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THE PRIMARY PRODUCTION OF PHYTOPLANKTON IN LAKE BALATON APRIL—SEPTEMBER 1972

SÁNDOR HERODEK and GIZELLA TAMÁS

Biological Research Institute of the Hungarian Academy of Sciences, Tihany, Hungary

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Numerous data are available on the number and biomass of planktonic algae in Lake Balaton (ENTZ et al., 1937; SEBESTYÉN et al., 1951; SEBESTYÉN, 1953; TAMÁS, 1955; 1967; 1969).

The chlorophyll content of the water (FELFÖLDY, 1963) and in the lake the photosynthesis of algae obtained from pure cultures (FELFÖLDY and KALKÓ, 1958; FELFÖLDY, 1959; 1962) were also studied. Several papers dealt with the light conditions of Lake Balaton (FELFÖLDY and KALKÓ, 1958; ENTZ and FILLINGER, 1961; 1962).

On the other hand a detailed study of the primary production of phytoplankton lagged behind. The production was too low to be measured by the O_2 technique (FELFÖLDY and KALKÓ, 1958), and our Institute was not equipped for ^{14}C measurements. Preliminary investigations by ^{14}C method were carried out in 1961 (BÖSZÖRMÉNYI et al., 1962).

We started in spring of 1972 to study the yearly cycle of the production of phytoplankton. Here the data concerning April—September are published, when the water temperature was above the mean temperature. The data of the other half-year will be published in a separate paper. The illumination, the composition, biomass and production of the phytoplankton were determined fortnightly in four depths. It is hoped that these data may contribute to the construction of the production biological model of the lake, and serve as reference point in studies on the process of eutrophication.

Materials and Methods

Investigations were carried out fortnightly irrespective of the weather. This way all meteorological factors had a probability to occur during the investigations corresponding to their frequency. The investigated point was two kilometres eastwards of Tihany. Water depth, temperature, Secchi transparency were determined at this point. The illumination was measured by Gemware Submarine Photometer (Model No. 268 WA 310) at the surface and at 25, 100, 200, 300 and 370 cm depths, the last value representing the bottom illumination. Total irradiation was measured by the Meteorological Station of Siófok. Water samples were taken in 250 ml glass flasks. Direct illumination of the water samples during further manipulations was avoided.

Of this water 100 ml was transferred into pyrex glass flasks, fitted with normal ground, made directly for this purpose by KUTESZ. They were used for the exposal. The remaining water was conserved by J_2/KJ and served algological determinations.

Algae were counted by UTERMÖHL's (1958) plankton microscope. The biomass was determined from the volume of individuals. In case of more complicated forms it was determined by modelling, while the form of other species was assumed to correspond to simple geometrical solids, and their volume was determined by calculation. Partly earlier (SEBESTYÉN, 1954; TAMÁS, 1955), partly recently determined values were used.

The methods of biomass determination were recently discussed by SCHNESEE and SCHWARTZ (1971), that of primary production measurement by HÜBEL (1971) and VOLLENWEIDER (1969).

To each sample used in primary production measurement 20 μCi $Na_2{}^{14}CO_3$ (Isotope Institute, Budapest) was added. Its specific activity was 290 μCi/mg. The samples were lowered to their original places, and in situ exposed from 10^h to 14^h. The bottles were kept horizontally (ELSTER and MOTSCH, 1966), and were suspended in such a manner that the buoy did not throw shade them. Dark parallel was always prepared. After 4 hours of exposure the samples were put in a dark box, transferred to the laboratory and filtered through a membran filter of 0.2 μ pore size (Sartorius Membranfilter GmbH).

In order to remove radioactive contamination, after the samples also 50 ml previously filtered inactive lake water was passed through the filters, then they were exposed to the fumes of concentrated HCl for four minutes. The filters were then dissolved in 10 ml Bray solution. One liter of this scintillation liquid contains in addition to dioxane 0.2 g POPOP, 4.0 g PPO, 60.0 g naphtalene, 20 ml ethylene glycol and 20 ml methanol. As the filters dissolved the algae were suspended in the liquid.

Radioactivity was measured by USB-2 liquid scintillation detector (Biuro Urzadzen Technici Jadrowej, Warszawa). Counting efficiency was determined separately for each sample by toluene-7-^{14}C internal standard (Isotope Institute, Budapest). In case of Geiger—Müller technique the samples must be dried before counting. During this procedure losses of ^{14}C content of the algae may occur up to 30% (WALLEN and GEEN, 1968). It is therefore a great advantage of the liquid scintillation technique, that it needs no dried samples.

