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Transformation of Light Energy into Chemical Energy: Photochemical Aspects of Photosynthesis[1]

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ABSTRACT

The physical and chemical events leading from the absorption of light by chlorophyll *a in vivo* to the production of the "reducing power" (reduced nicotinamide adenine dinucleotide phosphate) and the "high energy phosphate" (adenosine triphosphate) are reviewed here for the benefit of those students who have little understanding of the biophysical processes associated with photosynthesis and who are interested in appreciating the current status of the knowledge in this field. The capture of light energy, the fate of excitation, energy transfer, the trapping of energy, the Emerson enhancement effect, the *two* light reactions and the electron pathways in photosynthesis are discussed in this review; it cites detractors as well as supporters of the current dogma on photosynthesis.

LIGHT quanta absorbed by green plants, multi-colored algae, and photosynthetic bacteria are utilized for a large-scale conversion of light energy into chemical energy. This conversion of light energy into chemical free energy is the essential consequence of photosynthesis (Fig. 1). Photosynthesis, literally synthesis by light, occurs in thylakoids (double membranes closed in themselves, 123). In green plants (including multi-colored algae) chemical energy generated from light is used to synthesize carbohydrates, from carbon dioxide and water, with concomitant evolution of oxygen. In photosynthetic bacteria, however, oxygen is not evolved, and various hydrogen sources replace water as reductant. Recently, several symposia (69, 74, 109, 121, 130, 150, 152, 170), reviews (14, 33, 58, 85, 137, 146, 156, 157), and books (34, 66, 93, 158) have appeared that cover various aspects of green plant and bacterial photosynthesis.[3]

Green plant photosynthesis may be considered as a tripartite reaction (Fig. 2): the evolution of O_2 from water, the transfer of H-atoms (or electrons) from an intermediate (ZH) to another intermediate (X), the reduction of CO_2 by the reduced X, to form a carbohydrate. The light quanta captured by pigments are used to perform mainly the second step. Thus, in

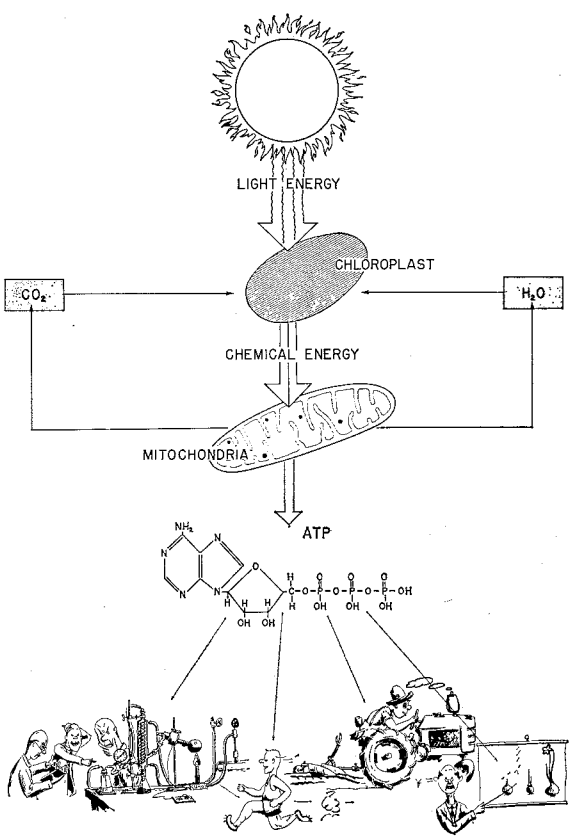

Fig. 1. Energy flow diagram.

[1] Talk delivered in a symposium, "Let There Be Light", at the Annual Meeting of the American Society of Agronomy, at Columbus, Ohio, November 2, 1965. Received for publication May 10, 1967. This review is addressed to those who are *not* engaged in plant physiology and photosynthesis research.

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[3] Abbreviations used in the figures and text: ADP — adenosine diphosphate; ATP — adenosine triphosphate; NADP — nicotinamide dinucleotide phosphate; NADPH — reduced NADP.

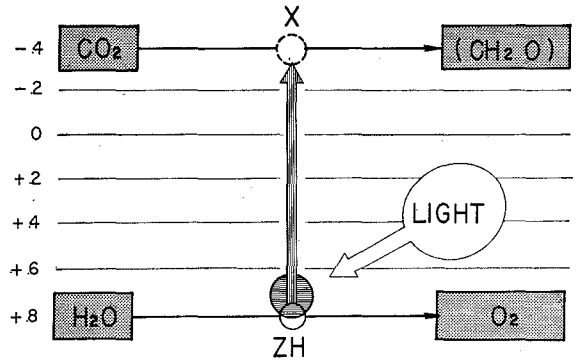

Fig. 2. Three phases of photosynthesis: (1) oxidation of ZH to Z and reduction of X to XH (vertical arrow); (2) evolution of oxygen by oxidation of water (H_2O) by Z made in phase 1 (bottom arrow); and (3) reduction of carbon dioxide (CO_2) to carbohydrate (CH_2O) by XH made in phase 1 (top arrow). The chemical identity of X and Z has not yet been definitely established. The oxidation-reduction potentials (E_0') of the different redox couples are shown on the left hand margin.

