ANNAL. BIOL. TIHANY | 27 | 201—208 | HUNGARIA 1960

APPARENT PHOTOSYNTHESIS OF *POTAMOGETON PERFOLIATUS* L. IN DIFFERENT DEPTHS OF LAKE BALATON

LAJOS J. M. FELFÖLDY

Received: 10th February, 1960

According to literary data dealing with the optical characteristics of the water of Lake Balaton not the lack of light is the major factor which hinders the growth of plants.

ULLYOTT and KNIGHT (1938) stated on the basis of light penetration measurement that "at the bottom of Lake Balaton there is an amount of light which is adequate for the growth of vegetation" and that "the sparseness of the flora is not due to a limitation by lack of light, but to the severity of the mechanical effects of wave action."

The intensity of photosynthesis in Lake Balaton was measured with pure algal cultures by FELFÖLDY and KALKÓ (1958) who found that "in Lake Balaton inhibited photosynthetic activity caused by insufficient light can be observed only in cloudy weather and in very turbid water. Losses imposed by the partial inhibition of photosynthesis near the water surface are most considerable".

In this paper experiments on the photosynthesis in the most widespread submersed aquatic plant of Lake Balaton *(Potamogeton perfoliatus* L.*)* are dealt with, with special regard to some methodical questions. Most investigations on the relation between depth of immersion and photosynthetic rate have been carried out with marine and freshwater algae (for literary data see: FELFÖLDY and KALKÓ 1958). There are, however, some investigators, notably RUTTNER (1926), SCHOMER (1934), MANNING *et al.* (1938), HOGESTU (1938, 1939), MEYER and HERITAGE (1941) MEYER *et al.* (1943), DUTTON and JUDAY (1944), BRILLIANT (1949), who have worked on this problem with vascular aquatics.

Similar experimental procedures have been followed by all of these investigators. The plants were put into glass containers of suitable size, which were then filled with lake water or with the desired nutrient solutions, stoppered and suspended at various depths under the water surface. In most cases the change of oxygen content in the vessels was determined by the usual WINKLER method, at the end of a given experimental period. Any gain in oxygen content over that of similary titrated blanks is an index of the amount of photosynthesis less respiration (*i.e.*, of apparent photosynthesis). When estimations of the absolute rate of photosynthesis are desired the rate of respiration is measured in black containers otherwise identical with the clear bottles.

This clear-black-bottle method is subject to certain limitations, as has been pointed out by several authors (EMERSON and GREEN 1934, BARKER 1935, GESSNER 1937, 1940, STEEMANN NIELSEN 1954, STEEMANN NIELSEN and AL KHOLY 1956, FELFÖLDY and KALKÓ 1958), therefore in this paper only data on apparent photosynthesis are given.

Material and methods

The plants were collected directly from Lake Balaton in the vicinity of the Biological Research Institute at Tihany. Collections were usually made the afternoon or the evening before a determination, the plants being kept overnight in a dark cool place in a large porcelain dish, containing filtered lake water.

Special care was taken for close uniformity as to size and shape in the choice of the plants in all determinations. In spite of this, however, the samples had no equal value and comparison was rather difficult. It became therefore necessary to study this problem seperately by methodical experiments.

The surface of the leaves in each sample was determined planimetrically. Each sample was cut into two halves. In one part the dry matter content was determined in an electric oven at 105° C and in the other chlorophyll determinations were made. The plant pigments were extracted by the method of MACKINNEY (PAECH and TRACEY 1955, IV. 159) with aqueous acetone. To obtain complete extraction, small amounts of powdered glass and calcium carbonate were added to the leaves. The extracted chlorophyll was not transferred to ether but was measured directly in 80% aqueous acetone at wave lengts 6630 and 6450 Å with the BECKMAN DU spectrophotometer.