The total carbonic acid content of the water was determined by pH measurement and by titrating three times 50 ml membrane filtered Balaton water by 0.1 N HCl against methylorange indicator. From the radioactivity of algae and the specific activity of the total carbonic acid content of the water, allowing for 5 percent isotope effect, the weight of the carbon taken up by the phytoplankton was calculated. Each value was reduced by that of the dark parallel. The results are given in this from, without further corrections. According to STEEMANN NIELSEN (1964) these values should be multiplied by 1,06 to obtain gross, and by 0.96 to obtain net production. By converting the biomass and production values to surface area the sample at 25 cm was taken as representing the water layer between 0 and 50 cm that at 1 m representing the 50—150 cm, the sample at 2 m the 150—250 cm, and the sample at 3 m the 250—350 cm layers. Accordingly, by adding the values of the lower three samples and the half value of the sample at 25 cm the biomass and production per cm² were obtained. These values were then converted into g biomass and mg C production/m² respectively. The biomass of the single species in the different depths is not given separately, but for brevity's sake only the harmonic mean of the four depths is given, i.e. calculations as above, and the results divided by 3.5.

Results and discussion

Water temperature, Secchi transparency, total irradiation, surface and underwater illumination data are presented in *Table 1*. Further characteristics of experimental days:

Apr. 5.	Overcast, at the beginning strong waves.
Apr. 18.	Overcast, at times sunshine. Moderate wind, moderate waves.
May 5.	Sunshine, calm. Barely rippling water.
May 16.	Overcast, at times sunshine. Wavy water.
May 31.	At first overcast, in the last two hours sunshine.
Jun. 13.	Sunshine with floating clouds. Moderate wind, rippling water.
Jun. 27.	Heavy storm on the previous day. Overcast, at times strong sunshine. Gently rippling surface, calm before the storm.
July 11.	The night before rather heavy storm. Overcast, drizzling. Storm with very strong wind and large waves.
July 27.	The day before heavy storm. Overcast. Light wind, big waves.
Aug. 10.	Calm for days. Sunshine. Dead calm. Stillness. Unruffled surface.
Aug. 24.	Four days storm and one day of very strong wind preceded the experiment. Sunshine, later clouds. Breeze. Unruffled surface, milky water.
Sept. 7.	After a cooler period rise in temperature, calm preceded the experiment. Strong sunshine with floating clouds. Medium then soft wind. Moderate waves then unruffled surface.
Sept. 28.	The day before relatively calm. Sunshine with floating clouds. Moderate wind, strong waves.

At the first experiment water temperature was 13° C, and returned to 13° C at the last one. As the mean temperature of the lake is 12° C, it can be said, that the half year above the mean temperature was investigated. This year the spring came before time, the summer was late. The water temperature attained 20° C first in June. During the heavy storm of 20–24th August the lake cooled down very much, and even in later times its temperature did not rise above 20° C.

Lake Balaton has a large surface, thus big waves are easily formed. On the other hand the lake is shallow, therefore the mud is easily stirred up by the waves. This renders the underwater light conditions extremely unstable. For example on the 10th of August, the Secchi transparency was 180 cm, and at 3 m depth the surface illumination was 20 percent, while on 11th of July the Secchi transparency was only 20 cm, and at 1 m depth only 2 percent of the surface illumination could be measured. Data of other days are between these two extremes. In general, light conditions of deeper layers depend more on the turbidity, i.e. on the wind, than on the cloud cover.

Altogether 108 alga species, 5 varieties and 1 form were found in the samples, collected from four different depths at 13 different days. Their distribution between the phyla was the following: Cyanophyta 12, Euglenophyta 9, Pyrrophyta 6, Chrysophyta 50, Chlorophyta 37.

For easier survey only those 22 species are listed separately in *Table II* whose biomass attained in some days 10 mg /m³. The biomass of the other species were summed up, and indicated in the *Table* for each phylum. As *Table II* shows the plankton was dominated unequivocally by diatoms till the middle of July. In this year they were replaced only at this time by the *Ceratium hirundinella* stand. Of the diatoms *Cyclotella bodanica* was the most dominant. In the first three months investigated this single species amounted to half of the total biomass of the phytoplankton. This year *Melosira granulata* became numerous only towards the middle of summer.

