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STUDIES ON THE OXIDATIVE ASSIMILATION OF UNICELLULAR ALGAE

I. EFFECT OF SUGARS ON THE RESPIRATION OF *CHLORELLA VULGARIS*

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In recent years the Botanical Department of the Biological Research Institute at Tihany has been engaged in the study of inorganic carbon sources of unicellular green algae (FELFÖLDY 1960a—e, 1962) performed in the interest of working out the principles of mass cultivation of algae.

In the last year this trend was extended to the investigation of organic carbon sources primarily with the aim of covering the carbon requirements of algae at least partly from organic materials and not only from photosynthesis giving much trouble in the technology of mass culturing of algae.

It was endeavoured to work out simple methods for determining the degree of sugar-utilization of our strains.

There is a great deal of evidence that the "dark metabolism" of photosynthesizing plants, algae also included, is essentially similar to that of non-photosynthetic organisms. From purely biochemical viewpoint, therefore, we would expect that almost any substrate or intermediate in the major pathways of energy metabolism might substitute for photosynthesis. This expectation is, in fact, fulfilled only partially and to varying degrees in various species of algae. Therefore, in dealing with the heterotrophy of algae we must be concerned not only with the question of how certain substrates function as carbon and energy sources for growth, but with the equally difficult questions of why the same compounds support growth of some species and not of others, and why, in a particular species, one substrate will support growth, while another, very closely related compound will not (DANFORTH 1962).

The degree of usefulness of the different sugars was measured by their stimulating effect on respiration, on basis of TAYLOR's (1960a, b) conclusion, that the kinetics of uptake of sugars stimulating respiration (glucose, mannose) differ, from those of simple diffusion, and sugars which do not stimulate respiration penetrate much more slowly, following the kinetics of simple diffusion (fructose, galactose, sorbose and various pentoses). These latter substances cannot be taken into consideration as carbon or energy-sources. The findings of BELCHER and FOGG (1958) that certain organic substances (also sugars) stimulate respiration but do not support growth in darkness were also considered notwithstanding that these were obtained in the case of diatoms.

The degree of oxidative assimilation of various organic substances is the specific property of the single algal strains and may serve as a key in the

physiological identification thereof. The degree of effect is, besides, dependent on age, physiological properties and conditions of the preparatory cultures of algae.

Material and methods

In the experiments the axenic strain 7K *Chlorella vulgaris* BEYER. originating from the collection of algae of the Biological Research Institute at Tihany was used.

Sugars used in the experiments are: Dl-Arabinose (Dr. Theodor Schuchardt — München), D-lyxose (Fluka Ag.), d-ribose (Zellstoff-fabrik Waldhof), D(+)xylose (Nutritional Biochemicals Corporation — Clevland), fructose (GyAK — Budapest), d-galactose (GyAK — Budapest), d-glucose (Merck — Darmstadt), d(+)mannose (Merck — Darmstadt), L-sorbose (Merck — Darmstadt), D-tagatose (L. Light and Co. Ltd. — England), L-rhamnose (Fluka Ag.), melibiose (GyAK — Budapest), saccharose (GyAK — Budapest), turanose (L. Light and Co. Ltd. — England), lactose (GyAK — Budapest), maltose (Spolek pro Chemickon — Czecho-Slovakia), raffinose (L. Light and Co. Ltd. — England), stachyose (L. Light and Co. Ltd. — England).

Algal material for the experiments was cultured in one litre Erlenmeyer flasks in KNOP—PRINGSHEIM nutrient solution containing only anorganic salts (PRINGSHEIM 1946) at a temperature of 19—22°C and at 9000 Lux light intensity provided by Tungsram "warmwhite" fluorescent tubes. 3 per cent carbon dioxide in air was bubled through the suspension. The cultures were kept under strictly aseptic conditions and reached a density of 1.0 g dry matter) litre within 6—7 days. For manometric measurements cells were separated by centrifuging a known volume of suspension and washed in a 1 : 1 dilution of KNOP—PRINGSHEIM nutrient solution and suspended therein. For experimental use starved cells (CRAMER and MYERS 1949) were prepared by aerobic incubation of harvested and washed suspensions in darkness for at least 24 hours and at temperature used for growth and manometry.

