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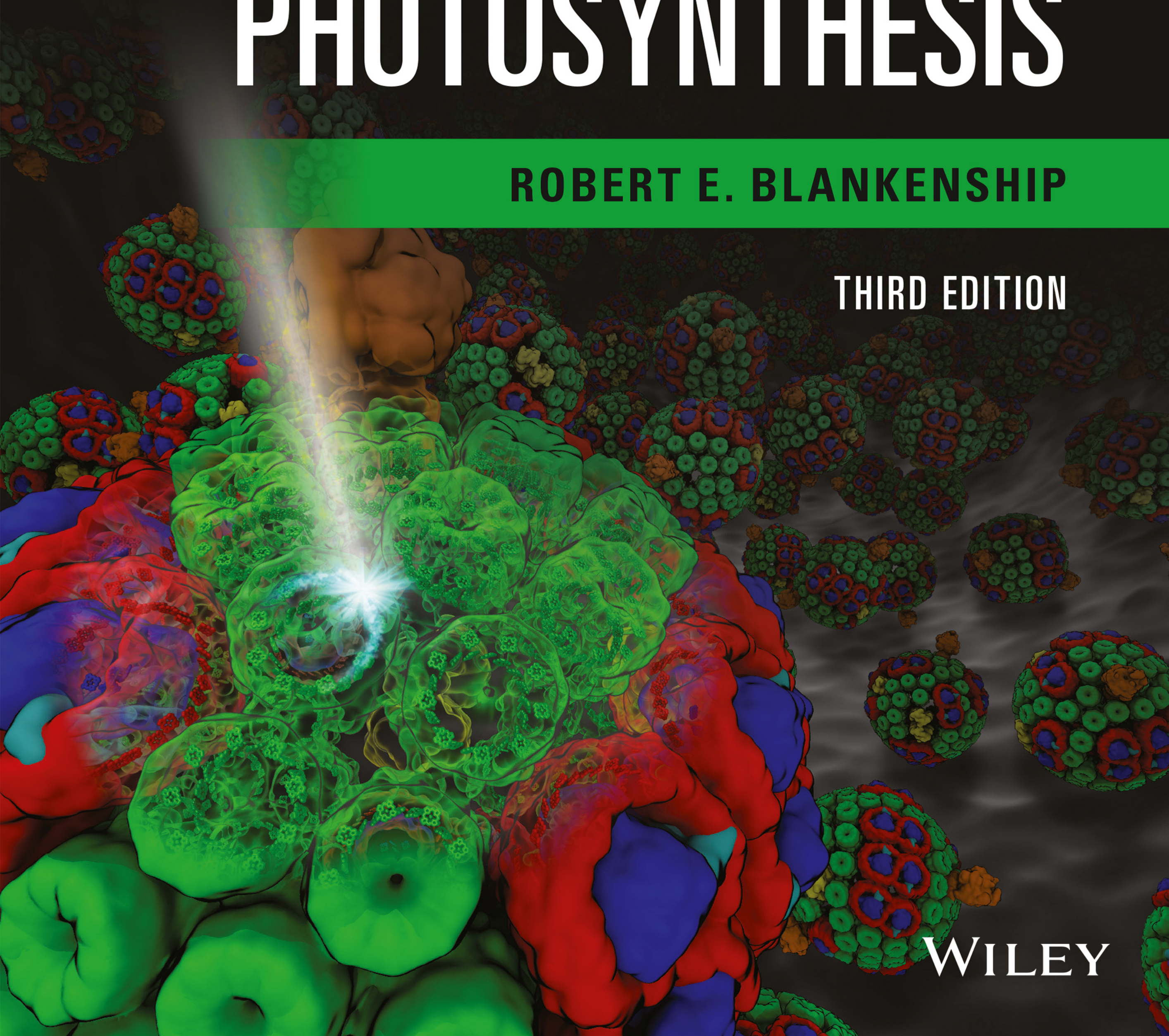
MOLECULAR MECHANISMS OF PHOTOSYNTHESIS

ROBERT E. BLANKENSHIP

THIRD EDITION



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Molecular Mechanisms of Photosynthesis

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Third Edition

Robert E. Blankenship
Tempe, AZ, USA

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I dedicate this book to the memory of my mother,
whose early and constant encouragement started me
down the road to a career in science.

Contents

Introduction to the third edition

It is now nearly 20 years since the first edition and more than 7 years since the second edition of *Molecular Mechanisms of Photosynthesis* were published. In that time, the scientific understanding of how photosynthesis works has continued to progress. The success of the first and second editions has prompted numerous requests for a third edition, which I am pleased to provide. I have tried to update the text to reflect this new understanding.

This book is an introduction to the basic concepts that underlie the process of photosynthesis as well as a description of the current understanding of the subject. Because it is such a complex process that requires some knowledge of many different fields of science to appreciate, it can be intimidating for a person who is not already conversant with the basics of all these fields. For this reason, a brief overview is provided in the first chapter, introducing and summarizing the main concepts. This chapter is then followed by a more in-depth treatment of each of the main themes in later chapters.

