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Metabolism of Carbochidrates in the Cell of Green Photosintesis Sulfur Bacteria

M. B. Gorishniy and S. P. Gudz

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1. Introduction

Green bacteria - are phylogenetic isolated group photosyntetic microorganisms. The peculiarity of the structure of their cells is the presence of special vesicles - so-called chlorosom containing bacteriochlorofils and carotenoids. These microorganisms can not use water as a donor of electrons to form molecular oxygen during photosynthesis. Electrons required for reduction of assimilation CO_2, green bacteria are recovered from the sulfur compounds with low redox potential.

Ecological niche of green bacteria is low. Well known types of green bacteria - a common aquatic organisms that occur in anoxic, was lit areas of lakes or coastal sediments. In some ecosystems, these organisms play a key role in the transformation of sulfur compounds and carbon. They are adapted to low light intensity. Compared with other phototrophic bacteria, green bacteria can lives in the lowest layers of water in oxygen-anoxic ecosystems.

Representatives of various genera and species of green bacteria differ in morphology of cells, method of movement, ability to form gas vacuoles and pigment structure of the complexes. For most other signs, including metabolism, structure photosyntetic apparats and phylogeny, these families differ significantly. Each of the two most studied families of green bacteria (*Chlorobium* families and *Chloroflexus*) has a unique way of assimilation of carbon dioxide reduction. For species of the genus *Chlorobium* typical revers tricarboxylic acids cycle, and for members of the genus *Chloroflexus* - recently described 3-hidrocsypropionatn cycle. Metabolism of organic compounds, including carbohydrates in the cells of representatives of genera *Chlorobium* and *Chloroflexus* remains poorly understood. Anabolism and catabolism of monomeric and polymeric forms of carbohydrates in the cells of green bacteria is discussed.

Representatives of the green sulfur bacteria family *Chlorobiaceae* and green nonsulfur bacteria family *Chloroflexaceae* grow with CO_2 as the sole carbon source. In addition, the
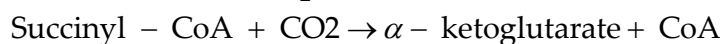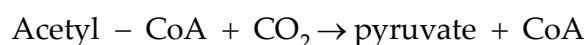
growth process, they can use some organic carbon sources, particularly carbohydrates. Species of the genus *Chlorobium* able to assimilate organic compounds is limited only in the presence of CO_2 and inorganic electron donors. Instead, representatives of the genus *Chloroflexus* grow on different carbon sources anaerobically and aerobically under illumination in the dark. Significant differences between species and genera *Chlorobium*, *Chloroflexus* due to the nature of their photosyntetic apparat. Despite the fact that members of both families contain the same types of chlorosoms, species of the genus *Chlorobium* reaction centers have photosystem I (PS I), while both species of the genus *Chloroflexus* contain reaction centers photosystem II (PS II). Because of the low redox potential (~ -0,9 V) of the primary electron acceptor in green sulfur bacteria, reaction center capable reduce ferredocsyn. In green bacteria nonsulfur bacteria redox potential of the primary acceptor is less negative (~ -0,5 V), resulting in these organisms synthesize reduction equivalents by reverse electron transport, like the purple bacteria. Thus, differences in the structure of the apparatus of green sulfur and green nonsulfur bacteria are reflected in their exchange carbohidrats compounds, and there fore also in their evolution and ecology.

In the evolution of autotrophic organisms formed several ways to assimilate CO_2, each of which is characterized by biochemical reactions that require the appropriate enzymes and reduction equivalents [9, 11]. The most common mechanism for CO_2 assimilation is Calvin cycle, which was found in most plants, algae and most famous groups of autotrophic prokaryotes. In green bacteria described two alternative ways of assimilation of CO_2. Revers cycle of tricarboxylic acids (RTAC) in green sulfur bacteria, first proposed by Evans in 1966. In 1989, Holo described 3-hidroksypropionat way that is characteristic of green non sulfur bacteria.

Larsen, using washed cells of *C. thiosulfatophilum*, for the first time found that they can absorb light in only small amounts of CO_2. They found that most carbon dioxide *C. thiosulfatophilum* records in an atmosphere containing H_2S, H_2 and CO_2. Most data on how carbon dioxide conversion and other compounds related to green sulfur bacteria genus *Chlorobium*, including *C. thiosulfatophilum*, *C. phaeobacteroides* and *C. limicola*.

Green sulfur bacteria can use some organic compounds (sugars, amino acids and organic acids). However, adding these compounds to the environment leads only to a slight stimulation of growth of culture in the presence of CO_2 and is to ensure that they are used only as additional sources of carbon [13]. In any case they are electron donors or major source of carbon. The use of these substances only if there among CO_2 and H_2S.