For the measurement of apparent photosynthesis the quantity of oxygen evolved was used. The samples were exposed in glass-stoppered 200 ml flasks, containing Balaton-water previously desoxygenized *in vacuo* (2—3 mg O_2/litre) (ZO BELL and ANDERSON 1936, FELFÖLDY and KALKÓ 1958). The oxygen content in the aliquots of water samples was measured by the WINKLER method modified by MAUCHA (1945, 362).

It was found in the course of preliminary experiments that when working with the apical portions of the plants shoots, otherwise generally used in similar experiments, inaccurate results were obtained. Photosynthetic experiments with isolated leaves have already been made by MEYER and co-workers (1943, 393), in the case of *Vallisneria americana*, by ARENS (1933) and STEEMANN NIELSEN (1947) in the case of *Potamogeton* species. Measurements were therefore made to decide upon the suitability of isolated leaves in such experiments.

As it can be seen from *Table 1*, in experiments of short duration the results obtained, when working with isolated leaves, were more reproducible than those obtained in the case of shoots. The portion of the stem disturbs both the determination of dry matter and that of the surface. The considerably lower values pertaining to the apical portions are probably due to the unequal illumination of the closely fitting leaves. Considering all these methodical difficulties, in the following the experiments were made with isolated leaves.

The results obtained in the course of experiments made in the laboratory, under standard conditions (22° C, *c.* 7000 Lux) are also very incongruous when calculated either on a dry matter or on a leaf surface basis. The samples

Table 1

Comparison between the apparent photosynthesis in the apical portions and in the isolated leaves of Potamogeton perfoliatus

Samples	Dry matter mg	Total leaf surface cm^2	mg O_2/1g dry matter per one hour	mg O_2/1dm² per one hour
Leaf	49,8	18,0	4,6	1,28
Two leaves	94,9	34,0	4,3	1,21
Apical portions with 10 leaves attached	112,4	41,4	4,7	1,28
,,	72,8	28,3	3,3	0,85
,,	113,9	70,0	1,4	0,23
A section of plant with 3 developed leaves	50,7	24,0	3,4	0,71
Two apical portions with 10—10 leaves attached	165,3	67,8	5,7	1,39

Surface illumination 11 300 Lux, temperature 22° C at 10 cm below water surface.

collected from the lake are very heterogeneous. Some shoots are of a light-green colour, with sparsely grown, small leaves, the others almost brown with closely grown big leaves. Experiments were also made to express the activity of apparent photosynthesis in mg O_2/1 mg chlorophyll units. To the experiments glass-stoppered vessels of 200 ml content were used. Each sample consisted of 4 leaves of medium size. These were put into the glass vessels, filled with previously desoxigenized (2,5 mg O_2/litre) and filtered (Delta paper № 368) Balaton Lake water. The vessels were exposed on a rotating shaking machine, at a temperature of 22° C and were illuminated by an incandescent lamp (*c.* 7000 Lux). After having taken aliquot samples of water from each vessel to compute their oxygen content, the leaves were removed from the vessels, dried with filter paper, and their surfaces planimetrically measured. Thereafter they were cut into two halves along the midrib. One half was used to determine the dry matter content, while the other was weighed, homogenized and its chlorophyll content determined. When the surface, wet weight, dry matter and chlorophyll content are known, apparent photosynthesis can be expressed in any unit.

As *Table 2* shows, the figures expressing photosynthetic rate of different samples in various units are incongruous due to the physiological inhomogeneity

Table 2

Photosynthetic activity of various Potamogeton samples under standard conditions, expressed in different units

Sample	Chlorophyll-a mg/1 g dry matter	Photosynthesis per one hour mg O_2 per		
		1 g dry-matter	1 dm² leaf surface	1 mg chlorophyll
Brown leaf I.	51,3	15,9	0,50	0,31
II.	48,7	12,6	0,39	0,26
V.	63,4	22,4	0,60	0,35
Light-green leaf I.	89,9	39,0	1,02	0,43
III.	94,5	59,4	1,47	0,63
V.	79,4	42,6	1,04	0,54

of the collected plants. In order to eliminate these differences and to obtain comparable results, different leaves of the same plant must be used.

