C_3 plants, which regulate the opening of stomatal pores for gas exchange in leaves, also lack rubisco and apparently use PEP carboxylase exclusively to fix CO_2.

Contributions of the late Martin Gibbs to this article are acknowledged.

Gerald A. Berkowitz; Archie R. Portis, Jr.; Govindjee

Bacterial Photosynthesis

Certain bacteria have the ability to perform photosynthesis. This was first noticed by Sergey Vinogradsky in 1889 and was later extensively investigated by Cornelis B. Van Niel, who gave a general equation for bacterial photosynthesis. This is shown in reaction (9).

$$2H_2A + CO_2 + \text{light} \xrightarrow[\text{enzymes}]{\text{bacteriochlorophyll}} \{CH_2O\} + 2A + H_2O \quad (9)$$

where A represents any one of a number of reductants, most commonly S (sulfur).

Photosynthetic bacteria cannot use water as the hydrogen donor and are incapable of evolving oxygen. They are therefore called anoxygenic photosynthetic bacteria. The prokaryotic cyanobacteria (formerly called blue-green algae) are excluded in this discussion of bacterial photosynthesis, since their photosynthetic system closely resembles that found in eukaryotic algae and higher plants discussed above. Anoxygenic photosynthetic bacteria can be classified in four major groups:

1. *Proteobacteria*. Two groups with somewhat different properties are known.

(A) Nonsulfur purple bacteria (Rhodospirillaceae). In these bacteria, H_2A is usually an organic H_2 donor, such as succinate or malate; however, these bacteria can be adapted to use hydrogen gas as the reductant. They require vitamins for their growth and usually grow anaerobically in light, but they can also grow aerobically in the dark by using respiration to utilize organic compounds from the environment. They are thus facultative photoheterotrophs. Examples of this group are *Rhodospirillum rubrum* and *Rhodobacter sphaeroides*.

(B) Sulfur purple bacteria (Chromatiaceae). These cannot grow aerobically, and H_2A is an inorganic sulfur compound, such as hydrogen sulfide, H_2S; the carbon source can be CO_2. These bacteria are called obligate photoautotrophic anaerobes. An example is *Chromatium vinosum* (alternate name: *Allochromatium vinosum*).

2. *Green sulfur bacteria* (Chlorobiaceae). These bacteria are capable of using the same chemicals as Chromatiaceae but, in addition, use other organic H_2 donors. They may then be called photoautotrophic and photoheterotrophic obligate anaerobes. An example of the green sulfur bacteria is *Chlorobium tepidum*.

3. *Green gliding bacteria* (Chloroflexaceae) [also known as filamentous anoxygenic phototrophs, FAP]. These are primarily photoorganotrophic bacteria which can grow under anaerobic conditions in light by photosynthesis or in aerobic conditions in the dark by using respiration to utilize organic compounds from the environment. They are thermophilic bacteria found in hot springs around the world. They also distinguish themselves among the photosynthetic bacteria by possessing mobility. An example is *Chloroflexus aurantiacus*.

4. *Heliobacteria* (Heliobacteriaceae). These are strictly anaerobic bacteria that contain bacteriochlorophyll *g*. They grow primarily using organic substrates and have not been shown to carry out autotrophic growth using only light and inorganic substrates. An example is *Heliobacterium chlorum*.

Like plants, algae, and cyanobacteria, anoxygenic photosynthetic bacteria are capable of photophosphorylation, which is the production of adenosine triphosphate (ATP) from adenosine diphosphate (ADP) and inorganic phosphate (P_i) using light as the primary energy source. Several investigators have suggested that the sole function of the light reaction in bacteria is to make ATP from ADP and Pi. The hydrolysis energy of ATP (or the proton-motive force that precedes ATP formation) can then be used to drive the reduction of CO_2 to carbohydrate by H_2A in reaction (9).

Photochemical apparatus. Photosynthetic bacteria do not have specialized organelles such as the chloroplasts of green plants. Electron micrographs of certain photosynthetic bacteria show tiny spherical sacs, with double-layered walls, as a result of invaginations which form stacks of membranes (**Fig. 12***a*). Other photosynthetic bacteria have invaginations which form thylakoids (Fig. 12*b*). These intracytoplasmic membranes, often called chromatophores, contain the photosynthetic apparatus and can be isolated easily by mechanical disruption of bacteria followed by differential centrifugation. Isolated chromatophores are often used for biochemical and biophysical studies of bacterial photosynthesis.