In the cells of *C. thiosulfatophilum* not identified Calvin cycle enzyme activity. The main role in the transformation of CO_2 is open in this group of bacteria (RTAC). Here in green sulfur bacteria is reduction of CO_2 assimilation. The cycle was proposed by the opening of phototrophic bacteria and other anaerobs two new ferredocsyn - dependent carboxylation reactions [13]:

$$Acetyl - CoA + CO_2 \rightarrow pyruvate + CoA$$
$$Succinyl - CoA + CO2 \rightarrow \alpha - ketoglutarate + CoA$$

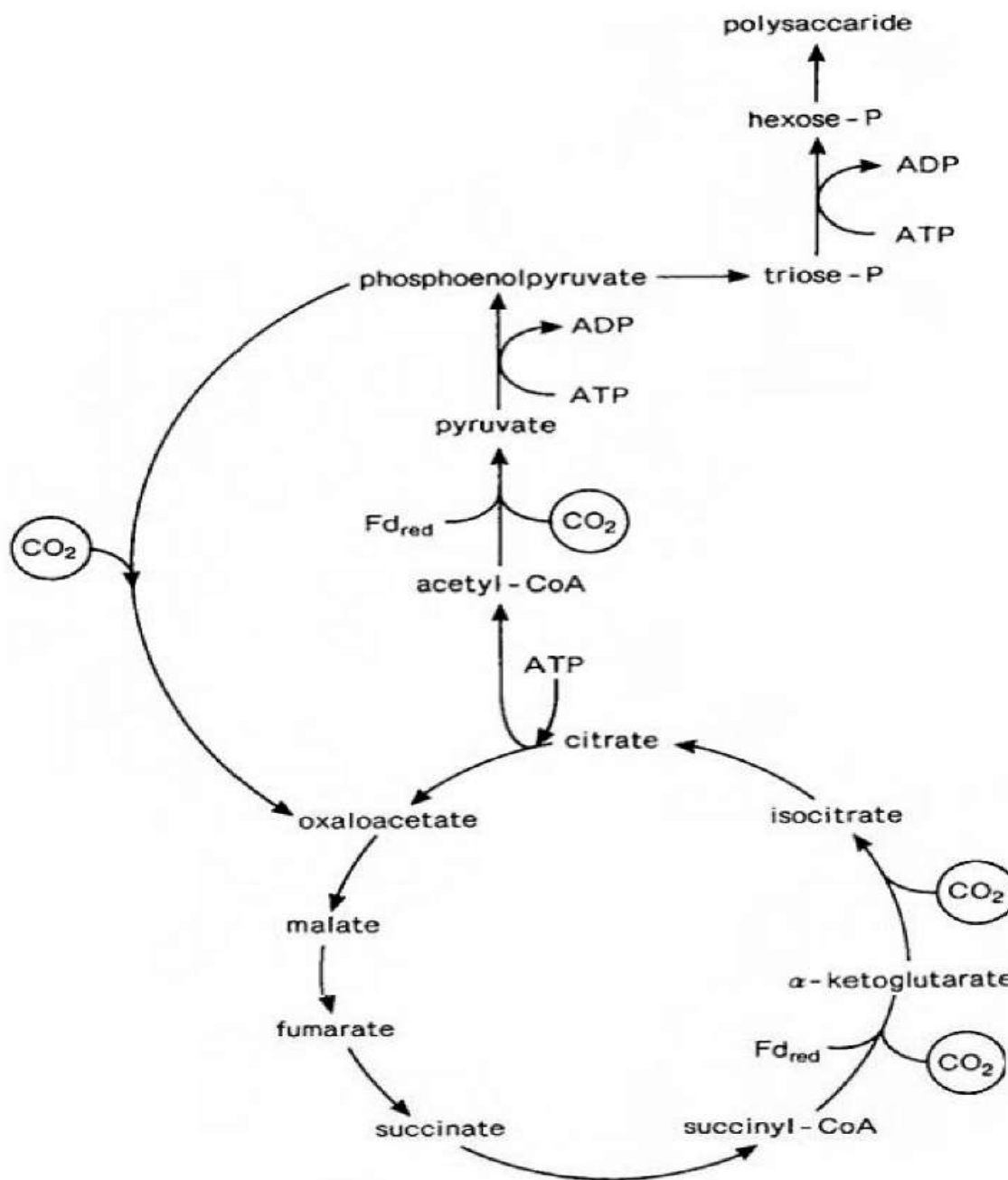They make possible (RTAC), in which two molecules of CO_2 formed a molecule of acetyl - CoA (Fig. 1).

Figure 1. The revers tricarboxylic acid cycle (RTAC) in *Chlorobium* .

First, revers tricarboxylic acid cycle (RTAC) considered an additional mechanism for better functioning of rehabilitation Calvin cycle of the genus *Chlorobium.* Assumed that its main function is the formation of precursors for the synthesis of amino acids, lipids and porphyrins, while restorative Calvin cycle given the main role in the synthesis of carbohydrates. However, the lack of activity in cells rubisco put the availability of restorative Calvin cycle in cells of *Chlorobium limicola* doubt. Confirmation of operation of

restorative tricarboxylic acid cycle in cells of green sulfur bacteria was discovered in them a key enzyme of this cycle. Using tracer and fractionation of isotopes of carbon have shown that (RTAC) is the only recovery mechanism for fixation of CO_2 in green sulfur bacteria, and the product cycle acetyl - CoA directly used for the synthesis of carbohydrates. It was also found that the genes of cells rubisco *Rhodospirillum rubrum*, not related of DNA isolated from cells of bacteria genus *Chlorobium*. Similar negative results were obtained using genes to cells rubisco *Anacystis nidulans*.