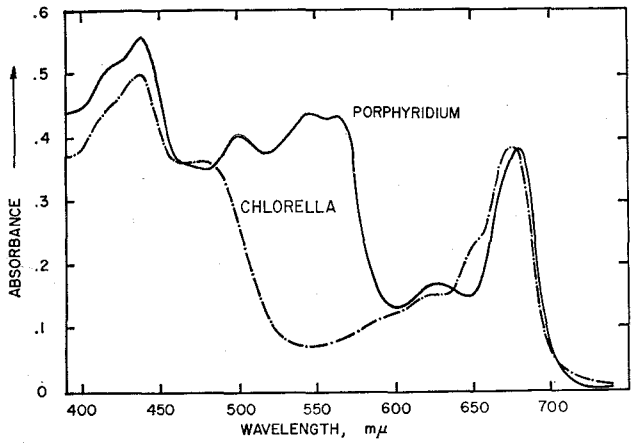

Fig. 3. Absorption spectra of a green alga (Chlorella; dashes and dots) and of a red alga (Porphyridium; solid line), measured by a Bausch and Lomb spectrophotometer (Spectronic 505) equipped with an integrating sphere. Absorption spectra of leaves of crop plants resemble those obtained for Chlorella.

photosynthesis, light energy is utilized for an oxidation-reduction reaction (reduction of X and oxidation of ZH) which could not occur without the supply of energy. The present review deals primarily with the photochemical aspects of green plant photosynthesis.

Capture of Light Energy

In order for light energy to be effective in any reaction it *must be* absorbed (the first law of photochemistry). For this purpose, plants contain an assortment of pigments, the alcohol-soluble chlorophylls *a* and *b* (green) and the carotenoids (yellow to orange). Certain plants have replaced chlorophyll *b* with other pigments, such as the water soluble pink pigment, phycoerythrin (red algae), or the blue pigment, phycocyanin (blue-green algae). These and other pigments (see Strain, 147) share in the capture of light energy (Fig. 3). Chlorophyll *a* is the only pigment that is common to all photosynthesizing plants and is thus considered to be the major pigment of photosynthesis; all other pigments are called "accessory".

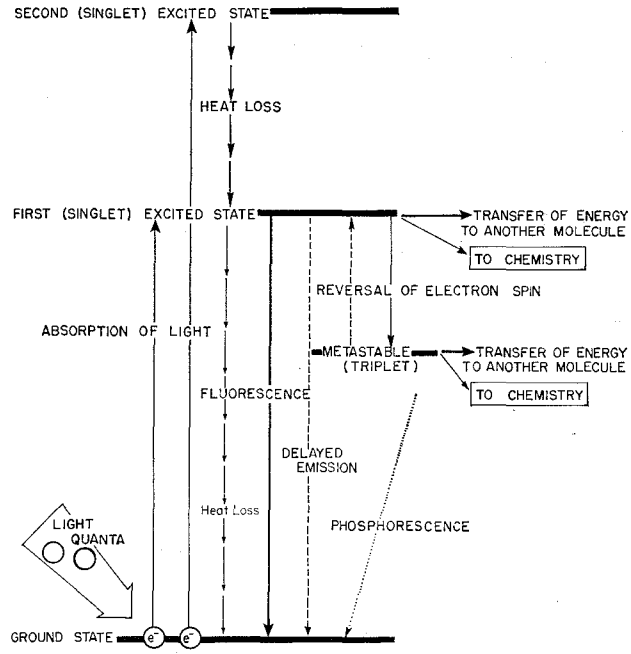

Fig. 4. Energy level diagram for chlorophyll (the vibrational and rotational levels are not shown).

The first act of photosynthesis is the absorption of light by one of the several chloroplast pigments. When a light quantum of a certain wavelength hits a pigment molecule, an electron in the outermost "shell" is "kicked up" into an empty, outer orbit (Fig. 4). The transition of the molecule from the ground state to the singlet excited state is extremely fast; it is over in 10^{-15} seconds. A molecule in the excited state has a new electron configuration (see Foerster, 53). It has an excess of free energy, namely that of the light quantum that it absorbed. This molecule is very unstable.