Experiments in Lake Balaton

Due to the methodical difficulties mentioned above, the experiments made in Lake Balaton were evaluated by the relative measurement method of MEYER and co-workers (1941, 1943).

The vessels containing partly desoxygenated Balaton-water and isolated leaves were immersed directly into the lake at a depth of 10 cm under the surface for 30 minutes. The purpose of this exposition was to allow time for the completion of the photosynthetic induction period and to bring the leaves into equilibrium with the reduced oxygen tension.

After this "preliminary run" the leaves were transferred to a second set of vessels and immersed at the same depth as during the first run. This second run is the "calibration run" and its purpose was to determine the relative photosynthetic capacity in all samples of plants used, while they were exposed to identical environmental conditions. The duration of the "calibration run" was one hour. At the end of this period water samples were taken for oxygen measurement, the leaves transferred to the third set of vessels and immersed into the lake at the depths of 10, 50, 100, 200, 250, 300 cm under the surface. Exposition period was one hour.

According to GESSNER (1937), MEYER and HERITAGE (1941) and also in our experiments, the photosynthesis will continue in submerged aquatics at a practically constant rate for long periods of time, even at fairly high light intensities, if environmental conditions, especially the oxygen content of water, are kept favourable and constant. Hence it seems to be a valid assumption that any differences in the rate of evolution of oxygen measured in the "experimental run" as compared to the "calibration run" with one given leaf, must be due to different light conditions at different depths of water.

Table 3

Comparative rates of apparent photosynthesis in Potamogeton perfoliatus L. at different depths on July 29, 1959 during a period of slight turbidity and cloudy weather

Sample N°.	Calibration run 10 : 00—11 : 00 A. M. mg O_2/1 g dry matter per one hour	Experimental run 11 : 30—12 : 30 Depth m	Experimental run 11 : 30—12 : 30 mg O_2/1 g dry matter per one hour	$100 \cdot \frac{\text{Experimental run}}{\text{Calibration run}}$
1	3,35	0,1	4,19	125
2	4,62	0,5	10,82	234
3	3,30	1,0	7,65	232
4	4,33	2,0	4,78	108
5	4,71	2,5	3,02	64
6	5,68	3,0	0,03	0,5

Transparency (Secchi-disk) = 0,74 m
Water temperature = 27° C
Light intensity at the surface = 5200 Lux (cloudy weather); Bunsen's vertical extinction coefficient (β_v) = 0,418; Metre transmission number (T_k) = 38,2; (Explanation of optical units see Felföldy and Kalkó 1958, 323).

Table 4

Comparative rates of apparent photosynthesis in Potamogeton perfoliatus L. at different depths on August 19, 1959, during a period of high turbidity

Sample N°.	Calibration run 10 : 00—11 : 00 A. M. mg O_2/1 g dry matter per one hour	Experimental run 12 : 00—13 : 00		$100 \cdot \frac{\text{Experimental run}}{\text{Calibration run}}$
		Depth m	mg O_2/1 g dry matter per one hour	
1	3,76	0,1	4,36	116
2	5,09	0,5	5,04	99
3	3,34	1,0	4,11	123
4	4,40	2,0	2,11	48
5	4,47	2,5	1,66	37
6	5,11	3,0	2,76	54

Transparency (Secchi-disk) = 0,35 m
Water temperature = 23° C
Light intensity at the surface = 25 400 Lux; Bunsen's vertical extinction coefficient (β_v) = 0,930; metre transmission number (T_k) = 12,0.

Table 5

Comparative rates of apparent photosynthesis in Potamogeton perfoliatus L. at different depths on August 24, 1959, during a period of very clear water

Sample N°.	Calibration run 10 : 30—11 : 30 A. M. mg O_2/1 g dry matter per one hour	Experimental run 12 : 00—13 : 00		$100 \cdot \frac{\text{Experimental run}}{\text{Calibration run}}$
		Depth m	mg O_2/1 g dry matter per one hour	
1	3,26	0,1	3,17	97
2	4,08	0,5	5,23	128
3	2,50	1,0	4,07	163
4	4,31	2,0	10,32	239
5	2,66	2,5	6,06	228
6	2,09	3,0	4,81	156

Transparency (Secchi-disk) = 0,83 m
Water temperature = 22,4° C
Light intensity at the surface = 91 000 Lux; Bunsen's vertical extinction coefficient (β_v) = 0,338; Metre transmission number (T_k) = 45,9.