The study of restorative (RTAC) can explain the inability of green sulfur bacteria photoheterotroph. Simultaneously with the operation of the mechanism fixation of CO_2 cycle intermediates also provide cells needed organic matter for the synthesis of fatty acids (from acetyl-CoA), amino acids (from pyruvate, α-ketoglutarat acid) and carbohydrates (with pyruvate). However, since the activity of α-ketoglutaratdehidrohenaz not found in species of the genus *Chlorobium*, this cycle can operate only in recreation and hence organic compounds can not oxidate with the formation of reduction equivalents .

Recovery (RTAC) provides fixation of CO_2, to be based on restorative carboxylation reaction of organic acids. Fixation of carbon dioxide occurs in three enzymatic reactions, two of which occur with photochemically reduced ferredoksyn, and one - the same way formed provided with (H^+). As a result of a turnover cycle of four molecules of CO_2 and 10 [H^+] using the energy of three molecules of ATP synthesized molecule oxaloacetat acid is the end product cycle.

Described as "short" version of the cycle, in which 2 molecules of CO_2 are fixed using for their restoration 8 [H^+] and the energy of ATP. The final product in this case is acetyl-CoA, which is used to build components of cells. Addition of acetate in the culture medium promotes the accumulation of biomass and stimulates the formation of reserve polysacharides in the cells of green sulfur bacteria. Representatives of the family *Chlorobiaceae*, including *Chlorobium limicola* and *C. thiosulfatophilum*, often accumulate in cells poliglycose and / or glycogen. Accumulation of polysacharides increases in carbon dioxide assimilation by cells under conditions of deficiency of nitrogen and phosphorus. Under certain conditions of cultivation the level of glycogen in the cells can exceed 12% of dry weight of cells. Formed spare polysaccharides play an important role in changing the conditions of cultivation of green sulfur bacteria, especially when ingested bacteria in the extreme conditions of growth.

Larsen and collaborators found that the bacteria *C. thiosulfatophilum* not grow on media containing traces of hydrogen sulfide (0.01%) and various organic compounds: alcohols, sugars, organic acids. Only media with acetic, lactic or pyruvatic acid was seen a slight increase in biomass under conditions of hydrogen sulfide and carbon dioxide in the environment. Regarding the nature of organic compounds green sulfur bacteria similar to purple sulfur bacteria.

Larsen found that washed suspensions of cells *C. thiosulfatophilum* the light can absorb only small amounts of CO_2. The greatest amount of carbon dioxide *C. thiosulfatophilum* assimilates in an atmosphere containing 86% N_2, 9,2% CO_2, 3,9% H_2S and 0,5% H_2. Most data on how

metabolic carbon dioxide and other carbon compounds obtained in experiments using *C. thiosulfatophilum* and *C. phaeobacteroides*.

Found that in cells *C thiosulfatophilum* not Calvin cycle enzyme activity. Important role in the assimilation of CO_2 is open in this group of microorganisms revers Crebs cycle, which was named Arnon cycle. This series provides a record of CO_2 through renewable carboxylation of organic acids. As a result of the work cycle in cells of green sulfur bacteria in the process of photosynthesis, glucose is formed, which is the first product of photosynthesis, carbohydrate nature. Ways to transform cells in green sulfur bacteria studied not enough. According to it becomes poliglucose, other authors believe that the glucose immediately polymerizes to form glycogen.

To detect sugars that accumulate in cells of *C. limicola* IMB- K-8 in the process of photosynthesis they were grown under illumination and in the presence of electron donor, which served as H_2S. After 10 days culturing cells destroy bacteria and cell less extract analyzed for the presence in it is reduced sugars. The total number of cell less extracts was determined by Shomodi-Nelson and for determination of glucose using enzymatic set "Diaglyc- 2". It turned out that the total number is reduced sugars determined by the method of Shomodi-Nelson did not differ from the rate obtained specifically for glucose.

It follows that the sugar is reduced *C. limicola* IMB- K-8 represented only glucose, which is the first carbohydrate, which is formed during photosynthesis.To test whether glucose in cells is in free or bound state spent acid hydrolysis cell less extract. It found that the content is reduced sugars increased approximately two fold. It follows that the glucose in the cells located in the free and in a bound state. In these experiments investigated the dynamics of accumulation of intracellular glucose bacterium *C. limicola* IMB- K-8 in the process of growth. It was found that the formation of glucose in the cells is observed throughout the period of growth and completed the transition culture stationary phase.

Growth of *C. limicola* IMB- K-8 and glucose in cells growing in culture in the light in a mineral medium with $NaHCO_3$ and Na_2S. We investigated the growth and accumulation of glucose in the cells of *C. limicola* IMB- K-8 for varying light intensity.

It was found that light intensity plays an important role in CO_2 assimilation in *C. limicola* IMB- K-8. More intensive process proceeded in low light, which does not exceed 40 lux. Reduction or increase in illumination intensity was accompanied by reduced productivity of photosynthesis.

On the intensity of photosynthesis reveals a significant influence of mineral nutrition of bacteria We shows the influence of different sources nitrogen and phosphorus supply of glucose in the cells *C. limicola* IMB- K-8.

Simultaneous limitation of growth of culture nitrogen and phosphorus accompanied by increase in glucose in the cells. Her level of these compounds for the deficit grew by about 60%. Separately salts of nitrogen and phosphorus showed much less effect In these experiments investigated how bacteria use glucose under various conditions of cultivation. This used washed cells were incubated under light and dark. When incubation of cells at the

light in the presence of CO_2 and H_2S levels of glucose in the cells practically did not change while under these conditions in the dark glucose concetration in the cells decreased about 2.5 times.

