水田における炭素循環に関する研究 第2報

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Cycling of Carbon in a Paddy Field

II. Biomass and gross production of algae*

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In the paddy field ecosystem, there are three kinds of producers, that is, rice plants, weeds and algae. They all participate in the carbon cycling through photosynthesis and respiration, supplying organic matter to consumers, decomposers, etc.

There are few studies on algae viewed as producers in the paddy field. Ichimura[5] estimated the standing crop of planktonic algae in a paddy field and their photosynthetic performance under field conditions. Kurasawa[7] made similar researches. Recently, Saito and Watanabe[10] estimated biomass and photosynthesis of algae both in the flooding water and on the soil surface in a paddy field in the Philippins.

However, the information available is too poor to delineate the whole picture of carbon cycling in the paddy field ecosystem.

The objectives of this study are to evaluate the biomass and organic matter production of algae in a paddy field and to examine the factors affecting them.

Materials and Methods

1. *The research field and the manner of manogement*

Observations in this study were conducted simultaneously with those in Part I of this series, using the same paddy field. The conditions and manners for managing the field were as described in the previous paper[14].

2. *Measurement of algal biomass*

As will be described later, algae in the field were grouped into three categories, i.e., benthic, semi-benthic and planktonic ones.

Samples for benthic and semi-benthic algae were collected randomly at 12 places in the field plus 2 places inside the chamber in which CO_2-exchange was measured. The sampling intervals were about 10 days. Size of the core used for the sampling was 20 cm^2 in bottom area. At the time of sampling, benthic algae were collected together with a thin layer of surface soil. The core which included benthic and semi-benthic algae and soil were ground in a mortar for a few minutes after adding a small amount of basic magnesium carbonate. The contents of the mortar were washed with 100% aceton into a bottle. After adding more aceton, the samples were stored in a refrigerator until chlorophyll was determined. Just before determining chlorophyll, concentration of the aceton was adjusted accurately to 90%. Chlorophyll-a (chl-a) was determined according to Lorenzen's method[8] after centrifuging the sample. As for specific absorption coefficient of chl-a, a value of 84 was applied (Wetzel and Westlake[12]).

Biomass of planktonic algae was measured by the following procedure. A 2-liter sample of the flooding water was collected from 12 places in the field and filtered through a grass fibre filter under a reduced pressure. The filter, on which planktonic algae were sedimented, was treated in the same way as core samples for benthic and semi-benthic algae. Using the resultant aceton solution of chlorophyll, chl-a was determined. At the same time with the collection of samples for planktonic algae, depth of the flooding

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water was measured at 50 places. Biomass of planktonic algae per unit area was calculated by multiplying chl-a concentration of the flooding water by the average water depth. Measurement of planktonic algae was done on May 28, June 18 and July 17.

In this paper, algal biomass is represented by the amount of chl-a obtained as above.

3. *Estimation of "community metabolic rate (CMR)" and algal photosynthesis (Pg)*

Amount of dissolved CO_2 in a whole water column of flooding water, i.e., DIC (concentration of total dissolved inorganic carbon) multiplied by depth of the flooding water (L), varies with time owing to (1) CO_2 uptake through algal photosynthesis, (2) CO_2 release through respiration of algae and other organisms (R), (3) CO_2 exchange between the atmosphere and the flooding water (CER), (4) loss of CO_2 into the soil accompanying percolating water (F_1) and (5) diffusion of CO_2 from the soil into the flooding water (F_2).

Theoretically, the variation in the amount of dissolved CO_2 in a whole column of flooding water is expressed by the following equation,

$$\frac{d(DIC \times L)}{dt} = -Pg + R + CER - F_1 + F_2 \quad \cdots\cdots\cdots\cdots(1)$$

where Pg, R, CER, F_1 and F_2 are expressed in terms of $mgCO_2/m^2/hr$, DIC, in $mgCO_2/l$ and L, in mm. CER in negative values indicates CO_2 evolution from the flooding water into the atmosphere and in possitive, CO_2 absorption.

