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Anaerobic Photosynthesis

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Chemical Formula

Numerous organic and inorganic electron donors can be utilized by anaerobic phototrophs to fix CO_2, with sulfide being one of the most common electron donors. The chemical formula for anaerobic photosynthesis coupled to hydrogen sulfide oxidation and elemental sulfur formation, one of the most common electron donors for anaerobic phototrophs, is expressed as:

$$CO_2 + 2H_2S + \textit{photons}\ \text{à} \rightarrow CH_2O + H_2O + 2S^0$$

As shown here, oxygen is not produced in this reaction leading to this process being referred to synonymously as "anoxygenic photosynthesis".

Definition

The process by which anaerobic phototrophic bacteria harvest light energy coupled to fixation of CO_2, without the use of water as an electron donor or the production of oxygen as a by-product.

History

The study of anaerobic photosynthesis stems back to the dawn of microbiology itself with the first documented observation made in 1876 by E. Ray Lankester who noted the formation of red-colored "crusts" in a bacterial enrichment culture from decaying organic matter. The first isolate of a purple anaerobic phototroph, *Rhodospirillum rubrum*, was obtained in 1887 from a Berlin tap water sample in which a mouse had died. In 1907, it was finally demonstrated conclusively that these purple phototrophic bacteria did not produce O_2 (Molisch 1907). The first green anaerobic phototroph, *Chlorobium limicola*, was described in 1906 by Georgii Nadson (1906), which was isolated and characterized by Cornelis van Niel (1932). Since then, huge advances have been made in our understanding of the metabolisms, physiology, lifestyle, and environmental importance of anaerobic phototrophs which is summarized below. A complete timeline of major

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advances in the study of anoxygenic photosynthesis can be found in Gest and Blankenship (2004)

Overview

Anaerobic photosynthesis is a process by which anaerobic phototrophic bacteria use energy from sunlight to drive the fixation of CO_2. In contrast to oxygenic photosynthesis, which is conducted by organisms such as cyanobacteria and plants, anaerobic photosynthesis does not couple CO_2 fixation to the oxidation of water and therefore does not produce oxygen as a by-product. Instead of using water as an electron donor, these phototrophs utilize numerous inorganic compounds including sulfide, ferrous iron, hydrogen, or even arsenite (Kulp et al. 2008) and nitrite (Griffin et al. 2007), as well as organic compounds. Several groups of bacteria are capable of conducting anaerobic photosynthesis including green sulfur bacteria (GSB), purple sulfur bacteria (PSB), purple non-sulfur bacteria (PNSB), *Acidobacteria*, *Heliobacteria*, and both red and green filamentous phototrophs such as *Chloroflexi* (Overmann and Garcia-Pichel 2013).

Anaerobic photosynthesis evolved before aerobic photosynthesis and was likely the dominant means of primary production in the Earth's ancient oceans, taking advantage of the anoxic, ferruginous, and sulfidic conditions that dominated for much of Earth's history (reviewed in Camacho et al. 2017). Anaerobic photosynthesis contributed significantly to early biogeochemical cycling, in particular by catalyzing oxidation of Fe(II) which led to the formation of vast deposits of Fe-rich rocks in the ancient oceans (see ► Photoferrotrophy). Distribution of anaerobic phototrophs became limited as high oxygen concentrations forced them to retreat into anoxic, sunlit niches. They are commonly found today in redox-stratified lakes, waterlogged sands and soils, sulfidic springs, and salt marshes. They are also found in extreme environments such as acidic and alkaline hot springs, salt marshes, soda lakes, and polar environments such as the high Arctic (Madigan 2003).

It is likely that the molecular pathways involved in anaerobic photosynthesis gave rise to aerobic photosynthesis (Blankenship 2010). Aerobic photosynthesis is a more complex molecular process than anaerobic photosynthesis, requiring two connected photosystems (Photosystem I and Photosystem II) to work in tandem. In order to harvest light energy, the chlorophyll-containing reaction center in Photosystem II is excited by light and readily passes an electron down the electron transport chain to a second chlorophyll-containing reaction center in Photosystem I. This second reaction center is excited by light and an electron passed down the second electron transfer chain, ultimately oxidizing NADP+ to NADPH. Anaerobic photosynthesis, on the other hand, requires only one photosynthetic reaction center, where the electron can either end up oxidizing NAD+ to create reducing equivalents or return to the reaction center in a process known as "cyclic photophosphorylation." The Type I reaction center found in the GSB and *Heliobacteria* is structurally similar to Photosystem I found in aerobic phototrophs, whereas the Type II reaction center found mainly in the purple bacteria and filamentous anaerobic phototrophs is similar to Photosystem II. It is therefore considered that the reaction centers in anaerobic phototrophs are the ancestors of Photosystems I and II. It is still debated, however, whether the photosystems were merged in one anaerobic phototroph shortly before the evolution of aerobic photosynthesis or whether ancient anaerobic phototrophs had both photosystems and later specialized to use just one (Allen 2005).

In addition to utilizing different electron transport chains from aerobic phototrophs, anaerobic phototrophs also employ different pigments for harvesting light. Anoxygenic phototrophs use bacteriochlorophylls for this purpose, which are similar to chlorophyll in aerobic photosynthesis. Chlorophyll has peak absorption of light in the red range of the spectrum, whereas bacteriochlorophylls have a maximum absorption in the near infrared. Anaerobic phototrophs, particularly the GSB, also utilize bacteriochlorophylls that are specifically adapted to harvest light at low intensities. This difference in both the wavelength and intensity of light utilized by anaerobic phototrophs can enable them to coexist alongside oxygenic phototrophs in the same environment where they can carve out independent niches based on the wavelength and intensity of light (e.g., de Beer et al. 2017).

To summarize, anaerobic photosynthesis is an ancient metabolism that helped significantly shape the biogeochemical evolution of the Earth, and it provided much of the genetic machinery later adapted for aerobic photosynthesis. Despite being relegated to more specialized environments following the evolution of aerobic photosynthesis, these organisms are still prevalent in many sunlit environments today where they contribute as primary producers and actively shape the biogeochemical cycling of elements such as sulfur and iron.

Cross-References

- ▶ Diversity and Evolution of Cyanobacteria
- ▶ Oxidation of the Atmosphere
- ▶ Photoferrotrophy
- ▶ Sulfide Oxidation
- ▶ Sulfidic Oceans

References and Further Reading

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