The electron in the excited state reached by absorption has an extremely short life. Brody (23; also see Brody and Rabinowitch, 26) and Terenin (151) independently measured the life time of the excited state of chlorophyll *in vivo* to be 0.6 to 1.5 $\times$ 10^{-9} seconds. Butler and Norris (28), Tomita and Rabinowitch (153), Murty and Rabinowitch (125) and Mueller and Lumry (124) have confirmed and extended the original measurements of Brody and Terenin. The electron in the excited state has several choices: *(1)* It may return to the ground state, emitting a light quantum (fluorescence). *(2)* It may return to the ground state by losing energy in small steps as heat (internal conversion). *(3)* The fall of the electron to the ground state may be coupled with electronic excitation in another pigment molecule ("resonance energy transfer"). *(4)* Its return to the ground state may be interrupted at a metastable (or triplet) state, in which it may stay for a long time ($\sim 10^{-3}$ sec). In the triplet state the electron has parallel spin to those in the ground state. The fall from this state down to the ground state may occur by loss of heat (internal conversion) or by emission of light (phosphorescence). *(5)* From the metastable state, the electron may be "kicked up" to the original singlet excited state by thermal agitation and may then fall back to the ground state emitting light (delayed-emission). *(6)* The elecron may be transferred to an "electron acceptor" (oxi-

dant) (either from the singlet excited or the triplet state) reducing the "oxidant" and leaving the pigment in the oxidized state.

In order to account for the high efficiency of photosynthesis, almost 90-95% of light quanta absorbed must be channeled to useful photochemical reactions (not heat, delayed emission, or fluorescence). The fluorescence yield of live cells is reasonably low; Latimer et al. (115) and Weber and Teale (162) found it to be around 2.5 to 3% in Chlorella.

Energy Transfer

When the quantum of light is absorbed by an accessory pigment *in vivo,* the energy does not stay in the pigment molecule that had initially absorbed it; instead it is transferred to chlorophyll *a* (4,37,38,65,161). When chlorophyll *b* is excited in chlorella,, the fluorescence of chlorophyll *b* is absent, but the fluorescence of chlorophyll *a* is observed (sensitized fluorescence). This shows transfer of excitation energy from chlorophyll *b* to chlorophyll *a*. By measuring the intensities of chlorophyll *a* fluorescence when chlorophyll *a* is directy excited and when the accessory pigments are excited, Duysens (38) caculated the efficiency of energy transfer from various accessory pigments to chlorohpyll *a* to range from 20 to 100%. The efficiency of energy transfer from carotenoids to chlorophyll *a* was lowest (~20%) in the blue-green aglae. In brown algae, the transfer efficiency from a special carotenoid (fucoxanthol) to chlorophyll *a* was rather high (70 to 80%). The transfer efficiency from the phycobilins (phycoerythrins and phycocyanin) to chlorophyll *a* was also high (70 to 90%). The highest (almost 100%) efficiency was from chlorophyll *b* to chlorophyll *a*. Brody and Brody (24), working with the red alga *Porphyridium cruentum,* and Govindjee and his coworkers (70, 133), working with the blue-green alga, *Anacystis nidulans,* have observed large changes in the efficiency of energy transfer from the phycobilins to chlorophyll *a* caused by growing algae with different pigment ratios and by preilluminating algae with different intensity and wavelength of light.

According to Foerster (53) (also see Duysens, 41), the efficiency of such resonance energy transfer depends upon the extent of the overlap of the fluorescence spectrum of the donor molecule with the absorption spectrum of the acceptor molecule, upon the average distance between them and the orientation of molecules with respect to each other.

When a chlorophyll *a* molecule absorbs a quantum of light, energy transfer to other chlorophyll *a* molecues may occur. This migration is demonstrated by almost complete depolarization of fluorescence when polarized light is used to excite chlorophyll *a* (3).

The Trapping of Energy

In 1936, Gaffron and Wohl (68) calculated that for the same chlorophyll *a* molecule to absorb 8 quanta of light, needed to evolve one O_2 molecule, it would take about an hour or more, and if there were no energy transfer between chlorophyll molecules, one would have to wait at least an hour before any measurable O_2 could be evolved when a plant is transferred from darkness to light, but in fact the O_2 evolution begins immediately. Therefore, Gaffron and Wohl (68) suggested that quanta absorbed in different molecules somehow assemble in special molecules (reaction centers or energy traps). Emerson and Arnold (46) had earlier discovered that when bright and short (10^{-5} sec) flashes of light are given to a plant, a maximum of one O_2 molecule is produced per flash per 2,400 chlorophyll molecules present. These findings, confirmed and placed on a more quantitative basis by Kok (101) also suggested an assemblage of chlorophyll *a* molecules somehow cooperating to evolve O_2. This assemblage is called the "photosynthetic unit". Since four H-atoms (or electrons) must be moved from H_2O to CO_2 to produce one O_2 molecule, it seems that about 600 chlorophyll molecules can cooperate to transfer one H-atom. As this transfer has been recently shown to occur in two steps, approximately 200 to 300 chlorophylls must cooperate in each primary reaction of photosynthesis. This is then the size of the "photosynthetic unit" (also see Kohn, 100). Light energy absorbed by any one of the pigment molecules in such a unit is assumed to migrate to a common reaction center. The chlorophyll *a* molecules associated with these centers function as the *"energy traps"*. These are molecules which are associated with the primary electron donors and acceptors of photosynthesis; they may thus undergo oxidation-reduction reactions upon illumination. It is at these selected pigment molecules that light energy is converted into chemical energy (see Clayton, 35, regarding the efficiency of "energy traps").