Obviously, in the dark using glucose as an energy source, turning towards Embdena-Meyerhof-Parnas. The level of intracellular glucose is reduced and the conditions of incubation of cells at the light in the environment without hydrogen sulfide, indicating that the use of glucose under these conditions as the sole source of renewable equivalents. In the dark, without glucose hydrogen sulfide is the only source of energy. Thus, the glucose formed by cells plays an important role in the life of cell *C. limicola* IMB - K-8. When staying in the light cells in the process of photosynthesis observed formation of glucose in the cells, and in darkness it is used to maintain cell viability.

2. Isolation, identification and patterns of accumulation poliglucose *C. limicola* IMB- K-8

Nature poliglucose formed in the cells of *C. limicola* IMB- K-8. As already mentioned above green sulfur bacteria in the process of growth can form glucose, a small part of which the cells are in a free state, and the part becomes glycogen. To test the ability of *C. limicola* IMB-K-8 form glycogen was held their extraction from the cells by the method. Grown under light conditions cells in acetic acid. Polisacharide precipitate obtained by adding to the supernatant concentrated ethanol. The obtained precipitate distroy 10M H_2SO_4 obtained hydrolyzate were separated by chromatography. As witnesses used the glucose and galactose, and atzer. After manifestation chromatography revealed only one spot, which is slowly moving in the system butanol - water and Rf value was identical to glucose. It follows that polisaharide that piled up in the cells *C. limicola* IMB- K-8, is polisaharide. As in the literature found allegations that members of *Chlorobium* form glycogen, we extracted polisaharide by Zacharova-Kosenko, which is specific for bacterial glycogen deposition. The formation of glycogen in the cells is only the lighting conditions and the presence of carbon dioxide and hydrogen sulfide in the culture medium. In the absence of H_2S and CO_2 accumulation of glycogen in the cells was observed. In microsections of cells grown under different light, the presence of carbon dioxide and hydrogen sulfide, clearly visible rozet not surrounded by a membrane, glycogen granules (Fig. 2).

Comparative analysis of selected polisaharide and glycogen company "Sigma" showed that the resulting sample shows identical chemical and physical properties: white crystalline powder soluble in water, not soluble alcohol, hydrolyzed in acidic medium to form glucose. Infrared spectroscopy etylaceton extract the studied sample and glycogen "Sigma" has shown that these substances are characterized by the presence of identical functional groups, O-H bonds (the interval 3608 - 3056 cm^{-1}), revealed specific absorption in the carbonyl group (1656 cm^{-1}),- CH2-group (2932 cm^{-1}), and -C-O-H groups (1048 cm^{-1}) and others, indicating the identity of the investigated sample of bovine liver glycogen (the drug company "Sigma") (Fig. 3.) Therefore, we first selected polisacharide of cells *C. limicola* IMB-K-8, which by the nature of the infrared spectrum identical with glycogen "bovine liver".

Accumulation of glycogen in the cells may be an indicator of flow speed. Therefore, we first selected polisacharide of cells *C. limicola* IMB- K-8, which by the nature of the infrared spectrum identical with glycogen "bovine liver". Accumulation of glycogen in the cells may be an indicator of flow speed.
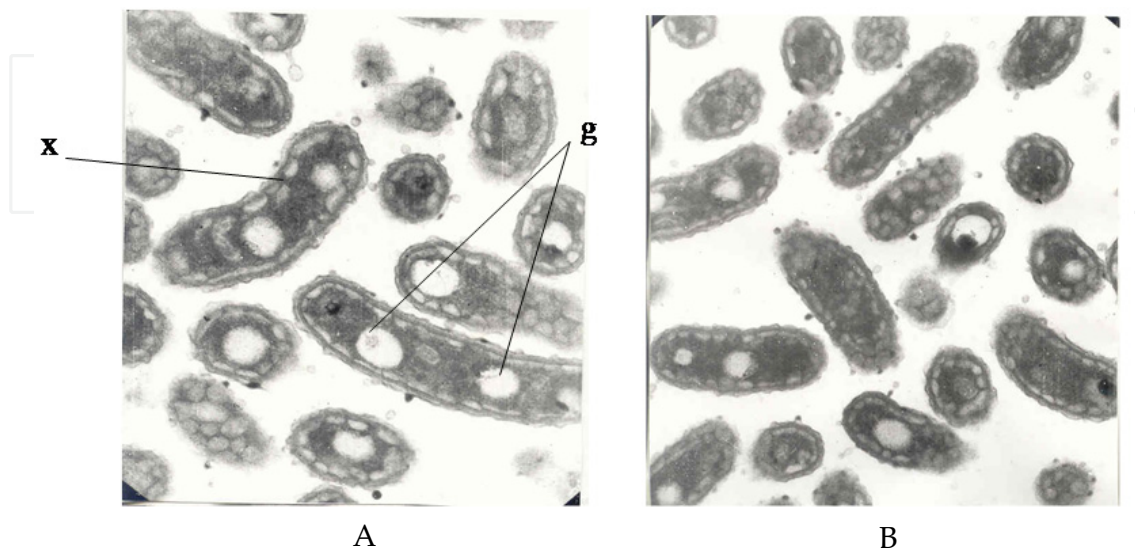

