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Historical corner

Dynamics of the history of photosynthesis research

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> *"Qu'on ne dise pas que je n'ai rien fait de nouveau ; la façon de présenter l'information est nouvelle."* Blaise Pascal

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Abstract

A personal view of the history of progress in photosynthesis research beginning in the seventeenth century and ending in 1992 is presented in a chart form. The 350-year time span is divided arbitrarily into seven periods by the "development junctures," which are likened to bamboo joints. The tempo of progress is reflected in the duration of the periods, starting from over 200 years for Period I, which progressively shortens in subsequent periods. This brief introduction highlights some of the events to show the dynamic nature of the progress in photosynthesis research.

1. The development junctures in the history of photosynthesis research

The history of photosynthesis research, as in other fields, has made many periodic, spectacular leaps – what we call "development junctures." Over the years, the progress of research seems to be gradual, but actually it is not as gradual as it seems. In the course of research, at some point or another, one often faces a "wall," beyond which nothing can be seen. At that point, transcending all the accepted ideas, some extraordinarily talented scholars begin to develop new experimental materials, procedures, and analytical methods, by which they break through the wall which had blocked further progress of research at the time. This leads to a "break through" by the efforts of the leading scholars who follow, and great progress is then made possible. As time goes by, another wall appears, and another group of talented scholars lead to another development. Thus, current understanding of photosynthesis has passed through many development junctures (which may be likened to the joints in bamboo).

To some of us, it may seem rather difficult or even impossible to divide the progress of photosynthesis research into several well-defined stages, considering its rapid developments in recent times encompassing many diverse areas. However, in order to fully understand the present stage of photosynthesis research, we need to comprehend what really led to certain discoveries; how much effort was behind a certain idea at the time it was presented; how subsequent research on that topic followed. Furthermore, it is very important to judge the impact of certain erroneous ideas; how they confused subsequent

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research for a while; and delayed the progress of the field.

With the above in mind, we present here several outstanding development junctures during the history of photosynthesis research and attempt to view the history of photosynthesis by dividing it, perhaps somewhat arbitrarily, into seven broad periods as the chart that follows this brief introduction shows.

2. Progress of photosynthesis research

2.1. Period I (From the beginning of the recognition of photosynthesis to *ca.* 1880)

This is the period when each element of photosynthesis, i.e. the nature of the components that are used as well as produced in the process, became established either by observations or by simple experiments. Thus the pioneering works during this period led to the generally accepted outline of photosynthesis. This period was culminated by the publication by the German scientist J. Sachs (1859-1862; I.18 [see ref. list]) of a treatise "Pflanzenphysiologie," that included discussions on the physiological aspects of photosynthesis. His work was followed up by his pupil W. Pfeffer (1874-1892; I.19), who also coined the term "photosynthetic assimilation."

2.2. Period II (*ca.* 1880 - *ca.* 1910)

The central figure in the research of this period was the English physiologist F. F. Blackman, who analyzed the relative rates of photosynthesis as affected by the various factors, and the interrelationships between them. He investigated in detail the relationship of the rate of photosynthesis and CO_2 concentration, light intensity, and temperature. As a result, he initiated the concept of a "limiting factor" (1905; II.2), which advocates that photosynthesis is not a simple photochemical reaction, but includes a reaction stage which does not require light. Later, this idea was tested by many researchers, the results were mixed, but in the end this theory was accepted.

Another trend during this period was the research on chlorophyll itself. Although it was recognized early (Dutrochet 1837; I.10) that chlorophyll was an important factor in photosynthesis, it was Willstätter and Stoll who attempted to explain the mechanism of photosynthesis through the various chemical characteristics of chlorophyll. Willstätter and Stoll published "*Untersuchungen über Chlorophyll*" (1913; II.3) and "*Untersuchungen über die Assimilation der Kohlensäure*" (1918; II.8), providing enormous amounts of information (both chemical and optical) on chlorophyll extracted from green leaves. However, in order to explain definitively and substantively the central role chlorophyll plays in photosynthesis, it is necessary to have knowledge on photosynthesis in other areas. This knowledge was lacking in those days. Thus, it was premature to study photosynthesis from the angle of chlorophyll chemistry alone.

Engelmann (1883; II.4) and Winogradsky (1887-1888; II.5) discovered photosynthetic bacteria, which have turned out to be important materials for current research in photosynthesis. During this period, we find an example of a misleading and erroneous hypothesis that was inspired by von Baeyer's research on formaldehyde (1864; II.9); many fruitless experiments were done in order to prove that formaldehyde was the initial carboxylation product formed in photosynthesis. This was a futile attempt and his hypothesis was later rejected by the experiment using carbon isotope ^{14}C.