Reaction centers. The pigment bacteriochlorophyll (BChl) is a necessary component for bacterial

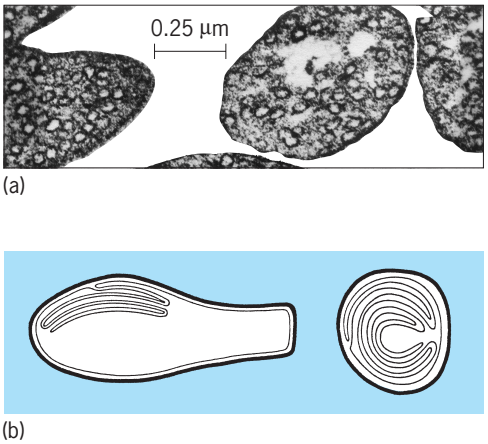


Fig. 12. Photosynthetic bacteria. (*a*) Electron micrograph of *Rhodobacter sphaeroides* with vesicle-like invaginations (*from T. W. Goodwin, ed., Biochemistry of Chloroplasts, vol. 1, Academic Press, 1966*). (*b*) Pictorial representation of a stacked invagination in a photosynthetic bacterium; at left is a longitudinal section and at right is a transverse section (*after R. Whittenbury and A. G. McLee, Archiv. für Mikrobiologie, 59:324–334, 1967*).

photosynthesis. There are specialized BChl molecules in bacteria which engage in the primary chemical reactions of photosynthesis. In addition to these specialized molecules, there are 40–50 BChl molecules referred to as antenna pigments, whose sole function is to harvest light energy and transfer it to reaction center molecules. This is similar to the photosynthetic unit of plants, algae, and cyanobacteria. Each reaction center contains a special pair (dimer) of BChl molecules that engage in chemical reactions after they trap the absorbed light energy. They are also called the energy traps of bacterial photosynthesis.

The energy trap in *Rhodobacter sphaeroides* has been identified as P870. Such identification is carried out with a difference (absorption) spectrophotometer. In this instrument a weak monochromatic measuring beam monitors the absorption of the sample; a brief but bright actinic light given at right angles to the measuring beam initiates photosynthesis. When photosynthesis occurs, changes in absorption take place. **Figure 13***a* shows the absorption spectrum of reaction centers isolated from *R. sphaeroides*. These changes are measured as a function of the wavelength of measuring light. A plot of the change induced in *R. sphaeroides* reaction centers by an actinic light flash, as a function of the wavelength of measuring light, is the difference absorption spectrum (Fig. 13*b*). This spectrum is due largely to the photooxidation of the BChl dimer, P870.

If P870 is the energy trap, then the following criteria must be met: (1) It must undergo a reduction or oxidation reaction, since this is the essential reaction of photosynthesis. The decrease in absorption at 870 nm (Fig. 13) is an oxidation reaction since chemical oxidants cause a similar change. (2) The quantum yield (number of trap molecules oxidized per absorbed photon) must be very high (close to 1.0). (3) The primary light reaction should occur at very low temperatures, down to 1 K (−460°F or −273°C). (4) The above photochemical reaction should be extremely fast, that is, in the picosecond range.

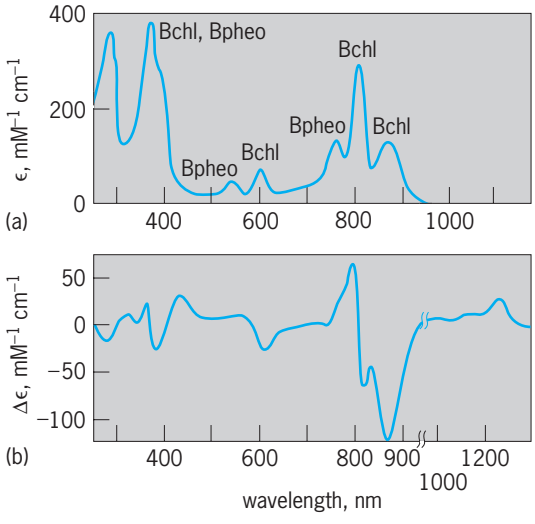


Fig. 13. Plots of (*a*) absorption spectrum and (*b*) the light-induced absorption changes in it, as occurring in reaction centers isolated from carotenoidless mutant R-26 of *Rhodobacter sphaeroides*. In *a*, bands attributed to bacteriochlorophyll and bacteriopheophytin are labeled BChl and BPheo, respectively. The ordinate in a is the millimolar extinction coefficient; in *b*, it is the differential extinction coefficient. (*After R. K. Clayton, Photosynthesis: Physical Mechanisms and Chemical Patterns, Cambridge University Press, 1980*)

