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# Seasonal Changes in the Primary Production and Chlorophyll *a* Amount of Sessile Algal Community in a Small Mountain Stream, Chigonosawa\*

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**Abstract.** Seasonal changes in major species, chlorophyll *a* amount and daily primary production of sessile algal community were investigated in a small mountain stream, Chigonosawa, during February of 1971 to February of 1972. Chlorophyll *a* amount varied over a wide range of 5-550 mg·m<sup>-2</sup> during the investigated period. Large amounts of chlorophyll *a* were observed when the green alga, *Cladophora* sp., or the diatoms, *Diatoma hiemale* and *Synedra ulna*, were dominant. The daily gross and net production varied seasonally within ranges of 16 to 680 mgC·m<sup>-2</sup>·day<sup>-1</sup> and -243 to 166 mgC·m<sup>-2</sup>·day<sup>-1</sup>, respectively. The daily gross production obtained was compared with that reported by other investigator for lower part of a Japanese mountain river. The optimal amount of chlorophyll *a* which maximizes the daily net production was calculated in each month. And seasonal changing pattern of the observed amount of chlorophyll *a* was compared with that of the optimal one. As an additional study, photosynthesis at saturated light and respiration of the suspended sessile algae under still water condition were compared with those of the algal community adhering onto stone under turbulent condition.

## Introduction

Information on the primary production of sessile algal community in shallow and rapid-running waters is still poor as compared with that of phytoplankton in lakes and oceans, though there are some interesting works on seasonal change in organic matter production (McCONNELL and SIGLER, 1959; KOBAYASHI, 1961a, b and 1972; TOMINAGA and ICHIMURA, 1966) and on the effect of current on lotic algal metabolism (McCONNELL and SIGLER, 1959; WHITFORD and SCHUMACHER, 1961; PFEIFER and McDIFFETT, 1975; RODGERS, Jr. *et al.*, 1978). Thus, further

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studies on the sessile algal production will be required for understanding the life of sessile algae in running waters.

The study site, a small mountain stream, Chigonosawa (very small tributary stream of the River Kiso, Central Japan) had been designated for study on the stream ecosystem by Otsu Hydrobiological Station, Kyoto University. KOBAYASHI (1972) reported already some characteristics of sessile algal community and organic matter production in this stream. However, his work was not a full investigation for understanding the actual state of seasonal changes in algal composition, amount of chlorophyll and primary production because it was on the basis of sporadical data obtained from four times-field surveys during 1964 to 1966.

The objectives of the present study are (1) to make clear the actual state of seasonal changes in algal composition, standing crop as chlorophyll *a* amount and daily primary production of sessile algal community at a fixed station in the Chigonosawa Stream, (2) to compare photosynthetic and respiratory rates of the sessile algae under suspended and still water conditions with those of the intact sessile algal community on stone under turbulent condition, and (3) to discuss the seasonal change in standing crop as chlorophyll *a* amount of sessile algae in connection with the optimal amount of chlorophyll *a* which maximizes the daily net production.

### Material and Methods

The samples were collected mostly every month during February of 1971 to February of 1972 at a fixed station. The observed station, being one of the typical riffles in the stream, was ca. 4 m long, 2–3 m wide and 5–20 cm deep.

*Determination of chlorophyll a:* Sessile algae which were brushed out from a given surface area of 8–10 pieces of stone with 15–30 cm in diameter were collected on the Whatman GF/C glass fiber filters. The amount of chlorophyll *a* on the filter was determined by the UNESCO method (UNESCO, 1969).

*Photosynthesis and respiration measurements:* Photosynthesis and respiration of sessile algae suspended at a concentration of chlorophyll *a* of ca.  $0.2 \text{ mg} \cdot \text{l}^{-1}$  were measured by the oxygen method under artificial light (Toshiba reflector lamp 500 W) and still water conditions. Incubation time was 3–5 hours.

In order to find a conversion factor from oxygen to carbon in photosynthesis, the photosynthesis was measured by the  $^{14}\text{C}$  technique in combination with the oxygen one using the suspended sessile algae in June and November of 1971. Incubation time by the  $^{14}\text{C}$  technique was 10 minutes. The rate thus obtained was regarded roughly as gross photosynthesis. The conversion factor of 0.33 from oxygen to carbon for photosynthesis was obtained from this experiment (Fig. 1a).

For a comparison of photosynthesis at saturated light and respiration of detached and suspended algae under still water condition with those of intact algal community adhering onto stone under turbulent condition, special experiment was undertaken. For measurements of photosynthesis and respiration of algal community on stone, suitable pieces of stone with sessile algal community were hanged in 600 ml-clear and dark separate flasks filled with the stream water. Turbulent motion of the water in the flasks was produced by means of a magnetic stirrer. Photosynthesis and respiration of the sessile algal community on stone were measured

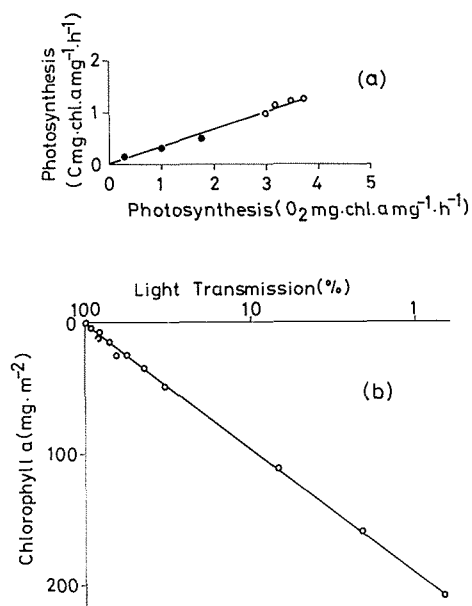


Fig. 1. a: Relationship between photosynthesis measured as "mg C · mg chl. a<sup>-1</sup> · h<sup>-1</sup>" by the <sup>14</sup>C technique and that as "mg O<sub>2</sub> · mg chl. a<sup>-1</sup> · h<sup>-1</sup>" by the oxygen method. Measured in June of 1971 (open circle) and in November of 1971 (solid circle).  
 b: Relation of light transmittance to the chlorophyll *a* amount of sessile algal community.

under different turbulent conditions. On the other hand, photosynthesis at various light intensities and respiration of suspended algae collected from the same stone used for the above experiment were measured under still water condition.

