Bacterial Photosynthesis Without Chlorophyll

David Bardell

THE EXISTENCE of all forms of life on Earth depends on photosynthesis, by which light energy of the sun is converted to chemical energy needed for the metabolic processes of organisms.

Plants and some species of bacteria can photosynthesize, since they contain chlorophyll, the critical light-absorbing molecule. Plant chlorophylls, which have minor differences in their chemical structure, are classified as *a*, *b*, *c*, *d*, and *e*. Bacterial chlorophylls differ in some chemical details from each other and from plant chlorophylls, and have been designated bacteriochlorophylls (Pfennig 1977).

Differences in chemical structure notwithstanding, plants and photosynthesizing bacteria have in common the possession of some form of chlorophyll and the effect of light on chlorophyll. The first event in photosynthesis with all kinds of chlorophyll is the absorption of light which causes the ejection of an electron from the molecule. This results in a positively charged chlorophyll molecule and an electron which has a negative charge. There are at least two known pathways for electrons in photosynthesis. Briefly, in one, the electron moves back via intermediates to the charged chlorophyll. In the other, the ejected electron does not return to chlorophyll, and the charge on chlorophyll is neutralized by an electron from a donor. Whatever the pathway, it is during movement of electrons that inorganic phosphate and adenosine triphosphate (ATP) the major source of usable energy in cell metabolism of all organisms.

Bacterial species of the genus *Halobacterium* require high concentrations of sodium chloride for growth, and in nature are found in pools of evaporated seawater and in places like the Dead Sea and the Great Salt Lake.

In recent years, while studying the structure of the microorganism, it was discovered that *Halobacterium halobium* could photosynthesize. The discovery of another bacterial species with the ability to photosynthesize was not too significant, but what was significant was the fact that *Halobacterium halobium* does not contain bacterial or plant chlorophyll. The light-sensitive molecule of *Halobacterium halobium* is rhodopsin, and it is located in the cell membrane of the microorganism. It is closely related to rhodopsin of animals, and has been designated bacteriorhodopsin (Stoeckenius 1976).

Rhodopsin is well known as the light-sensitive molecule in retinal cells of the eyes of all vertebrate and some invertebrate animals. In vision, the absorption of light causes a change in shape of the rhodopsin molecule, and this sets in action a series of events which results in the sensation of vision. Rhodopsin is changed back to its original shape by an enzyme, and can then be stimulated again by light.

The cell membrane of *Halobacterium halobium* absorbs much light in the green-yellow part of the visible light spectrum, and consequently has a purple color. It is light with a wavelength around 570 nanometers which excites bacteriorhodopsin. Photosynthesis is not brought about by a change in shape of bacteriorhodopsin, with the movement resulting from changes in the conformation of the molecule driving the conversion of light to chemical energy, although it would not be unreasonable to expect this from the way rhodopsin reacts to light in the visual process.

The synthesis of ATP during photosynthesis in plants and bacteria takes place during movement of electrons. Therefore, it might be expected that light absorbed by bacteriorhodopsin would eject an electron, and the process would then be essentially that which is observed in the usual form of photosynthesis. However, this is not the case. Not only is the light-absorbing molecule different from chlorophyll, but photosynthesis by *Halobacterium halobium* involves a moving proton, or hydrogen ion (H +), and not a moving electron.

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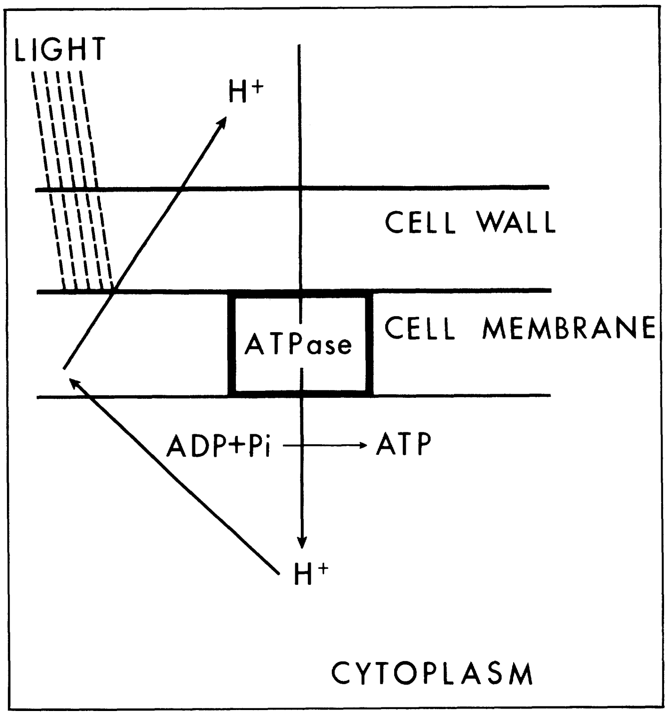