All the above criteria are fulfilled by P870, and thus it is the reaction center of bacterial photosynthesis in *Rhodobacter sphaeroides*. Among other reaction centers that have been identified and studied extensively are P890 in *Chromatium vinosum*, P960 in *Rhodopseudomonas viridis* (also called *Blastochloris viridis*), P840 in *Chlorobium limicola* and P798 *Helicobacterium chlorum*. Each species of bacteria has only one type of reaction center, unlike plants, algae, and cyanobacteria, which utilize two types of reaction centers, PSI and PSII, that include P680 and P700, respectively. The reaction centers from oxygenic photosynthetic organisms have been identified by means similar to those used for bacterial reaction centers. Reaction centers have been isolated as pure proteins, which has served the important function of providing a well-defined system in which primary reactions of photosynthesis can be studied. A milestone in bacterial photosynthesis was reached in the early 1980s by the crystallization and determination of the three-dimensional structure of *Rhodopseudomonas viridis* reaction centers by Hartmut Michel, Johann Deisenhofer, and Robert Huber, who received the 1988 Nobel Prize in Chemistry for their work. These crystals enabled an atomic resolution of the molecular structure of the reaction center to be obtained.

Although isolated reaction centers are able to absorb light and convert it to chemical energy, the antenna pigment system in chromatophores (or in whole cells) absorbs most (>90%) of the light. The antenna transfers this energy to the reaction center. Antenna BChl molecules are bound to protein in a specific manner; this binding and pigment-pigment interactions modify the properties of the pigment and define the absorption maxima and the width of the absorption band. An example is B800 (B represents BChl, and the number indicates the wavelength of one of the absorption peaks in nanometers) found in *Rhodobacter sphaeroides* (**Fig. 14**).

Components of photosynthetic bacteria. These bacteria contain the usual components of living material: proteins, lipids, carbohydrates, deoxyribonucleic acid (DNA), ribonucleic acid (RNA), and various metals. However, the specific components of interest to the electron transport system of bacterial photosynthesis are quinones, pyridine nucleotides, and various iron-containing proteins (cytochromes, ferredoxins, Rieske iron-sulfur centers, and others) in addition to the photosynthetic pigments which capture light energy.

In contrast to plastoquinones found in plants, bacteria contain substituted benzoquinones called ubiquinones (UQ or coenzyme Q) and substituted naphthoquinones called menaquinones (MK or vitamin K_2) which act as electron acceptors. The purple bacteria have a pool of UQ (about 25 UQ per reaction center) which mediates transfer of electrons and protons between protein complexes in the

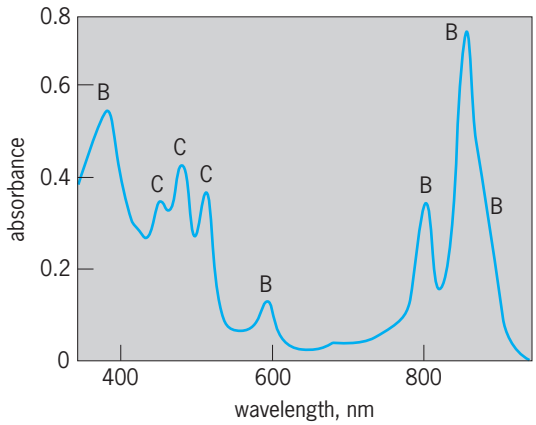


Fig. 14. Absorption spectrum of chromatophores from the bacterium *Rhodobacter sphaeroides*. Absorption bands attributed to BChl *a* are labeled as B, and those attributed to carotenoids as C. (*After R. K. Clayton, Photosynthesis: Physical Mechanisms and Chemical Patterns, Cambridge University Press, 1981*)

chromatophore membrane. However, MK is found only in some bacteria, sometimes in a smaller quantity (about 1–2 MK molecules per reaction center) than the more plentiful UQ. In these organisms, menaquinone's function is probably limited to electron transfer within the reaction center. Other organisms contain only menaquinone. In contrast to plants which contain NADP, the major pyridine nucleotide in bacteria is nicotinamide adenine dinucleotide (NAD); it is present in large quantities and seems to be active in photosynthesis. Among the various cytochromes, the *c*-type cytochromes and the *b*-type cytochromes are the important ones for bacterial photosynthesis.