Photosynthesis is perhaps the best possible example of a scientific field that is intrinsically interdisciplinary. Our discussion of photosynthesis will span time scales from the cosmic to the unimaginably fast, from the origin of the Earth 4.5 billion years ago, to molecular processes that take only a few femtoseconds. This is a range of over 32 orders of magnitude. Appreciating this extraordinary scale will require us to learn a range of vocabularies and concepts that stretch from geology through physics and chemistry, to biochemistry, cell and molecular biology, and finally to evolutionary biology. Any person who wishes to appreciate the big picture of how photosynthesis works, and how it fits into the broad scope of scientific inquiry, needs to have at least a rudimentary understanding of all of these fields of science. This is an increasingly difficult task in this age of scientific specialization, because no one can truly be an expert in all areas. This book attempts to provide the starting point for a broadly based understanding of photosynthesis, incorporating key concepts from across the scientific spectrum. The emphasis throughout the book will be on molecular-scale mechanistic processes.

Many of the concepts that we will explore throughout the bulk of this book require an understanding of basic concepts of physical chemistry, including thermodynamics, kinetics, and quantum mechanics. It is beyond the scope of our broad, and therefore necessarily brief, treatment of photosynthesis to provide a comprehensive background in these areas that form the core of the mechanistic aspects of the subject. However, some modest understanding of these physical principles is essential to be able to appreciate the essence of the photosynthetic process. This is addressed in an appendix that introduces the physical basis of light and energy. This appendix can either be read as a preface to the bulk of the book or consulted as needed as a reference.

The book is aimed toward advanced undergraduates and beginning graduate students in a range of disciplines, including life sciences, chemistry, and physics, as well as more senior scientists seeking to learn about the remarkable process of photosynthesis. An understanding of basic principles of chemistry, physics, and biology is assumed.

Robert E. Blankenship

Acknowledgements

I thank my former advisors Ken Sauer and Bill Parson for initiating me into the fascinating world of photosynthesis. Their guidance, support, and friendship have been invaluable to me during the course of my career.

I thank the many friends and colleagues from around the world for reading and commenting on some material, for helpful discussions on specialized topics, and for kindly providing figures for publication. These include (in alphabetical order) Carl Bauer, Oded Béjà, Gary Brudvig, Don Bryant, Julian Eaton-Rye, Gyozo Garab, Govindjee, Beverley Green, Martin Hohmann-Marriott, Werner Kühlbrandt, Haijun Liu, Yuval Mazor, Johannes Messinger, Tom Moore, Jian-Ren Shen, and Junko Yano.

The beautiful graphic that adorns the cover of the book is courtesy of Melih Sener. This is an updated version of the graphics that were on the covers of the first and second editions.

Special thanks to my editor Rebecca Ralf and to Kerry Powell from Wiley-Blackwell for help with the production.

Finally, I thank my wonderful family, Liz, Larissa, and Sam, for their constant love and support.

About the companion website

This book is accompanied by a companion website:

https://www.wiley.com/go/blankenship/molecularphotosynthesis3e

The website includes:

- Powerpoints of all figures from the book for downloading
- PDFs of all tables from the book for downloading

Chapter 1

The basic principles of photosynthetic energy storage

1.1 What is photosynthesis?

Photosynthesis is a biological process whereby the Sun's energy is captured and stored by a series of events that convert the pure energy of light into the free energy needed to power life. This remarkable process provides the foundation for essentially all life and has over geologic time profoundly altered the Earth itself. It provides all our food and most of our energy resources.

Perhaps the best way to appreciate the importance of photosynthesis is to examine the consequences of its absence. The catastrophic event that caused the extinction of the dinosaurs and most other species 65 million years ago almost certainly exerted its major effect not from the force of the comet or asteroid impact itself, but from the massive quantities of dust ejected into the atmosphere. This dust blocked out the Sun and effectively shut down photosynthesis all over the Earth for a period of months or years. Even this relatively short interruption of photosynthesis, miniscule on the geological time scale, had catastrophic effects on the biosphere.

Photosynthesis literally means "synthesis with light." As such, it might be construed to include any process that involved synthesis of a new chemical compound under the action of light. However, that very broad definition might include a number of unrelated processes that we do not wish to include, so we will adopt a somewhat narrower definition of photosynthesis:

> Photosynthesis is a process in which light energy is captured and stored by a living organism, and the stored energy is used to drive energy-requiring cellular processes.

This definition is still relatively broad and includes the familiar chlorophyll-based form of photosynthesis that is the subject of this book, but also includes the very different form of photosynthesis carried out by some micro organisms using proteins related to rhodopsin, which contain retinal as their light-absorbing pigment. Light-driven signaling processes, such as vision or phytochrome action, where light conveys information instead of energy, are excluded from our definition of photosynthesis, as well as all processes that do not normally take place in living organisms.