*Estimation of primary production:* The daily primary production of sessile algae was estimated by the chlorophyll method (cf. TOMINAGA and ICHIMURA, 1966) using photosynthesis-light curve, amount of chlorophyll *a*, daily change in light intensity on the surface of algal community and light extinction coefficient in the community. The daily change in light intensity on the top of the community was measured mostly every hour from sunrise to sunset at the station.

To find relationship between thickness (amount) of chlorophyll *a* of the community and light attenuation, suspended sessile algae with different chlorophyll *a* concentrations were prepared and collected on HA Millipore filters and desiccated at ca. -20°C under vacuum condition. The desiccated filters were made transparent with cedar oil. Light transmittance of the respective samples on the transparent filters was measured using the lamp mentioned before and a photometer (Toshiba SP-1). As a result, light intensity in the community (*I*) could be expressed as the equation,  $I = I_0 \exp(-0.023x)$ , where *I*<sub>0</sub> is light intensity at the top of sessile algal community and *x* is chlorophyll *a* thickness (mg · m<sup>-2</sup>) of the community (Fig. 1b).

Formulae used for the calculation of the daily primary production of the sessile algal community are explained in the results.

## Results and Discussion

### 1. Seasonal changes in some physical variables.

It is very important for understanding the sessile algal production in small mountain streams to know short-term or seasonal fluctuation of physical variables such as precipitation, water temperature and light as well as chemical parameters.

Seasonal changes in some physical variables at the stream or at the sampling station are shown in Figs. 2 and 3. Water depth at a small lock near the station fluctuated greatly from mid spring (April) to the beginning of autumn (September) because of much precipitation, while it was relatively stable and maintained low levels in other seasons with less precipitation (Fig. 2a and b). It is considered that current velocity at the station changed frequently in a large scale from April to September.

Monthly mean water temperature varied seasonally from 1.1 in January of 1971 to 14.1°C in August during the investigated period. The monthly mean water temperatures in January and February of 1971 were lower than those in the corresponding months of 1972 (Fig. 2c).