Density of suspension was adjusted on basis of dry matter determinations. This was achieved by filtering a known volume of suspension through weighed filter paper disc and drying it at 105°C to constant weight.

Respiration was measured with the usual WARBURG technique in 20 ml conical vessels by placing 2 ml algal suspension into the main compartment (= 12 mg dry matter), 0.1 ml 2M KOH solution into the center well, and in every case nutrient solution containing sugar of 5 μM quantity into the side arm. Measurements were performed at 25 $\pm$ 0.1°C temperature in darkness (a double walled bag made of black cloth was pulled on the vessels). Endogenous respiration was measured in the first 60—80 minutes of experiment. Thereafter the sugar solution was dipped into the main compartment. A separate vessel containing 5 μM glucose was used also parallel in case of every sugar investigated for the purpose of obtaining a basis for the comparison of the stimulating effect of the various sugars on respiration.

Rates of respiration are expressed in terms of Q_{O_2} with the usual dimensions of μl O_2/mg dry weight. hour. It is not a simple matter to correct these values by ground respiration. After KRATZ and MYERS the amount of endogenous O_2 should be considered as 100 and exogenous Q_{O_2} as per cent of this value *(Table 2)*.

In order to obtain more knowledge on the properties of the strain 7K *Chlorella vulgaris*, the degree of glucose utilization was also measured. According to MYERS and coworkers (1947) this may be computed from the quantitative relations between consumed sugar and oxygen. For this purpose the knowledge of the respiratory quotient (R. Q.) pertaining to the given conditions is necessary.

R. Q. was determined by WARBURG's indirect method (WARBURG 1924, FRENCH et al. 1935). The method may be rendered convenient if the pH of suspension is adjusted to 5 because in that case carbon-dioxide retention is negligible. MYERS et al. (1947) show that the respiration of the *Chlorella pyrenoidosa* strain used in their experiment does not change considerably between pH 3.8 and 6.8 (see also KANDLER 1954, STEEMAN NIELSEN 1955, BERGMANN 1955, DANIEL 1956, GRIFFITHS et al. 1960). The relation between pH and respiration in strain 7K *Chlorella vulgaris* is presented in *Table 1.*

Table 1 — 1. Táblázat

Changes of respiration in Chlorella vulgaris
at different pH values of suspension
Chlorella vulgaris légzésváltozása
a szuszpenzió különböző pH értékei mellett

pH	Q_{O_2} ground — alap	Q_{O_2} glucose — glukóz
3.95	1.2	6.5
5.00	1.3	6.5
5.99	1.3	6.6
7.42	1.2	6.5

In case of low pH values the effect produced on ground- and glucose-respiration was small. Accordingly two vessels were used for R. Q. measurements. Into the center well of the one (I) 2M KOH solution, into that of the other (II) 3N H_2SO_4 solution was placed for the determination of oxygen and carbon dioxide respectively. The values were computed by using the following formulae:

$$x_{O_2} = h^{I} \cdot K^{I}_{O_2}; \quad x_{CO_2} = h^{II} \cdot K^{II}_{CO_2} - \frac{K^{II}_{CO_2}}{K^{II}_{O_2}} \cdot x_{O_2} \quad \text{where}$$

$x_{O_2} = \mu$l oxygen consumed,

$x_{CO_2} = \mu$l CO_2 released

h^{I} and h^{II} = manometer readings at manometers I and II (mm).

$K^{I}_{O_2}$= constant of the first vessel computed for oxygen determinations.

$K^{II}_{O_2}$ resp. $K^{II}_{CO_2}$ = constants of the second vessel, computed for O_2 and CO_2 determinations respectively.

pH measurements were performed with BECKMAN GS pH-meter.

Results

1. Respiratory experiments

Out of the 18 sugars examined stimulating effect on the respiration of strain 7K *Chlorella* was produced by the following ones: xylose, glucose, fructose, galactose, mannose, sucrose and raffinose. The results are presented numerically in *Figures 1—3* and *Table 2*.