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What constitutes a photosynthetic organism? Does the organism have to derive all its energy from light to be classified as photosynthetic? Here, we will adopt a relatively generous definition, including as photosynthetic any organism capable of deriving some of its cellular energy from light. Higher plants, the photosynthetic organisms that we are all most familiar with, derive essentially all their cellular energy from light. However, there are many organisms that use light as only part of their energy source and, under certain conditions, they may not derive any energy from light. Under other conditions, they may use light as a significant or sole source of cellular energy. We adopt this broad definition because our interest is primarily in understanding the energy storage process itself. Organisms that use photosynthesis only part of the time may still have important things to teach us about how the process works and therefore deserve our attention, even though a purist might not classify them as true photosynthetic organisms. We will also use both of the terms "photosynthetic" and "phototrophic" when describing organisms that can carry out photosynthesis. We will usually use photosynthetic to describe higher plants, algae, and cyanobacteria that derive most or all of their energy needs from light, and phototrophic to describe bacteria or archaea that can carry out photosynthesis but often derive much of their energy needs from other sources.

The most common form of photosynthesis involves chlorophyll-type pigments and operates using light-driven electron transfer processes. The organisms that we will discuss in detail in this book, including plants, algae, and cyanobacteria (collectively called **oxygenic** organisms because they produce oxygen during the course of doing photosynthesis) and several types of **anoxygenic** (non-oxygen-evolving) bacteria, all work in this same basic manner. All these organisms will be considered to carry out what we will term "chlorophyll-based photosynthesis." The retinal-based form of photosynthesis, while qualifying under our general definition, is mechanistically very different from chlorophyll-based photosynthesis, and will not be discussed in detail. It operates using *cis–trans* isomerization that is directly coupled to ion transport across a membrane (Ernst *et al.*, 2014). The ions that are pumped as the result of the action of light can be either H^+, Na^+, or Cl^- ions, depending on the class of the retinal-containing protein. The H^+-pumping complexes are called bacteriorhodopsins, and the Cl^--pumping complexes are known as halorhodopsins. No light-driven electron transfer processes are known thus far in these systems.

For many years, the retinal-based type of photosynthesis was known only in extremely halophilic Archaea (formerly called archaebacteria), which are found in a restricted number of high-salt environments. Therefore, this form of photosynthesis seemed to be of minor importance in terms of global photosynthesis. However, in recent years, several new classes of microbial rhodopsins, known as proteorhodopsin, heliorhodopsin, and others, have been discovered (Béjà *et al.*, 2000; Pushkarev *et al.*, 2018; Inoue *et al.*, 2020). Proteorhodopsin pumps H^+ and has an amino acid sequence and protein secondary structure that are generally similar to bacteriorhodopsin. The proteobacteria that contain proteorhodopsin are widely distributed in the world's oceans, so the rhodopsin-based form of photosynthesis may be of considerable importance. Recent evidence suggests that the proteorhodopsins are responsible for a significant amount of primary productivity in the ocean (Gómez-Consarnau *et al.*, 2019).

As mankind pushes into space and searches for life on other worlds, we need to be able to recognize life that may be very different from what we know on Earth. Life always needs a source of energy, so it is reasonable to expect that some form of photosynthesis (using our general definition) will be found on most or possibly all worlds that harbor life. Photosynthesis on such a world need not necessarily contain chlorophylls and perform electron transfer. It might be based on isomerization such as bacteriorhodopsin, or possibly on some other light-driven process that we cannot yet imagine (Kiang *et al.*, 2007a, b; Schweiterman *et al.*, 2018).

1.2 Photosynthesis is a solar energy storage process

Photosynthesis uses light from the Sun to drive a series of chemical reactions. The Sun, like all stars, produces a broad spectrum of radiation output that ranges from gamma rays to radio waves. The solar output is shown in Fig. 1.1, along with absorption spectra of some photosynthetic organisms. Only some of the emitted solar radiation is visible to our eyes, consisting of light with wavelengths from about 400 to 700 nm. The entire visible range of light, and some wavelengths in the near infrared (700–1000 nm), are highly active in driving photosynthesis in certain organisms, although the most familiar chlorophyll *a*-containing organisms cannot use light with a wavelength longer than 700 nm.