By dividing the figure representing oxygen evolution during the "experimental run" for each sample by the figure representing oxygen evolution during the "calibration run" for the same sample and multiplying by 100, a convenient index of the relative rate of apparent photosynthesis during the "experimental run" is obtained for that leaf. Such indices are upon a comparable basis (MEYER and HERITAGE 1941, 20).

At the end of July and in August 1959 several experiments were made in Balaton Lake water of different turbidity. Three series of these experiments are summarized in *Tables 3—5*. The results of the experiments carried out in slightly cloudy weather are shown in *Table 3*. As the figures in the last column show, the optimum photosynthesis was found between 2—3 meters under water surface. The situation was entirely different in the other series of experiments, made in optically almost clear water and in a sunny day, as it is shown by the data of *Table 5*. Optimal photosynthesis was found at about 2 m. No direct optimum is shown by the data of *Table 4* (the water is very turbid). It is striking that photosynthesis was not considerably inhibited even at the depth of 3 meters. The rather low value (0,5) at 3 meters in *Table 3* follows from the fact that the vessels reached the muddy surface of lake bottom and were partly covered by the settlings of the disturbed mud. In each series of experiments, when carried out in clear water and bright sunshine, there was a marked inhibition due to light oversaturation.

The experiments made in this vascular aquatic gave similar results to those made with algal suspensions (FELFÖLDY and KALKÓ 1958).

It can be stated on the basis of these measurements that in Lake Balaton, due to its shallowness, lack of light cannot act as a limiting factor either in the life of phytoplankters or in the case of vascular aquatics.

Grateful acknowledgement is made here to Miss JULIANNA RIESZ for her helpful technical assistance in experimental works and to Mrs. ZSUZSA F. KALKÓ for the English translation.

Summary

Experiments were made in the apparent photosynthesis of *Potamogeton perfoliatus* L. The results may be summed up as follows:

1. For photosynthetic experiments of short duration (only few hours) isolated leaves are more suitable than the apical portions of shoot.

2. As the calculations made on a dry matter, leaf surface or chlorophyll content basis show, the photosynthetic rate of the leaves of different plant specimens collected from natural habitats are very incongruous. Leaves of the same plant gave good and comparable results. The effect of various light intensities in different depths of water can be correctly measured by the relative measurement method of MEYER and co-workers (1941, 1943).

3. According to these studies, the photosynthetic activity of higher aquatic plants is never inhibited by lack of light on clear summer days, even if the water is very turbid.

4. Inhibition due to oversaturated light can be studied in the uppermost layers of optical clear water.

5. Compensation point of photosynthesis and of respiration can not develop in summer days in the shallow water of Lake Balaton.

LITERATURE

ARENS, K. (1933): Physiologisch polarisierter Massenaustausch und Photosynthese bei submersen Wasserpflanzen I. — *Planta* **20**, 621—658.

BRILLIANT, V. A. (1949): Influence of previous shading on photosynthesis of higher and lower aquatic plants. — *Dokl. Akad. Nauk SSSR.* **64**, 397—400. *British Abst.* A. III. 1951, 1135.)

DUTTON, H. J. and C. JUDAY (1944): Chromatic adaptation in relation to color and depth distribution of fresh-water phytoplankton and large aquatic plants. — *Ecol.* **25**, 273—282.

EMERSON, R. and L. GREEN (1934): Manometric measurements of photosynthesis in the marine alga Gigartina. — *J. Gen. Physiol.* **17**, 817—842.