Since the energy "traps" must be present in low concentration (less than 1% of the total concentration of pigments) a very sensitive instrument is required to detect any orxidation-reduction changes in them. Duysens (39), Witt (166), Kok (103), and Coleman et al. (36) have successfully applied the technique of difference spectroscopy for detecting small changes in absorbance in illuminated plants (Fig. 5). Kok

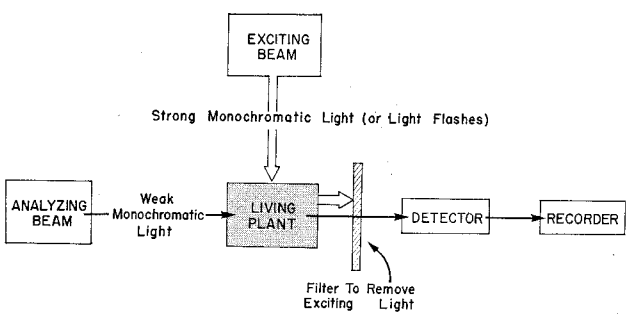

Fig. 5. Sketch of a difference spectrophotometer. The analyzing beam (of low intensity) is split into two beams; one goes through the sample (living plant) and the other around the sample (not shown in the diagram). Both beams fall on the detector (a photomultiplier). The intensity of the beam that is sent around the sample is adjusted to match the intensity of the light transmitted by the sample; a zero reading is obtained on the recorder. Upon turning on the exciting beam (of high intensity), changes in absorption are observed and recorded. By varying the wavelength of the analyzing beam, a difference spectrum (that is, the difference between the absorption spectrum of cells illuminated with strong exciting light and non-illuminating cells) is obtained; it gives information concerning the pigments that undergo oxidation or reduction during photosynthesis. By varying the wavelength of the exciting beam, an action spectrum (that is, the curve showing the effectiveness of different wavelengths of light in producing the change) is obtained; it provides information concerning the pigments that sensitize the absorption changes.

(102, 106), who discovered an absorbance change at 700 mμ (and 433 mμ) due to oxidation of a tiny quantity of a chlorophyll *a* (P700), has suggested that this "P700" is one of the energy traps of photosynthesis. In the energy traps, the formation of oxidants (positively charged ions) and reductants (negatively charged ions) occurs. The conversion of light energy into chemical energy thus takes place at these centers. Most workers believe (see Robinson, 137) that P700 is the energy trap for the so-called pigment system I and that the energy trap for pigment system II is still to be discovered. However, Franck and Rosenberg (58) believe that there is only one type of energy trap which serves both the pigment systems.

After the primary reactions have taken place, the primary products must not be allowed to react with each other. It has been suggested (see Rabinowitch, 134) that oxidation of H_2O may occur on one side of a lamella and reduction of CO_2 on the other side, thus preventing back reactions between the primary products.

The "Red Drop", The Emerson Enhancement Effect and Two Light Reactions

Emerson and coworkers (48,49,50) observed that the quantum efficiency (number of moles of O_2 evolved per mole quanta absorbed) of photosynthesis becomes abnormally low when light is primarily absorbed by chlorophyll *a* (red drop) (Fig. 6). The "red drop" was observed particularly clearly in the red alga Porphyridium (22). In 1957, Emerson et al. (48) discovered a "synergistic" effect in photosynthesis. When light of a certain wavelength (which is absorbed primarly by accessory pigments) is combined with far-red light (absorbed primarily by chlorophyll *a*), the production of oxygen in the combined beams is greater than the sum of the production in the two beams given separately. The enhancement (E) is calculated as:

$$E = \frac{RO_2 \text{ (combined beams) minus } RO_2 \text{ (short wave beams)}}{RO_2 \text{ (short or long wave beam)}}$$

On the basis of this synergistic effect which we call *Emerson enhancement effect,* Emerson (45) suggested that photosynthesis requires two light reactions. Emerson and co-workers (45, 47, 51) measured the action spectra of the enhancement effect by measuring the enhancement (E) as a function of the wavelength (λ) of the "short-wave" beam, while the far-red beam (720 mμ) was kept constant (Fig. 7). Later, Blinks (19) and Fork (55) measured another action spectra of enhancement (E), in phycoerythrin containing algae, by measuring enhancement (E) as a function of the wavelength (λ) of the "long or short-wave" beam while green light (absorbed by phycoerythrin) was kept constant.