Pigments. Most photosynthetic bacteria contain BChl *a*, a tetrahydroporphyrin. The chlorophyll of green plants, algae, and cyanobacteria, by contrast, is a dihydroporphyrin. In diethyl ether, BChl *a* has absorption maxima at 365, 605, and 770 nm. The infrared band of various antenna BChl *a* has maxima at 800 (B800), 850 (B850), or 890 nm (B890). These antenna absorption bands in the bacterial cell are due to the formation of complexes of BChl *a* with different proteins. *See* CHLOROPHYLL.

The reaction center protein (composed of L, M, and H subunits) from *Rhodobacter sphaeroides* binds four BChl *a* and two bacteriopheophytin (BPh; similar to BChl but does not contain magnesium). Two of the BChl form the energy trap P870. Another BChl and a BPh are involved in the transfer of electrons within the protein. The exact locations of these chromophores in the reaction center protein was first established in the crystals of *Rhodopseudomonas viridis* reaction centers (**Fig. 15***a*). Similar information is now available for *Rhodobacter sphaeroides* reaction centers (Fig. 15*b*).

The bacterium *Rhodopseudomonas viridis* utilizes an antenna with an infrared absorption band at 1015 nm. The isolated BChl from this species has absorption maxima at 368, 582, and 795 nm in diethyl ether, and has been designated BChl *b*. The reaction center of *R. viridis*, P960, uses BChl *b* and BPh *b* much in the same way as P870 in other bacteria utilizes Bchl *a*. Here, there is an "uphill" energy transfer from the antenna to its reaction center.

The green bacterium *Chlorobium* sp. contains a small amount of BChl *a* but a large quantity of another type of chlorophyll called chlorobium chlorophylls, BChl *c*, *d* or *e*, depending on the species. The BChl *a* has been shown to be associated with the reaction center, and some antenna complexes while the BChl *c* acts only as antenna. It is located in

