273-283.
- DAVISON, I. and J. O. DAVISON (1987): The effect of growth temperature on enzyme activities in the brown alga *Laminaria saccharina*. *Br. phycol. J.*, **22**, 77-87.
- DREW, E. A. (1973): Primary production of large marine algae measured *in situ* using uptake of ^{14}C . In UNESCO (ed.), *Monogr. Oceanogr. Methodol.*, 3. A Guide to the Measurements of Marine Primary Production under Special Conditions. Paris. p. 22-26.
- DRING, M. J. (1982): *The Biology of Marine Plants*. Edward Arnold Publ., London. 199pp.
- GAO, K. and I. UMEZAKI (1988): Comparative photosynthetic capacities of the leaves of upper and lower parts of *Sargassum* plants. *Bot. mar.*, **31**, 231-236.
- HAROUN, R., Y. YOKOHAMA and Y. ARUGA (1989): Annual growth cycle of the brown alga *Ecklonia cava* in central Japan. *Scient. Mar.* **53**, 349-356.
- HAYASHIDA, F. (1977): On age and growth of a brown alga, *Ecklonia cava* KJELLMAN, forming aquatic forest. *Bull. Jpn. Soc. Sci. Fish.*, **43**, 1043-1051 (in Japanese with English summary).
- HOGETSU, K., M. HATANAKA, T. HANAOKA and T. KAWAMURA (1977): Productivity of Biocenoses in Coastal Regions of Japan. *JIBP Synthesis*, Vol. 14. Univ. Tokyo Press, Tokyo. 394 pp.
- JASSBY, A. D. (1978): Polarographic measurements of photosynthesis and respiration. In J. A. Hellebust and J. S. Craigie (eds.), *Handbook of Phycological Methods. Physiological and Biochemical Methods*. Cambridge Univ. Press, Cambridge. p. 285-295.
- JEFFREY, S. W. and G. F. HUMPHREY (1975): New spectrophotometric equations for determining chlorophylls *a*, *b*, *c*₁ and *c*₂ in higher plants, algae and natural phytoplankton. *Biochem. Physiol. Pflanzen*, **167**, 191-194.
- KAIN, J. M. (1979): A view of the genus *Laminaria*. *Oceanogr. Mar. Biol. Ann. Rev.*, **17**, 101-161.
- KATAYAMA, N., Y. TOKUNAGA and Y. YOKOHAMA (1985): Effect of growth temperature on photosynthesis-temperature relationships of a tide pool alga *Cladophora rudolphiana* (Chlorophyceae). *Jpn. J. Phycol.*, **33**, 312-316.
- KING, R. J. and W. SCHRAMM (1976): Determination of photosynthetic rates for the marine algae *Fucus vesiculosus* and *Laminaria digitata*. *Mar. Biol.*, **37**, 209-213.
- KIRK, J. T. O. (1983): *Light and Photosynthesis in Aquatic Ecosystems*. Cambridge Univ. Press, Cambridge. 401 pp.
- KREMER, B. P. (1978): Determination of photosynthetic rates and ^{14}C photoassimilatory products of brown seaweeds. In J. A. Hellebust and J. S. Craigie (eds.), *Handbook of Phycological Methods. Physiological and Biochemical Methods*. Cambridge Univ. Press, Cambridge. p. 269-283.
- LITTLER, M. M. and D. S. LITTLER (1985): *Handbook of Phycological Methods. Ecological Field Methods: Macroalgae*. Cambridge Univ. Press, Cambridge. 617 pp.
- LOBBAN, C. S., P. J. HARRISON and M. J. DUNCAN (1985): *The Physiological Ecology of Seaweeds*. Cambridge Univ. Press, Cambridge. 242 pp.
- LÜNING, K. (1980): Control of algal life-history by daylength and temperature. In J. H. PRICE, D. E. G. IRVINE and W. F. FARNHAM (eds.), *The Shore Environment. Vol 2: Ecosystems*. Academic press, London. p. 915-945.
- LÜNING, K. (1981): Photobiology of seaweeds: ecophysiological aspects. *Proc. 10th Inter. Seaweed Symp.* p. 35-55.
- LÜNING, K. and M. J. DRING (1985): Action spectra and spectral quantum yield of photosynthesis in marine macroalgae with thin and thick thalli. *Mar. Biol.*, **87**, 119-129.
- MAEGAWA, M. and W. KIDA (1984): Ecological studies on *Eisenia bicyclis* and *Ecklonia cava* communities - IV. Seasonal change in allometric relation of *Ecklonia* frond. *Bull. Fac. Fish., Mie Univ.*, **11**, 199-206 (in Japanese with English summary).
- MAEGAWA, M., Y. YOKOHAMA and Y. AURGA (1987): Critical light conditions for young *Ecklonia cava* and *Eisenia bicyclis* with reference to photosynthesis. *Hydrobiologia*, **151/152**, 447-455.
- MATSUYAMA, K. (1983): Photosynthesis of *Undaria pinnatifida* SURINGAR f. *distans* MIYABE et OKAMURA (Phaeophyceae) from Oshoro Bay. II. Photosynthetic rates in several portions of the thallus. *Sci. Rep. Hokkaido Fish. Exp.*

