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Introduction to Photosynthesis: Energy Conversion by Plants and Bacteria

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ABBREVIATIONS

ADP (ATP)	Adenosine di (tri) phosphate
BChl	Bacteriochlorophyll
Chl	Chlorophyll
Cyt	Cytochrome
ESR	Electron spin (paramagnetic) resonance
NAD$^+$ (NADP$^+$)	Nicotinamide adenine dinucleotide (phosphate)
NMR	Nuclear magnetic resonance
PS	Photosystem
RC	Reaction center

ABSTRACT

In photosynthesis, plants, cyanobacteria, and photosynthetic bacteria use absorbed radiant energy to drive the synthesis of a variety of chemicals. In this process, energy liberated in the fusion of hydrogen in the sun is stored within a period of 10 min of its release in a chemically stable form that can last for hundreds of millions of years. Photosynthesis produces the food, much of the energy (past photosynthesis), and a vast number of materials we depend upon for our survival and comfort. The reactions begin when pigment molecules, acting as an antenna, absorb incident photons, and transfer the excitation energy over the array. The onset of photochemistry occurs when the excitation energy is trapped at a reaction center resulting in the initial charge separation. In plants and cyanobacteria, this light-driven oxidation–reduction occurs in two distinguishable reaction

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centers that interact in series. One of these photosystems (PSII) is involved in the oxidation of H_2O and consequent evolution of oxygen. The other PS (I) provides the charge separation that eventually results in the reduction of $NADP^+$. In addition to this linear electron transport, at least under certain conditions, there is a cyclic flow of electrons around PSI, as well as an electrogenic loop between the two photosystems. The components that mediate these light-driven reactions are for the most part located in highly complex membranes, the thylakoids, that resist ion translocation. The transfer of electrons from H_2O to $NADP^+$ is coupled to the accumulation of protons. The energy stored in the proton concentration difference, together with that stored in an electric field due to separation of protons and electrons across the membrane, is used by the coupling factor enzyme to synthesize ATP. The photosynthetic bacteria differ in that they do not evolve oxygen and there is but one photosystem. In green photosynthetic bacteria, the light reaction can drive linear electron transport from a donor (other than H_2O) to NAD^+. In the purple and brown bacteria, light drives cyclic electron transport that results in a transmembrane electric potential and a transmembrane proton concentration difference. The stored energy is used to synthesize ATP, again by the coupling factor enzyme. Subsequent reverse electron flow, driven by ATP, transfers electrons from a hydrogen donor (e.g., H_2S) to NAD^+. This volume is concerned with elucidating these aspects of photosynthesis, especially the extent to which the above general statements are applicable, and the modifications, additions, and new concepts that must be considered in order to have a complete molecular understanding. Carbon fixation, photorespiration, and other aspects of plant biology pertaining to photosynthesis (e.g., molecular biology, biosynthesis of membranes, translocation of photosynthates, effects of environment, and plant productivity) are discussed in the Volume II (Govindjee, 1982).

I. Introduction

Photosynthesis is the process by which plants, cyanobacteria, and photosynthetic bacteria convert radiant energy into a chemically stable form. The pathways of energy in the course of this energy transduction are complex, involving many components and several physical and chemical mechanisms. The process is initiated when light is absorbed by an antenna molecule within the photosynthetic membrane. The absorbed energy is transferred over the array; its fate is determined by whether it is trapped at a reaction center and used to do chemically useful work or whether it is emitted as a photon or lost as heat. Although several different pigments are involved in the light-gathering process, the fundamental importance of chlorophyll (Chl) or bacteriochlorophyll (BChl) is clear from the fact that this molecule is common to all photosynthetic antenna systems, as well as reaction centers (RC). Most if not all of the Chl is bound to protein and exhibits different electronic behavior in the membrane than *in vitro*. In this volume the nature of the Chl excited states is discussed by Shipman (Chapter 6, this volume), and the transfer of

excitation energy over the light-gathering molecules is discussed by Pearlstein (Chapter 7, this volume). In the past, it was thought that there was one chemical form of Chl *a* in plants. Recent developments indicating that there are other chemical forms of this ubiquitous molecule are discussed by Rebeiz and Lascelles (Chapter 15, this volume).