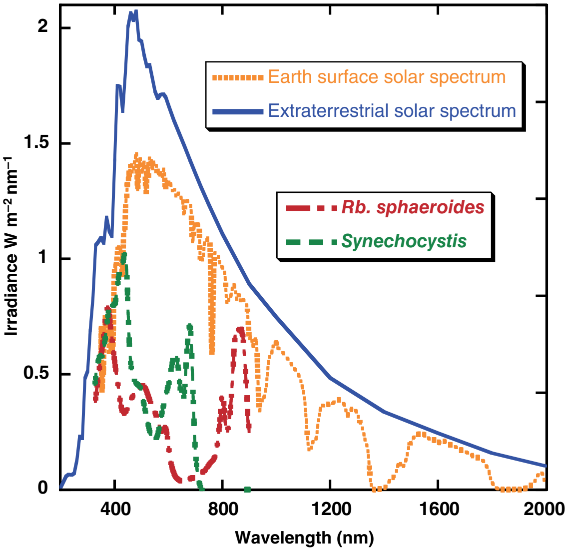


Figure 1.1 Solar irradiance spectra and absorption spectra of photosynthetic organisms. Solid curve: intensity profile of the extraterrestrial spectrum of the Sun; dotted line: intensity profile of the spectrum of sunlight at the surface of the Earth; dash-dot line: absorbance spectrum of *Rhodobacter sphaeroides*, an anoxygenic purple photosynthetic bacterium; dashed line: absorbance spectrum of *Synechocystis* PCC 6803, an oxygenic cyanobacterium. The spectra of the organisms are in absorbance units (scale not shown).

The spectral region from 400 to 700 nm is often called **photosynthetically active radiation** (PAR), although this is only strictly true for chlorophyll *a*-containing organisms. Recently, some oxygenic photosynthetic organisms that utilize radiation outside the PAR region have been discovered. These are discussed in detail in Chapters 2 and 7.

The sunlight that reaches the surface of the Earth is reduced by scattering and by the absorption of molecules in the atmosphere. Water vapor and other molecules such as carbon dioxide absorb strongly in the infrared region, and ozone absorbs in the ultraviolet region. The ultraviolet light is a relatively small fraction of the total solar output, but much of it is very damaging because of the high energy content of these photons (see Appendix for a discussion of photons and the relationship of wavelength and energy content of light). The most damaging ultraviolet light is screened out by the ozone layer in the upper atmosphere and does not reach the Earth's surface. Wavelengths less than 400 nm account for only about 8% of the total solar irradiance, while wavelengths less than 700 nm account for 47% of the solar irradiance (Thekaekara, 1973).

The infrared wavelength region includes a large amount of energy and would seem to be a good source of photons to drive photosynthesis. However, no organism is known that can utilize light of wavelength longer than about 1000 nm for photosynthesis (1000 nm and longer wavelength light comprises 30% of the solar irradiance). This is almost certainly because infrared light has a very low energy content in each photon, so that large numbers of these low-energy photons would have to be used to drive the chemical reactions of photosynthesis. No known organism has evolved such a mechanism, which would in essence be a living heat engine. Infrared light is also absorbed by water, so aquatic organisms do not receive much light in this spectral region.

The distribution of light in certain environments can be very different from that shown in Fig. 1.1. The differing spectral content, or color, of light in different environments represents differences in **light quality**. In later chapters, we will encounter some elegant control mechanisms that organisms use to adapt to changes in light quality. In a forest, the upper part of the canopy receives the full solar spectrum, but the forest floor receives only light that was not absorbed above. The spectral distribution of the filtered light that reaches the forest floor is therefore enriched in the green and far-red regions and is almost completely lacking in the red and blue wavelengths.

In aquatic systems, the intensity of light rapidly decreases as one goes deeper down the water column, owing to several factors. This decrease is not uniform for all wavelengths. Water weakly absorbs light in the red portion of the spectrum, so that the red photons that are most efficient in driving photosynthesis rapidly become depleted. Water also scatters light, mainly because of effects of suspended particles. This scattering effect is most prevalent in the blue region of the spectrum, because scattering by small particles is proportional to the frequency raised to the fourth power. The sky is blue because of this frequency-dependent scattering effect. At water depths of more than a few tens of meters, most of the available light is in the middle, greenish part of the spectrum, because the red light has been absorbed and the blue light scattered (Falkowski and Raven, 2007; Kirk, 2011). None of the types of chlorophylls absorb green light very well. However, other photosynthetic pigments, in particular some carotenoids (e.g. fucoxanthin, peridinin), have intense absorption in this region of the spectrum and are present in large quantities in many aquatic photosynthetic organisms. At water depths greater than about 100 m, the light intensity from the Sun is too weak to drive photosynthesis.

1.3 Where photosynthesis takes place

Photosynthesis is carried out by a wide variety of organisms. In all cases, lipid bilayer membranes are critical to the early stages of energy storage, such that photosynthesis must be viewed as a process that is at heart membrane-based. The early processes of photosynthesis are carried out by pigment-containing proteins that are integrally associated with the membrane. Later stages of the process that occur on a slower (e.g. millisecond) time scale are mediated by proteins that are freely diffusible in the aqueous phase.