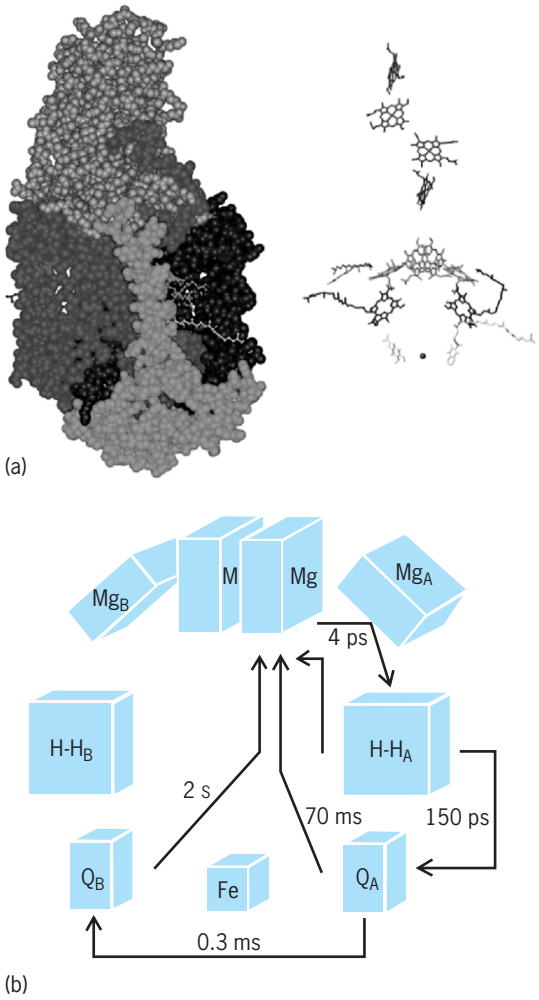


Fig. 15. Reaction centers of bacteria. (*a*) Structure of the reaction center of the purple nonsulfur bacterium *Rhodopseudomonas viridis* as determined by x-ray analysis of the crystalline preparation. In this diagram, the left side shows the complete structure in a space-filling representation. On the right side, the protein has been removed for clarity and only the components of the electron transport chains are shown (*after R. E. Blankenship, Molecular Mechanisms of Photosynthesis, Blackwell Science, Oxford, 2002*). (*b*) A simplified representation of the donor-acceptor complex based on the x-ray data and on spectroscopic data for *Rhodobacter sphaeroides*. The blocks define the aromatic ring systems of bacteriochlorophyll (M-Mg and Mg), bacteriopheophytin (H-H), the quinones (Q), which are ubiquinone and menaquinone, and Fe^{2+}. M-Mg is the primary electron donor, a dimer of bacteriochlorophyll *a* (*Rhodobacter sphaeroides*) or *b* (*Rhodopseudomonas viridis*). Subscripts A and B label the two potential electron transfer pathways, of which only pathway A appears active. The arrows show the various electron transfer reactions with their half-times. Note that Q_B is absent in the crystal of *Rhodopseudomonas viridis* (*after J. F. Norris and G. Van Brakel, Photosynthesis, in Govindjee, J. Amesz, and D. C. Fork, eds., Light Emission by Plants and Bacteria, Academic Press, 1986*).

chlorosome complexes, which are appressed to the cytoplasmic side of the cell membrane and contain about 200,000 molecules of chlorobium chlorophyll.

The second group of pigments is the carotenoids, which have absorption peaks from 450 to 550 nm. The carotenoids of photosynthetic bacteria are of great variety and include some which are found in green plants, for example, the lycopenes. However, some are typical only of bacteria: γ-carotene, which is found in large quantities in green sulfur bacteria, and spirilloxanthol, which is found mainly in purple bacteria. Carotenoids function to prevent photooxidation and destruction of antenna bacteriochlorophyll. They also function in bacterial photosynthesis by transferring their absorbed energy to bacteriochlorophyll. Similar roles are found for carotenoids in plants and cyanobacteria.

Transfer of excitation energy. Light energy absorbed by the carotenoids is transferred to BChl with varying efficiency (30–90%), as demonstrated by the method of sensitized fluorescence. (Similar methods have been used for demonstrating energy transfer from carotenoids, chlorophyll *b*, and phycobilins to chlorophyll *a* in oxygenic photosynthesizers.) When light energy is absorbed by carotenoids, only the fluorescence of bacteriochlorophyll (B875) is observed. By the same method, energy transfer with efficiencies approaching 100% has been demonstrated from B800 to B850 to B875. The high quantum yield (almost 1.0) of P870 oxidation, when bacteria are excited in the antenna pigments, is a clear demonstration of an extremely efficient excitation energy transfer by antenna pigments and trapping in reaction centers.

The lifetime of the excited state of antenna BChl in the bacterial cell is of the order of 30–50 ps. The excitation energy must be channeled from the antenna pigments to the energy traps within this time for efficient photosynthesis to occur. In reaction center preparations, it takes only 3 ps to create a definitively stable charge separation (see below) after the absorption of light. Moreover, the lifetime of the physical state or states preceding P870 oxidation is <3 ps. Thus, it appears that within a few picoseconds of receiving excitation energy, the reaction center has converted the absorbed light energy into chemical energy. Similar reactions occur in plants, algae, and cyanobacteria.

Mechanisms of electron transport. The first act of photosynthesis is the absorption of light by various pigments. As discussed above, light energy absorbed by the carotenoids B800 and B850 is transferred to B875 and finally to the reaction centers, where the primary reaction occurs: the oxidation of the reaction center BChl dimer leads to bleaching of P870 and reduction of an acceptor (**Fig. 16**). In the current model, P (short for P870 and so on) is oxidized to P^+ and an intermediate I is reduced to I^- within a few picoseconds; I includes a BChl monomer and a BPh molecule. The reduced I^- transfers the electron to an iron-quinone complex, reducing the primary quinone (Q_A) to a semiquinone within 100–200 ps. For most anoxygenic bacteria, Q_A is ubiquinone, though for those containing both menaquinone and ubiquinone the menaquinone functions as Q_A. Although an iron atom is in this complex and is within 0.5–1.0 nm of the quinone, its presence is not necessary for the reduction of Q_A, nor does the iron undergo redox changes. The function of this nonheme iron in the reaction center is unknown. In plants, algae, and cyanobacteria, PSII contains Q_A, which is a bound plastoquinone; the function of the iron there is also unknown.