Following the absorption of light the initial photochemistry occurs at RC complexes, where the excitation energy is trapped and drives the transfer of an electron from a high potential primary donor [Chl or BChl] to a low potential electron acceptor. This electrochemical energy, stored in the initial charge separation, is used to drive all subsequent electron and proton transfer reactions in photosynthesis. After this time it is no longer meaningful to consider the initially absorbed photon energy as localized; the energy becomes divided into several different forms. The constraints of achieving high efficiency and high rates in this process are substantial as indicated by the complexity of RCs. The structure and function of RCs are discussed by Okamura, Feher, and Nelson (Chapter 5, this volume). The nature of the primary charge separation and of the early donors and acceptors is discussed by Parson and Ke (Chapter 8, this volume).

The RC complexes, the light-harvesting pigments, many of the electron and proton carriers, as well as other proteins (e.g., kinase), are constrained within or on a highly complex membrane. This membrane is relatively resistant to proton movement and forms a closed vesicle, so that there is an inner and outer aqueous phase. The structure and function of these membranes are discussed by Kaplan and Arntzen (Chapter 3, this volume). What is known about the orientation of components and complexes within the membrane is described by Breton and Vermeglio (Chapter 4, this volume).

Unique to plants and cyanobacteria is their ability to oxidize water and release molecular oxygen. They differ from the photosynthetic bacteria in that they have two distinguishable RCs rather than one. The two RCs of PSI and PSII are connected in series by electron and hydrogen-carrying components. Photosystem I uses the absorbed energy to transfer an electron to a low potential acceptor that via intermediates reduces $NADP^+$. Photosystem II contains the RC and components that oxidize water, releasing molecular oxygen, protons, and electrons that reduce the PSI RCs. The steps involved in oxygen evolution and the release of water protons are discussed by Wrydzynski (Chapter 10, this volume). Contributions to this understanding from measurements of thermoluminescence are described by Inoue and Shibata (Chapter 11, this volume).

In plants, cyanobacteria, and photosynthetic bacteria, the light-driven transfer of electrons involves Chl (BChl), pheophytin (bacteriopheophytin), quinones, cytochromes (Cyt) c and b, FeS centers, plastocyanin, and other electron and hydrogen carriers. In addition to the linear transport in plants and cyanobacteria, there is under some conditions cyclic transport around PSI. Evidence is now available suggesting an electrogenic loop between the two photosystems and in photosynthetic bacteria. Coupled to this multifarious electron transport is proton translocation. The numerous electron and hydrogen carriers and the variety of transport pathways, loops, and cycles are discussed by Cramer and Crofts (Chapter 9, this volume).

A portion of the energy initially stored in the primary charge separation goes into producing a pH gradient via electron transfer-driven proton translocation. In addition, energy is stored in an electric field as a consequence of the separation of electrons and protons across the membrane. Further contributions to the electric potential energy may come from cyclic electron transport around PSI and from an electrogenic "Q-cycle." These two forms of stored energy—electrical potential energy and the proton gradient—combine together to drive the phosphorylation of ADP by the coupling factor protein. Details of the membrane potential are discussed by Junge and Jackson (Chapter 13, this volume), the process and energetics of ATP synthesis by Ort and Melandri (Chapter 12, this volume), and the structure and function of the reversible ATPase enzyme by McCarty and Carmeli (Chapter 14, this volume).

The intent in this volume is to present a conceptual, integrated explanation of plant and bacterial photosynthesis. This comparative approach is especially evident in the following chapter in which Wraight discusses current attitudes in photosynthesis starting from van Niel's observations on bacterial and plant photosynthesis in the early 1930s.

II. Basic Concepts from Earlier Work

In the following chapters, the reader is assumed to be familiar with a number of concepts concerning photosynthesis that have been introduced and modified over the last 50 years. Together they provide the basis for the current description of photosynthesis. In this section, the salient features of several of these ideas are briefly sketched and referenced. A notable omission is a discussion of van Niel's contributions, which are detailed in the next chapter.