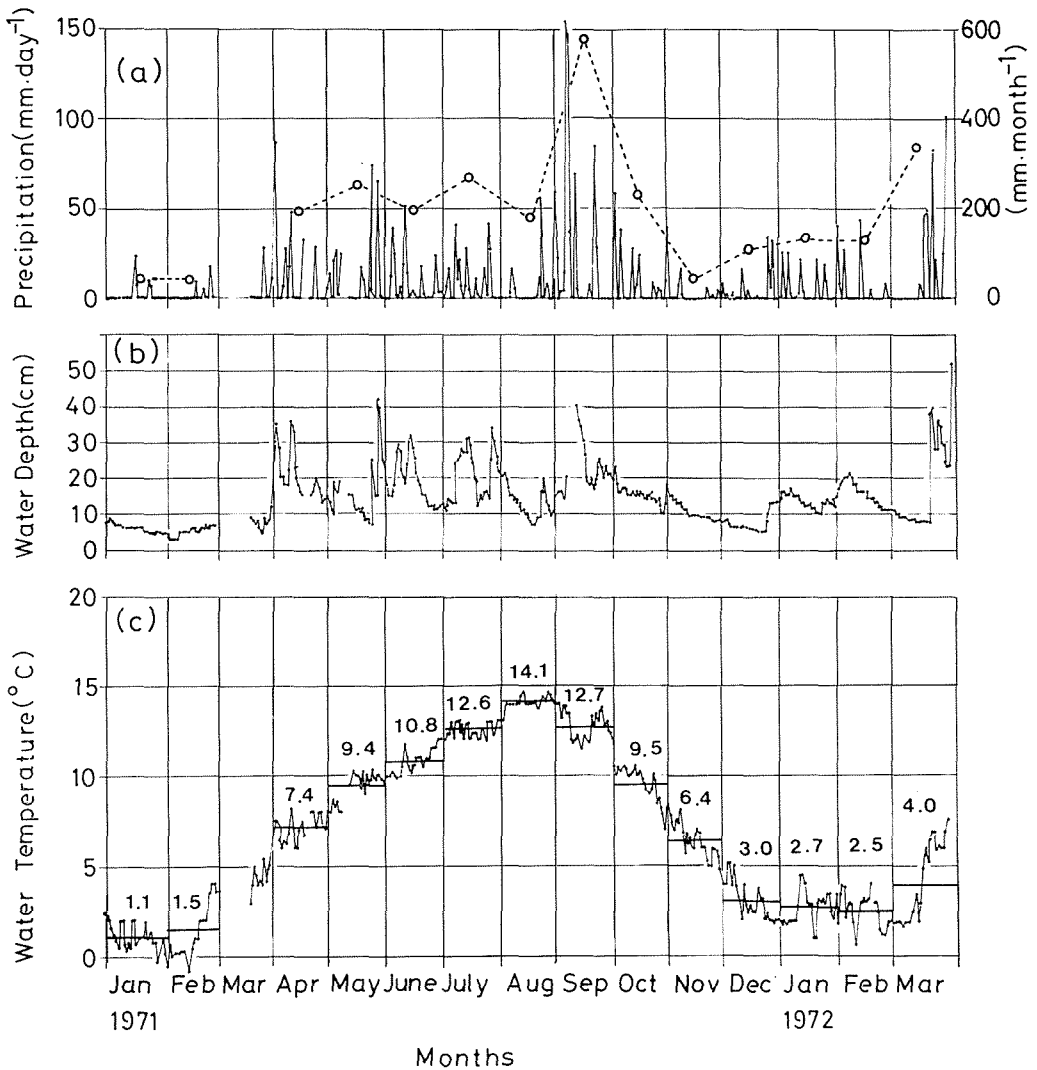


Fig. 2. Seasonal changes in precipitation near the sampling station (a), water level at a small lock near the station (b) and water temperature at the station (c). Open circle in Fig. 2a and numerals in Fig. 2c show monthly precipitation and monthly average of water temperature, respectively.

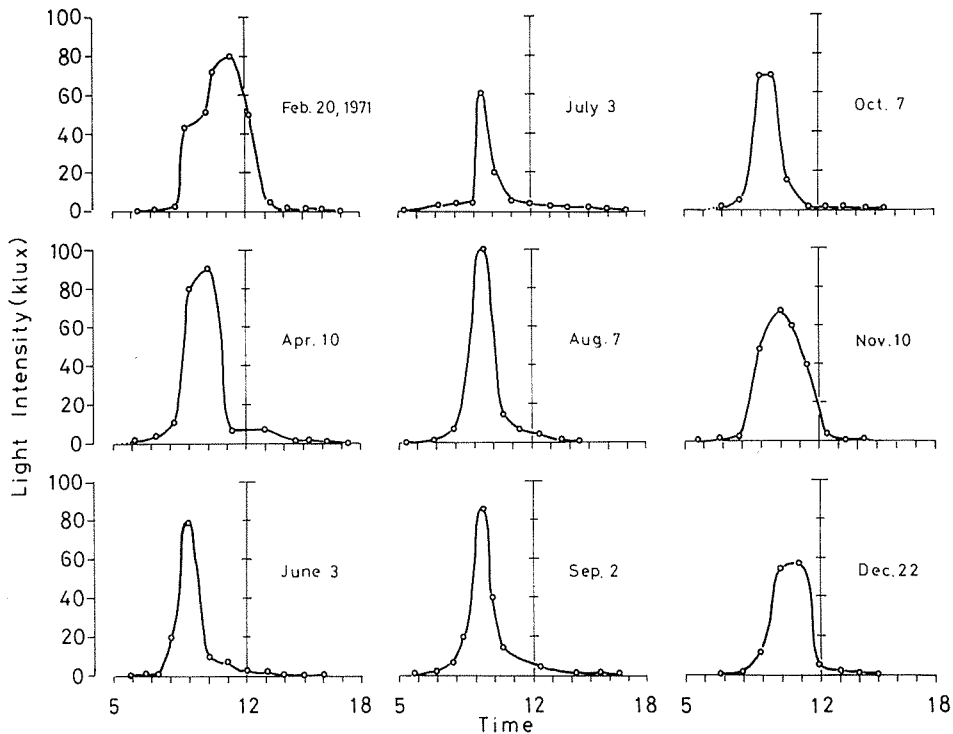


Fig. 3. Daily changes in light intensity on the surface of sessile algal community at the station in each month.

Such an annual variation of monthly mean water temperature seems to be closely related to precipitation.

The Chigonosawa Stream is surrounded three sides by mountains and covered with trees and bushes. Consequently, the stream bed is exposed directly to the sun for only a few hours. According to КОБАЯШИ (1972), duration of insolation ranges from 0.7 to 4.6 hours in summer and 2.0 to 4.5 hours in winter at 9 points in the Chigonosawa Stream. The observed station was exposed for only one hour in the morning to direct sunshine in summer (Fig. 3). In winter, duration of insolation tended to be longer by defoliation of surrounding trees and bushes. The daily primary production of sessile algal community in small mountain streams like the Chigonosawa Stream appears to be limited strongly by short duration of insolation.

## 2. Seasonal changes in the algal composition and chlorophyll *a* amount.

Seasonal changes in blue-green algae, diatoms and green algae at the station are shown in Fig. 4a as a percentage of the total algal cell numbers. In general, the filamentous blue-green alga, *Homeothrix* sp., was relatively abundant during the sampling period. Sessile algal community in spring-summer was dominated by *Homeothrix* sp. and the green algae, *Cladophora* sp. and *Ulothrix* sp. and in autumn-winter by *Homeothrix* sp. and/or the diatoms, *Diatoma hiemale* and *Synedra ulna*. There were noticeable differences in algal composition and standing crop as chlorophyll *a* amount between February of 1971 and 1972 (Fig. 4b). The algal community in February of 1971 consisted mainly of *D. hiemale* and *S. ulna* and the amount of chlorophyll

$a$  was  $300\text{--}550\text{ mg}\cdot\text{m}^{-2}$ . On the other hand, it was dominated by *Homeothrix* sp. and the chlorophyll  $a$  amount was  $5\text{--}25\text{ mg}\cdot\text{m}^{-2}$  in February of 1972. The extremely high standing crop in February of 1971 was brought about by dense populations of *D. hiemale* and *S. ulna*. What is the reason for such a great difference in population density of these diatoms between February of 1971 and 1972? The Chigonosawa Stream was very stable during January-February of 1971 under the lowest water level, while in January-February of 1972 it was not so stable under relatively high water level (cf. Fig. 2b). It is considered that populations of *D. hiemale* and *S. ulna* could develop densely in February of 1971 under long time stable condition with the lowest current velocity, while they could not increase well in February of 1972 because of being scraped away by relatively high current velocity.