The photooxidized donor BChl dimer, P^+, can be

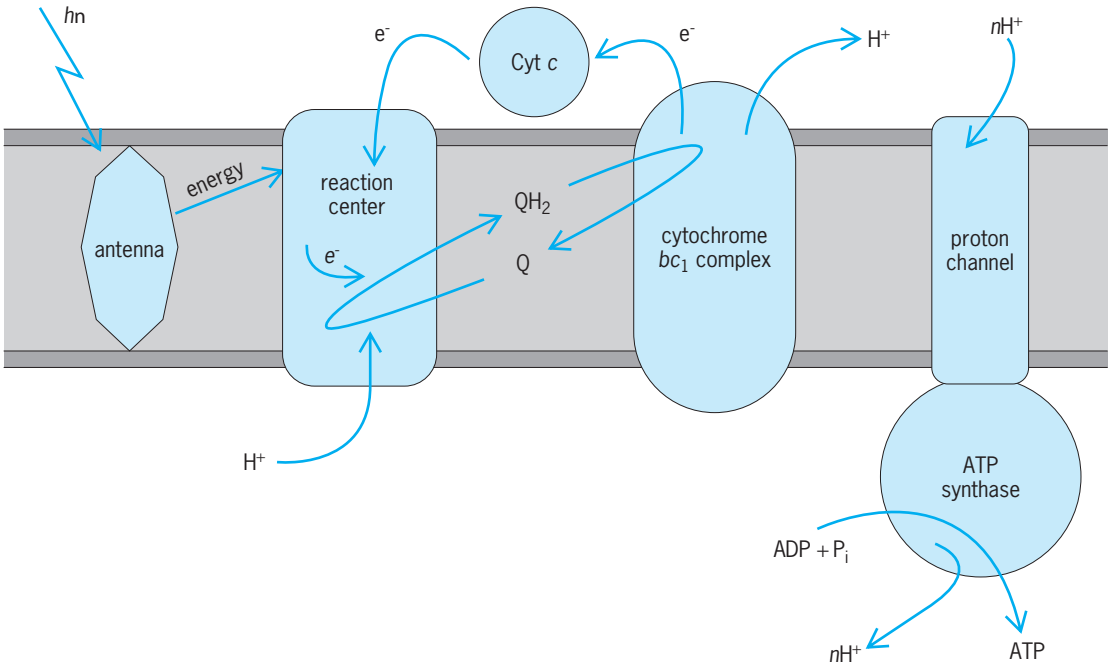


Fig. 16. Electron and proton transport in purple photosynthetic bacteria. For details and explanation of symbols, see the text. The shapes of the proteins are largely hypothetical.

re-reduced by a cytochrome *c* in 1–30 μs, thus oxidizing the cytochrome. In *Rhodobacter sphaeroides* and a number of other species, this cytochrome is soluble Cyt c_2. In other bacteria (for example, *Rhodopseudomonas viridis*) the cytochrome that donates electrons to P^+ is an integral part of the reaction center. The photochemical reactions and the electron transfers in the reaction center are summarized in reaction (10). After this set of reactions, the

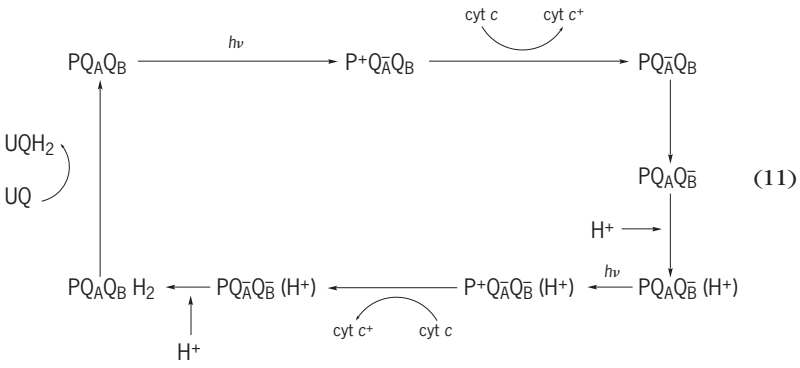
$$PIQ_A \xrightarrow{h\nu} P^*IQ_A \xrightarrow{3\ ps} P^+I^-Q_A \xrightarrow{200\ ps} P^+IQ_A^- \xrightarrow[1\text{–}30\ \mu s]{\text{cyt } c \quad \text{cyt } c^+} PIQ_A^- \qquad (10)$$