On the basis of his action spectra measurements, Emerson concluded (45,47) that one light reaction is sensitized by chlorophyll *a* and the other by accessory pigments, and the "red drop" occurs in the wavelength range where chlorophyll *a* becomes the prime absorber of light energy. The conclusion that accessory pigments alone can sensitize some reactions was hard to accept, as light absorbed in many accessory pigments is transferred with high efficiency (80-100%) to chlorophyll *a* (4,37,38,65,161). In 1960, Govindjee

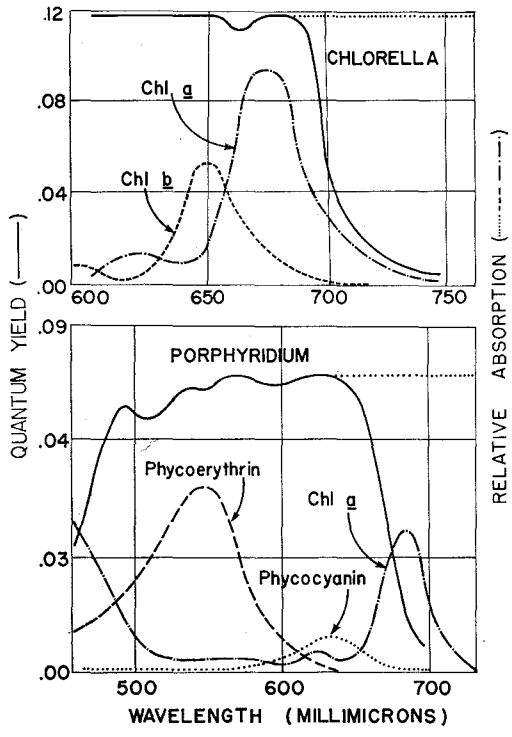

Fig. 6. Quantum yield of oxygen evolution as a function of wavelength of light (solid line). Absorption curves for chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl *b*), phycocyanin and phycoerythrin are also shown. The top graph is for the green alga Chlorella and the bottom for the red alga Porphyridium. The low efficiency under red and far-red illumination (the red drop) is restored to full efficiency by supplementary short-wave illumination (dotted curve). This enhancement is known as the "Emerson enhancement effect" (redrawn from the data of R. Emerson and his co-workers [22,48,50,51]).

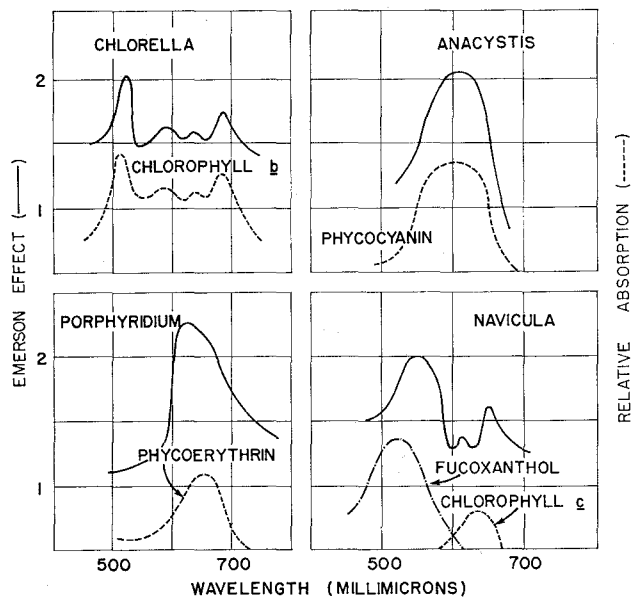

Fig. 7. Action spectra of the Emerson enhancement effect in Chlorella, Anacystis (a blue-green alga), Navicula (a diatom) and Porphyridium (solid curves). Absorption spectra of the accessory pigments are also shown by dashed curves (after R. Emerson and co-workers [47,51]).

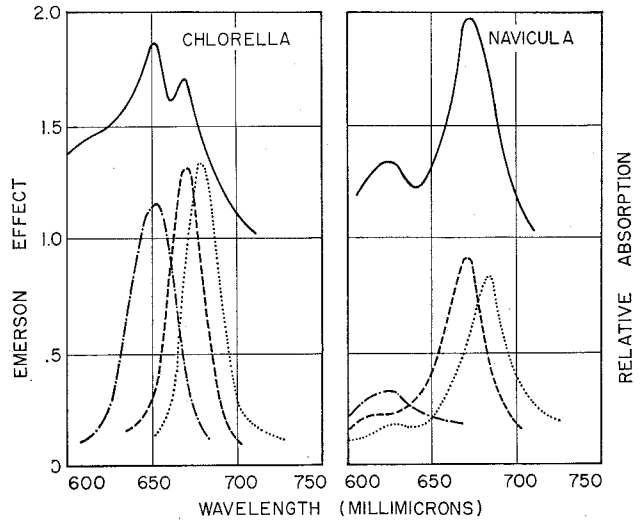

Fig. 8. Detailed action spectra of the Emerson enhancement effect in Chlorella and Navicula in 600 to 700 mμ range (solid curves). The absorption curves for chlorophyll *b* (peak at 650 mμ; dashes and dots), chlorophyll *c* (peak at 630 mμ; dashes and dots), chlorophyll *a* 670 (dashes) and chlorophyll *a* 680 (dots) are also shown (after Govindjee et al. [75,83,84] and Cederstrand et al. [32]).