As F_1 is defined as the mass flow of CO_2 with percolating water into the soil, it can be rewritten,

$$F_1 = -\frac{dL}{dt} \times DIC \cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots(2)$$

from the formulae (1) and (2)

$$Pg - R - F_2 = -\frac{d(DIC \times L)}{dt} + \frac{dL}{dt} DIC + CER \cdots\cdots\cdots\cdots\cdots(3)$$

consequently,

$$Pg - R - F_2 = \frac{1}{t_2 - t_1} \times \frac{L_2 + L_1}{2} (DIC_1 - DIC_2) + CER \cdots(4)$$

where DIC_1, DIC_2 and L_1, L_2 are the values of DIC and L at the time t_1 and t_2, respectively.

($Pg—R—F_2$) represents the situation of carbon metabolism of the flooding water community which consists of algae, small animals, etc., although F_2 comes from the outside of the community. Thus, ($Pg—R—F_2$) will be called "community metabolic rate" or CMR in this paper.

Out of data necessary for calculating CMR, those for DIC and CER were obtained as described in the previous paper[14]. L inside the chamber in which CER and DIC were measured was estimated from the water depth outside the chamber. Correction was made for the difference in the level of soil surface between the inside and outside of the chamber. But it was assumed that there was no difference in water level between the inside and outside.

Observations in this study were conducted under decreasing flooding water, for under reverse conditions mass flow of CO_2 from the soil into the water occurred.

4. *Observation of environmental conditions inside and outside the chamber*

Principal environmental factors were observed inside and outside the chamber according to the method in the previous paper[14].

Results and Discussion

1. *Seasonal trend of the algal community compcsition*

According to the visual observation, algae in the paddy field were grouped into 3 categories. The first one involves algae which grow on the soil surface forming thin carpet-like colonies. With microscopic observation, these colonies were found to be composed of diatoms, green algae and blue green algae. Just after transplanting of rice seedlings, the colonies formed many air bubbles on the surface in the daytime. As a result, they separated from the soil and floated in the flooding water. In this paper, algae of this kind are called "benthic algae".

The second group of algae are filamentous poly-cellular green algae. The major part of the filament floats in the flooding water but a part of it attaches to or penatrates into the soil. Algae of this kind are tentatively called "semi-benthic algae" in this paper.

The third group of algae are planktonic ones. They seemed to be unicellular and are called "planktonic algae" in this paper.

According to visual and microscopic observation, the composition of algal community changed with time. At the early stages, benthic algae were dominant. In the second half of the rice growing period, semi-benthic algae predominated. Planktonic algae looked inferior during rice growing season, although they had a short bloom just after transplanting of rice seedlings.

Further changes in specific composition in each group of the algal community were also observed. Blue green algae in benthic group appeared in considerable population just after transplanting, when algal bloom occurred, but thereafter declined. On the other hand, benthic diatoms did not show such a large change. Dominant species in the last one month, when the field had been drained, seemed to belong to semi-benthic group. However, they were a little different in the appearance from those dominant in the flooding period.

2. *Seasonal trend of algal biomass*

Biomass of algae expressed as the amount of chl-a per unit land area is presented in Fig. 1. Table 1 shows proportion of biomass of planktonic algae to total algal biomass. The proportion was about 5% even at its bloom. Further, there was a possibility that on May 28 the sample for planktonic algae was contaminated by fragments of benthic algae. Considering these, we concluded that biomass of planktonic algae was very little compared with that of other groups during the rice growing seasons. Therefore, we examined the movement of algal biomass based simply on that of the benthic and semi-benthic group in the following observation.

Table 1. Biomass of planktonic algae, benthic algae and semi-benthic algea, expressed as the amount of chlorophyll-a(chl-a).

