For the photosynthetic CO_2 reduction
only those hydrogen compounds can serve as H-donors
in which the hydrogens can be sufficiently activated
by the organism. Then it is quite conceivable that
organisms exist which cannot use H_2O as a H-donor
because they cannot activate the H in this compound
sufficiently. These organisms might, however,
be typically photosynthetic in case some other
H compound is present containing the hydrogen
in a form in which these organisms
can bring about a sufficient activation

Cornelis B. van Niel

Chapter 9

The power of photosynthesis, even in almost complete darkness

This title probably means that some bacteria are able to "see" tiny amounts of light.

Correct, but first we need to see how microorganisms take advantage of bright sunlight.

Photosynthesis had a decisive impact on evolution. When the world was still anaerobic, the ability to convert light energy into metabolically useful energy provoked a first revolution. It was not only the generation of ATP from light but also the possibility to oxidize compounds such as hydrogen sulfide or ferrous ions (Fe^{2+}) as sources of the reducing power required for CO_2 reduction. So sulfate and ferric ions (Fe^{3+}) became available for the first time, and these compounds allowed new microbiological processes to evolve, such as those carried out by the sulfate-reducing bacteria. The second revolution occurred with the emergence of oxygenic photosynthesis and, with it, the development of the aerobic world (see Chapter 5). These processes should be examined more closely.

You described the bacteriorhodopsin of some archaea as a light-driven proton pump, the second type of photosynthesis, in Chapter 8. Are you now talking about the first type of photosynthesis?

Yes, and this type is much more complex. It's found all over the world and involves the phototrophic anaerobic bacteria; the oxygen-evolving cyanobacteria; the algae in oceans, lakes, and streams; and all the green plants on the continents. All of these organisms have a machinery called the photosynthetic apparatus. When we look at the flora around us, at the flowers, the meadows and the forests, we are of course aware that all this is the result of photosynthesis, but normally we don't think about the machinery required to capture light and take advantage of its energy. The conversion of light energy into other forms of energy is no easy task.

Discover the World of Microbes: Bacteria, Archaea, and Viruses, First Edition. Gerhard Gottschalk.

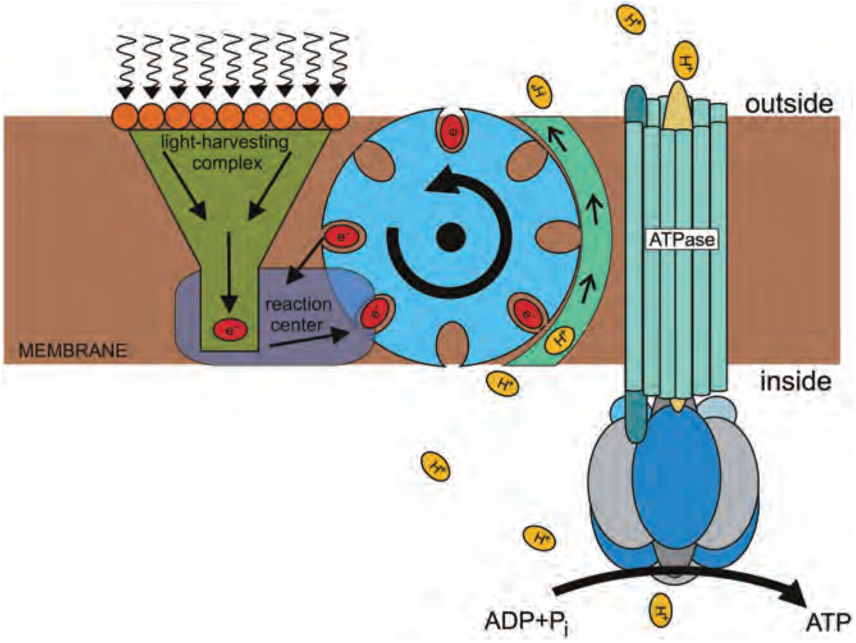

Figure 20 The photosystem as it appears in purple bacteria carrying out anoxygenic photosynthesis. Light is harvested and the excitation energy is channeled to the reaction center in which electrons (red) are released. They are pushed through a cycle of carriers and, driven by this cycle, protons (yellow) are translocated from inside to outside. The electrons return to the reaction center (cyclic electron flow). The resulting proton gradient is then used for ATP synthesis. The driving force is the high redox energy of the electrons released, which is lost stepwise in the cycle.

Think of the sophisticated technologies that have been developed to “harvest” light in photovoltaic plants.