Figure 2. Microsections of cells *C. limicola* IMB- K-8, grown under different light intensity (A - 40lk, B - 100lk): g – glycogen granules, x – chlorosomu.
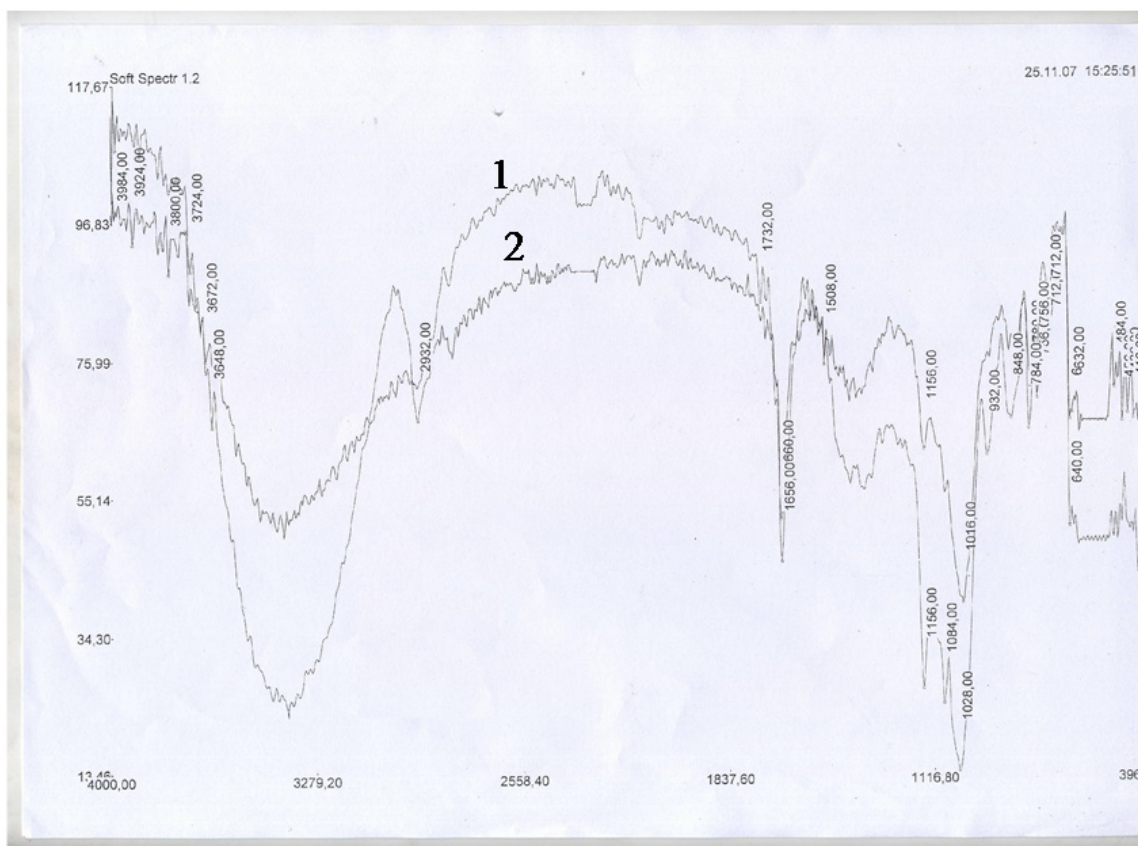

Figure 3. Infrared spectrum of glycogen company "Sigma" (1) and glycogen cells of *C. limicola* IMB- K-8 (2)

The laws of accumulation and utilization of glycogen *C. limicola*. In the presence of light *C. limicola* IMB- K-8 can use organic compounds only, subject to the availability of hydrogen sulfide as an additional source of carbon and continue in their presence actively assimilate carbon dioxide. Assimilation green sulfur bacteria carbon dioxide and organic compounds leads not only to form cells of substances necessary for their growth, but can also affect the synthesis of glycogen. Assuming in these experiments, we investigated the influence of organic carbon sources of power in the process of accumulation of this compound. It turned out that adding to the medium glucose, sucrose, maltose, lactate, not accompanied by changes in intracellular glucose and glycogen.

Only adding to the environment pyruvate and acetate stimulated the growth of glycogen content in cells of *C. limicola* IMB- K-8 which clearly explains the functioning of the studied bacteria cycle Arnon, in the process which produced acetate. Notably, cells with elevated levels of glycogen synthesis that is caused by the addition of pyruvate and acetate, in contrast to cells grown in the presence of other sources of carbon, used almost entirely endogenous glucose. Only adding to the environment pyruvate and acetate stimulated the growth of glycogen content in cells of *C. limicola* IMB- K-8 which clearly explains the functioning of the studied bacteria cycle Arnon, in the process which produced acetate. Notably, cells with elevated levels of glycogen synthesis that is caused by the addition of pyruvate and acetate, in contrast to cells grown in the presence of other sources of carbon, used almost entirely endogenous glucose.