In eukaryotic photosynthetic cells, photosynthesis is localized in subcellular structures known as **chloroplasts** (Fig. 1.2). The chloroplast contains all the chlorophyll pigments and, in most organisms,

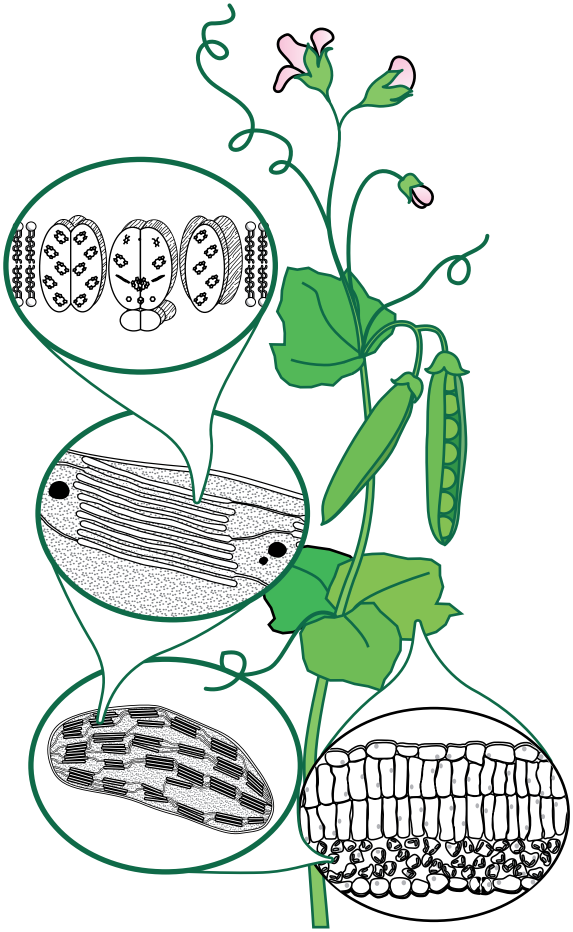


Figure 1.2 Exploding diagram of the photosynthetic apparatus of a typical higher plant. The first expansion bubble shows a cross-section of a leaf, with the different types of cells; the dark spots are the chloroplasts. The second bubble is a chloroplast; the thylakoid membranes are the dark lines; the stroma is the stippled area. The third bubble shows a grana stack of thylakoids. The fourth bubble shows a schematic picture of the molecular structure of the thylakoid membrane, with a reaction center flanked by antenna complexes. *Source:* Courtesy of Aileen Taguchi.

carries out all the main phases of the process of photosynthesis. Synthesis of sucrose and some other carbon metabolism reactions require extrachloroplastic enzymes. Chloroplasts are about the size of bacteria, a few micrometers in diameter. In fact, chloroplasts were derived long ago from symbiotic bacteria that became integrated into the cell and eventually lost their independence, a process known as **endosymbiosis** (see Chapter 12). Even today, they retain traces of their bacterial heritage, including their own DNA, although much of the genetic information needed to build the photosynthetic apparatus now resides in DNA located in the nucleus.

An extensive membrane system is found within the chloroplast, and all the chlorophylls and other pigments are found associated with these membranes, which are known as **thylakoids**, or sometimes called **lamellae**. In typical higher plant chloroplasts, most of the thylakoids are closely associated in stacks and are known as **grana thylakoid membranes**, while those that are not stacked are known as **stroma thylakoid membranes**. The thylakoid membranes are the sites of light absorption and the early or primary reactions that first transform light energy into chemical energy. The nonmembranous aqueous interior of the chloroplast is known as the **stroma**. The stroma contains soluble enzymes and is the site of the carbon metabolism reactions that ultimately give rise to products that can be exported from the chloroplast and used elsewhere in the plant to support other cellular processes.

In prokaryotic photosynthetic organisms, the early steps of photosynthesis take place on specialized membranes that are derived from the cell's cytoplasmic membrane. In these organisms, the carbon metabolism reactions take place in the cell cytoplasm, along with all the other reactions that make up the cell's metabolism.

1.4 The four phases of energy storage in photosynthesis

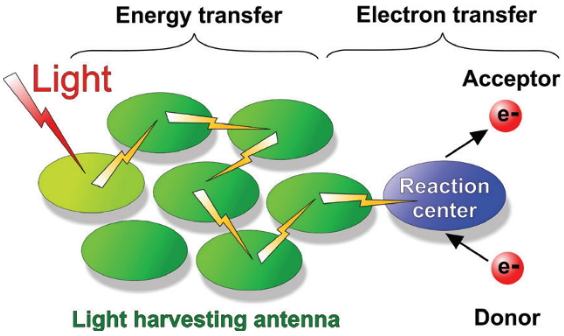
It is convenient to divide photosynthesis into four distinct phases, which together make up the complete process, beginning with photon absorption and ending with the export of stable carbon products from the chloroplast. The four phases are as follows: (1) light absorption and energy delivery by antenna systems, (2) primary electron transfer in reaction centers, (3) energy stabilization by secondary processes, and (4) synthesis and export of stable products.