Date		Planktonic algae	Benthic and semi-benthic algae (mgchl-a/m²)	Total biomass
May	28	3.2	56.9	60.1
June	18	0.42	31.3	31.7
July	17	0.16	41.9	42.1

Fig. 1 shows the biomass of these two groups. There was large variation in algal biomass among samples collected on one and the same day. This large variation shows uneven distribution of algae in the field. However, it is apparent that the mean value increased with time until late in the season. The amount of chl-a ranged from 30 to 183 mg/m² in this study. The range is equivalent to 40–244 mg chl-(a+b) if we assume the chl-a/chl-b ratio to be 3. According to Aruga[1)], the amount of total chlorophyll is 11–123 mg/m² for mesotrophic lakes and 100–290 mg/m² for eutrophic lakes. Therefore, the values obtained in this study are comparable to those for mesotrophic or eutrophic lakes.

The increase in algal biomass with time can be attributed to slower turnover of algae in the late season as will be described later. The change in the turnover rate of biomass may have been based on the alter-

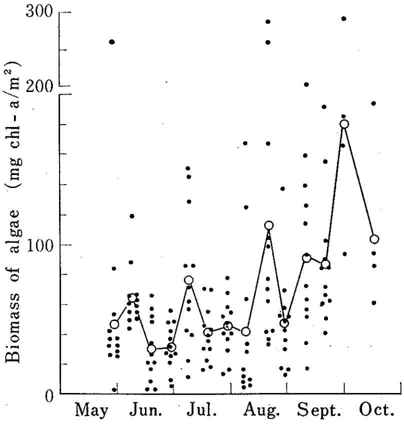

Fig. 1. The seasonal trend in the algal biomass.

● : value for each sample taken at various places on the same day.

○ : average for those.

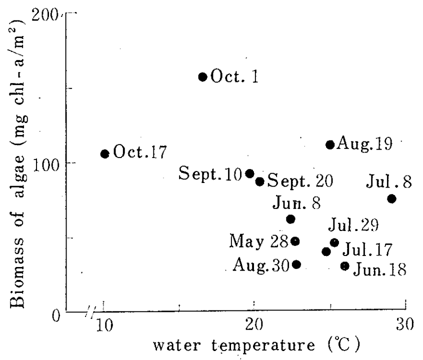

Fig. 2. Relationship between algal biomass and water temperature. Values of water temperature are the average for the period 3days before algal sampling.

nation of dominant species, from benthic to semi-benthic, because the latter were much larger in size and seemed to have longer life span compared with the former. What factor, then, is responsible for the alternation of the dominant species?

A fairly close relationship was detected between water temperature and algal biomass (Fig. 2). This may be taken to suggest that water temperature is the main cause for the alternation of dominant species. The increase in biomass of algae with lowering temperature was mainly caused by increase in biomass of semi-benthic algae according to visual observation. This coinsides with the evidence reported by YAMAGISHI and HASHIZUME[12] that the optimum temperature for emergence of filamentous algae, in this paper called semi-benthic, in a paddy field has been fairly low.

After spraying "Sumichion®", a kind of insecticide, algal biomass tended to increase temporalily (Figs. 1 and 2, Jul. 8 and Aug. 19). The same tendency was detected in a preliminary experiment conducted in 1977. These facts suggest that grazing pressure acts as one of the factors determining the level of algal biomass in the flooding water and on the soil surface in paddy fields.

As will be described later, the turnover rate of algae decreases with time, or in accordance with the successional change in dominant algal species. The lowering in turnover rate might be partly due to decrease in the grazing rate, as it is well known that the larger the cell size of phytoplankton is, the lower the rate of predation is. Moreover, HARGRAVE and GEEN[4] observed that filamentous green algae and other chain-forming diatoms were not eaten by copepods. Thus, the change in water temperature might result in the change in algal biomass through the alternation in dominant species.

3. *Diurnal changes in the community metabolic rate (CMR) and the gross photosynthetic rate (Pg)*

The diurnal patterns of CMR are presented in Fig. 3 with those of intensity of photosynthetic active radiation on the surface of flooding water (PARt). The PARt values were obtained as the product of total solar radiation on the leaf canopy with 0.535 and transmittance of the leaf canopy for PAR. Factor 0.535 is the average proportion of PAR to total solar radiation (short wave) reported by KISHIDA[6]. The transmittance of rice canopy was measured using silicon photocells sensitive to visible rays.