A. Photosynthetic Unit and Two Light Reactions

In the early 1930s, Emerson and Arnold (1932a) measured O_2 evolution by *Chlorella* using short flashes of light. They inferred from their data that photosynthesis involves a rapid light reaction that is temperature-independent over physiological ranges, followed by a temperature-dependent dark reaction faster than about 20 msec at 25°C. They then went on to ask a simple question that has had a strong influence on subsequent photosynthesis research: If one uses a single, short flash of light to drive photosynthesis, how many CO_2 molecules are reduced per chlorophyll molecule? The experiment depended upon producing light flashes that were intense enough to saturate the photochemistry yet short enough to avoid turning over the reaction more than once. After summing thousands of flashes, they determined that, on the average, a maximum of one O_2 molecule could be evolved per 2480 Chl molecules per flash (Emerson and Arnold, 1932b). From these early experiments emerged the concept of the *photosynthetic unit,* a group of Chl molecules capable of acting cooperatively to reduce one molecule of CO_2. Originally, the concept of a photosynthetic unit was necessarily vague and, as a consequence, flexible. The nature of the cooperativity and the site and components involved in the photochemistry were not known. In trying to explain the cooperativity of a large number of molecules in a photochemical reaction, Gaffron and Wohl (1936a,b) suggested that absorbed quanta are transferred between Chl molecules until they can be trapped and the energy used to drive a photochemical reaction. [The accompanying volume (see Govindjee, Vol. II, 1982) is dedicated to the memory of H. Gaffron.] Years later, experimental demonstration of energy transfer between different pigments was provided by fluorescence studies in which energy absorbed by one type of pigment sensitized fluorescence from a spectrally distinct pigment, Chl *a* (Dutton *et al.,* 1943; Duysens, 1952; French and Young, 1952). Energy transfer between the Chl *a* molecules was established by measurements showing depolarization of the Chl fluorescence (Arnold and Meek, 1956; Goedheer, 1957; Mar and Govindjee, 1972; Whitmarsh and Levine, 1974; Wong and Govindjee, 1981).

The next major development in the concept of the photosynthetic unit was the characterization of the energy trap or RC in photosynthetic bacteria by Duysens (1952; also see Duysens *et al.,* 1956). He observed that illumination of bacteria led to a decrease in absorbance that he attributed to a bleaching of a small fraction of the BChl. He envisioned a special BChl trapping excitation energy from the antenna pigments and

the energy driving a charge separation reaction. Bessel Kok (to whom this volume is dedicated) observed a similar bleaching in plants near 700 nm that was attributed to a special chlorophyll a (P700), the plant reaction center (Kok, 1956, 1957, 1961). These observations made possible a fairly clear picture of the early events in photosynthesis: absorption of a photon by the antenna complex, transfer of excitation energy over the array, trapping of the energy at a special RC complex, where the energy is used to transfer an electron from the RC Chl to the primary acceptor.

A major breakthrough in the study of RCs was their biochemical isolation in photosynthetic bacteria by Reed and Clayton (1968). This opened the search for the mechanisms and components involved in the trapping of energy, primary charge separation, and stabilization by the early donors and acceptors. A search that has now reached into the picosecond time domain (Kaufmann *et al.,* 1975; Rockley *et al.,* 1975).

In the late 1950s, it became evident that two distinguishable light reactions were involved in plants. The experiments of Emerson and co-workers (Emerson, 1957, 1958; Emerson *et al.,* 1957; Emerson and Rabinowitch, 1960) showed that at low light intensities the rate of photosynthesis in combined far-red and shorter wavelength light was greater than the sum of the rates driven by the beams separately (Emerson enhancement effect). Emerson assumed that one reaction was sensitized by auxiliary pigments (e.g. Chl b) and the other by Chl a. This assumption was incompatible with Duysens' (1952) conclusion that 100% of the energy absorbed by Chl b is transferred to Chl a. The discovery of bands due to short wavelength forms of Chl a and accessory pigments in the action spectra of the Emerson enhancement effect resolved this problem (Govindjee and Rabinowitch, 1960; French *et al.,* 1960): one reaction was sensitized by a short wavelength form of Chl a and the other by pigments including a long wavelength form of Chl a.

B. Kok and A. Jagendorf wrote in 1963: "Every so often someone manages to remove another stone from the wall through which we all want to see, and the crowds tend to flock around the new peep hole [p. ix]." This was the case with Emerson's discovery. Kautsky *et al.* (1960) also suggested the existence of two light reactions to explain Chl a fluorescence changes with time of illumination (Kautsky effect). The relation of Chl a fluorescence to the two photosystems was clarified when it was shown that far-red light quenched the high level of fluorescence excited by short wavelength light (Govindjee *et al.,* 1960; Butler, 1962; Duysens and Sweers, 1963). Hill and Bendall (1960) proposed that the two light reactions operate in series. This proposal, now known as the Z scheme, accounted for a number of observations and has now gained general acceptance in the field of photosynthesis. The two photosystems are

named I and II. PSII is the site of H_2O oxidation and results in the reduction of plastoquinone, whereas PSI oxidizes plastoquinol and reduces $NADP^+$. These reactions involve a series of electron and hydrogen carriers. Crucial experiments contributing to the early acceptance of this scheme include those of Duysens *et al.* (1961) showing the antagonistic effect of PSI and PSII on the Cyt *f* redox state; Kok (1959) and Kok and Gott (1960) showing the opposite effect of PSI and PSII light on the redox state of P700; Boardman and Anderson's (1964) biochemical separation of the two photosystems; and the studies of Levine and co-workers (see Levine, 1969) demonstrating the inhibition of electron transport in mutants lacking various electron carriers.