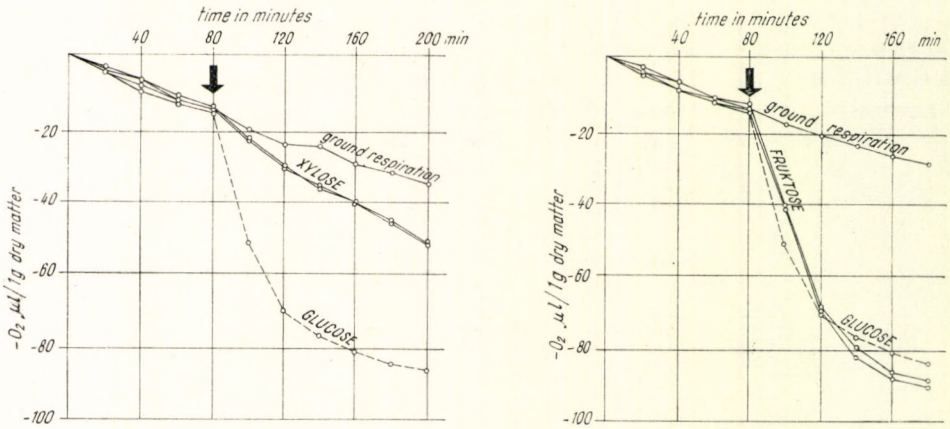

Fig. 1. — 1. ábra. The effect of fructose and xylose on the respiration of *Chlorella vulgaris* — A fruktóz és xilóz hatása a *Chlorella vulgaris* légzésére.

Table 2 — 2. Táblázat

Stimulating influence of various sugars on the respiration of the algal strain 7K Chlorella vulgaris
Különböző cukrok stimuláló hatása 7K Chlorella vulgaris alga törzs légzésére

Sugar — Cukor	Q_{O_2} ground respiration — alap légzés	Substrate respiration — Szubsztrátum légzés	Substrate respiration in % of the Q_{O_2} value of ground respiration — Szubsztrátum légzés az alap légzés Q_{O_2} értékének százalékában
Xylose	0.75	1.41	188
Glucose	0.71	6.70	945
Fructose	0.70	4.97	710
Galactose	0.80	1.62	202
Mannose	0.70	4.37	624
Sucrose	0.69	5.77	838
Raffinose	0.83	1.39	168

As the *Figures* and *Table 2* show the respiration of strain *Chlorella* is most intensively stimulated by glucose, next to which fructose comes producing a similar effect. Except for some special algal strains *(Chlorella:* FINKLE et al. 1950, *Synechococcus:* DYER and GAFFORD 1961) and the majority

of acetate flagellates (HUTNER and PROVASOLI 1951) glucose proved to be an useful substrate for all algal strains investigated (SAUNDERS 1957, GIBBS 1962).

Mannose which proved to be unefficacious in case of other *Chlorella* strains (NEISH 1951, SAMEJIMA and MYERS 1958) increased considerably the respiration of strain 7K *Chlorella*. Further experiments are needed to determine whether less efficaceous sugars as xylose, galactose and raffinose are utilized or not. The saccharose respiration of the 7K *Chlorella* is most extraordinary

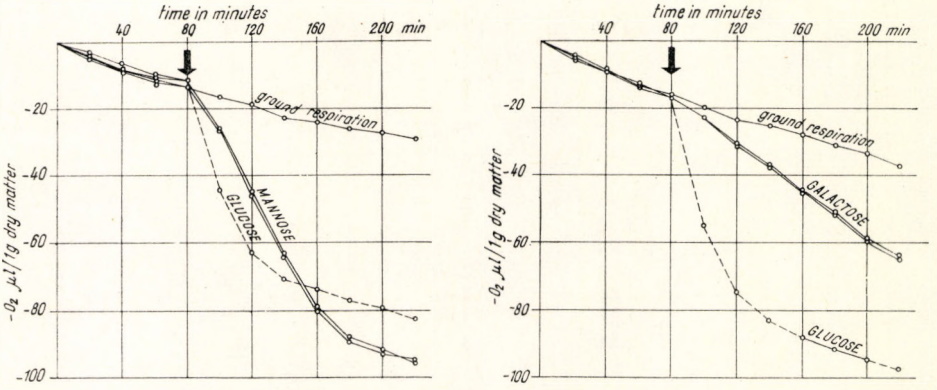

Fig. 2. — *2. ábra.* The effect of mannose and galactose on the respiration of *Chlorella vulgaris* — A mannóz és galaktóz hatása a *Chlorella vulgaris* légzésére.

because this substance is either not utilizable (MYERS et al. 1947, NEISH 1951, SAMEJIMA and MYERS 1958) or only barely utilized (SPECTOR 1956) by most *Chlorella* species in general. Utilization of this substance by *Tribonema equale* only after a three weeks long lag period was observed by BELCHER and FOGG (1958). In the experiments reported here the increase in respiration observed immediately after the addition of the substrate was similar to that observed in the case of glucose.