The results obtained give grounds to assert that *C. limicola* IMB- K-8 the most effective use as an additional source of carbon nutrition acetate. It is used only in the presence of hydrogen sulfide and carbon dioxide in the environment and occurs through the inclusion of this compound in the Arnon cycle with the formation of cell components and glycogen. In the presence of pyruvate and acetate in the environment there are some differences in photoreduction CO_2 cells.

So when the concentration of CO_2 in the atmosphere 60mM observed maximum cell growth and increased by 50% the level of glycogen. A slight reduction of carbon dioxide in the environment (20%) accompanied by a reduction in biomass, while increasing the level of glycogen in the cells by about 30%. Further reduction of CO_2 was accompanied by decrease in the intensity of photosynthesis. Increase in glycogen levels in cells with the shortage of carbon dioxide in the atmosphere, apparently, can be explained by inhibition of pyruvate carboxylation reaction and its conversion in to oksaloatsetat and then using it in a constructive metabolism. Note that formed in the process of photosynthesis annoxy carbohydrates not allocated to the environment and stockpiled exclusively in the cell. As evidenced by a negative test for glucose and other sugars is reduced before and after hydrolysis of culture broth. To find ways of further use of glycogen in these experiments, free cells of *C. limicola* IMB K-8 with a high content of polisacharide, incubated in light and in darkness, and then determined the level of glycogen in the cells and analyzed the nature of the organic matter accumulating in the environment. It turned out that the absence of light and presence of CO_2 and H_2S in the medium, cells of *C. limicola* IMB K-8 used a significant amount of glycogen, which testified to a significant reduction of its level in cells.

Analysis of the products of glucose catabolism, obtained after deposition of the mixture (acetone - petroleum ether) from the environment showed that the cells incubated in the dark in the environment accumulate organic compounds as evidenced by their elemental analysis (C-40.25%, H-4.5 %, N-0%). Infrared spectrometry etylatseton hoods showed that these substances are characterized by the presence of O-H bonds (the interval 3608 - 3056cm^{-1}), CH$_3$-CH$_2$ bonds (1456sm^{-1}) and specific absorption in the carbonyl (1656 cm^{-1}) and methyl group (2920 cm^{-1}) and R-COOH groups (2700 cm^{-1}) and others that indicate the presence in culture fluid of carboxylic acids (Fig. 4).
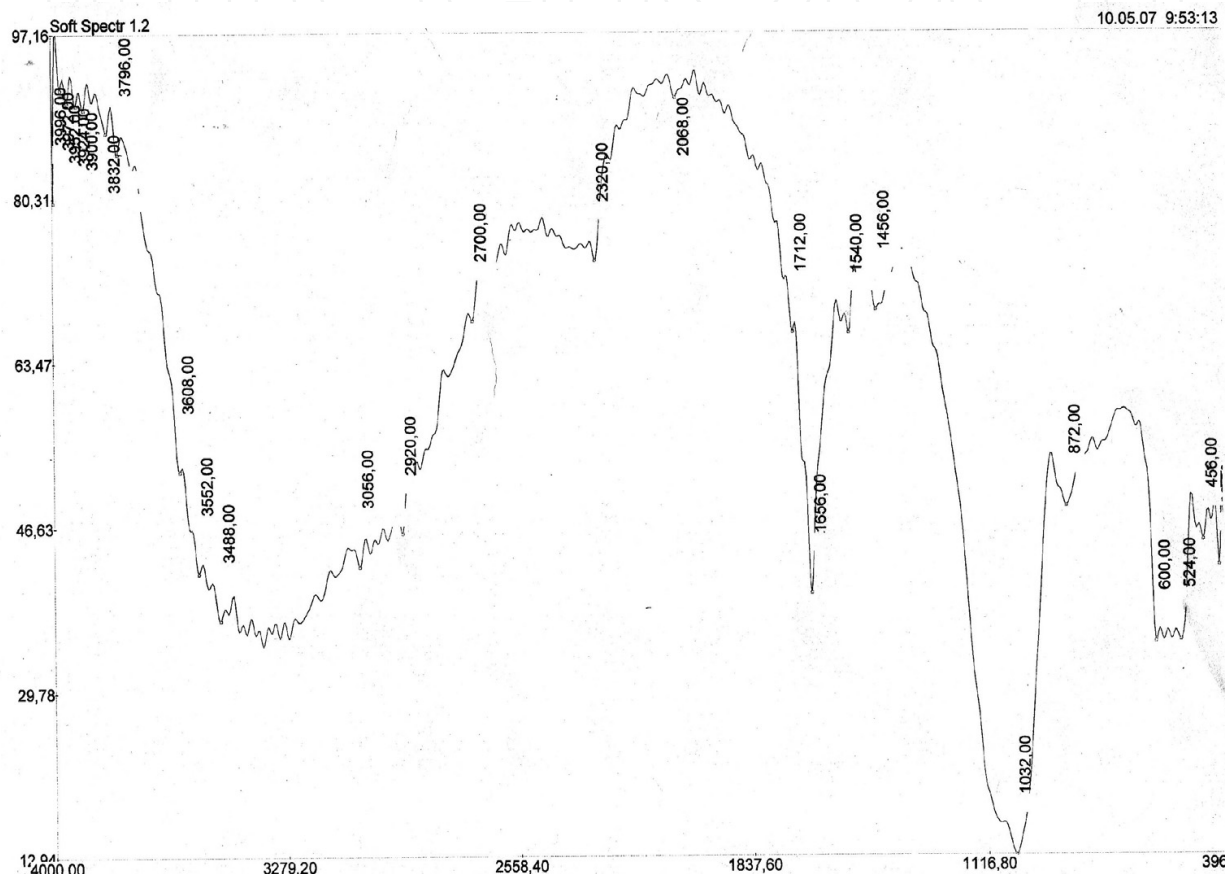