With the introduction of the Z scheme and the observation that O_2 evolution involves a four-step process within a single photosystem (i.e., PSII does not act cooperatively to evolve oxygen; see later), the concept of a photosynthetic unit could be defined as approximately 600 Chl molecules including PSII and PSI and an electron transport chain that could independently evolve oxygen and reduce $NADP^+$. Thus, it was inferred that 300 Chl molecules per RCII or RCI is the minimum unit size for one photosystem. This number was obtained by dividing 2400 by 8 (the minimum quantum number of O_2 evolution; see Emerson, 1958). Although it was shown that the chains could exchange electrons at the level of plastoquinone, the visualization of a photosynthetic unit was often overly rigid (see Myers, 1974). Recently two experimental results may force yet another modification of our description of a photosynthetic unit. First, Melis and Brown (1980) argued that the ratio of PSII to PSI varies considerably depending upon the organism and growth conditions. And second, evidence is accumulating that the grana stacks of thylakoid membranes are enriched in PSII and the stroma and edge regions of grana contain PSI (Andersson and Anderson, 1980). These latter studies raise questions concerning the mobility of large protein complexes within the membrane as well as the problem of long distance electron transport between the two photosystems. It would seem that the original photosynthetic unit concept is too simple to accommodate the complex interactions between the two photosystems that are presently being suggested.

In reading this volume, one may get the impression that there is unanimous agreement concerning the current general description of the light reactions in photosynthesis. However, Arnon and co-workers (1981) recently attacked the very premise of the Hill-Bendall Z scheme. Arnon and co-workers propose that PSII oxidizes H_2O and reduces $NADP^+$ in a two quanta reaction. In this scheme PSI is concerned only with cyclic electron flow. In general, it appears to us that Arnon and co-

workers have attempted to explain their results in terms of a radically new scheme before thoroughly searching for more modest explanations of their data. It is difficult to explain in their scheme (also see Arnold, 1976) the existence of the Emerson enhancement effect in $NADP^+$ reduction (R. Govindjee et al., 1962, 1964; Joliot et al., 1968; Avron and Ben-Hayyim, 1969; McSwain and Arnon, 1972) and the antagonistic effect of PSI and PSII light on P700 (Kok and Gott, 1960) and Cyt f (Duysens et al., 1961), among several other established observations.

B. Oxygen Evolution

A cursory examination of the equation for the oxidation of H_2O ($2H_2O \rightarrow O_2 + 4H^+ + 4e^-$) suggests the involvement of four steps in the evolution of oxygen. In experiments that were somewhat similar in design to those of Emerson and Arnold (1932b) and Allen and Franck (1955), Joliot et al. (1969) measured the relative amount of O_2 evolved in a short flash in dark-adapted cells of Chlorella and chloroplasts as a function of flash number. These influential experiments depended upon a rapid, sensitive polarographic method to detect oxygen (Joliot and Joliot, 1968). Joliot et al. found that the oxygen yield exhibited a periodicity of 4 that became damped out as the flash number became large. Shortly thereafter Kok et al. (1970) provided the simplest scheme to account for the periodicity and its damping. In this scheme, one PSII RC interacts with a single oxygen-evolving site. Each photochemical reaction, driven by a single photon, results in providing oxidizing equivalents that are accumulated at the oxygen-evolving site. Upon accumulation of four oxidizing equivalents, O_2 is evolved and the site returns to its lowest oxidation state. In this model, there is no exchange of equivalents between different oxygen-evolving sites i.e., they are independent with respect to oxygen evolution (reviewed by Joliot and Kok, 1975).

The components involved in the oxygen-evolving site and their interaction with the RC are still largely unknown. The importance of Mn has been demonstrated in a number of separate studies (e.g., Cheniae, 1970; Blankenship and Sauer, 1974; Yamashita and Tomita, 1974). A dynamic function of Mn was first suggested by NMR and ESR studies of Wydrzynski and co-workers (1976; Govindjee et al., 1977; Wydrzynski and Sauer, 1980).