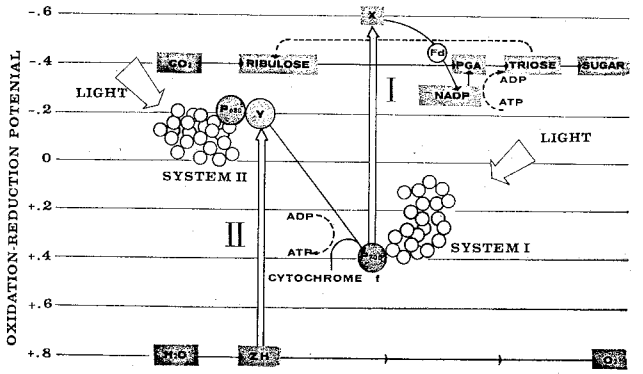

Fig. 9. The "uphill" hydrogen-atom transfer in photosynthesis. ZH and Y are, respectively, hypothetical primary hydrogen donor and acceptor for the light reaction II. P680 is the hypothetical energy trap of pigment system II. Cytochrome *f* and X are, respectively, the primary hydrogen donor and acceptor for the light reaction I. P700 is the energy trap of pigment system I. Fd stands for ferredoxin, ribulose for ribulose diphosphate, NADP for nicotinamide adenine dinucleotide phosphate, PGA for phosphoglyceric acid, triose for phosphoglyceraldehyde. The left-hand margin shows the oxidation reduction potential (E_o') of various intermediates (based on the original schemes of Hill and Bendall [88], Duysens and Amesz [42] and Kok and Hoch [108]).

and Rabinowitch (75,83,84,135) re-investigated the action spectra of the Emerson effect. Detailed measurements on Chlorella (a green alga) and Navicula (a diatom) showed that light absorbed in one form of chlorophyll *a*, "Chl *a* 670", also enhances photosynthesis in far-red light (Fig. 8). French et al. (64) independently observed the same chlorophyll *a* band in the action spectrum of the Emerson effect in Chlorella. These results led us to believe that for complete photosynthesis, two forms of chlorophyll *a*, Chl *a* 670 (a form that preferentially receives energy from accessory pigments) and Chl *a* 680, need to be simultaneously excited. This was a more satisfactory picture, since the high efficiency of energy transfer from accessory pigments to chlorophyll is taken into account. In red algae and blue-green algae, the Emerson enhancement effect shows a very small band at 670 mμ; often this band is absent. The distribution of Chl *a* 670 and Chl *a* 680 is not simple. Chl *a* 670 is preferentially present in pigment system II in Chlorella but almost all of Chl *a* 670 and Chl *a* 680 are present in the pigment system I of the phycobilin-containing algae (see ref. 32).

Myers and co-workers (92,126-129) and French and co-workers (59-63), working on the Emerson effect, also concluded that photosynthesis requires the cooperation of two light reactions that are sensitized by different pigment systems. Other groups of investigators have provided evidence for the operation of two light reactions and two pigment systems from measurements of: Emerson enhancement effect (9, 12, 15-17, 20, 55, 63, 67, 71, 76, 78, 79, 82, 87, 90, 91, 108, 120, 122, 132), transient oxygen effects (62, 159, 160), oxidation-reduction reactions of cytochromes (7, 42, 43, 88, 167, 168) of P700 (97, 98, 104, 105, 107, 140, 142, 143), quinones (1, 99, 163) and of plastocyanin (57, 94, 95, 110, 112) and of measurements of 520 mμ absorbancy change (56, 77, 139, 169), fluorescence (27, 30, 31, 40, 44, 80, 81, 86, 96, 113, 114, 116, 131, 138) and delayed emission (2, 8, 13, 72, 73), NADP reduction (89, 119), and phosphorylation (18, 54, 108, 148, 149). Research with physical separation of pigment systems (21, 30) and with mutants of algae (15, 117, 118) has confirmed the two light reactions-two pigment systems hypothesis.

Electron Pathways

A model of photosynthesis (electron transport) in which the two light reactions occur in a series was first proposed by Hill and Bendall (88). Independently, Duysens et al. (43), Kok and Hoch (108) Losada et al. (119), Kautsky et al. (96), and Witt et al. (167, 168) (also see Rumberg et al., 141) came to similar conclusions.