Lake Balaton is rich in benthic algae, and the storm turns the lake upside down. The importance of benthic algae in the plankton compared to the euplanktonic forms has been frequently discussed. The present data show, that in clear or moderately disturbed water, i.e. in most cases the plankton is dominated by euplanktonic algae. Benthic elements do not attain one fifth of the total biomass. On the other hand during a storm this ratio suddenly increases. In a heavy storm on the 11th July the biomass of the phytoplankton was doubled by the benthic elements. Of the tychoplanktonic algae the largest biomass was given by *Surirella robusta* var. *splendida*. The biomass of Cyanophyta, Euglenophyta and Chlorophyta phyla are inferior.

The vertical distribution of the phytomass *(Table III)* was always uneven, but in the average of the phytomass values measured in the different days there are no differences by depths. Generally phytoplankton shows an even vertical distribution.

The primary production at the different depths *(Table IV)* varied much from time to time. Usually the maximal production was at 1 m, in clearer water at 2 m depths. At 3 m the production is much lower, in two third of the measurements there was scarcely any production at all. At the surface the production was usually inhibited by the excessive light. There are however significant deviations from this most frequent picture. At the 13th of June the whole water column exhibited a high production. This day yielded the highest production per surface area. The water was very clear, at 3 m 6 percent of the surface illumination was recovered. In the most transparent water on the 10th of August by 180 cm Secchi transparency and 20 percent illumination

TABLE I

Environmental factors

Date	IV. 5.	IV. 18.	V. 2.	V. 16.	V. 31.
Water temperature °C	13	13	15	16	19
Total irradiation during exposal cal/cm²	166	141	227	113	99
Total irradition in the whole day cal/cm²	346	294	519	189	226
Secchi transparency cm	42	45	51	51	55
Illumination at the surface Klux	—	62.4	66.4	40.5	8.1
Illumination in the different depths in percent of the surface illumination					
25 cm	—	50.0	64.7	59.5	63.1
100 cm	—	23.4	26.5	29.8	14.8
200 cm	—	3.9	7.3	8.3	4.2
300 cm	—	0.8	1.0	2.6	1.6
	—	—	—	—	0.9

at 3 m the higher levels were inhibited by light, and the production showed the maximum at 3 m.

In storm the situation was reversed. On the 11th of July, when the illumination at 1 m was only 2 percent, already in this layer and underneath there was no significant production. On the other hand tremendous production was measured at the surface, due to the huge amount of benthic algae, brought up by the storm *(Table II)*.

Similar, but less extreme was the situation during a storm on the 27th of July. On this day 7 percent of the surface light penetrated down 1 meter depth, enabling intensive photosynthesis. At 2 m with 1 percent illumination the production fell to a very low level.

From the means of the 13 days *(Fig. 1)* it appears that the vertical distribution of the algae is even, but the same biomass displays quite different productions in different depths. At 2 m the insufficiency of light is already apparent, while at 3 m only one fourth is produced by the same biomass than at 1 m. The means of the different levels are calculated from values of very different dispersions. At 1 and 2 m there is relatively less variation in the production from one day to the other. At the surface on the other hand the production is usually low owing to inhibition by the excess of light, while in storm it is extremely increased by benthic algae. At 3 m the results show great variability because here serious light insufficiency is caused in two thirds of the cases by turbidity, on the contrary in clear water the production is similar to that of the higher levels. Light saturation at the bottom must be even rarer.

The production as related to surface area *(Fig. 2.)* is relatively even, with values varying between 83 and 168 mg C/m^2/4 hours. The differences between the values of the different experimental days are less to be attributed to seasonal changes, than to the different weather conditions of the single days. Smaller differences, resulting from changes in plankton constituents, temperature and water chemism are masked by the effects of the fluctuation in water transparency. Only the last three measurements indicate the autumnal decline of production. The highest values were obtained in the clearest water (13th June, 27th July). In storm the production related to surface area was

VI. 13.	VI. 27.	VII. 11.	VII. 27.	VIII. 10.	VIII. 24.	IX. 7.	IX. 28.
23	19	22	23	24	17	20	14
250	283	95	51	256	164	199	124
485	538	269	221	550	306	399	217
78	55	20	28	110	33	111	41
70.2	66.4	18.0	8.7	54.5	42.5	46.5	38.4
55.6	53.0	40.0	59.0	82.1	61.4	70.8	57.5
30.6	26.5	2.0	6.9	48.2	6.8	43.8	12.5
13.9	6.3	0.0	1.1	32.1	1.4	24.0	2.5
5.5	1.8	0.0	0.1	19.6	0.3	12.5	0.5
2.8	0.9	0.0	0.0	12.1	0.1	8.3	0.3

