Anoxygenic Photosynthesis in Photolithotrophic Sulfur Bacteria

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Hydrogen sulfide is a toxic compound that can affect various groups of water microorganisms. Photolithotrophic sulfur bacteria including *Chromatiaceae* and *Chlorobiaceae* are able to convert inorganic substrate (hydrogen sulfide and carbon dioxide) into organic matter deriving energy from photosynthesis. This process takes place in the absence of molecular oxygen and is referred to as anoxygenic photosynthesis, in which exogenous electron donors are needed. These donors may be reduced sulfur compounds such as hydrogen sulfide.

Keywords: hydrogen sulfide ; toxicity ; waste water treatment ; anoxygenic photosynthesis

1. Introduction

Hydrogen sulfide is a colorless gas with a characteristic odor that is soluble in various liquids including water. In nature, hydrogen sulfide is an intermediate of the sulfur cycle. The main producers of hydrogen sulfide in the environment are sulfate-reducing microorganisms [1][2][3][4][5][6]. Hydrogen sulfide occurs in volcanic gases and it is produced by some microbial metabolic processes during decomposition of plant and animal proteins. Hydrogen sulfide is highly toxic, and even in small doses can cause fatal poisoning. It inhibits the enzyme cytochrome *c* oxidase and thus prevents tissues from using molecular oxygen (O_2) [7][8]. This is mainly manifested in the central nervous system by paralysis of the respiratory center. In some cases, it may accumulate in aquatic environments. However, this accumulation can have fatal consequences for such ecosystems. As a result of hydrogen sulfide poisoning, mass deaths of aquatic animals and fish occur. Furthermore, the decomposition of these organisms leads to a further increase in the amount of hydrogen sulfide. Another problem with hydrogen sulfide-polluted water is that it is very difficult and very expensive to detoxify contaminated water [1]. Moreover, in most cases, it is practically impossible to remove all of hydrogen sulfide with currently existing methods.

Photolitotrophic sulfur bacteria are a group of microorganisms that includes the families *Chlorobiaceae* (green sulfur bacteria) and *Chromatiaceae* (purple sulfur bacteria) [9]. These names refer to their coloration, which are due to the different content of photosynthetic pigments, such as bacteriochlorophylls and carotenoids [10]. These specialized bacteria have developed a special form of photosynthesis, the so-called anoxygenic photosynthesis, which takes place under anaerobic conditions and oxidizes reduced sulfur compounds as an electron donor [11]. The process of anoxygenic photosynthesis thus differs from oxygenic photosynthesis, which is characteristic of cyanobacteria and plants. Green sulfur bacteria (GSB) and purple sulfur bacteria (PSB) of the above families may metabolize hydrogen sulfide. High concentrations of this compound often occur in aqueous layers of molecular sulfur-rich sediment, which is reduced by two groups of microbial communities: sulfate-reducing and sulfur-reducing microorganisms. The sulfate or sulfur is being used as a terminal electron acceptor in anaerobic respiration. On the one hand, sulfur anoxygenic phototrophs oxidize sulfur compounds to sulfates and molecular sulfur, and on the other hand, these compounds are reduced. Therefore, the described microorganisms are in close interaction with one another and are involved in the sulfur cycle in water layers and occur in nature in general [12].

Although *Chlorobiaceae* and *Chromatiaceae* have been known for almost a century, they have not been thoroughly studied, as very few researchers have dealt with this group of microorganisms [10][11][13]. However, these interesting bacteria could be used in the biotechnology industry due to their ability to utilize hydrogen sulfide.

2. General Characteristics of Photoautotrophic Bacteria

The most remarkable and at the same time common feature of all GSB and PSB are the ability of anoxygenic photosynthesis based on bacteriochlorophyll-mediated processes [10]. Different anoxygenic phototrophic bacteria contain several types of bacteriochlorophylls and various carotenoids as pigments, which function to transform light into chemical energy and give cultures a strong coloration that differs in pigment content from different shades of green, yellow-green, brown-green, brown, red, pink, purple, up to blue [14]. Photosynthesis in phototrophic sulfur bacteria depends on the O_2 content of the environment because the synthesis of their photosynthetic dyes is suppressed by O_2. Unlike cyanobacteria and eukaryotic algae, phototrophic sulfur bacteria are unable to use water as an electron donor and do not produce O_2. They use only one photosystem and require electron donors with a lower redox potential than water. Sulfur and its reduced compounds are most often used as donors, but also hydrogen and many other small organic molecules [9].

Green sulfur bacteria form a phylogenetically consistent and isolated group of bacteria. They differ in that inside their cells there are special light-harvesting complexes called chlorosomes, which contain bacteriochlorophylls and carotenoids. GSB also differ from other phototrophic organisms in the chemical structure of bacteriochlorophyll antennas. The same antenna composition was found only in the phylogenetically distant family *Chloroflexaceae* [13]. Chlorosomes of GSB contain bacteriochlorophyll (BChl) c, d, or e. Green-colored bacteria contain mainly BChl c or d; others are colored orange or brown, due to the high content of carotenoids [15].

Unlike GSB, PSB do not contain chlorosomes and their photosynthetic apparatus, including pigments, is stored in one or more of the extended intracellular systems of the cytoplasmic membrane. These systems consist of folds, tubules, vesicles, or lamellae. The most common photosynthetic dye found in PSB is bacteriochlorophyll a or b. *Chromatiaceae* also contains a large number of auxiliary dyes, such as spirilloxynthine, rhodopine, or okenone carotenoids [16].