Photosynthesis is conceived of as a set of (at least) *five* reactions, two of which are the light reactions (I and II) and three are dark reactions (Fig. 9). Since, in the steady state, all reactions must operate simultaneously at the same rate, the numbering is arbitrary. We begin with reaction II (Duysens (43) terminology), the reaction most closely associated with O_2 evolution. The final result of this set of reactions is the oxidation of water to O_2 and the reduction of cytochromes. Light absorbed by accessory pigments (pigment system II; such as chlorophyll *b* in green plants, and phycobilins in red and blue-green algae) is ultimately transferred to hypothetical chlorophyll *a* molecules (P680), which are assumed to be in a favorable position to act as an "energy trap" (or "reaction center"). The primary light reaction is suggested to be an electron (or hydrogen atom) transfer from the unknown H-donor, ZH ($E_o' > +0.8$ V) to the unknown H-acceptor, Y ($E_o' \approx$ perhaps -0.2 V)[4] sensitized by excited P680:

$$(1) \quad ZH + Y + P680^* \longrightarrow Z + YH + P680.$$

[4] There is no evidence for Y having an E_o' of -0.2 V. We suggest this value for the sake of symmetry; in this way both light reactions (I & II) overcome a potential difference of 1.0 V.

The oxidation product, the strong oxident Z, being then utilized to evolve oxygen from water:

(2) $$2Z + H_2O \longrightarrow 1/2\ O_2 + 2ZH$$

The weak reductant (YH), which may be Duysens QH (44) or Kautsky's A (96) may react first with a plastoquinone (PQ) and then a *b* type cytochrome (Cb). The suggested path of electron transfer from YH to P700 (the energy trap of light reaction I) is:

(3) $$YH \rightarrow PQ \rightarrow Cb \rightarrow \text{cytochrome f} \rightarrow \text{Plastocyanin} \rightarrow P700$$
$$ADP \quad ATP$$

Enough energy is released in the "downhill" reaction from cytochrome of *b* type (Cyt. b_3) to cytochrome *f* that phosphorylation may be coupled with it. Recently, evidence has been found by Trebst (154), Wessels (164), and Avron (6) for such a coupling. The role of cytochrome *b* has not been definitely established and there is disgreement as to the position of plastocyanin (PC). Fork and co-workers (57, 112) have suggested that plastocyanin is before cytochrome *f* whereas the work of Levine and Gorman (118) on mutants of chlamydomonas suggests that plastocyanin is after cytochrome *f*.

The pigment system that sensitizes reaction I (system I) is mainly composed of Chl *a* 680 (Chl a_1) and P700. Light quanta directly absorbed by P700 molecules or transferred to them "send" the P700 molecules into an excited state (P700*). The primary light reaction is suggested to be a photo-oxidation of P700 ($E_{o'} = +0.4$ V) and a reduction of an unknown intermediate X ($E_{o'} \approx -0.6$ V);

(4) $$X + P700^* \rightarrow X^- + P700^+$$

The final result of the set of reactions (I) is the oxidation of cytochrome *f* (*i.e.*, production of a weak oxidant) and the reduction of NADP (production of a strong reductant). It has been recently suggested (5,165) that ferredoxin (Fd), previously known as "photosynthetic pyridine nucleotide reductase" (145), is the primary oxidant of light reaction I of photosynthesis. Ferredoxin has $E_{o'}$ of about −0.41 to −0.49 v. However, chloroplasts are capable of reducing externally added oxidants having oxidation-reduction potentials as low as −0.6 V (Kok et al., 111). It is now generally believed that NADP is reduced by a reaction of NADP with reduced X, via ferredoxin and NADP reductase (R) (see San Pietro and Black, 144).

The path of electrons from H_2O to CO_2 may then be summarized as follows:

(5) $$H_2O \rightarrow Z \rightarrow (P680?) \rightarrow Y(\text{or } Q) \rightarrow PQ \rightarrow Cb \rightarrow Cf \rightarrow PC \rightarrow$$
$$\downarrow O_2 \qquad \uparrow light_{II} \qquad ADP \quad ATP$$
$$(P700) \rightarrow X \rightarrow Fd \xrightarrow{(R)} NADP \rightarrow CO_2$$
$$\uparrow light_I \qquad (CH_2O)$$

Two products, ATP and reduced NADP, are needed for the reduction of CO_2 in the Calvin cycle (see Bassham, 10, 11; Calvin and Baasham 29; and Evans et al., 52 for a discussion of the path of carbon in photosynthesis). The hypothesis so far discussed suggests that reduced NADP is produced by a series of two light reactions, and ATP is obtained in a reaction that connects the two light reactions. (Evidence for "cyclic phosphorylation" has accumulated in recent years but we do not deal with it here.)

Alternate Hypotheses

An alternate hypothesis for two light reactions is the "parallel formulation" of Gaffron (67). In this hypothesis, the oxidents made by the two light reactions react with H_2O to evolve O_2 and the reductants made by the light reactions somehow cooperate to reduce (CO_2) to the (CH_2O) level. French and Fork (61) and Brody and Brody (25) have also proposed parallel formulations. Hoch and Owens (90) and more recently Govindjee et al. (81) have proposed hypotheses in which light reaction I makes high energy intermediates which are somehow used to evolve O_2 from H_2O or to reduce ferredoxin (Fig. 10).