According to KOBAYASHI (1972), the algal community in the Chigonosawa Stream was composed of diatoms dominated by *Achnanthes laceolata* in summer (August, 1964), blue-green algae by *Homeothrix janthina*, *Chamaesiphon minutus* and *Phormidium autumnale* in autumn (October,

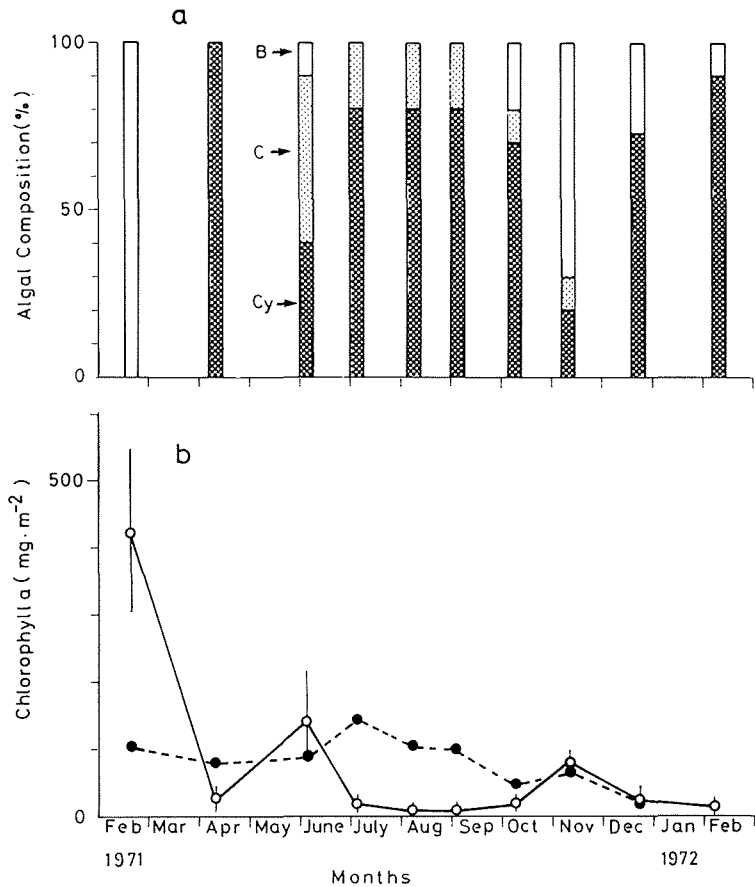


Fig. 4. a: Seasonal variation of the percentage of total cell numbers for blue-green algae (Cy), diatoms (B) and green algae (C) in the sessile algal communities. b: Seasonal changes in the observed amount of chlorophyll  $a$  (solid line) and the optimal amount (broken line) which gives the maximum daily net production. Vertical bars: varying range of the amount of chlorophyll  $a$  observed on 8-10 pieces of stone.

1965) and spring (March, 1966), and diatom-gold brown algae by *D. hiemale* and *Hydrurus foetidus* in winter (February, 1965). Dominant species in a given month during 1964–1966 do not always correspond with those in the present observation. This fact suggests that seasonal changing pattern of the dominant species in the Chigonosawa Stream is very complicated and differs from year to year.

Seasonal variation of the amount of chlorophyll *a* is shown in Fig. 4b. The amount varied over a wide range of 5–550 mg·m<sup>-2</sup> during the investigated period. Large amounts of chlorophyll *a* were observed in February (300–550 mg·m<sup>-2</sup>), June (89–224 mg·m<sup>-2</sup>) and November (60–98 mg·m<sup>-2</sup>) in 1971. These large amounts were brought about mainly by the propagations of *D. hiemale* and *S. ulna* in February, *Cladophora* sp. in May, and *S. ulna* in October. Rises and falls of *D. hiemale*, *S. ulna* and *Cladophora* sp. seem to have influence on seasonal variation of standing crop of the sessile algae in this stream.

TOMINAGA and ICHIMURA (1966) observed large amounts of chlorophyll of 300–500 mg·m<sup>-2</sup> in winter and 100–200 mg·m<sup>-2</sup> in other seasons from lower part of mountain region of the River Arakawa, and MCCONELL and SIGLER (1959) reported 300 mg·m<sup>-2</sup> as an annual mean amount of chlorophyll in canyon section of Rogan River. KOBAYASHI (1969a) reported that chlorophyll amount in canyon section or upper part of the River Arakawa ranged from 0 to 144 mg·m<sup>-2</sup>. The amount of chlorophyll *a* in the Chigonosawa Stream is low in comparison with that of the former two reports with a few exceptions, but corresponds with that in canyon section of the River Arakawa. At upper part of Japanese mountain rivers or streams, it may be difficult, excepting a few cases, for sessile algae to maintain their high standing crop because they are restricted in their growth by shorter duration of insolation and scraped away frequently by flooding.