In all cases, CMR increased with PARt after sunrise to the highest value at the middle of the day and then decreased. The amplitude of the diurnal cycles of CMR became smaller with days after transplanting in accordance with decrease in light transmittance of the rice canopy.

As CMR is the sum of CO_2 release through respiration of organisms (R), diffusion of CO_2 from the soil into the flooding water (F_2) and CO_2 uptake through algal photosynthesis (Pg), it is possible to calculate Pg as CMR−(R+F_2), if we can estimate daytime (R+F_2). Considering the nature of (R+F_2), it is expected that this is strongly affected by water temperature. In the flooding period, however, no apparent correlation was detected between water temperature and CMR at night (at night, Pg=0, so CMR=−R−F_2). Therefore, Pg was estimated assuming that (R+F_2) was constant all the day and equal to the average level at night. The level is presented by a broken line in each of Fig. 3 a-d. On the other hand, after drainage, a

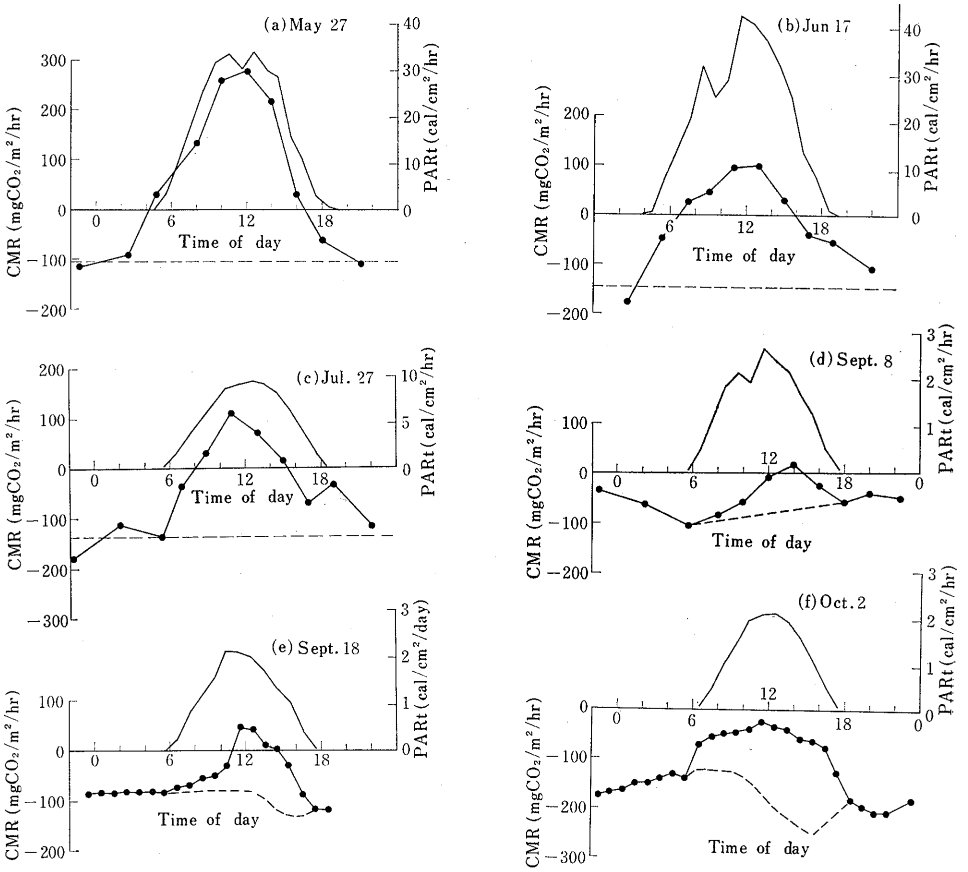

Fig. 3. Diurnal variations in the community metabolic rate (CMR) and photosynthetically active radiation under the rice leaf canopy (PARt). Broken lines represent the estimated rates of community respiration. See the text in detail.

negative correlation was detected between soil temperature and CMR at night on each day. Therefore, $(R+F_2)$ in the daytime was estimated from the soil temperature at each time of day and soil temperature-CMR relationship at night. $(R+F_2)$ values estimated by this procedure are shown by broken lines in Fig. 3e, f. Thus gross photosynthesis of algae on unit land basis derived on the above-mentioned assumptions is presented by the distance between the thick full line and the broken line in Fig. 3.