Figure 4. Infrared spectrum of culture fluid components *C. limicola* IMB K-8 cells under incubation in the dark

These results are consistent with data Sirevag, under which the cells incubated with *C. thiosylfatophillum* in the dark in culture fluid accumulated carboxylic acids: acetate (the main component that makes up 70%), propionate and succinate. They are the authors produced by reactions of glycolysis, pyruvate decarboxylation and other reactions.

Under the conditions of incubation, washed cells *C. limicola* IMB K-8 in light of the formation of organic compounds in the culture fluid was observed, and the total content of glucose after hydrolysis of glycogen, not significantly different from control. We shows the dynamic changes in the concentration of glucose (after hydrolysis of glycogen) and the accumulation of carboxylic acids during incubation of cells *C. limicola* IMB K-8 in the dark.

As seen from for 40h incubation, the contents of glycogen (for glucose) in the incubation mixture decreased almost three times while there was accumulation of carboxylic acids in the environment. Thus, synthesized by cells during photosynthesis *C. limicola* IMB K-8 - glucose and glycogen play an important role in the life of these bacteria during their stay on the light and in darkness. In the first case in the photoreduction CO_2 observed accumulation of glucose and its conversion into glycogen. In the darkness degradation glycogen to glucose, catabolism of which provides energy and constructive metabolism of green sulfur bacteria

In addition to the family *Chlorobiaceae* green bacteria carry the family *Chloroflexaceae*, which is called green nonsulfur bacteria. Green nonsulfur bacteria form filaments capable of sliding movement, optional anaerobes that can use organic compounds as sources of carbon and energy. By type of metabolism they phototropy under anaerobic conditions and under aerobic heterotrophs. Their cells contain bakteriohlorophily and carotenoids. Some molecules of green pigments nonsulfur bacteria contained directly in the cytoplasmic membrane, and part of chlorosom. Protein membrane chlorosom similar representatives of families *Chlorobiaceae* and *Chloroflexaceae*. Slow growth of photoavtotroph on the environment of sulphide was first described Median of employes in 1974. The representatives of green nonsulfur bacteria detected actively functioning oxidative tricarboxylic acid cycle. Like most photobacter bacteria genus *Chloroflexus* can grow using CO_2 as the sole carbon source. Found that green nonsulfur bacteria can use hydrogen sulfide as electron donor for photosynthesis and *Chloroflexus aurantiacus* may molecular hydrogen in the process reduce CO_2.

Found that one of the key enzymes - piruvatsyntaza that catalyzes the formation of pyruvate from acetyl-CoA and CO_2 detects activity in *Ch. aurantiacus*. The activity of other specific enzymes that are restorative (RTAC) was absent. On this basis it was concluded that cells of these bacteria, acetyl-CoA is synthesized from CO_2. The mechanism of this synthesis is different from what is in *C. limicola*.

Holo and Grace in 1987 found that in autotrophic conditions is inhibiting the tricarboxylic acid cycle and gliocsilate shunt, and in the cells is a new metabolic pathways in which acetyl-CoA is an intermediate product. Later Holo found that in autotrophic conditions *Ch. aurantiacus* converts acetyl-CoA in 3-hidroksypropionat, which is an intermediate product in the fixation of CO_2. Further to its transformation leads to the formation of malate and succinate. The results were confirmed by Strauss in 1992, which showed that the autotrophic cell growth *Ch. aurantiacus* isolated succinate and many 3-hidroksypropionat in the period from the late exponential phase to early stationary.

When culture *Ch. aurantiacus* was placed in an environment of ^{13}C labeled succinate and analyzed the different components of cells using ^{13}C spectroscopy, which determines the distribution of ^{13}C isotope in various compounds of cells, the results confirmed the role as an intermediate metabolite 3-hidroksypropionatu in CO_2 fixation.

Hidrokspropionat role as intermediate in the fixation of CO_2 was investigated Fuchs and Staff in experiments using ^{13}C. The relative amount of ^{13}C after growth *Ch. aurantiacus* in the