### 3. *A comparison of photosynthesis and respiration of suspended sessile algae under still water condition with those of sessile algal community on stone under turbulent condition*

Photosynthesis and respiration of sessile algae have been measured by two ways; using suspension of sessile algae under static condition (KOBAYASHI, 1961b and 1972; TOMINAGA and ICHIMURA, 1966; UEDA, 1975) or using stone or rock with full amount of sessile algae under static or flowing condition (MCCONELL and SIGLER, 1959; OKINO, 1970; HANSMANN *et al.*, 1971; PFEIFER and McDIFFETT, 1975; BOTT *et al.*, 1978; RODGERS, Jr. *et al.*, 1978).

To compare photosynthesis at saturated light and respiration of suspended algae under still water condition with those of sessile algal community on stone under turbulent condition, comparative experiments were performed on July 2 in 1971 and November 26 in 1973. In these experiments, it was impossible to measure the current velocity in vessel including a stone with algal community because turbulent motion was produced by changing the number of revolution of a magnetic stirrer. Gradation of turbulent motion was expressed by an arbitrary unit. To examine whether the rate of photosynthesis of the sessile algal community on stone was the same as the one at saturated light or not, light intensities from the top to the bottom in the algal mat used for the experiments were calculated roughly from the equation,  $I = I_0 \exp(-0.023x)$ , formulating a relation of light transmission to amount of chlorophyll *a* (*x*) of the community (cf. Fig. 1b). Light intensities thus obtained were 35 klux at the top and 25 klux at the base of the mat in the first experiment on July 2 and 35 klux and 6 klux in the second



one on November 26. Combining ranges of light intensities from the top to the base of the community with the photosynthesis-light curves of the suspended algae, photosynthesis of the sessile algal communities on stone in both experiments will be regarded as the rate under light saturated condition (Fig. 5a' and b'). Hence, photosynthesis of the algal community on stone obtained can be compared directly with that of the suspended algae at saturated light.

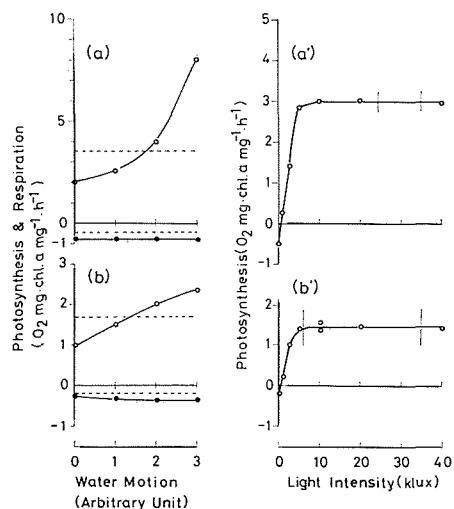


Fig. 5. a and b: Gross photosynthesis at saturated light (open circle) and respiration (solid circle) of sessile algal communities on stone against different turbulent motion. Broken lines: Gross photosynthesis at saturated light and respiration of the sessile algae under suspended and static conditions (see a' and b').

a' and b': Photosynthesis-light curves of the suspended sessile algae. Vertical bars show the light intensities on the surface and on the base of the sessile algal communities on stone used for experiments.

a and a': results of the experiment on July 2, 1971.

band b': results of the experiment on November 26, 1973.

Photosynthesis of the sessile algal community on stone increased with increase in turbulent motion, though there was difference in changing pattern of photosynthesis against turbulence between the both experiments (Fig. 5a and b). Photosynthesis in the first experiment was noticeably enhanced at the greatest turbulence and reached 450% of that under still water condition, whereas in the second experiment it was 235% increase. In both experiments, the current plateau for photosynthesis was not observed (RODGERS, Jr. *et al.*, 1978). On the other hand, enhancement effect of turbulence on respiration of sessile algal community on stone was not significant.

As pointed out by some workers (McCONNELL and SIGLER, 1959; WHITFORD and SCHUMACHER, 1961; PFEIFER and McDIFFETT, 1975; RODGERS, Jr. *et al.*, 1978), it is true that metabolisms of lotic algae are enhanced by turbulent motion. However, the degree of enhancement effect of turbulence seems to differ among metabolisms such as photosynthesis and respiration. In the case of the Chigonosawa Stream, turbulent motion was more effective for photosynthesis than respiration.

Photosynthesis of the suspended algae at saturated light corresponded to that of the sessile algal community on stone under a given turbulent condition (cf. Fig. 5a and b). Therefore, photosynthesis of the suspended algae can be regarded as photosynthesis of the sessile algal community on stone under a certain flowing condition. Respiration of the suspended algae showed a tendency to be lower than that of the algal community on stone and ranged from 60 to 70%. It is unknown why respiration of the sessile algae under suspended condition was lower.

## 4. Seasonal change in daily primary production of the sessile algal community

The daily primary production of sessile algal community was estimated by the chlorophyll method (cf. TOMINAGA and ICHIMURA, 1966) using photosynthesis-light curves of the suspended algae (Fig. 6), mean concentration of chlorophyll *a* (Fig. 4b), relation of light transmission to chlorophyll *a* amount of the sessile algal community (Fig. 1b) and daily changes in light intensity on the top of algal mat at the observed station (Fig. 3). The mathematical model used here has been advanced by SAEKI (1960), KUROIWA and MONSI (1964) for calculation of daily photosynthesis of terrestrial plant communities and by IKUSIMA (1970) for that of aquatic plant communities. The model by SAEKI (1960) was on the basis of the summation method, while the model by KUROIWA and MONSI (1964) and IKUSIMA (1970) was on the basis of the integration one. Their equations were derived from the MONSI and SAEKI's theory which hourly net photosynthesis of the foliage was calculated as a function of light intensity.