4. *Light-photosynthesis relationship*

The relationship between Pg and PARt derived from their diurnal changes are shown in Fig. 4. In these figures, Pg is expressed as the amount of carbon assimilated per unit weight of chl-a. The forms of light-photosynthesis curves are not regular nor consistent probably due to errors in estimating Pg. It is apparent, however, that Pg increases with PARt without signs of light-saturation until the highest PARt attained, for example, 30 cal/cm^2/hr on May 27 and 40 cal/cm^2/hr on June 17. It is also clear that the slope of light-photosynthesis curve became larger with time.

The benthic algae which are dominant in the early season appeared to inhabit among soil particles near the soil surface, as observed by HARGRAVE[3] in the sediments of Marion Lake. GARGAS[2] found that more than 50% of gross production of algae in the surface sediments to the depth of 10 mm was done in 2–10 mm depth

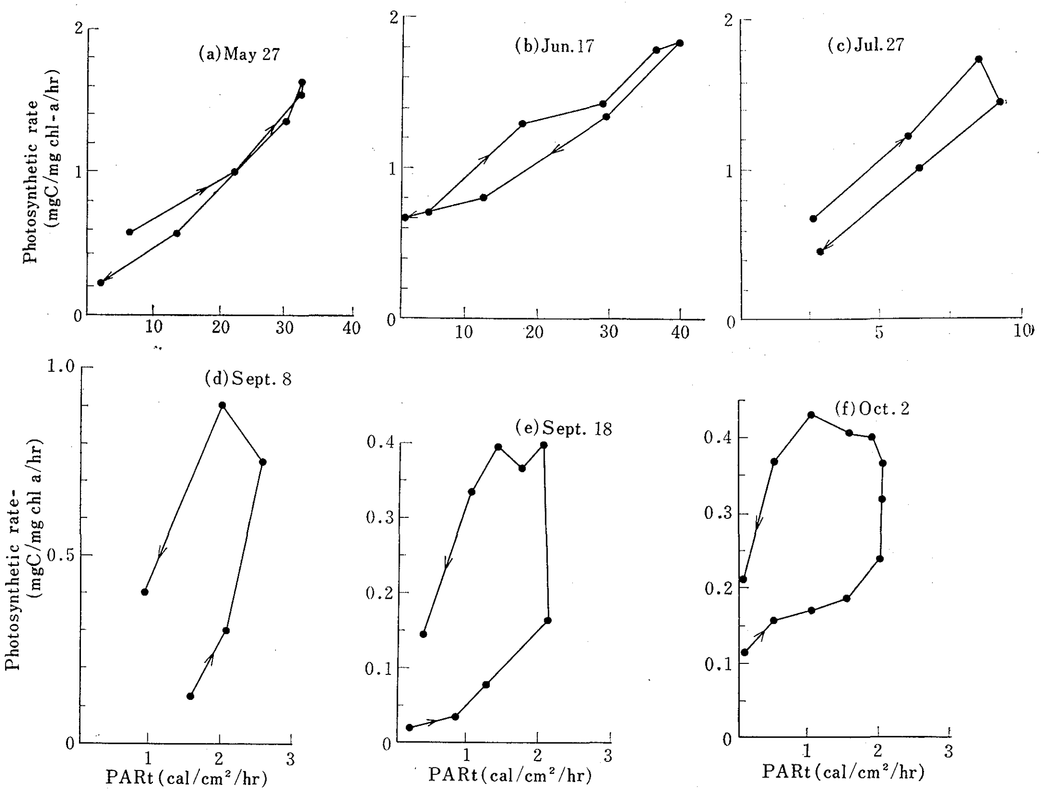

Fig. 4. Relationships between the gross photosynthetic rate of algae on chlorophyll-a basis and photosynthetically active radiation under the rice leaf canopy (PARt).

layer when sediments were dispersed within the water. If this hold true for the present case, a large part of gross production of benthic algae may have been done under disadvantageous conditions in receiving light. This may explain the gentler slope of the light-photosynthesis curve in the early season when benthic algae were dominant.