The photosynthetic apparatus consists of several components (Figure 20). Light is absorbed by carotenoids that are part of the light-harvesting centers. The light energy is then converted into a flow of electrons that hit the reaction center pigments. They consist of special chlorophyll molecules. The reaction center then initiates a cyclic electron flow, which functions like the wheel of a water mill. It pumps protons from one side of the cytoplasmic membrane to the other, and the resulting proton gradient can be coupled to the synthesis of ATP as discussed in Chapter 8.

This is the principle of anoxygenic photosynthesis as carried out, for example, by the brightly colored purple bacteria (Figure 8). Not all microorganisms carrying out anoxygenic photosynthesis contain beautiful, purple-colored carotenoids. Other groups contain yellowish carotenoids capable of absorbing shorter-wavelength light that reaches greater depths in bodies of water. This, however, is not the only adaptation of the green sulfur bacteria for growth in deeper layers of water or where it’s turbid. Furthermore, these microorganisms contain super antennae, chlorosomes, which enable them to absorb the tiniest amounts of light.

They don't look through binoculars, as the purple bacteria do, but through a telescope. They are even so efficient that they are able to thrive in the Black Sea. Let's ask Joerg Overmann (Braunschweig, Germany) under which conditions green sulfur bacteria can grow in this habitat:

> "Green sulfur bacteria are much less flexible than any other phototrophic bacterium with regard to their metabolism: they obligately depend on light to obtain energy, on carbon dioxide as carbon source, and on sulfide to feed electrons in their photosynthetic system and to ultimately reduce that carbon dioxide and form progeny. Because of their narrow ecological niche, natural populations of green sulfur bacteria are only found in certain lakes or sandy beaches where microbial processes lead to sulfide production in deeper layers still reached by underwater light. Green sulfur bacteria thus face a dilemma – they are confined to lower light levels than any other phototrophic organism. This is probably the reason, why green sulfur bacteria have developed the largest photosynthetic antenna of all photosynthetic organisms to absorb light: it has been determined that a single cell contains about fifty million bacteriochlorophyll molecules.
>
> In the Black Sea, the inflowing river water cannot mix with the heavier, deeper water that originates from the Mediterranean. As a result, only the upper 100 m contain oxygen, algae, crustacea, jellyfish and fish, etc., whereas the entire 2100 m below that are completely free of oxygen and higher life forms. Consequently, the Black Sea currently represents the largest anoxic water body on Earth. Our recent measurements of underwater light intensities employing especially sensitive quantum meters revealed unprecedented low values. The light intensities at 100 m depth equals the light of a small candle seen at a distance of 60 m in a pitch dark night. Yet, one type of phototrophic green sulfur bacterium has been found to be capable of growing even under these extreme environmental conditions.
>
> After earlier anecdotal reports on the occurrence of different anoxygenic phototrophic bacteria in the 1950s and 1970s, a U.S.–Turkish expedition in May 1988 detected traces of bacteriochlorophyll *e*, a unique pigment of green sulfur bacteria, at about 100 m depth. This represents the deepest occurrence of these bacteria so far. In the following years, we could show that only a single type of green sulfur bacteria occurs in this environment and were able to isolate and study it. The Black Sea strain is able to increase its photosynthetic antenna to twice the size of its relatives, thereby increasing the light energy harvested even further. Most notably, however, the cells are capable of surviving very long periods in the dark because they require much less maintenance energy than any other bacterium investigated so far. Recently, we found that the Black Sea bacterium is actually distributed across the major part of the Black Sea. Thus, this bacterium holds the world record for low-light adaptation, low maintenance energy requirement and probably represents the largest contiguous population of phototrophic bacteria known to date."