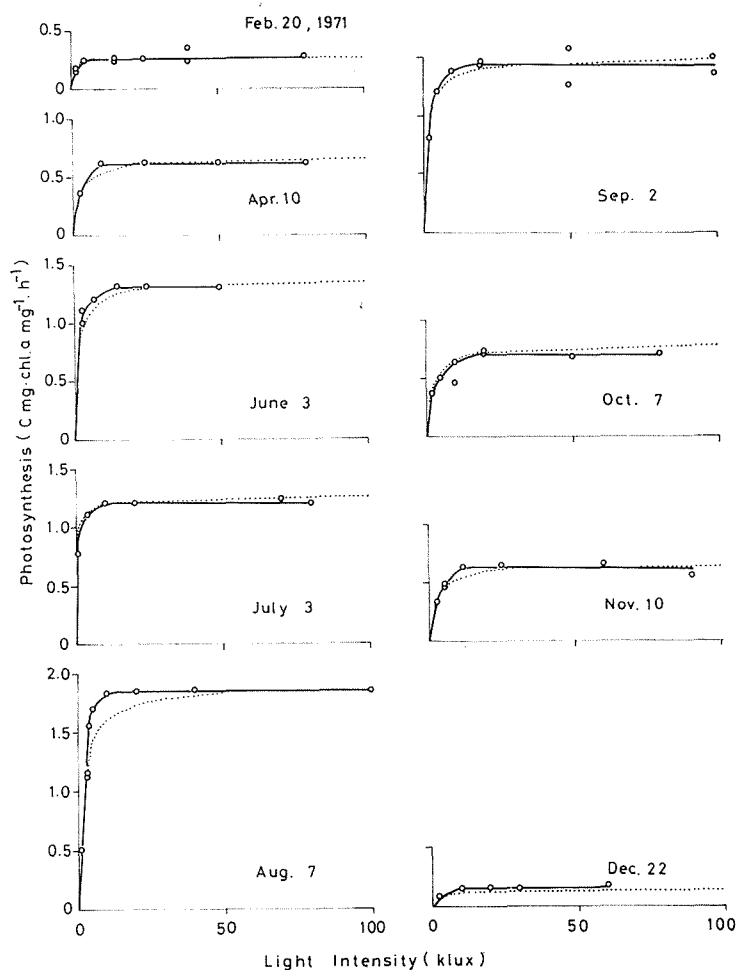


Fig. 6. Photosynthesis-light curves of the suspended algae (solid line) and the curves approximated by hyperbola (dotted line) in the respective months.

The photosynthesis-light curve is represented approximately by the equation,

$$P = \frac{bI}{1+aI} \quad (1)$$

where  $P$  is the photosynthesis ( $\text{mg C} \cdot \text{mg chl. } a^{-1} \cdot \text{h}^{-1}$ ),  $I$  is light intensity (klux), and  $a$  and  $b$  are parameters determined by the experimental data (Fig. 6). The light intensity in sessile algal community is expressed by the equation

$$I(x) = I_0 \exp(-ax) \quad (2)$$

where  $I_0$  = the light intensity (klux) on the top of algal mat,

$x$  = the depth from the top of the algal mat, figured as the amount of chlorophyll  $a$  ( $\text{mg} \cdot \text{m}^{-2}$ ),

$a = 0.023$  determined from Fig. 1b.

As  $I_0$  changes in process of time  $t$  during a day.

$$I_0 = I_0(t) \quad (0 \leq t \leq T) \quad (3)$$

where  $t=0$  represents the time of sunrise and  $t=T$  represents the time of sunset.

The daily gross production ( $P_g$ ) can be expressed by

$$P_g (\text{mg C} \cdot \text{m}^{-2} \cdot \text{day}^{-1}) = \int_0^T dt \int_0^A P dx \quad (4)$$

where  $A$  is the amount of chlorophyll  $a$  ( $\text{mg} \cdot \text{m}^{-2}$ ).

On the other hand, the daily respiration ( $R$ ) is given by

$$R (\text{mg C} \cdot \text{m}^{-2} \cdot \text{day}^{-1}) = rAT_0 \quad (5)$$

where  $r$  = respiration rate ( $\text{mg C} \cdot \text{mg chl. } a^{-1} \cdot \text{h}^{-1}$ ),

$T_0 = 24$  hours.

Here, we assume that the respiration rate is constant independent of time and thickness in the strata of the algae. The daily net production ( $P_n$ ) can be obtained from the equations (1), (2), (3), (4) and (5),

$$P_n = \int_0^T dt \int_0^A \frac{bI_0(t) \exp(-ax)}{1+aI_0(t) \exp(-ax)} dx - rAT_0 \quad (6)$$

As the light intensity at the study site did not change symmetrically from sunrise to sunset, the daily change in the light intensity could not be expressed as an equation. Hence, the daily gross production was estimated by integration of the respective values of hourly gross production from sunrise to sunset. For calculation of the hourly gross production, intermediate values approximated by segment of line connecting two neighbouring observed values were used as  $I_0(t)$ .