2. Oxidative assimilation of glucose

The stoichiometry of oxidative assimilation was investigated by numerous workers (MYERS et al. 1947, CRAMER and MYERS 1949, TAYLOR 1950, SYRETT 1951, DANIEL 1956, FUJITA 1959, etc.). In the knowledge of the respiratory quotient under the experimental conditions it is possible to compute the respired and absorbed proportions of the substrate from the amount of oxygen required for complete utilization of a known amount of substrate. Results of twelve RQ determinations are tabulated in *Table 3* (R. Q. = 1.03). The amounts of oxygen consumed during the glucose experiments were readed off from curves constructed similar to the *Figures 1—3*. Location of the exact position of the breaks in the curves is made with some uncertainty. The amount of oxygen required by the substrate is here arbitrarily estimated as the oxygen uptake from the last point on the initial endogenous respiration curve to the first point on the final endogenous respiration curve. Only small differences occur if the extrapolated intersections of the curves are used instead.

Table 3 — 3. Táblázat

Determination of R. Q. in 7K Chlorella vulgaris in the presence of glucose (by the indirect method of Warburg at pH 4.4)
R. Q. meghatározás 7K Chlorella vulgarisban glukóz jelenlétében (Warburg indirekt módszerével 4,4 pH mellett)

Q_{O_2}	Q_{CO_2}	R. Q.
3.57	3.60	1.01
3.69	4.10	1.11
2.66	2.66	1.00
3.36	3.26	0.97
2.46	2.81	1.14
2.46	2.50	1.02
3.16	3.05	0.97
3.86	3.74	0.97
2.66	2.66	1.00
3.24	3.02	0.94
2.36	2.69	1.14
3.54	3.76	1.06
average — átlag:		1.03

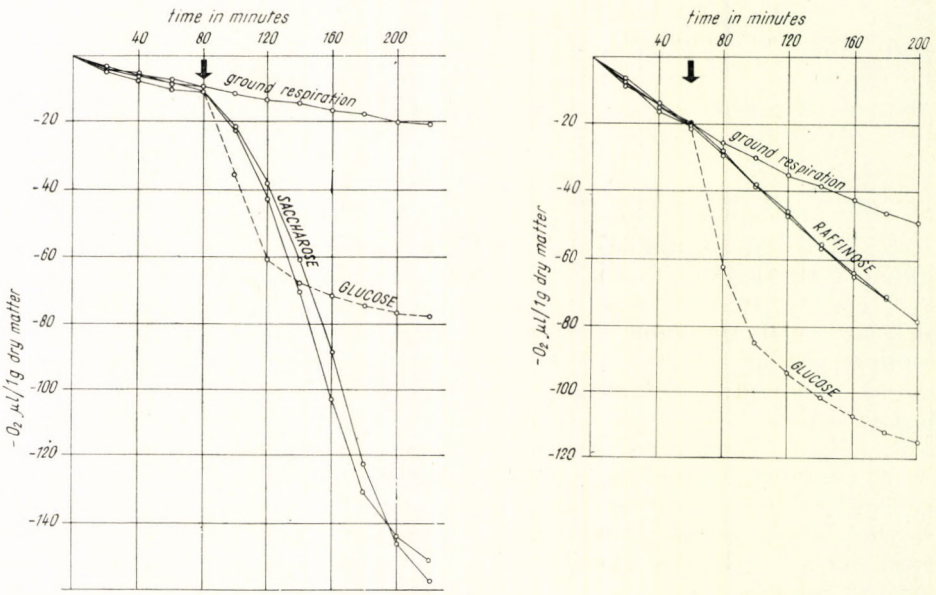

Fig. 3. — 3. ábra. The effect of saccharose and raffinose on the respiration of *Chlorella vulgaris* — A szaharóz és raffinóz hatása a *Chlorella vulgaris* légzésére.