electron is transferred from Q_A^- to Q_B (a bound UQ), producing $Q_AQ_B^-$. In a subsequent absorption of a photon, the $Q_A^-Q_B^-$ state is created, which is followed by electron transfer from Q_A^- to Q_B^-, forming Q_BH_2 with the uptake of two protons. The bound quinol (Q_BH_2) is replaced by a UQ molecule. This cycle is known as the two-electron gate and is summarized in reaction (11) [omitting the early photochemical steps illustrated in reaction (10)]. The same cycle occurs in photosystem II, except that the electron donor to P^+ is tyrosine Z, and Q_BH_2 is another plastoquinol instead of ubiquinol. The molecular detail is so similar in oxygenic and anoxygenic photosynthesizers that many of the herbicides which act to inhibit PSII electron transfer from Q_A^- to Q_B are also potent inhibitors of electron transfer from Q_A^- to Q_B in photosynthetic bacteria. However, one difference involves a unique role of CO_2/HCO_3^- in reaction (11) in PSII of plants and cyanobacteria, but not in photosynthetic bacteria. Bicarbonate has been shown to be bound on the electron acceptor side of PSII, but not in photosynthetic bacteria.

Protons are taken up from the cytoplasm at the same time as the electrons reduce the quinones. The first proton does not bind directly to the semiquinone (Q_A^- or Q_B^-), but instead it binds to a protonatable amino acid of the reaction center. The net result from the absorption of two photons is the formation of a ubiquinol in the membrane, the oxidation of two Cyt *c*, and the removal of two protons from the cytoplasm of the bacterial cell. In plants and cyanobacteria, the quinol is plastoquinol, and it is water that is ultimately oxidized.

The doubly reduced ubiquinone (QH_2, quinol) through a cyclic pathway serves to re-reduce the oxidized cytochrome (cyt c^+). This cyclic reaction (Fig. 16) is coupled to the production of ATP via the creation of a proton gradient (more accurately a proton motive force) across the membrane. Just as in plants, the proton motive force (which includes two components: a membrane potential, and a proton gradient) is used to drive ATP synthesis. Protons move down the potential gradient through the ATPase to contribute energy to drive the ADP + $P_i \rightarrow$ ATP reaction.

This overall mechanism is consistent with P. Mitchell's chemiosmotic theory. The quinol produced by the two-electron gate mechanism binds



to the cytochrome *b-c* complex (an integral membrane protein) which contains two *b* cytochromes, a *c* cytochrome, a Rieske iron-sulfur center, and two quinone-binding sites. Plants also contain a similar complex, where cytochrome *b* is replaced by cytochrome b_6, and cytochrome *c* is replaced by cytochrome *f*. The mechanism is strikingly similar, on a molecular level, to that of noncyclic electron transfer from photosystem II to plastocyanin via the plastoquinone pool and the cytochrome *b-f* complex. In all likelihood, it includes a pathway called a Q cycle by Mitchell; this cycle incorporates two different redox-linked pathways for the electrons. For each quinol oxidized by this complex, two molecules of Cyt *c* are reduced, two protons are removed from the quinol, an additional two protons are removed from the cytoplasm, and these four protons are released into the intermembrane space. Absorption of two photons leads to the translocation of four protons across the membrane. Structural and mechanistic data on ATPases indicate that 3–5 H^+'s are needed to make an ATP (Fig. 16).

The mechanism described here for the generation of ATP from light energy is largely from studies on *Rhodobacter sphaeroides* and is generally valid for other purple photosynthetic bacteria.

The mechanisms for oxidizing the reduced substrate H_2A [reaction (9)] are known in much less detail than those for photophosphorylation. Most substrates feed electrons into the quinone pool, and the resulting quinol can be used by the cytochrome *b-c* complex. An example is succinate, which reduces quinone via a succinate dehydrogenase. In bacteria that have a low potential cytochrome *c* bound to the reaction center (such as Cyt c_{551} in *Chromatium vinosum*), electrons from some substrates can possibly be fed into the reaction center through this cytochrome. The electrons for the reduction of NAD^+ in purple photosynthetic bacteria are from the quinone pool, but these electrons require additional energy gained from the hydrolysis of ATP or action of the proton motive force.