TABLE II

The biomass of the

	5. IV.	18. IV.	2. V.	16. V.	31. V.
Cyanophyta					
Microcystis flos-aquae	—	—	—	—	—
Aphanizomenon flos-aquae	—	—	—	—	—
Other species	35	3	33	33	20
Total	35	3	33	33	20
Euglenophyta					
Total	45	—	13	3	21
Pyrrophyta					
Cryptomonas erosa	—	—	3	—	—
Ceratium hirundinella	2	16	21	26	29
Peridinium inconspicuum	—	—	—	—	—
Other species	—	—	—	—	—
Total	2	16	24	26	29
Chrysophyta					
Chromulina sp.	5	—	—	1	113
Amphora ovalis	104	37	46	27	20
Cyclotella bodanica	1898	2005	1544	592	1218
Cyclotella ocellata	541	443	200	90	254
Cyclotella quadriiuncta	210	71	111	1	6
Cymatopleura elliptica	32	114	30	19	18
Cymatopleura solea	230	10	12	5	7
Diploneis elliptica	—	—	—	—	—
Melosira granulata	2	18	—	21	86
Navicula gracilis	6	—	—	4	—
Navicula radiosa	114	—	35	—	—
Nitzschia acicularis	684	292	51	17	11
Nitzschia amphibia	—	—	—	27	13
Nitzschia hungarica	45	47	62	92	30
Nitzschia sigmoidea	52	14	43	36	19
Surirella robusta	4	—	32	30	73
Surirella turgida	4	1	30	—	—
Other species	133	71	134	28	176
Total	4064	3123	2330	1242	2044
Chlorophyta					
Closterium aciculare	—	2	—	5	22
Oocystis solitaria	39	11	37	20	49
Other species	54	44	34	21	84
Total	93	57	71	46	155
Sum total of all algae	4239	3199	2471	1350	2269
g/m^2	14.8	11.2	8.6	4.7	7.9

low. The benthic algae brought up by the waves can but partly compensate for the darkness of deeper regions.

The mean production during the four hours and the standard error of this mean were 118 ± 8 mg C/m^2. Owing to the low standard error a 20 percent increase in the following years detected by measurements of similar frequency could be regarded as significant difference. The average length of day time in this half-year is 14 hours. To extrapolate the production of the 4 hours of exposure to the whole day time, it was multiplied by 3.5. The mean daily production is 413 mg C/m^2/day, the maximal production is 588 mg C/m^2/day. According to VINBERG (1961) lakes with 300—700 mg C maximal daily production belong to the mesotrophic category. The maximal daily *phytoplankton 10^6 μ^3/l*

13. VI.	27. VI.	11. VII.	27. VII.	10. VIII.	24. VIII.	7. IX.	28. IX.
—	86	—	—	257	—	3	—
—	—	3	6	32	56	199	7
7	139	119	145	103	17	86	64
7	225	122	151	392	73	288	71
36	87	46	20	34	76	26	8
34	48	43	129	47	1	90	11
138	147	341	1022	840	234	870	54
—	134	—	7	4	2	—	—
—	222	38	182	86	19	15	—
172	551	422	1340	977	256	975	65
89	57	46	165	108	56	49	28
9	45	87	33	—	9	—	71
2255	1934	558	335	93	223	—	228
458	384	125	62	10	62	18	29
50	129	—	—	—	—	—	—
34	25	36	58	—	—	—	84
2	6	158	29	—	—	—	24
—	—	—	—	—	—	—	105
242	316	1257	310	1	74	—	4
—	26	284	22	—	—	—	133
—	—	—	—	—	—	—	87
2	15	42	7	—	7	—	39
4	5	110	29	6	25	—	81
—	37	226	40	—	—	—	172
7	2	146	41	—	35	—	32
27	113	1072	786	—	—	—	45
—	189	229	20	—	—	—	17
52	171	431	146	52	135	91	239
3231	3454	4807	2083	270	626	158	1418
134	17	5	60	412	160	162	193
140	26	—	54	13	40	44	30
70	108	178	99	69	92	83	20
344	151	183	213	494	292	289	243
3790	4468	5580	3807	2167	1323	1736	1805
13.3	15.6	19.5	13.3	7.6	4.6	6.1	6.3

production of Lake Balaton falls within this range. According to the yearly gross production, oligotrophic lakes produce 10—30, mesotrophic lakes 30—70 eutrophic lakes 70—200 and hypertrophic lakes 200—400 g C/m^2. During the six months investigated the primary production of Lake Balaton was 0.413 g $C/m^2 \times 183 = 75.6$ g C/m^2/half-year, i.e. the production attained already the yearly level of eutrophic lakes.