Knowing, that to the full oxidation of 5 μM glucose 30 μM (733.8 μl) oxygen is required at a temperature of 25°C and pressure of 760 Hg mm it is possible to compute easily the proportions of oxidized and assimilated glucose *(Table 4)*.

Table 4 — 4. Táblázat

Oxidative assimilation of 5 μM glucose by 7K Chlorella vulgaris
5 μM glukóz oxidatív asszimilációja 7K Chlorella vulgaris esetében

μM O_2 respired — ellélegzett O_2 μM-ban	Per cent of glucose oxidized — Oxidált glukóz %	μM O_2 respired — Ellélegzett O_2 μM-ban	Per cent of glucose oxidized — Oxidált glukóz %
2.37	7.9	2.50	8.3
2.32	7.8	2.41	8.0
2.27	7.6	2.41	8.0
2.45	8.2	2.32	7.8
2.50	8.3	2.54	8.5
2.50	8.3	2.37	7.9
		average — átlag:	8.05

Discussion

It has been demonstrated that the strain 7K *Chlorella vulgaris* has a quite intense metabolic rate. The measure of the endogenous respiration decreases to a fairly constant level even under a starvation period of 24 hours (Genevois 1927, Daniel 1956). Such starved cells are closely analogous to the resting cells commonly used in studies of this type performed on other organisms (Myers et al. 1947).

As it is seen from *Table 2* seven sugars stimulated the respiration of this strain. Other *Chlorella* strains known from literary data display more poorish reactions. Mannose and sucrose is ineffective, and the effectiveness of xylose is also questionable (Samejima and Myers 1958). Evidences on raffinose utilization of some algal strains is presented only by Beckwith (1933) and Watanabe (1937).

The strain examined in this work assimilates glucose very intensively, since only about 8% of it is lost by respiration *(Table 3)*. This fraction agrees fairly well with the value recorded by Syrett (1951) for *Chlorella vulgaris:* 9.7% and Griffiths (1963) for the Emerson strain of *Chlorella vulgaris:* 10%, but is considerably less than those quoted by Myers et al. (1947) for *Chlorella pyrenoidosa:* 15%, Daniel (1956) for different *Chlorella strains:* about 13% and Taylor (1950) for *Scenedesmus quadricauda:* 16%.

A number of workers presented evidence on the negative responses of *Chlorella* strains to sucrose and galactose. Griffiths and coworkers (1960) suggest that the growth promoting effect of these oligosaccharides is produced only after an "adaptive" periode and respiration itself is not stimulated by these substances.

The assumption that the strain investigated in this work may have a good oligosaccharide utilization is indicated both by the very intensive sucrose-

respiration and the well measurable promoting effect of galactose. These results may have importance also in practice, because saccharose is the most cheap organic source economically.

Summary

A range of sugars have been tested as respiratory substrates using 7K *Chlorella vulgaris* BEYER. axenic strain of the Algal Collection of the Hungarian Biological Research Institute as test organism.

Much higher rates of respiration were obtained with glucose, fructose, mannose and sucrose. Much smaller effect was observed with xylose, galactose and raffinose. Sustained respiration was not observable with any other sugars tested (arabinose, lyxose, ribose, sorbose, tagatose, rhamnose, melibiose, turanose, lactose, maltose and stachyose).

The respiratory quotient of glucose respiration may be taken as 1.03. The pH between 4—7.4 was ineffective either on endogenous respiration rate or on the exogenous ones.

The oxidative assimilation of starved resting cells of this strain is very good, only about 8 per cent of the absorbed glucose was completely oxidized, the remainder being presumably converted into algal dry matter. A considerable sucrose utilization is indicated by the intensive respiratory increase in consequence of sucrose, and its ecological wiev points are also emphasized.

Sincere thanks are expressed to Dr. L. J. M. FELFÖLDY, head of the Botanical Department for his interest in this work and the author takes also pleasure in acknowledging the helpful assistance of Mrs. ZSUZSA F. KALKÓ and Mrs. BRIGITTA SZABÓ under these experiments.