Alternatively, especially in some green bacteria, the primary stable acceptor of electrons in the reaction center may not be a quinone but an acceptor with a negative enough oxidation-reduction potential to directly reduce NAD^+. In several green bacteria, this electron acceptor has been shown to be an iron-sulfur (Fe·S) center instead of a quinone. The midpoint redox potential of this Fe·S center is much lower than that for the quinone acceptor in

the purple photosynthetic bacteria. This Fe·S center can then directly reduce a ferredoxin, and this can drive the $NAD^+ \rightarrow NADH$ reaction. The reduced ferredoxin may also feed electrons into a cytochrome *b* complex from which a soluble Cyt *c* could be reduced, thus allowing cyclic electron transfer to occur. This scheme is very reminiscent of PSI-driven reactions in oxygenic photosynthesis. However, not all green photosynthetic bacteria follow the above pattern, but instead they resemble more the purple photosynthetic bacteria.

The reduced pyridine nucleotide NADH and the ATP made in the light reactions are then utilized to convert carbon sources into carbohydrates. The pathway of carbon in anoxygenic photosynthetic bacteria involves a reversed tricarboxylic acid (Krebs) cycle or another cycle called the hydroxyproprionate cycle. *See* BACTERIAL PHYSIOLOGY AND METABOLISM.

Govindjee; Robert E. Blankenship; R. J. Shopes

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Phototransistor

A semiconductor device with electrical characteristics that are light-sensitive. Phototransistors differ from photodiodes in that the primary photoelectric current is multiplied internally in the device, thus increasing the sensitivity to light. For a discussion of this property *see* TRANSISTOR.

Some types of phototransistors are supplied with a third, or base, lead. This lead enables the phototransistor to be used as a switching, or bistable, device. The application of a small amount of light causes the device to switch from a low current to a high current condition. *See* PHOTOELECTRIC DEVICES.

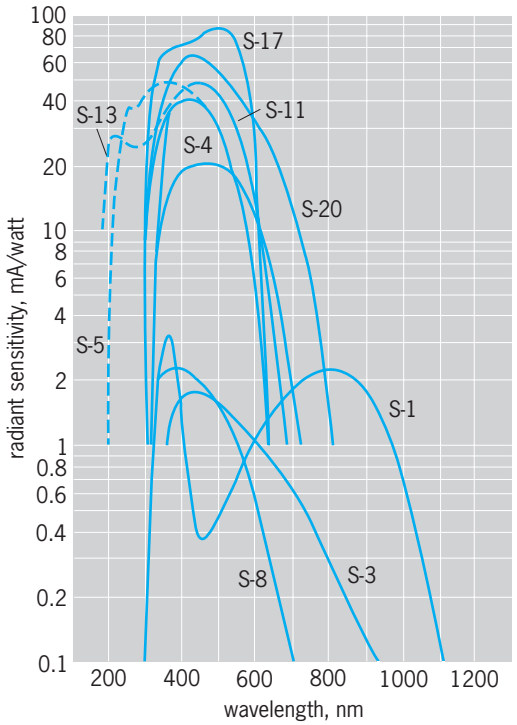
W. R. Sittner

Phototube

An electron tube comprising a photocathode and an anode mounted within an evacuated glass envelope through which radiant energy is transmitted to the photocathode. A gas phototube contains, in addition, argon or other inert gas which provides amplification of the photoelectric current by partial ionization of the gas. The photocathode emits electrons when it is exposed to ultraviolet, visible, or near-infrared radiation. The anode is operated at a positive potential with respect to the photocathode. *See* ELECTRICAL CONDUCTION IN GASES; ELECTRON TUBE.

Characteristics. A phototube responds to radiation over a limited range of the spectrum that is determined by the photocathode material. Radiant sensitivity, shown in the **illustration** as a function of wavelength, is the photoelectric current emitted per unit of incident monochromatic radiant power. Sensitivity on the short-wavelength side of the curves is limited by the transmittance of the glass envelope. Electron affinity of the photocathode determines the long-wavelength threshold of sensitivity. *See* PHOTOEMISSION.

Typical phototube characteristics are summarized in the **table**. Quantum efficiency, or photoelectron yield, is the number of electrons emitted per incident photon. It is tabulated at the wavelength of maximum response. For photometric applications a useful parameter is luminous sensitivity: the photoelectric current per lumen incident from a specified source of light. A source commonly used



Curves of the average spectral sensitivity characteristics of some typical phototubes.