- Sta., 25, 195-200 (in Japanese with English summary).
- MIZUSAWA, M., A. KAGEYAMA and Y. YOKOHAMA (1978): Physiology of benthic algae in tide pools I. Photosynthesis-temperature relationships in summer. *Jpn. J. Phycol.*, 26, 109-114.
- NOVACEK, I. (1984): Development and phenology of *Ecklonia radiata* at two depths in Goat Island Bay, New Zealand. *Mar. Biol.*, 81, 189-197.
- OOHUSA, T. (1980): Diurnal rhythm in the rates of cell division, growth and photosynthesis of *Porphyra yezoensis* (Rhodophyceae) cultured in the laboratory. *Bot. mar.*, 23, 1-5.
- RAMUS, J., S. I. BEARLE and K. L. HOWARD (1976): Changes in photosynthetic pigment concentration in seaweeds as function of water depth. *Mar. Biol.*, 37, 223-229.
- SAKANISHI, Y., Y. YOKOHAMA and Y. ARUGA (1988): Photosynthesis measurement of blade segments of brown algae *Ecklonia cava* KJELLMAN and *Eisenia bicyclis* SETCHELL. *Jpn. J. Phycol.*, 36, 24-28.
- SMITH, W. O. (1981): Photosynthesis and productivity of benthic macroalgae on the North Carolina continental shelf. *Bot. mar.*, 24, 279-284.
- STEEMANN NIELSEN, E. (1975): Marine Photosynthesis with Special Emphasis on the Ecological Aspects. Elsevier Sci. Publ., Amsterdam. 141 pp.
- TALLING, J. F. (1957): Photosynthetic characteristics of some freshwater plankton diatoms in relation to underwater radiation. *New Phytol.*, 56, 29-50.
- WHEELER, W. N. (1980): Pigment content and photosynthetic rate of the frond of *Macrocystis pyrifera*. *Mar. Biol.*, 56, 97-102.
- YOKOHAMA, Y. (1971): Photosynthesis-temperature relationships in several benthic marine algae. *Proc. VIIth Inter. Seaweed Symp.* p. 286-291.
- YOKOHAMA, (1973a): Photosynthetic properties of marine benthic green algae from different depths in the coastal area. *Bull. Jpn. Soc. Phycol.*, 21, 70-75.
- YOKOHAMA, Y. (1973b): A comparative study on photosynthesis-temperature relationships and their changes in marine benthic algae. *Int. Revue ges. Hydrobiol.*, 58, 467-476.
- YOKOHAMA, Y. and S. ICHIMURA (1969): A new device of differential gas-volumeter for ecological studies on small aquatic organisms. *J. Oceanogr. Soc. Japan*, 25, 75-80.
- YOKOHAMA, Y. and M. MAEGAWA (1988): Measurements of photosynthesis and respiration of large samples by "Productmeter", a differential gas-volumeter. *Jpn. J. Phycol.*, 36, 29-36.
- YOKOHAMA, Y., N. KATAYAMA and K. FURUYA (1986): An improved type of "Productmeter", a differential gas-volumeter, and its application to measuring photosynthesis of seaweeds. *Jpn. J. Phycol.*, 34, 37-42.
- YOKOHAMA, Y., J. TANAKA and M. CHIHARA (1987): Productivity of the *Ecklonia cava* community in a bay of Izu Peninsula on the Pacific coast of Japan. *Bot. Mag. Tokyo*, 100, 129-141.

鍋田湾における褐藻カジメの光合成特製の季節変化

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要旨：カジメの光合成特性の季節変化を明らかにするため、伊豆下田の鍋田湾に生育するカジメを用いて1986年4月から1987年4月まで毎月1回の測定を行った。差動式ガス検容計により、側葉の光合成速度及び呼吸速度を測定した。光合成-光曲線は測定した月により側葉ごとに異なったが、全ての側葉が新しい冬季にはほとんど同じであった。葉面積当たりでは、最も若い側葉はより古い側葉に比べて高い純光合成速度を示し、光飽和光合成速度の最高値 ($44\sim 49 \mu\text{O}_2 \cdot \text{cm}^{-2} \cdot \text{h}^{-1}$) は初春に、最低値 ($19\sim 31 \mu\text{O}_2 \cdot \text{cm}^{-2} \cdot \text{h}^{-1}$) は秋季(生殖期)に見られた。乾燥重量当たりでは、光飽和光合成速度は側葉の厚さと逆の関係にあり、最高値は第2側葉で、最低値は第11側葉で得られた。クロロフィル a 当りでは、乾燥重量当りの場合と同様の傾向が認められたが、光飽和光合成活性はそれぞれ大きな季節変化を示さなかった。第2側葉以外の各側葉の呼吸速度は年間を通して安定していたが、第2側葉では側葉の形成期にあたる11月及び2月に高い極大値がみられた。カジメの光合成は、その生育過程と密接に関連している。カジメの葉状部は、それを取りまく水中の光環境に応じて色素濃度を調節している。