Recent experiments by Dismukes and co-workers (see, e.g., 1982) on low temperature ESR spectra of Mn in thylakoid membranes, following exposure to a series of single turnover light flashes at room temperature, have provided the most direct evidence for the dynamic function of Mn during O_2 evolution.

Measurements of proton release from PSII as a function of flash number revealed that an oxygen-evolving enzyme does not actually accumulate four oxidizing equivalents releasing O_2 and four protons in one step. There is general agreement that protons are released at least as early as the second flash (Fowler, 1977; Junge *et al.*, 1977; Saphon and Crofts, 1977; also see Förster *et al.*, 1981).

The early experiments of Ruben *et al.* (1941) provided experimental evidence for van Neil's argument that H_2O was the source of O_2 in photosynthesis. This concept has been challenged by Warburg (1964), Metzner (1975), and by Stemler (1980). Although there is general agreement that the ultimate source of O_2 is H_2O (Metzner, 1966; Stemler and Radmer, 1975; Radmer and Ollinger, 1980), Metzner *et al.* (1979) and Stemler (1980) believe that the immediate source of oxygen may be HCO_3^- or CO_2. The involvement of CO_2 in water oxidation is presently unsettled, although it has been shown that CO_2 plays a role in electron transport between the two photosystems (see review by Vermaas and Govindjee, 1981).

C. Photophosphorylation

Light-driven phosphorylation was first demonstrated in chromatophores from photosynthetic bacteria by Frenkel (1954) and in chloroplasts by Arnon *et al.* (1954). The mechanism by which energy-transducing membranes couple electron flow to ATP synthesis has fascinated researchers to this day. Although the process is complex, tied to charge transfer in ways that only recently have been revealed (e.g. Q cycle), it was in the early 1960s that Mitchell (1961, 1966) offered a conceptually simple and profoundly influential hypothesis to explain the coupling of electron transport to phosphorylation. For this work he received the Nobel prize in 1978. He suggested that electrons transfer results in the vectorial translocation of protons across a membrane; the resulting proton chemical gradient then provides the energy for the phosphorylation of ADP. Not long after this, attention was focused on his proposal by the experiments of Jagendorf and co-workers in which they showed chloroplasts could exhibit light-induced pH changes (Jagendorf and Hind, 1963) and an acid–base jump synthesis of ATP (Jagendorf and Uribe, 1966). These and other contributions are covered extensively in this volume (see Chapters 12–14).

D. Light Emission

A fraction of the radiant energy absorbed by photosynthetic organisms is emitted as light. The features of the emitted radiation are deter-

mined in part by the absorbing pigments, the excitation energy transfer, the fluorescing pigments, and the orientation of these pigments. In addition, the fluorescence is sensitive to a wide variety of photosynthetic events. These include the redox state of the reaction center, donors, and acceptors of PSII, proton translocation, thylakoid stacking and unstacking, ionic strength, and the midpoint potential of Cyt b-559, to name a few. Although the dependence of the fluorescence upon these phenomena is often indirect and difficult to quantitate and separate from one another, fluorescence measurements have been used to monitor and characterize a wide variety of events and components. One of its main attractions is that it offers a nondestructive means of probing various photosynthetic reactions (Papageorgiou, 1975; Butler, 1977; Lavorel and Etienne, 1977). As an example, one of the most fruitful uses of fluorescence has been to establish the existence and measure the midpoint potential of PSII electron acceptors by monitoring the fluorescence intensity as a function of the ambient redox potential (see, e.g., Cramer and Butler, 1969; Golbeck and Kok, 1978; Horton and Croze, 1979; Klimov *et al.*, 1980).

Delayed fluorescence (delayed light emission, luminescence) and thermoluminescence were first observed by Strehler and Arnold (1951) and by Arnold and Sherwood (1957), respectively. Delayed fluorescence is due to a back reaction in which the initial charge separation recombines at the RC providing the energy for the emission of a photon. Thermoluminescence is delayed fluorescence observed during the slow heating of a sample or after a sudden temperature jump (Mar and Govindjee, 1971). Both of these processes have been used to investigate components involved in the early events in the primary charge separation (Lavorel, 1975; Malkin, 1977; Govindjee and Jursinic, 1979; Inoue and Shibita, Chapter 11, this volume).