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TANULMÁNYOK AZ EGYSEJTŰ ALGÁK OXIDATÍV ASSZIMILÁCIÓJÁRÓL*

Összefoglalás

Tóth László

Megvizsgáltuk 18 cukornak a hatását — Intézetünk törzsgyűjteményéből származó — 7K *Chlorella vulgaris* BEYER. törzsünk légzésére.

Törzsünk légzését a legintenzívebben a glukóz serkenti, hozzá hasonló mértékben a fruktóz következik. A mannóz, mely több *Chlorella* törzs esetében hatástalan, 7K törzsünk légzését lényegesen befolyásolta. Kisebb mértékben hatásosak voltak még a xylóz, galaktóz és raffinóz *(1—3. ábra, 2. táblázat)*.

Igen feltűnő törzsünk szaharóz légzése, ami igen jó hasznosítási lehetőségre utal. Gyakorlati fontossága is lehet, ezért külön tanulmány tárgyát fogja képezni *(3. ábra, 2. táblázat)*.

Vizsgált törzsünk légzésére hatástalanok voltak a következő cukrok: arabinóz, lyxóz, ribóz, szorbóz, tagatóz, ramnóz, melibióz, turanóz, laktóz, maltóz, sztahyóz.

7K *Chlorella* törzsünk alaposabb megismerése érdekében megmértük glukóz hasznosítási fokát is, amit az elfogyott cukor és a fogyasztott oxigén arányából számíthatunk ki akkor, ha ismerjük a vizsgált törzs — vázolt körülmények közötti — légzési együtthatóját (R. Q.). *(3. táblázat)*.

Az R. Q. meghatározást WARBURG indirekt módszerével végeztük, aminek egyik feltétele, hogy a szuszpenzió folyadék fázisában a pH 5 alatt legyen a széndioxid retenció miatt és a vizsgált törzs légzése az alacsony pH mellett ne változzék lényegesen *(1. táblázat)*.

A glukóz oxidatív asszimilációjára vonatkozó eredmények szerint törzsünk a glukózt igen nagy mértékben hasznosítja, mintegy 8%-át lélegzi csak el. *(4. táblázat)*

НАБЛЮДЕНИЯ ПО ОКИСЛИТЕЛЬНОЙ АССИМИЛЯЦИИ ОДНОКЛЕТОЧНЫХ ВОДОРОСЛЕЙ

I. ВЛИЯНИЕ РАЗЛИЧНЫХ САХАРОВ НА CHLORELLA VULGARIS BEYER

Л. Тот

Изучалось влияние 18 сахаров на дыхание штамма Chlorella vulgaris Beyer — 7К происходящегося из коллекции института.

Дыхание этого штамма наиболее интенсивно увеличивается под влиянием глюкозы, и за ним следует фруктоза. Манноза, являющаяся неэффективной у многих штаммов Chorella, у щтамма 7К вызивала значительное изменение дыхания. В меньшей мере были еще эффективными ксилоза, галактоза и рафиноза (Рис. № 3, Таблица № 2).

Бросается в глаза употребление сахарозы с этим штаммом которое указывает на возможности ее усвоения. Употребление сахарозы может иметь и практическое значение, поэтому мы будем отдельно изучить (Рис. № 3 Таблица № 2).

На дыхание изучаемого штамма оказались неэффективными: арабиноза, люксоза, рибоза, сорбоза, тагатоза, раммоза, мелибиоза, тюраноза, лактоза, малтоза и стахюоза.

С целью подробного ознакомления с штанном Chlorella 7К был измерен и коэффициент полезного действия глюкозы, который высчитается по соотношению употребляемого сахара и кислорода, в том случае, если дыхательный коэффициент (RQ) изучаемого штамма известен в данных экспериментальных условиях.

Измерение дыхательного коэффициента производили при применении непрямого метода Варбурга, согласно которому Ph жидкой фазы суспенсии должен быть ниже 5 из — за ретенции углекислоты и дыхание изучаемого штамма не должно существенно меняться при низкой Ph. (Таблица № 1.).

Согласно нашим данным, полученным при изучении окислительной ассимиляции глюкозы, изучаемый штамм в значительной мере утилизирует глюкозы, и для своего дыхания употребляет только 8% всей глюкозы (Таблица № 4).

* I. Különféle cukrok hatása a *Chlorella vulgaris* BEYER légzésére.