5. *Daily gross production* (*ΣPg*), *the turnover rate and efficiency of solar energy utilization* (*Eg*) *in each period of rice growing season*

Using the data presented in Fig. 3, daily total gross production (ΣPg) was estimated and related with daily total PARt (ΣPARt) (Fig. 5). ΣPg increased proportionally with ΣPARt and then attained a plateau.

In Fig. 5, ΣPg under a large ΣPARt was obtained in the early season. Therefore, the relationship represents not only the direct effect of ΣPARt on ΣPg but also the influence of environmental factors and difference in dominant algal species. Consequently, on the heavily cloudy day in the early season, the ΣPg values may be different from the value estimated on the basis of the ΣPARt-ΣPg curve. But such a case is considered to be very few. Thus, the average daily gross production in each period was estimated according to the following procedure,

$$\overline{\Sigma Pg'} = \overline{\Sigma Pg} \times Ca \quad \cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots (5)$$

where $\overline{\Sigma Pg}$ is the average daily gross production on chl-a basis in a period estimated from the curve in Fig. 5 and the average ΣPARt in the same period ($\overline{\Sigma PARt}$). Ca is the average amount of chl-a per unit land area in the same period obtained as an arithmetic mean of the amounts of chl-a at the beginning and the end of the period. $\overline{\Sigma Pg'}$ is the average gross production in the period expressed as mgC/m²/day.

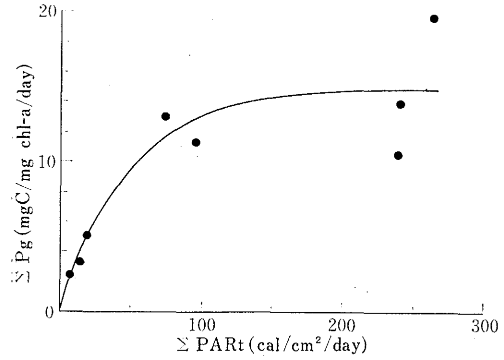

Fig. 5. Relationships between the daily total of algal gross productionon chlorophyll-a basis (ΣPg) and that of photosynthetically active radiation under the rice leaf canopy ($\Sigma PARt$).

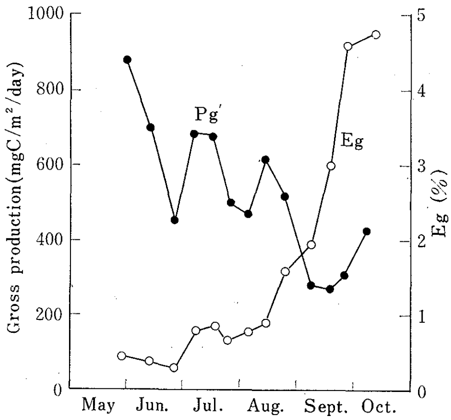

Fig. 6. Seasonal trends in the daily total gross production of algae on land area basis ($\overline{\Sigma Pg'}$) and the efficiency of photosynthetically active energy for algal photosysnthesis (Eg).

The efficiency of solar energy utilization for gross production in a period (Eg) was calculated as follows:

$$Eg(\%) = \frac{\overline{\Sigma Pg'} \times fc}{\overline{\Sigma PARt}} \times 100 \cdots\cdots\cdots\cdots\cdots (5)$$

where fc is the convertion factor from unit weight of carbon to the calorific value, being evaluated at 10 kcal/gC, after Odum⁹⁾.