The terms **light reactions** and **dark reactions** have traditionally been used to describe different phases of photosynthetic energy storage. The first three phases that we have identified make up the light reactions, and the fourth encompasses the dark reactions. However, this nomenclature is somewhat misleading, in that all the reactions are ultimately driven by light, yet the only strictly light-dependent step is photon absorption. In addition, several enzymes involved in carbon metabolism are regulated by compounds produced by light-driven processes. We will now briefly explore each of the phases of photosynthetic energy storage, with the emphasis on the basic principles. Much more detail is given in the later chapters dedicated to each topic.

1.4.1 Antennas and energy transfer processes

For light energy to be stored by photosynthesis, it must first be absorbed by one of the pigments associated with the photosynthetic apparatus. Photon absorption creates an excited state that eventually leads to charge separation in the reaction center. Not every pigment carries out photochemistry; the vast majority function as antennas, collecting light and then delivering energy to the reaction center where the photochemistry takes place. The antenna system is conceptually similar to a satellite dish, collecting energy and concentrating it in a receiver, where the signal is converted into a different form (Fig. 1.3). Energy transfer in antenna systems is discussed in more detail in Chapter 5.

The antenna system does not do any chemistry; it works by an energy transfer process that involves the migration of electronic excited states from one molecule to another. This is a purely physical process, which depends on a weak energetic coupling of the antenna pigments. In almost all cases, the pigments are bound to proteins in highly specific



(a)

(b)

Figure 1.3 (a) Schematic diagram illustrating the concept of antennas in photosynthetic organisms. Light is absorbed by a pigment, which can be either a type of chlorophyll or an accessory pigment. Energy transfer takes place in which the excited state migrates throughout the antenna system and is eventually delivered to the reaction center where electron transfer takes place, creating an oxidized electron donor and a reduced electron acceptor. (b) Radio telescope as an analogy to the photosynthetic antenna. The dish serves as the antenna, collecting energy and delivering it to the receiver, which transduces it into a signal. *Source:* NASA.

associations. In addition to chlorophylls, common antenna pigments include carotenoids and open-chain tetrapyrrole bilin pigments found in phycobilisome antenna complexes.

Antenna systems often incorporate an energetic and spatial funneling mechanism, in which pigments that are on the periphery of the complex absorb at shorter wavelengths and therefore higher excitation energies than those at the core. As energy transfer takes place, the excitation energy moves from higher- to lower-energy pigments, at the same time heading toward the reaction center.

Antenna systems greatly increase the amount of energy that can be absorbed compared with a single pigment. Under most conditions, this is an advantage, because sunlight is a relatively dilute energy source. Under some conditions, however, especially if the organism is subject to some other form of stress, more light energy can be absorbed than can be used productively by the system. If unchecked, this can lead to severe damage in short order. Even under normal conditions, the system is rapidly inactivated if some sort of photoprotection mechanism is not present. Antenna systems (as well as reaction centers) therefore have extensive and multifunctional regulation, protection, and repair mechanisms.

The number of antenna pigments associated with each reaction center complex varies widely, from a minimum of a few tens of pigments in some organisms to a maximum of several thousand pigments in other types of organisms. The pigment number and type largely reflect the photic environment that the organism lives in. Smaller antennas are found in organisms that live in high intensity conditions, while the large antennas are found in environments where light intensity is low.

1.4.2 Primary electron transfer in reaction centers

The transformation from the pure energy of excited states to chemical changes in molecules takes place in the photosynthetic reaction center. The reaction center is a multisubunit protein complex that is embedded in the photosynthetic membrane. It is a pigment–protein complex, incorporating chlorophyll or bacteriochlorophyll and carotenoid pigments as well as other cofactors such as quinones or iron sulfur centers, which are involved in electron transfer processes. The cofactors are bound to extremely hydrophobic polypeptides that thread back and forth across the nonpolar portion of the membrane multiple times.

The reaction center contains a special dimer of pigments that in most or all cases is the **primary electron donor** for the electron transfer cascade. These pigments are chemically identical (or nearly so) to the chlorophylls that are antenna pigments, but their environment in the reaction center protein gives them unique properties. The final step in the antenna system is the transfer of energy into this dimer, creating an excited dimer that has been electronically excited to a higher energy level.

The basic process that takes place in all reaction centers is described schematically in Fig. 1.4a. A chlorophyll-like pigment (P) is promoted to an excited electronic state, either by direct photon absorption or, more commonly, by energy transfer from the antenna system. The excited state of the pigment is chemically an extremely strong reducing species. It rapidly loses an electron to a nearby electron acceptor molecule (A), generating an ion-pair state P^+A^-. This is the "primary reaction" of photosynthesis. The energy has been transformed from electronic excitation to chemical redox energy. The system is now in a very vulnerable position with respect to losing the stored energy. If the electron is simply transferred back to P^+ from A^-, a process called **recombination**, then the net result is that the energy is converted into heat and rapidly dissipated and is therefore unable to do any work. This pathway is possible because the highly oxidizing P^+ species is physically positioned directly next to the highly reducing A^- species.