FIGURE 1. Diagrammatic representation of photosynthesis by *Halobacterium halobium*. Light causes the loss of a protòn, hydrogen ion (H +), from bacteriorhodopsin located in the cell membrane of the microorganism. The proton, which goes to the external environment of the bacterium, is brought back into the cell via the enzyme ATPase, which spans the membrane. It is during transport of the proton through ATP ase that inorganic phosphate (Pi) reacts with adenosine diphosphate (ADP) to form energy-rich adenosine triphosphates (ATP). The negative charge on bacteriorhodopsin due to loss of a proton is neutralized by the proton after it re-enters the bacterium.

In photosynthesis by *Halobacterium halobium*, light absorbed by bacteriorhodopsin causes a proton to be eliminated from the molecule into the external environment of the microorganism, leaving bacteriorhodopsin with a negative charge. The resulting membrane potential, positive on the outside of the cell and negative on the inside, drives a backflow of protons into the microorganism. It is during backflow of a proton through the enzyme ATPase that ATP is produced. The enzyme is located in, and completely transverses, the cell membrane, Thereafter, the negative charge on bacteriorhodopsin is neutralized by the proton, and the cycle is then repeated (fig. 1). Evidence indicates that intermediates are involved in the release of the proton from the cell and in reprotonation of bacteriorhodopsin, and this is an area of active research (Stoeckenius 1976).

The cell membrane of *Halobacterium halobium* is rich in bacteriorhodopsin, and it has been demonstrated experimentally that the movement of protons in and out of microorganisms is reflected in a reversible change in the pH of the medium in which the microorganisms are growing. The medium becomes more acid as protons are released from bacteriorhodopsin and then less acid as the protons return.

The necessity for light in the unusual pathway leading to ATP production has been demonstrated. In the absence of light, or in the presence of light of the wrong wavelength to excite bacteriorhodopsin, ATP is not synthesized.

A key role for membrane ATPase in the pathway is also known. If, under experimental conditions, protons are made to enter the cell while the enzyme is inhibited, ATP is not synthesized, thus demonstrating the role of membrane ATPase in joining inorganic phosphate by a high-energy bond to ADP.

All photosynthetic organisms must have a mechanism to produce ATP during periods of darkness. *Halobacterium halobium* does so by cellular respiration. The microorganism has no known fermentative pathways for the production of ATP, pathways which occur in numerous species of bacteria (Stoeckenius 1976).

In the past two decades, as a result of research on photosynthesis and cellular respiration, the production of ATP as electrons pass along a chain of electron-transport molecules has become well entrenched in college and high school biology textbooks. At specific points along the chain, sufficient energy is released for synthesis of ATP from inorganic phosphate and ADP. This mechanism for ATP synthesis has been challenged, particularly by Peter Mitchell of England. Based on his own experimental work, started more than twenty years ago, Mitchell has proposed that ATP is produced by a "chemiosmotic" process. Mitchell was awarded the Nobel Prize in chemistry in 1978 for this work (Freedman 1978). According to the chemiosmotic theory, the movement of electrons along a chain of electron-transport molecules creates conditions which cause protons to cross the inner membrane of mitochondria, or the membranes of thylakoids in chloroplasts. This movement of protons results in an electrical-charge gradient across the membrane, which in turn drives the protons back across the membrane. As the protons move back, membrane ATPase synthesizes ATP from ADP and inorganic phosphate.

Although the mechanisms of photosynthesis by *Halobacterium halobium* and the chemiosmotic theory differ with respect to the process by which protons are moved to the outside of a membrane, they do have in common the production of ATP by membrane ATPase as protons are returned across the membrane.

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FIGURE 1. Color-coded muscular system of *Rana catesbeiana*.

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That rhodopsin is the essential light-absorbing pigment of the photosynthetic mechanism of *Halobacterium halobium* is now firmly established Be that as it may, relatively few biology teachers, or other professional biologists, are aware of this method of photosynthesis that does not require chlorophyll.

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