The average biomass of the phytoplankton is 10.3 g. The average daily production, if 1 g C corresponds to 10 g biomass was 4.13 g. This means that the mass of phytoplankton is renewed in each 2.5 days. As in other lakes this value is 2—10 days, (Gessner, 1959), the turnover time of the phytoplankton is relatively short.

TABLE III

The biomass of the phytoplankton at different depths 10^6 μ^3/100 ml

Depth, cm	5. IV.	18. IV.	2. V.	16. V.	31. V.	13. VI.	27. VI.	11. VII.	27. VII.	10. VIII.	24. VIII.	7. IX.	28. IX.
25	344	362	261	169	212	244	460	765	490	129	55	184	214
100	328	296	229	123	235	354	496	620	435	169	103	206	258
200	550	322	134	134	250	449	383	634	391	250	125	151	147
300	434	320	372	131	203	401	455	317	262	273	209	159	120

TABLE IV

The production of the phytoplankton at different depths µg C/100 ml/4 hours

Depth, cm	5. IV.	18. IV.	2. V.	16. V.	31. V.	13. VI.	27. VI.	11. VII.	27. VII.	10. VIII.	24. VIII.	7. IX.	28. IX.
25	3.46	3.35	1.36	3.69	3.99	6.25	1.81	17.53	8.06	1.87	2.53	1.42	3.76
100	6.11	5.99	5.13	4.73	4.66	4.84	3.67	0.60	4.49	2.82	6.02	2.87	3.94
200	4.59	2.58	3.71	3.39	7.50	5.72	5.86	0.38	0.81	4.75	1.05	2.82	1.90
300	0.32	2.43	2.90	0.12	0.83	4.09	1.06	0.42	0.65	7.96	0.28	2.89	0.58

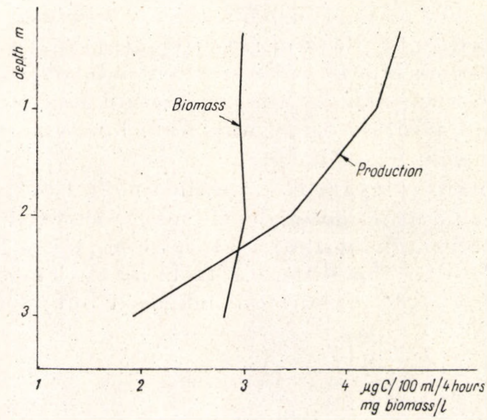

Fig. 1. The average biomass and production of the phytoplankton at different depths

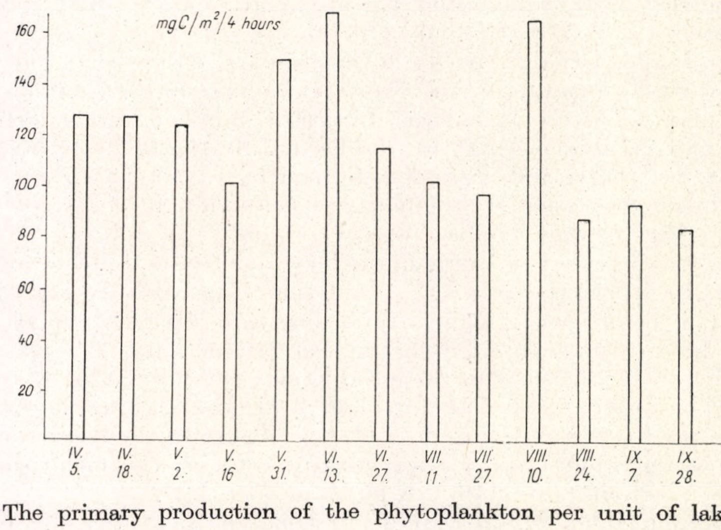

Fig. 2. The primary production of the phytoplankton per unit of lake surface

Due to rapid turnover, the daily production is relatively high as compared to the biomass, and due to the long productive period the yearly production is high as compared to the daily production. This way it is possible, that by relatively low phytomass, the daily production corresponds to the mesotrophic, the yearly production to the eutrophic level. The not too high mass of algae provides more food for other organisms than in lakes with a slower renewal of algae, or with shorter productive period.