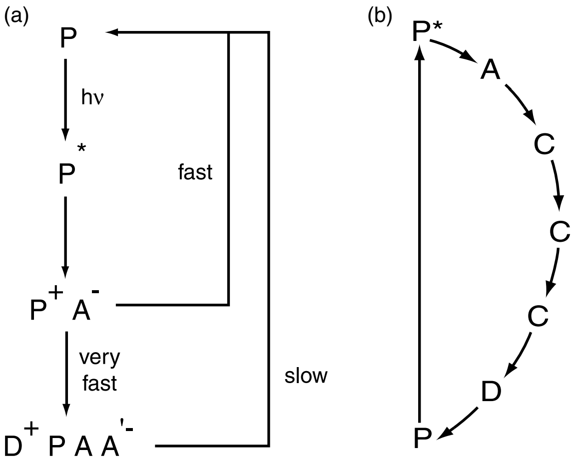


Figure 1.4 (a) General electron transfer scheme in photosynthetic reaction centers. Light excitation promotes a pigment (P) to an excited state (P*), where it loses an electron to an acceptor molecule (A) to form an ion-pair state P^+A^-. Secondary reactions separate the charges, by transfer of an electron from an electron donor (D) and from the initial acceptor A to a secondary acceptor (A′). This spatial separation prevents the recombination reaction. (b) Schematic diagram of cyclic electron transfer pathway found in many anoxygenic photosynthetic bacteria. The terms fast, slow, and very fast are relative to each other. The vertical arrow signifies photon absorption: P represents the primary electron donor: D, A, and C represent secondary electron donors, acceptors, and carriers.

The system avoids the fate of recombination losses by having a series of extremely rapid **secondary reactions** that successfully compete with recombination. These reactions, which are most efficient on the acceptor side of the ion-pair, spatially separate the positive and negative charges. This physical separation reduces the recombination rate by orders of magnitude.

The final result is that within a very short time (less than a nanosecond) the oxidized and reduced species are separated by nearly the thickness of the biological membrane (~30 Å; 1 Å = 0.1 nm). Slower processes can then take over and further stabilize the energy storage and convert it into more easily utilized forms. The system is so finely tuned that in optimum conditions the photochemical **quantum yield** of products formed per photon absorbed is nearly 1.0 (see Appendix). Of course, some energy is sacrificed from each photon in order to accomplish this feat, but the result is no less impressive.

1.4.3 Stabilization by secondary reactions

The essence of photosynthetic energy storage is the transfer of an electron from an excited chlorophyll-type pigment to an acceptor molecule in a pigment–protein complex called the reaction center. The initial, or primary, electron transfer event is followed by separation of the positive and negative charges by a very rapid series of secondary chemical reactions. This basic principle applies to all photosynthetic reaction centers, although the