presence of ^{13}C and ^{13}C 3-hidroksypropionatu acetate. From the samples were labeled ^{13}C marker central intermediate metabolite as trioz and dicarboxylic acids. These experiments showed that cell growth *Ch. aurantiacus* was determined by adding ^{13}C 3-hidroksypropionat for several generations of cells, where it was concluded that this substance is a precursor of all cellular compounds *Ch. aurantiacus*. Thus, 3-hidroksypropionat functions in the body of *Ch. aurantiacus* as a central intermediate metabolite. The data obtained with labeled acetate, also confirmed the key role 3-hidroksypropionat as intermediate in the cyclic mechanism of CO_2 fixation (Fig. 5).
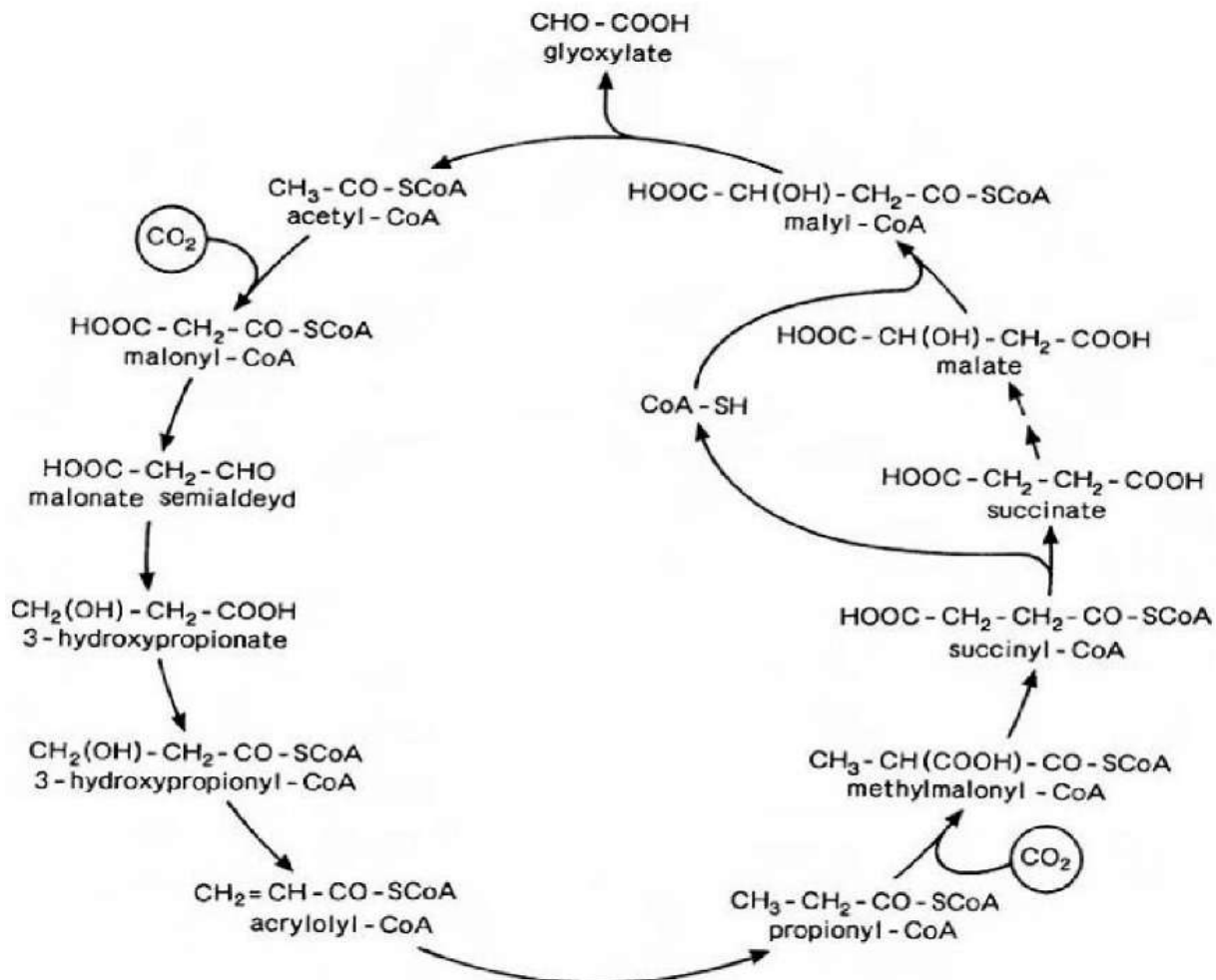

Figure 5. 3-Hidroksypropionatnyy cycle CO_2 fixation (Holo 1989 p.)

For a final check of the cycle Strauss and Fuchs had enzymatic studies and showed that the cells of green bacteria is nonsulfur activity of all enzymes required for assimilation cycle 3-hidroksypropionat reduction of carbon dioxide. In this cycle acetyl - CoA in malonil - CoA and then, reducing turns through 3-hidroksypropionat to propionil - CoA.

Thus, in green bacteria nonsulfur *Ch. aurantiacus* operating mechanism of autotrophic fixation of CO_2, the key intermediates which are 3-hidroksypropionat.. The final product of this cycle is glyoxylate, who fotoheterotrofiv becomes a backup compound poli -β-hidrocsybutyrat.

Thus, green bacteria families *Chlorobiaceae* and *Chloroflexaceae,* despite the similarity of their photosintetic system, assimilation of CO_2 reduction carried out in different ways. In the family *Chlorobiaceae* CO_2 fixation reactions proceeding with revers tricarboxylic acid cycle. Carbohydrates - products of photosynthesis, they lay in store as glycogen, which is used in extreme conditions for energy and carbon. Green nonsulfur bacteria family *Chloroflexaceae* used for CO_2 fixation reaction 3-hidroksypropionat way. Under these conditions produced a poli-β-hidroksybutyrat, which, like glycogen in the family *Chlorobiaceae*, is used in the energy and constructive exchanges.

Author details

M. B. Gorishniy and S. P. Gudz
National University of Lviv Ivan Franko, Lviv, Ukraine

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