E. Carbon Fixation and Photorespiration

This volume is concerned with the bioenergetics of what are primarily membrane-bound events commonly known as the light reactions in photosynthesis. These reactions provide the energy, via ATP and reduced NADP, for the reduction of CO_2. The pathway of carbon in photosynthesis was traced by Calvin and co-workers (Bassham *et al.*, 1954). Calvin received a Nobel prize for these studies in 1961. A major development in carbon fixation was the discovery by Kortschak *et al.* (1965) that sugarcane plants fixed carbon initially into a C_4 rather than a C_3 acid. This was followed by a delineation of the detailed pathways in many

plants, now known as C_4 plants, by Hatch and Slack (1966). Another significant discovery in this field relating to photorespiration was the observation that ribulosebisphosphate carboxylase is also an oxygenase (Ogren and Bowes, 1971). These and other topics relating to productivity and efficiency are discussed in the Volume II in this series (Govindjee, 1982).

III. Concluding Remarks

The study of the light-driven reactions in photosynthesis depends on a variety of techniques and approaches involving a wide spectrum of scientific disciplines. The primary aim of the research has been to characterize photosynthetic processes at a molecular level. Currently, as our description of photosynthesis becomes more detailed in terms of basic physicochemical principles, attention is being focused on the relationship between photosynthesis and plant productivity and on the possibility of altering or modifying photosynthetic reactions or applying principles learned from these reactions to develop a practical system of solar energy conversion. For example, can light-driven reduction of protons produce H_2 on a scale that is practical (Rao and Hall, 1977)? Can improving photosynthesis significantly increase productivity (Good and Bell, 1980; Hesketh *et al.*, Chapter 11, in Govindjee 1982)? Emphasis is placed upon producing biomass from nonedible plants, especially on marginal lands (Rolfe and White, 1979). Attempts are also being made to grow plants that produce petroleum-like substances (Calvin, 1977).

IV. Literature

The present volume is an expansion of the book edited by Govindjee (1975) in this series. The unique feature of this volume is the integration of plant and bacterial work. Several topics (fluorescence, delayed fluorescence, pigment–protein complexes, and ion transport) that were covered previously are not thoroughly covered here. The topics of CO_2 fixation and plant productivity, not covered at all in the earlier book, now appear in a separate volume (Govindjee, 1982).

Several symposia volumes, edited books, special journal issues, and single authored books have appeared since 1975. (For earlier reviews, see Govindjee, 1975.) Some of these are listed below. Symposia volumes include the proceedings of the three International Congresses on Photo-

synthesis Research edited by Avron (1975), Hall *et al.* (1978) and Akoyunoglou (1981); other more specialized conference proceedings are those edited by Olson and Hind (1977) on protein complexes; Packer *et al.* (1977) on bioenergetics of membranes; Akoyunoglou and Argyroudi-Akoyunoglou (1978) on chloroplast development; Metzner (1978) on O_2 evolution; Chance *et al.* (1979) on electron tunneling, and Trumpower (1981) on quinones. Multiauthor books on various aspects of photosynthesis are those edited by Barber (1976) on intact chloroplasts; Barber (1977) on primary processes; Trebst and Avron (1977) on electron transport and photophosphorylation; Clayton and Sistrom (1978) on photosynthetic bacteria; Barber (1979) on model systems; Hatch and Boardman (1981) on several aspects of photosynthesis; Alfano (1982) on ultrafast laser spectroscopy; and Barber (1982) on electron transport and photophosphorylation. A special issue on ultrafast reactions in photosynthesis was edited by Govindjee (1978). Other books are those edited by Burris and Black (1976) on CO_2 metabolism and plant productivity, San Pietro (1980a) on energy production, and San Pietro (1980b) on methods in photosynthesis. An excellent single-authored book on photosynthesis is that by Clayton (1980).

For an up-to-date knowledge, the reader should consult the recent issues of various journals including: *Annual Review of Plant Physiology, Archives of Biochemistry and Biophysics, Biochemical and Biophysical Research Communications, Biochemistry, Biochimica et Biophysica Acta (Bioenergetics), Biokhimiya, Biofizika, Biophysical Journal, Doklady Akademy Nauk SSSR, FEBS Letters, Journal of Biological Chemistry, Journal of Theoretical Biology, Photobiochemistry and Photobiophysics, Photochemistry and Photobiology, Photosynthesis Research, Photosynthetica, Physiologia Plantarum, Plant and Cell Physiology, Plant Physiology, Plant Science Letters, Proceedings of the National Academy of Sciences, U.S.A.,* and *Zeitschrift für Naturforschung.*

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