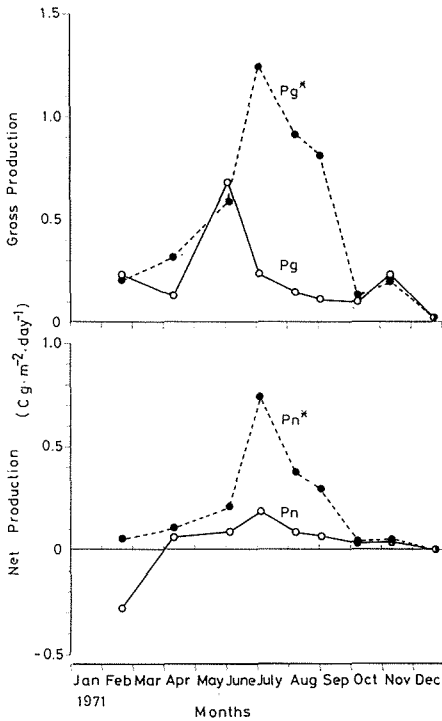


Fig. 7. Seasonal changes in daily gross production (Pg) and daily net production (Pn) of sessile algal community. Pg\*: daily gross production calculated from the optimal amount of chlorophyll *a* which gives the maximum daily net production (Pn\*).

Seasonal changes in the daily gross and net production of sessile algal community are shown in Fig. 7. The daily gross and net production varied seasonally over ranges of 16 (December) to 680 mg C·m<sup>-2</sup>·day<sup>-1</sup> (June) and -243 (February) to 166 mg C·m<sup>-2</sup>·day<sup>-1</sup> (June), respectively. The daily net production in February showed a highly negative value. This value resulted from the fact that the daily respiration of the community exceeded far the daily gross production due to extremely large amount of chlorophyll *a*.

There are very few informations on the daily production of the sessile algae in canyon section or in upper part of Japanese mountain rivers or streams, excepting the two papers by KOBAYASHI (1961b and 1972). In order to compare his data with the present ones, the authors calculated roughly the daily gross production expressed as "mg C·m<sup>-2</sup>·day<sup>-1</sup>" using his data of the daily gross production per chlorophyll unit (mg O<sub>2</sub>·mg chl.<sup>-1</sup>·day<sup>-1</sup>) and chlorophyll amounts, and conversion factor of 0.33 from oxygen to carbon unit. The daily gross production thus obtained ranged from 0 to 593 mg C·m<sup>-2</sup>·day<sup>-1</sup> in canyon section of the River Arakawa and from 211 to 380 mg C·m<sup>-2</sup>·day<sup>-1</sup> in the Chigonosawa Stream. A comparison of these values with the present ones indicates that the daily gross production of sessile algal community seems not to exceed 1,000 mg C·m<sup>-2</sup>·day<sup>-1</sup> in small mountain streams like the Chigonosawa and in canyon section of Japanese rivers.

TOMINAGA and ICHIMUA (1966) reported that the daily gross production in lower part of mountain region of the River Arakawa varied seasonally from 2,500 mg O<sub>2</sub> (ca. 910 mg C)·m<sup>-2</sup>·day<sup>-1</sup> in January to 11,000 mg O<sub>2</sub> (ca. 4,110 mg C)·m<sup>-2</sup>·day<sup>-1</sup> in July. The daily gross production of sessile algal community in canyon section of the River Arakawa and in the Chigonosawa Stream is very low as compared with that in lower part of the River Arakawa. What

are the reasons for such a noticeable difference in the daily gross production between them? The following reasons will be suggested:

- (1) Canyon section of the River Arakawa and the Chigonosawa Stream are very different in light condition from lower part of the River Arakawa. After KOBAYASHI (1961b and 1972), the open sky is 20–50% of the whole celestial hemisphere in canyon section of the River Arakawa, and 3.1–29.9% during the period of foliation and 16.9–39.2% during the defoliation period in the Chigonosawa Stream, whereas it was 60–80% in lower part of mountain region of the River Arakawa. This fact suggests that the daily primary production of sessile algal community in the canyon section and in the Chigonosawa Stream is strongly limited by shorter duration of insolation.
- (2) As described in the previous section, in general, standing crop as chlorophyll or chlorophyll *a* amount in upper part of the River Arakawa and in the Chigonosawa Stream is less than that in lower part of the River Arakawa. The standing crop in the upper part and in the Chigonosawa Stream may not be enough to increase the daily gross production.
- (3) After TOMINAGA and ICHIMURA (1966), photosynthetic activity of the suspended algae in lower part of the River Arakawa is 2–3 times higher than that in the canyon section and in the Chigonosawa Stream. They speculated that lower photosynthesis in the canyon section is related mainly to lower water temperature and nutrient concentration.

Relatively low daily gross production of the sessile algae in the Chigonosawa Stream seems to be closely related to shorter duration of insolation and lower standing crop and photosynthesis.

As shown in Fig. 5a and b, in the case of a rapid stream, photosynthesis of the suspended algae showed lower rate than that of the natural sessile algal community on stone. Therefore, we should mind the fact that, in the present study, the daily primary production estimated by the chlorophyll method may have been underestimated in certain months with high current velocity.

##### 5. *An attempt to estimate the optimal amount of chlorophyll a in reference to the maximal daily net production*

MONSI and SAEKI (1953) and KUROIWA and MONSI (1964) advanced the equations to obtain the optimum leaf area index (the leaf area index which gives the maximum daily surplus production) in terrestrial plants. It is interesting to know whether chlorophyll *a* amounts observed in the respective months are optimal amounts which give the maximum daily net production or not.

The dependence of daily net production on the *A* (chlorophyll *a* amount) corresponding to thickness of the sessile algal mat was investigated. Here, we assume that photosynthesis-light curves of the sessile algae in the respective months do not change significantly even if chlorophyll *a* fluctuates from the observed amount to the optimal one.