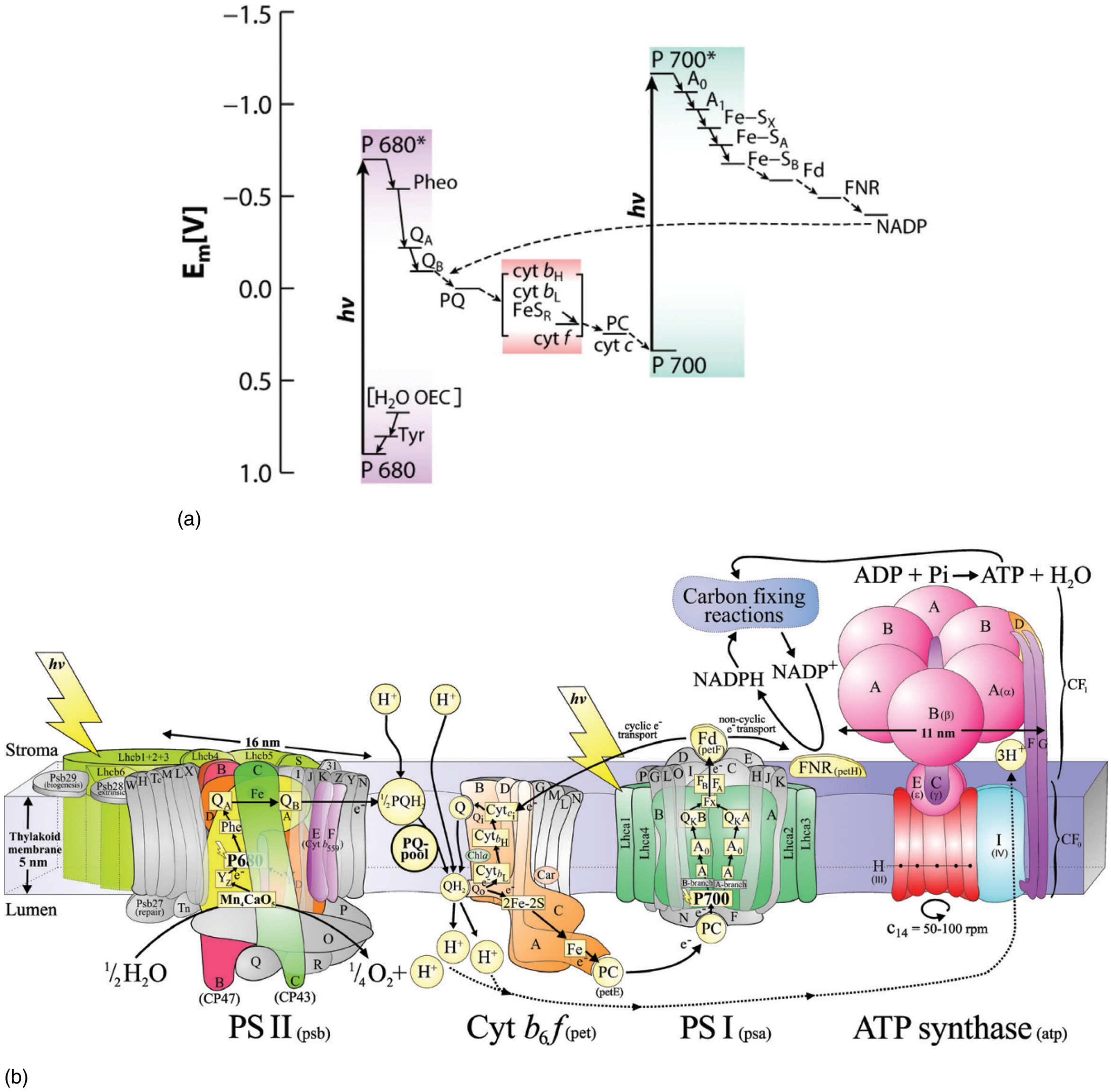


Figure 1.5 Schematic diagram of the noncyclic electron transfer pathway found in oxygenic photosynthetic organisms. The upper diagram (a) is an energetic picture of the electron transport pathway, incorporating the major reactions of photosynthesis into what is called the Z-scheme of photosynthesis. The lower diagram (b) is a spatial picture, showing the major protein complexes whose energetics are shown in the Z-scheme, and how they are arranged in the photosynthetic membrane. Neither view alone gives a complete picture, but together they summarize much information about photosynthetic energy storage. *Source:* (a) Hohmann-Marriott and Blankenship (2011) (p.532)/Annual Reviews. Reproduced with permission of *Annual Reviews*. (b) Courtesy of Dr. Jonathan Nield.

details of the process vary significantly from one system to the next.

In some organisms, one light-driven electron transfer and stabilization is sufficient to complete a **cyclic electron transfer chain**. This is shown schematically in Fig. 1.4b, in which the vertical arrow represents energy input to the system triggered by photon absorption, and the curved arrows represent spontaneous, or downhill, electron transfer processes that follow, eventually returning the electron to the primary electron donor. This cyclic electron transfer process is not in itself productive unless some of the energy of the photon can be stored. This takes place by the coupling of proton movement across the membrane with the electron transfer, so that the net result is a light-driven difference of pH and electrical potential, or electrochemical potential gradient across the two sides of the membrane. This electrochemical potential gradient, called a **protonmotive force**, is used to drive the synthesis of ATP.

The more familiar oxygen-evolving photosynthetic organisms have a different pattern of electron transfer. They have two photochemical reaction center complexes that work together in a **noncyclic electron transfer chain**, as shown in Fig. 1.5. The two reaction center complexes are known as Photosystems I and II. Electrons are removed from water by Photosystem II, oxidizing it to molecular oxygen, which is released as a waste product. The electrons extracted from water are transported via a quinone and the cytochrome b_6f complex to Photosystem I and, after a second light-driven electron transfer step, eventually reduce an intermediate electron acceptor, $NADP^+$ to form NADPH.

Protons are also transported across the membrane and into the thylakoid lumen during the process of the noncyclic electron transfer, creating a protonmotive force. The energy in this protonmotive force is used to make ATP (see Chapter 8).

Reaction centers and electron transfer processes in anoxygenic bacteria are discussed in more detail in Chapter 6, while these processes in oxygenic photosynthetic organisms are discussed in more detail in Chapter 7.

1.4.4 Synthesis and export of stable products

The final phase of photosynthetic energy storage involves the production of stable high-energy molecules and their utilization to power a variety of cellular processes. This phase uses the intermediate reduced compound, NADPH, generated by Photosystem 1, along with the phosphate bond energy of ATP to reduce carbon dioxide to sugars. In eukaryotic photosynthetic organisms, phosphorylated sugars are then exported from the chloroplast. The carbon assimilation and reduction reactions are enzyme-catalyzed processes that take place in the chloroplast stroma. These reactions are discussed in more detail in Chapter 9.

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