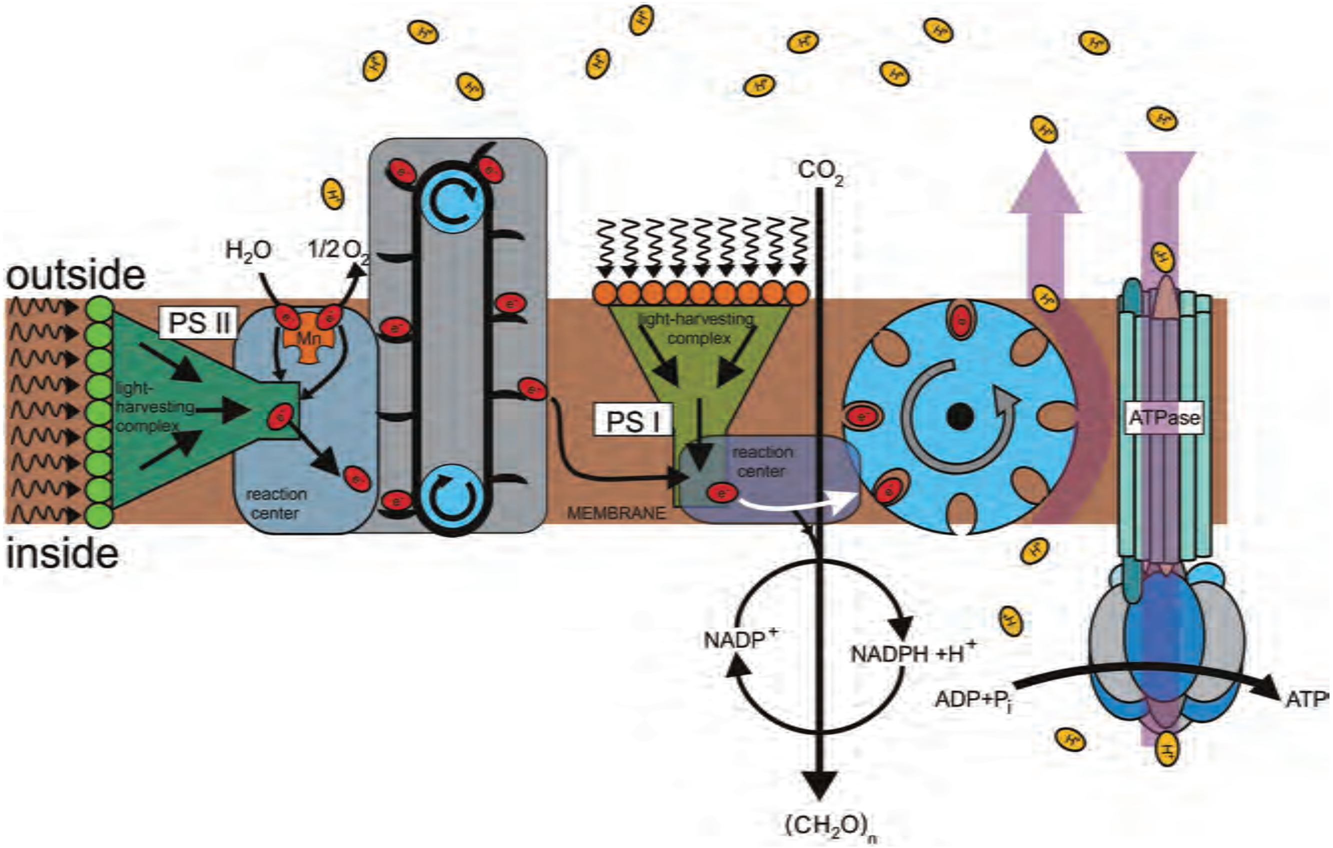

Figure 21 Oxygenic photosynthesis requires the interplay of two photosystems. PS I generates electrons (red) that travel through the carrier cycle but are also used to provide reducing power for the reduction of CO_2. This results in a lack of electrons that no longer reach the reaction center of PS I. The pool of electrons is replenished by the action of PS II. Ultimately, these electrons come from water, which is cleaved by a manganoprotein complex. As mentioned in Figure 20, the redox energy is important. At the reaction center of PS II, it is so high that water can be oxidized to oxygen and the electrons are pulled all the way through the carrier system to reduce $NADP^+$.

What an impressive report: photosynthesis at a depth of 100 meters, but performed by a highly specialized species of the green sulfur bacteria.

As already mentioned, the transition of H_2S to H_2O as source of reducing power was a dramatic step in evolution that was taken with the emergence of the cyanobacteria on our planet. They represent the first important group of organisms capable of carrying out an oxygenic photosynthesis.

What is the mechanistic difference between anoxygenic and oxygenic photosynthesis?

There's a big difference. The anoxygenic photosynthesizers have one photosystem. This system is not potent enough to remove the two hydrogen atoms from the water molecule. As already mentioned, water is the gold among the suppliers of reducing power. Two photosystems are required, and their combined action makes the whole system extremely powerful. It is like going from a propeller engine to a jet engine. Instead of air, photosystem II sucks in electrons and generates a manganese-containing protein so deficient in electrons that it can separate water into oxygen, protons, and electrons (Figure 21). Recent findings indicate that the photosystem of the green sulfur bacteria is the ancestor of photosystem I and that photosystem II originated from the purple bacteria. Isn't that a miracle, two types of bacteria performing anoxygenic photosynthesis coexisted for hundreds of million years. Combination of their photosystems in one cell and further evolution took place. As a result, cyanobacteria appeared performing an oxygenic photosynthesis. They are the pathfinders of eukaryotic phototrophs, of algae and plants, and their importance cannot be overexaggerated. We have asked an expert on cyanobacteria, Jack C. Meeks, (Davis, California, USA), to summarize the importance of the cyanobacteria during evolution and today:

> "Cyanobacteria are defined by their oxygenic photoautotrophic mode of energy and carbon metabolism. They are the most nutritionally independent organisms in the biosphere, requiring only light, water, CO_2 and a few macro- (N, P and S) and microinorganic nutrients for growth. To appreciate the ecological role of cyanobacteria, it is important to recognize that, although ATP is the primary cellular energy currency, reduced carbon compounds (biomass) are the major ecological energy currency in supporting growth of fermenting and respiring organisms. Fueled by an energy source from outside of the biosphere (sunlight), anoxygenic photosynthesis, utilizing H_2S and H_2 as electron donors, was (and is) an efficient mechanism for the production of reduced carbon, and the emergence of the two different types of reaction centers of anoxygenic photosynthesis undoubtedly led to the diversification of fermentative and respiratory metabolism in other organisms. However, the abundance of water as an electron donor, and its essential requirement as the solvent of life, gave oxygenic photosynthesis by cyanobacteria an enormous competitive advantage. Moreover, oxygen, the waste product of the photolysis of water, is a

biological toxin because of its interaction with reduced biomolecules and conversion to reactive oxygen species (ROS, see Chapter 5), which damage DNA and proteins. To this day, the vast majority of anoxygenic phototrophic bacteria cannot grow as phototrophs in the presence of oxygen. Thus, cyanobacteria improved their competitive advantage by converting illuminated habitats from an anoxic to oxic state and essentially eliminating their photosynthetic bacterial competitors in the oxic environments. Many cyanobacteria also reduce (fix) atmospheric N_2 to NH_3 (see Chapter 11), thereby enhancing both their nutritional independence and the value of their metabolites. In this regard, they also show their nutritional needs to be simpler than their progeny eukaryotic algae. From an ecological perspective, nutritional independence also implies that cyanobacteria are less susceptible to biological selective pressures than are nutritionally dependent organoheterotrophs, or even chemolithoautotrophs.

The photosynthetic production of oxygen by cyanobacteria was, arguably, the most dramatic event in the continued evolution of life on Earth. Its effect on ancestral microorganisms was discussed in Chapter 5. One can speculate on its impact in the evolution and diversification of eukaryotes. Eukaryotic cells have many unique characteristics that distinguish them from the bacteria and archaea. With respect to one character, it now appears that all existing eukaryotes have, or had, mitochondria. In some anaerobic eukaryotic microorganisms, the mitochondria have been reduced in structural and functional complexity, and exist as membrane-enclosed hydrogenosomes or mitosomes. Phylogenetic analyses indicate that mitochondria arose following an endosymbiotic association between an unknown anaerobic phagocytic partner cell and a respiring bacterium. A question to ask is: what was the selective pressure that stabilized such an endosymbiosis? Much attention has been given to the advantage of respiratory electron transport coupled to ATP synthesis; i.e. energy metabolism. Clearly, mitochondria have evolved elaborate translocation mechanisms for small (ATP, ADP and other metabolites) and large (proteins) molecule communication with the partner cytoplasm and nucleus. An alternative hypothesis suggests an oxygen protective role in mitochondrial endosymbiosis. Since the mechanisms for detoxification of ROS appear to be universal in bacteria and eukaryotes, the oxygen protective role has credence, with the genetic information transferred from the tolerant endosymbiont to the intolerant eukaryote nucleus. In this scenario, a eukaryotic cell with a stabilized mitochondrial endosymbiont could tolerate the oxygen produced by cyanobacterial primary producers.

A second, sequential, endosymbiotic event with a cyanobacterium then led to the chloroplasts of algae and plants. This event greatly reduced the competition for organic substrates by the partner cell, which could now live on CO_2 as carbon source. This competitive advantage would have stabilized the endosymbiosis.

> These two endosymbiotic events in response to the selective pressures of oxygen tolerance and reduced-carbon/energy acquisition could have resulted in quite rapid diversification of the two early eukaryotic lines. The microbial photoautotrophic line led to terrestrial plants, with their highly successful light-harvesting morphology. The selective pressure on the microbial organoheterotrophic line was for external nutrient (biomass) acquisition, ultimately leading to the evolution of highly effective means for harvesting prey."

We learned a lot from Jack Meeks' contribution. It is not only ATP synthesis that stabilized the endosymbiosis ultimately leading to animals and to plants. It is also the oxygen-protective role and, in the case of plants, the ability to grow on CO_2 as carbon source. Further aspects of endosymbiosis will be discussed in Chapter 27.