The turnover rate of algae, i.e. daily net production per algal biomass was calculated in terms of carbon, assuming the carbon/chl-a ratio to be 30 gC/gchl-a after WETZEL and WESTLAKE¹²⁾ and the Pn/Pg ratio, 60% after STEEMAN NIELSEN¹¹⁾.

The results are shown in Table 2 and Fig. 6. $\overline{\Sigma Pg'}$ was the highest in the first period, amounting 881 mgC/m²/day. After that it decreased with time to fall to a level of 300–400 mgC/m²/day in the last few periods. The reduction in $\overline{\Sigma Pg'}$ was much

Table 2. Gross production, the turnover rate and efficiency of solar energy utilization for gross production (Eg) of algae.

Period	Algal biomass (mgchl-a/m²)	$\overline{\Sigma PARt}$* (cal/cm²/day)	Gross production $\overline{\Sigma Pg}$ (mgC/mgchl-a/day)	Gross production $\overline{\Sigma Pg'}$ (mgC/m²/day)	Eg (%)	Turnover rate (day⁻¹)
I May 27-June 7	59.5	198	14.8	881	0.44	0.30
II June 8-June 16	47.2	193	14.8	699	0.36	0.30
III June 17-June28	31.3	156	14.7	458	0.29	0.29
IV June 29-July 6	53.7	86.3	12.8	688	0.80	0.26
V July 7-July 16	57.7	78.6	11.9	686	0.87	0.24
VI July 17-July 28	42.7	73.3	11.5	490	0.67	0.23
VII July 29-Aug. 7	44.3	60.5	10.7	474	0.78	0.21
VIII Aug. 8-Aug. 18	78.3	60.5	8.0	626	0.90	0.16
IX Aug. 19-Aug. 29	80.5	49.7	6.5	523	1.66	0.13
X Aug. 30-Sep. 9	71.1	32.2	4.1	292	1.99	0.082
XI Sep. 10-Sep. 19	91.7	9.2	3.0	275	3.00	0.060
XII Sep. 20-Sep. 30	136	6.7	2.3	312	4.63	0.046
XIII Oct. 1-Oct. 17	145	9.1	3.0	435	4.78	0.060
Whole period (144 days)	74.7	9976 cal/cm²		71.0 gC/m²	0.71	0.190

* Average daily total photosynthetically active radiation under rice leaf canopy.

less than that in $\overline{\Sigma \mathrm{PARt}}$. There may be two reasons for this. One is increase in algal biomass with time. The other is increase in the photosynthetic efficiency on chl-a basis indicated by the increased slope of the light-photosynthesis curve (Fig. 3).

The turnover rate of algae was the highest in the early season (0.30 day^{-1} in the period I and II) and lowered gradually with time. In the last period, it was only 0.046 day^{-1}. The above-mentioned facts clearly show that higher levels of algal biomass in the later periods can be attributed to a much slower turnover rate in algal biomass. The mean turnover rate for the whole period was 0.13 day^{-1}. This rate is comparable to the average rate for ocean (0.09 day^{-1}) obtained by Ryther and the rate for Lake Suwa (0.16 day^{-1}) by Hogetsu, as reported by Aruga1).

Eg was low in the early periods, increased with time and attained the maximum value in the last period. The Eg value in the last period was more than ten times as large as those in the early periods. The increase in Eg with time can be ascribed to the increase in algal biomass and in the efficiency of PARt utilization on chl-a basis.

6. *Total amount of algal gross production in the whole rice growing season*

Total amount of algal gross production in the whole experimental period (144 days) derived from the data in Table 2 amounted to 71 gC/m^2 (0.49 gC/m^2/day). The magnitude is close to the value obtained by Saito and Watanabe10) in a field in the Philippins. Comparing these values with those in lakes, 0.18–1.72 gC/m^2/day1), it may be tentatively concluded that paddy fields have a high algal productivities comparable to those in eutrophic lakes.