The primary production in this half-year, extrapolated to the whole Lake Balaton was some 453 000 metric ton of planctonic algae. This amount is 22 times higher than that estimated by ENTZ (1954) from the low phytomass of the 1940 s (TAMÁS, 1955) for the whole year.

The question may arise, how much did the productivity of the lake change since the first primary production measurements in 1961. It cannot be answered in an exact manner, since there are essential differences between the two set of experiments. BÖSZÖRMÉNYI et al. (1962) exposed the samples only at 1 m depth for six hours, and measured radioactivity by the GEIGER—MÜLLER tube. In this experiment the production was measured at four different depths, the exposition time was four hours and radioactivity was measured by liquid scintillation.

In order to obtain comparable data the amount of carbon bound by 100 ml sample in one hour at 1 meter depth was calculated. These values were 0.70 and 1.07 μgC/100 ml/h in 1961 and 1973 respectively. Part of this difference may originate in the different techniques. Thus by all probability the productivity of the phytoplankton increased but moderately in the last decade.

Summary

The biomass of phytoplankton, the illumination and primary production were measured fortnightly at four depths.

In the samples 108 alga species, 5 varieties and 1 form were found. Algae were counted by UTERMÖHL microscope. The biomass of each species and the total phytoplankton were calculated from the number of algae and from the volume of individuals. Until the middle of July the plankton was dominated by diatoms, the largest mass was formed by Cyclotella bodanica. Ceratium hirundinella became the dominating species first in the second half of the summer. The average biomass was 10.3 g/m^2.

Transparency is very unstable in the lake, due to the frequent swirling up of the mud. In storm the primary production stops already at 1 m depth because of light insufficiency while after a long calm period in the clear water the deepest layer (3 m) exhibited the highest production.

In general at the surface the production is inhibited be excessive illumination, the maximum is found at 1 or 2 m, and at 3 m the same mass of algae produced four times less than at 1 m, owing to the insufficient light.

The mean production and the standard error of the mean during the four hours expositions were 118 $\pm$ 8 mg C/m^2.

The average daily production was estimated to be 413 mg C/m^2, the primary production during the half-year to 76 g C/m^2.

This primary production corresponds to that of the slightly eutrophic akes.

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A BALATON FITOPLANKTONJÁNAK ELSŐDLEGES TERMELÉSE 1972. ÁPRILIS–SZEPTEMBERBEN

Herodek Sándor és *Tamás Gizella*

Összefoglalás

Fél éven keresztül kéthetente mértük négy különböző mélységben a fitoplankton tömegét, a megvilágítást és az elsődleges termelést.

A mintákban 108 algafajt, 5 változatot és 1 formát találtunk. Az egyedszámot Utermöhl módszerével határoztuk meg. Az egyedszám és az egyedek átlagos térfogata alapján kiszámítottuk az egyes fajok és az egész fitoplankton biomasszáját. Július köze-

péig a planktonban a kovamoszatok uralkodtak, a legnagyobb tömeget a *Cyclotella bodanica* képezte. A *Ceratium hirundinella* a nyár második felében vált uralkodó fajjá. A biomassza átlaga 10,3 g/m² volt.

A Balaton vizének átlátszósága nagyon változékony az iszap gyakori felkeveredése miatt. Viharban már egy méter mélyen sincs termelés a fényhiány miatt, míg hosszú szélcsend után a víz annyira tiszta volt, hogy a termelés maximuma a legmélyebb (3 m) rétegben alakult ki. Általában a felszínen fénygátlás van, a termelés maximuma egy-két méterre esik, három méter mélyen pedig a fényhiány miatt ugyanakkora algatömeg csak negyedannyit termel, mint egy méteren.

Négyórás expozíció alatt a termelés átlaga és az átlag standard hibája 118 ± 8 mg C/m² volt. Ebből számítva az átlagos napi termelés 413 mg C/m², a fél év alatti termelés 76 g C/m² volt. A fél évi termelés eléri a természetes eutróf tavak szintjét. Ezt az algatömeg gyors, 2,5 naponkénti megújulása, és a hosszú vegetációs periódus teszi lehetővé.