Warburg (see Vennesland, 155) and, more recently, Arnon (5) have considered one light reaction hypothesis, but these authors have disregarded all the existing data obtained in the laboratories of other investigators in the last 10 years. Perhaps, other hypotheses can also be constructed. However, most of the available data — collected in the majority of the laboratories — favor the Hill-Bendall type hypothesis in which two light reactions occur in series (see 136).

SUMMARY

Photosynthesis is a unique process on earth, in which energy of sunlight is massively converted into chemical energy. (For a summary of events in time when plants are transferred from darkness to light, see Fig. 11.) All life draws upon this energy source.

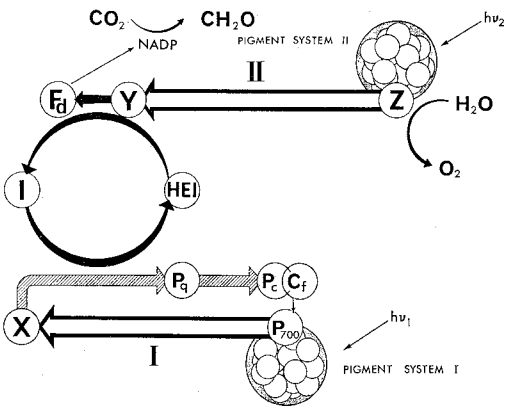

Fig. 10. Alternate model for the "uphill" transfer of hydrogen atoms in photosynthesis (after Govindjee et al. [81]). The main features of this scheme are: (1) the purpose of light reaction I (bottom part of figure) is the production of a high energy intermediate (HEI). Electron carriers such as cytochrome f (Cyt f), plastocyanin (P_c and plastoquinone (P_q), "X" and P_{700} are parts of this reaction sequence. (2) The "HEI" produced by light reaction I supplies energy for the reduction of ferredoxin (Fd) by reduced Y; Y being the primary electron acceptor in system II. Reduced Y is postulated to have a potential slightly less negative ($E_{o'} \sim -0.2$ V) than that of Fd; there is a deficiency in reductive power that is overcome by energy from HEI. (3) Light reaction II involves the oxidation of Z and the reduction of Y ($E_{o'}$ of Z $\approx +0.8$ V). (4) It is further suggested that a pool of "HEI" may exist and other energy requiring reactions in chloroplasts may also draw upon this pool.

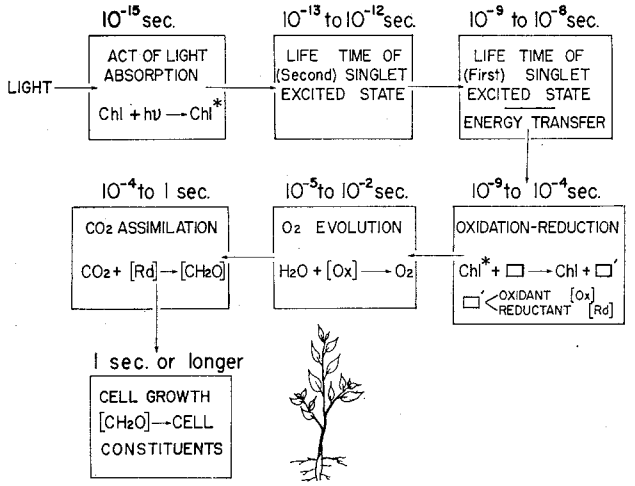

Fig. 11. A summary of events leading from light absorption to cell growth (10^{-15} sec to 1 sec) (based on a diagram by Kamen [93]).

Photosynthetic plants contain "photosynthetic units". Each unit is composed of approximately 200 to 300 pigment molecules (accessory pigments and chlorophyll *a*) and one reaction center (or energy trap). Light energy absorbed by any molecule in the photosynthetic unit is transferred to the "energy traps" (or reaction centers). At these centers, the primary reactions (oxidation-reduction reactions) occur; the light energy is converted to chemical energy.

Recent experiments, beginning with the discovery of the "Emerson enhancement effect", have led to a picture that suggests the operation of *two* light reactions in photosynthesis. In most popular hypotheses, these reactions occur in series. The light reaction II produces a strong oxidant which oxidizes H_2O to O_2 and a weak reductant. The light reaction I, however, produces a weak oxidant and a strong reductant that reduces NADP to $NADPH_2$. ATP formation is coupled to a reaction of the weak oxidant (made by light reaction I) and the weak reductant (made by light reaction II). Both $NADPH_2$ and ATP — the end products of the light reactions — are needed to reduce CO_2 to the carbohydrate (CH_2O) level.

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