FELFÖLDY, L. J. M. and ZSUZSA F. KALKÓ (1958): The rate of photosynthesis and underwater radiation in Lake Balaton. Observations of summer 1957. — *Annal. Biol. Tihany* **25**, 303—329. (In Hungarian with English summary.)

GESSNER, F. (1937): Untersuchungen über Assimilation und Atmung submerser Wasserpflanzen. — *Jb. wiss. Bot.* **85**, 267—328.
HOGETSU, K. (1938): Über den Einfluss von Aussenfaktoren auf die Atmungs- und Assimilationsleistungen der Süsswasserpflanzen. — *Bot. Mag. (Tokyo)* **52**, 573—582. (*Bot. Zbl.* **34**, 43, 1941.)
HOGETSU, K. (1939): Untersuchungen über die Lage des Kompensationspunktes der Wasserpflanzen im Kizakisee. — *Bot. Mag. (Tokyo)* **53**, 428—442. (*Bot. Zbl.* **35**, 140—141, 1942.)
MANNING, W. M., C. JUDAY and M. WOLF (1938): Photosynthesis of aquatic plants at different depths in Trout Lake, Wisconsin. — *Trans. Wisc. Acad. Sci.* **31**, 377—410.
MAUCHA, R. (1945): Hydrochemische Halbmikro-Feldmethoden. — *Arch. f. Hydrobiol.* **41**, 352—391.
MEYER, B. S., F. H. BELL, L. C. THOMPSON and EDYTHE I. CLAY (1943): Effect of depth of immersion on apparent photosynthesis in submersed vascular aquatics. — *Ecol.* **24**, 393—399.
MEYER, B. S. and A. C. HERITAGE (1941): Effect of turbidity and depth of immersion on apparent photosynthesis in Ceratophyllum demersum. — *Ecol.* **22**, 17—22.
PAECH, K. and M. V. TRACEY (1955): Modern Methods of Plant Analysis. Vol. IV. — Springer, *Berlin*, 1—766.
RUTTNER, F. (1926): Über die Kohlensäureassimilation einiger Wasserpflanzen in verschiedenen Tiefen des Lunzer Untersees. — *Internat. Rev. ges. Hydrobiol. u. Hydrogr.* **15**, 1—30.
SCHOMER, H. A. (1934): Photosynthesis of water plants at various depths in the lakes of northeastern Wisconsin. — *Ecol.* **15**, 217—218.
STEEMANN NIELSEN, E. (1947): Photosynthesis of aquatic plants with special reference to the carbon-sources. — *Dansk Bot. Ark.* **12**, (8), 1—71.
STEEMAN NIELSEN, E. and A. A. AL KHOLY (1956): Use of ^{14}C -technique in measuring photosynthesis of phosphorus or nitrogen deficient algae. — *Physiol. Plant.* **9**, 144—153.
ULLYOTT, P. and F. C. E. KNIGHT (1938): Light penetration into Lake Balaton. — *Arb. Ung. Biol. Forsch. Inst.* **10**, 254—268.
ZoBELL, C. E. and D. Q. ANDERSON (1936): Observations on the multiplication of bacteria in different volumes of stored sea water and the influence of oxygen tension and solid surfaces. — *Biol. Bull.* **71**, 324—342.

FOTOSZINTÉZIS-MÉRÉS *POTAMOGETON PERFOLIATUS* L. HÍNÁRRAL A BALATON KÜLÖNBÖZŐ MÉLYSÉGEIBEN

Felföldy Lajos

Összefoglalás

A Balatonról szóló irodalmi adatok szerint a tó sekély volta miatt fényhiány sehol sem szab határt a növényzet életének. Magasabbrendű növényekkel azonban még nem történtek ilyen irányú kísérletek.