Differentiating the equation (6) with respect to *A*,

$$\frac{dP_n}{dA} = \int_0^T \frac{bI_0(t) \exp(-\alpha A)}{1 + aI_0(t) \exp(-\alpha A)} dt - rT_0 \quad (7)$$

Differentiating the equation once more,

$$\frac{d^2P_n}{dA^2} = \int_0^T \frac{-\alpha bI_0(t) \exp(-\alpha A)}{\{1 + aI_0(t) \exp(-\alpha A)\}^2} dt \quad (8)$$

It is found that  $\frac{dP_n}{dA}$  is monotone decreasing function with respect to  $A$  because  $\frac{d^2P_n}{dA^2}$  is negative. If there exists a positive value  $A^*$  such that the equation (7) becomes zero when  $A=A^*$ ,

$$\begin{aligned} \frac{dP_n}{dA} > 0 & \quad \text{for } 0 \leq A < A^* \\ \frac{dP_n}{dA} < 0 & \quad \text{for } A^* < A \end{aligned}$$

Therefore,  $P_n$  takes the maximum value when  $A=A^*$  (cf. Kuroiwa, 1979). Because  $\frac{dP_n}{dA}$  approaches a negative value  $-\tau T_0$  as  $A$  goes to infinity, the condition on the existence of  $A^*$  is that the value of the equation (7) for  $A=0$  is positive. From the equation (6), the maximum daily net production  $P_n^*$  is expressed by

$$P_n^* = \int_0^T dt \int_0^{A^*} \frac{bI_0(t) \exp(-\alpha x)}{1+aI_0(t) \exp(-\alpha x)} dx - \tau A^* T_0 \quad (9)$$

and the equation determining the value of  $A^*$  is

$$\int_0^T \frac{bI_0(t) \exp(-\alpha A^*)}{1+aI_0(t) \exp(-\alpha A^*)} dt = \tau T_0 \quad (10)$$

If the time dependence of the light intensity can be approximated by the next symmetric function (KUROIWA and MONSI, 1964; IKUSIMA, 1967; KUROIWA, 1968)

$$I_0 = I_{\max} \sin^2\left(\frac{\pi t}{T}\right), \quad (11)$$

the integral in the equation (10) can be calculated and an explicit form of  $A^*$  can be obtained (cf. Appendix).

As mentioned before, the equation (11) cannot be used because the daily change in the light intensity at the station was not symmetric. Therefore, the value of  $A^*$  satisfying the equation (10) was determined by numerical calculation of computer, using the intermediate values between observation time as  $I_0(t)$ .

Seasonal changes in the values of  $A^*$ ,  $P_n^*$  and  $P_g^*$  (daily gross production at  $A^*$ ) thus obtained are shown in Figs. 4b and 7. The optimal amount of chlorophyll  $a$  which gives the maximum daily net production ( $P_n^*$ ) varied seasonally from 22.1 mg·m<sup>-2</sup> in December to 146.6 mg·m<sup>-2</sup> in July. As a general trend, the observed amount of chlorophyll  $a$  of sessile algal community was very low from April to September as compared with the optimal amount, while from October to December it was not so different from the optimal one (Fig. 4b). Taking into consideration the seasonal change in water level at a small lock near the station, the stream bed during April-September with relatively low amount of chlorophyll  $a$  seems to be physically unstable (cf. Fig. 2b). After TETT *et al.* (1978), sessile algal biomass varies irregularly by the degree of flooding during short-term period. Further, HORNER and WELCH (1981) pointed out that chlorophyll amount decreased in high velocity. One of the reasons for such relatively

low amount of chlorophyll *a* in physically unstable seasons may be ascribed to the possibility that considerable amounts of sessile algae are scraped away frequently by small-scale flooding. In contrast with this, the observed amount of chlorophyll *a* in February of 1971 exceeded far the optimal amount.

In comparison of seasonal change in the observed amount of chlorophyll *a* with that in the optimal amount, it can be expected that in the Chigonosawa Stream, standing crop of sessile algal community does not reach the optimal level in seasons with much precipitation, while it is equal to or exceeds the optimal level in seasons with less or little precipitation.

In the present study, seasonal change in standing crop of the sessile algal community with reference to the optimal standing crop was discussed only on the basis of physical process through precipitation. In some cases, however, variation of the standing crop may be brought about by grazing of herbivorous aquatic insects.

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### Appendix

Applying the equation (11) to the equation (10), we get

$$\int_0^T \frac{bI_{\max} \sin^2\left(\frac{\pi t}{T}\right) \exp(-\alpha A^*)}{1 + aI_{\max} \sin^2\left(\frac{\pi t}{T}\right) \exp(-\alpha A^*)} dt = rTo \quad (\text{A1})$$

Putting  $\frac{\pi t}{T} = \tau$  and  $\frac{\exp(\alpha A^*)}{aI_{\max}} = k^2$ , (A1) is rewritten as

$$\int_0^\pi \frac{\sin^2 \tau}{k^2 + \sin^2 \tau} d\tau = \frac{\pi a r T o}{b T} \quad (\text{A2})$$

Integration of the left side gives  $\pi\left(1 - \frac{k}{\sqrt{k^2+1}}\right)$ , and

$$k^2 = \frac{(bT - arTo)^2}{arTo(2bT - arTo)} \quad (\text{A3})$$

Because  $A^* = \frac{1}{\alpha} \ln(ak^2I_{\max})$ , the explicit form of  $A^*$  can be obtained as

$$A^* = \frac{1}{\alpha} \ln \left\{ \frac{I_{\max}(bT - arTo)^2}{rTo(2bT - arTo)} \right\} \quad (\text{A4})$$