Summary

Biomass and photosynthesis of algae in a paddy field were examined during the whole rice growing season. Results obtained are as follows:

1. Total algal biomass expressed as the amount of chlorophyll-a(chl-a) per unit land area was small in the early season, increased with time and attained the highest value at the last stage of rice growth. The value ranged between 30–183 mgchl-a/m^2 depending on the time.
2. In the early season, benthic algae were dominant and in the later season "semi-benthic" i.e. filamentous algae predominated. The alternation in dominant species was considered to be brought about by lowering water temperature with time.
3. The algal photosynthetic rate varied in phase with intensity of photosynthetically active radiation incident on water surface (PARt). The amplitude of the diurnal cycles of the photosynthetic rate on unit land area basis was large in the early season and diminished with time as the rice canopy closed.
4. No sign of saturation was detected in the light-photosynthesis relationship in the range of light intensity attained. The slope of the light-photosynthesis curve on chl-a basis got steeper with time.
5. Daily gross photosynthesis was largest at the earliest period of the rice growing season (881 mgC/m^2/day) and decreased with time. In the last period it fell to a level of 300–400 mgC/m^2/day.
6. Efficiency of photosynthetically active radiation energy for gross production was low in the early season (0.24–0.42%), increased with time and attained the highest value at the last stage (4.78%).
7. The turnover rate of algal carbon was high at the early stages (0.30 day^{-1}) and decreased with time. At the last stage, it was only 0.046 day^{-1}. This low turnover rate might explain why algal biomass increased with time in the later half of rice growing season in spite of reduction in the daily gross production caused by decline in PARt.
8. Total gross production in the whole experimental period (144 days) amounted to 71 gC/m^2/day. The magnitude is comparable to those for eutrophic lakes.

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* In Japanese with English summary
** In Japanese

〔和文摘要〕

水田における炭素循環に関する研究

第2報　ソウ類の種類，現存量および総生産量の季節的変動

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水田生態系においてソウ類は，イネ，雑草とともに一次生産者として光合成を行ない，生産物を消費者や分解者に供給している．本報告は，ソウ類の現存量・光合成量の季節的推移を調べ，併せてその変動の要因について検討を行なったもので，得られた結果は次の通りである．

1．ソウ類の現存量は，イネ作付期間中の初期に小さく，季節のすすみに伴い増加した．特に稲生育中期以降の増加が顕著であった．クロロフィル量であらわした現存量は 30～183 mg/m^2 で中栄養湖ないしは富栄養湖のそれに相当した（第1図）．

2．ソウ類は主に土壌表面に付着するものとミドロ類で，浮遊性のものは極めて少なかった（第1表）．初期には付着性ソウ類が，後期にはミドロ類が優占した．このような優占種の交替は水温の低下によりもたらされるものと推察された（第2図）．

3．ソウ類の光合成速度の日中における経過は日射強度のそれとほぼ並行した（第3図）．両者の日変化から求めた光-光合成曲線には，光飽和の傾向が認められなかった．光合成速度をクロロフィル当りでみた時，光-光合成曲線の勾配は水稲の初期に緩く，季節のすすみに伴い大きくなった（第4図）．この変化は，付着性ソウ類からミドロ類への優占種の変化と対応するものと考えられた．

4．1日当りの総生産量は，初期 881 mgC/m^2 であったが次第に低下し，後期には 300～400 mgC/m^2 となった（第2表，第6図）．

5．水稲の葉層を通過し田面に到達した光合成有効放射の総生産への利用効率は初期には 0.24～0.42% と低く，その後次第に増加し，最大値は 4.78% と極めて高い値を示した（第2表．第6図）．

6．ソウ類のターンオーバーレートは初期には大きい（0.3 回/日）が後期にはその 10% 程度（0.04 回/日）に低下した（第2表）．このことが季節のすすみに伴い田面に到達する光の強度が低下し，光合成量が減少するにもかかわらず，現存量が増加した要因と考えられた．

7．測定期間中（5月27日より10月17日までの144日間）の総生産量は 71 gC/m^2，1日当り 0.49 gC/m^2 で，この値は富栄養湖における一次生産量に匹敵する．

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