1959 nyarán természetes termőhelyekről származó hínár-anyaggal végeztünk kísérleteket. Tekintettel a növényanyag heterogén voltára, előkísérletekkel, próbáltuk megtalálni a leghelyesebb módszert a különféle mélységben rendelkezésre álló fénymennyiség hatásának számszerű kifejezésére. Megállapítottuk, hogy rövid lejáratú kísérletekhez az egyébként szokásos hajtás-csúcs vagy hajtás-darabka helyett jól használhatók izolált levelek *(1. táblázat)* és, hogy bármilyen egységben fejezzük ki a fotoszintézis gyorsaságát (szárazanyagra, levélfelületre vagy egységnyi klorofill mennyiségre vonatkoztatva), a minták heterogenitásának foka nem csökken *(2. táblázat)*. Ezért MEYER és munkatársainak (1941, 1943) relatív mérő módszerét alkalmaztuk: a 2—4 izolált levélből álló mintákat csiszoltdugós üvegben, szűrt és részben oxigéntelenített Balaton-vízben, először 10 cm mélyen exponáltuk egy óra hosszat („calibration run" a *3—5. táblázat*-ban), majd új üvegekbe, friss, szűrt és oxigén-szegényített vízbe téve át őket, függesztettük különféle mélységbe („experimental run" a *3—5. táblázat*-ban). A kísérleti expozíció alatt kapott oxigénmennyiséget a kalibrációs kísérletben keletkezett oxigén százalékában fejezve ki, jellemző és jól reprodukálható eredményhez jutunk.

A *3—5. táblázat*-okban ismertetett kísérleti eredmények szerint a Balatonban derült nyári időben biztosan nem alakul ki fényhiány a *Potamogeton* fotoszintézise szempontjából, még igen zavaros vízben sem. Ezzel szemben a fénytúltelítettség bizonyos fokig gátlólag hat az asszimilációra a felső vízrétegekben, különösen optikailag tiszta vízben.

A Balatonban a fotoszintézis és légzés kompenzációs pontja, a tó sekélysége miatt sehol sem jelentkezhet.

ИЗМЕРЕНИЕ ФОТОСИНТЕЗА НА ТИНЕ *POTAMOGETON PERFOLIATUS* L. В РАЗЛИЧНЫХ ГЛУБИНАХ ОЗЕРА БАЛАТОНА

Лайош Фельфэлди

Выводы

По литературным данным об озере Балатоне вследствие мелководя недостаток в свете нигде не ограничивает жизнь растительности. Однако, с точки зрения высших растений такие опыты до сих пор не были проведены.

Летом 1959 г. были проведены опыты с тиной, происходящей из естественного местонахождения. Имея в виду неоднородность растительного материала, были проведены предварительные попытки для численного выражения влияния количества света, имеющегося в различных глубинах. Было установлено, что для проведения краткосрочных опытов вместо обыкновенного кусочка побеговой почки или побега хорошо применимы изолированные листья (таблица № 1) и несмотря на единицу выражения скорости фотосинтеза (отнесенную к сухому веществу, листовую поверхность или единице количества хлорофила), степень неоднородности образцев не уменьшается (таблица № 2). В результате этого был применен метод относительного измерения Мейера и его сотрудников (1941 г., 1943 г.): образцы из 2—4 изолированных листьев в колбе с притертой пробкой, наполненной фильтрованной и частично обескислороженной водой Балатона, впервые были экспонированы на глубине 10 см в течение часа («calibration run» в таблицах 3—5), а затем после перемещения в новые колбы, наполненные свежей, фильтрованной и бедной кислородом водой, были подвешены на различных глубинах («experimental run» в таблицах №№ 3—5). Выражая количество кислорода, полученного при опытной экспозиции, в проценте кислорода, образовавшегося при калибровочном опыте, получается характерный и хорошо воспроизводимый результат.

По опытным данным, изложенным в таблицах №№ 3—5, в озере Балатоне даже в весьма мутной воде, в ясное летнее время не наступает недостаток света с точки зрения фотосинтеза Potamogeton. По сравнению с этим, чрезвычайное повышение количества света в некоторой мере мешает ассимиляции в верхних слоях воды, особенно в оптически чистой воде.

В озере Балатоне компенсационная точка фотосинтеза и дыхания вследствие мелководя озера нигде не возникает.