Due to their limited physiological flexibility, the ecological niche of GSB is rather narrow. All known species are typically aquatic microorganisms and inhabit illuminated anoxygenic layers of lakes or littoral sediments. In some of these ecosystems GSB play a major role in the transformation of carbon and sulfur compounds. Another phenotypic feature of ecological significance is the adaptation to very low light intensities. Compared to other phototrophic microorganisms, GSB are able to inhabit the lowest parts or sediments of ecosystems. The cells of most species belong morphologically to the most inconspicuous members of natural bacterial communities. An exception are phototrophic consortia, which are permanent associations of GSB with chemolithotrophic bacteria. At present, these phototrophic consortia represent one of the most developed symbioses in the prokaryotic world [13].

Purple sulfur bacteria inhabit the same sites as green sulfur bacteria, and some may even live in a symbiosis-like relationships with them. In general, however, *Chromatiaceae* live above *Chlorobiaceae* because they need higher light intensity and lower hydrogen sulfide concentrations for photosynthesis [10].

Both GSB and PSB are of the gram-negative type. All GSB described so far are rods and their size is around 1 μm. PSB are more diverse in shape; the shape of cells varies from species to species, from cocci, through rods, to spirals. However, it can also vary during the cell life cycle depending on external conditions. PSB are slightly larger than GSB and reach a size of up to 3 μm. Most types of PSB are motile with one or more flagella, while GSB lack a flagellum and are therefore immobile. Some GSB species, such as *Chlorobium limicola*, form streptococcal-like chains. In addition, these chains may, depending on the culture conditions, be coated with a mucous layer. PSB occur either singly or in pairs. For later oxidation, the PSB store sulfur inside the cell in so-called granules, and the GSB store it outside the cell, where they are held at the membrane by special mechanisms. Some PSB species have gas sacs inside the cell that allow them to float in a low-density environment [17].

3. Anoxygenic Photosynthesis

The conversion of light into chemical energy is an essential process for life, and photosynthetic reaction centers play a major role in this mechanism. These are special complexes of proteins and chlorophylls in the nucleus of the photosynthetic system, which are excited after irradiation and absorption, thus releasing energy that allows electrons to pass through the photosynthetic membrane. Two types of reaction centers are known. The first type is photosystem 1 (PS1), which is found in chloroplasts of cyanobacteria and GSB. The second type is photosystem 2 (PS2), which is found in chloroplasts and cyanobacteria. This type of reaction center is also found in PSB [18].

3.1. The Photosystem of the Family Chlorobiaceae

In the case of GSB, the antenna complex is found in special formations called chlorosomes. These chlorosomes are located on the inner side of the inner cell membrane and perform the function of absorbing light radiation and transferring energy to the photosynthetic reaction center. They differ from all known photosynthetic antenna complexes due to their pigment–pigment arrangement, instead of the typical pigment–protein, such as the *Chromatiaceae*. Chlorosomes contain lipids, small amounts of protein, carotenoids (chlorobactein, neurosporein, and lycopene) and bacteriochlorophylls. The function of proteins in chlorosomes has not been elucidated, but they are thought to ensure the stability of bacteriochlorophylls and maintain the stable ovoid shape of chlorosomes. In addition to chlorosomes, GSB contain another unique antenna complex, called the Fenna–Matthews–Olson (FMO) protein. This protein transports electrons from chlorosomes to the reaction center. Most proteins containing bound bacteriochlorophylls are insoluble in water, with the exception of FMO protein [19].

In the case of GSB, the energy of light radiation is transmitted to the reaction center by means of chlorosomes. These structures described above capture high radiation efficiency, thanks to the huge amount of bacteriochlorophylls contained (about 200,000 molecules per chlorosome). The reaction center contains an average of 500 bacteriochlorophyll molecules, and one chlorosome binds to up to forty such reaction centers. Bacteriochlorophylls are arranged in chlorosomes in tubules with an absorption maximum between 720–750 nm. The energy transfer of light radiation passes through these tubules to the so-called baseplate, formed by bacteriochlorophyll, and from there the energy passes into the FMO protein (absorption maximum FMO 808 nm). Via FMO protein, energy is already transferred to the reaction center of the photosynthetic apparatus of *Chlorobiaceae* [20].

3.2. The Photosystem of the Family Chromatiaceae

The antenna system in PSB consists of two main types of light-harvesting complexes, LH1 and LH2. The LH1 complex is found in all species of this family and surrounds the reaction center and forms with it the so-called core of the photosynthetic complex. The LH2 complex is located in the periphery of this nucleus and does not occur in some species. Both LH1 and LH2 are large oligomers composed of heterodimers of transmembrane polypeptides (α and β) associated with bacteriochlorophylls and carotenoids. Although both subunits are structurally almost identical, the LH1 complex absorbs light radiation of a longer wavelength (870–960 nm) than the LH2 complex (800–850 nm).

The LH1 complex is evenly distributed around the reaction center and forms a closed and slightly elliptical cylinder composed of 16 pairs of helical αβ-polypeptides, 32 bacteriochlorophyll a, 16 carotenoids (spirilloxanthin) and 16 Ca^{2+} ions. The ratio between the content of pigments and Ca^{2+} ions is stoichiometrically constant. As with LH2, α-polypeptides are found inside LH1 and β-polypeptides outside the ring [21].The LH2 complex is a typical membrane protein of cylindrical structure, containing 27 bacteriochlorophylls and 9 carotenoids. It contains 9 αβ-heterodimers that form a circular aggregate [22].

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