2.3. Period III (*ca.* 1910 - *ca.* 1938)

Otto Warburg (October 8, 1883 - August 1, 1970) was the center of research activities during this period. Until his research, knowledge concerning the photosynthetic process was fragmented and mostly qualitative. Warburg perfected the manometer to enable the measurement of gas exchange accurately (1919-1920; III.2), and introduced the unicellular green alga, *Chlorella*, as a new experimental material. This alga is not only easy to cultivate but also easy to handle in large quantities. Moreover, unlike higher-plant leaves used in the past, there was no need to worry about the problem of opening and closing of the stomata or gas diffusion; it became an excellent and popular experimental material for photosynthesis research. Warburg also studied systematically and quantitatively the inhibition of photosynthesis by using various toxic chemicals, thus opening a way to analyze photosynthesis through its inhibition by known chemicals. However, because of his arrogance, he ignored some of the new information obtained by others. Sometimes, by presenting an erroneous theory, such as the unreasonably high quantum yield of photosynthesis, he disturbed the scientific world of his days, and even delayed the progress of the field. Nevertheless, in our opinion, he was a giant in photosynthesis research and made numerous contributions.

Warburg, using the new experimental material (*Chlorella*) and the new measuring method (manometry), pursued his research vigorously and confirmed the mechanism that photosynthesis consists of (1) a light reaction in which light participates directly, and (2) a dark reaction where light does not participate directly (1919-1920; III.2).

Influenced by his father, Emil Warburg, a scholar in optics, Otto Warburg was familiar with optical instruments, which he introduced effectively into the research of photosynthesis. He set up new measuring equipment and measured, for the first time, the maximum quantum yield of photosynthesis (1922-1923; III.3) and conducted flashing-light experiments (1919-1920; III.2). Later, many scholars worked in the areas pioneered by Warburg and established an important main stream of contemporary photosynthesis research. However, Warburg's extremely high quantum yield of photosynthesis were subsequently challenged by his own student Robert Emerson: the value is now settled as 0.12 in favor of Emerson (IV.5).

Another main stream of this period was the general formulation of photosynthesis advocated by van Niel (1929; III.9). He made good use of a suggestion by Thunberg (1923; III.10) that phosynthesis is a redox system involving CO_2 reduction and H_2O oxidation, and came up with the general equation for photosynthesis. In other words, the main function of photosynthesis is CO_2 reduction by hydrogen donors. The hydrogen donor may be different depending on the organism which performs the photosynthesis, but the process of CO_2 reduction is the same in all photosynthetic organisms:

In the case of plants and cyanobacteria (oxygenic):

$$CO_2 + 2\ H_2O + h\nu \rightarrow [CH_2O] + O_2 + H_2O$$

In the case of photosynthetic bacteria (anoxygenic):

$$CO_2 + 2\ H_2S + h\nu \rightarrow [CH_2O] + 2\ S + H_2O$$

or $CO_2 + 2\ H_2 + h\nu \rightarrow [CH_2O] + H_2O$

General equation for photosynthesis is then:

$$CO_2 + 2\ H_2A + h\nu \rightarrow [CH_2O] + 2\ A + H_2O$$

Although the concept of redox reactions was also provided by Wurmser (1925-1930; III.8), van Niel's work is clearly responsible for research on photosynthetic bacteria that followed this period (however, see Gest [1993] under III.9). The idea of van Niel was singularly responsible for the modern thinking on the mechanism of photosynthesis. Soon after the establishment of this unitary concept of photosynthesis by van Niel, the very important new concept of the "chlorophyll-containing photosynthetic unit" was advanced by Emerson and Arnold in 1932 (III.4). This concept continued to gain strength (Arnold and Kohn [1934; IV.7]; Gaffron and Wohl [1937; IV.8]; and Wohl [1937-1941; IV.8]).

2.4. Period IV (*ca.* 1938 - *ca.* 1954)

During this period many new streams sprang up in the history of photosynthesis research. One of them was the discovery of what we call the "Hill reaction" by Robin Hill (1937-1939;IV.24). Oxygenic photosynthesis takes place in chloroplasts of plant cells. However, in the suspensions of extracted (non-intact) chloroplasts obtained by grinding plant leaves, the ability to perform normal photosynthesis is lost although Jensen and Bassham later (1966; IV.33) succeeded in preparing active intact chloroplasts which can perform CO_2 fixation. Under the usual circumstances, the decomposition and complete reconstruction, which were very effective means for studying fermentation and respiration, could not be easily applied to photosynthesis research. However, Hill, by adding an oxidizing agent to the chloroplast preparation extracted from green leaves, found the photochemical oxygen-evolution reaction (1937-1939; IV.24) and thus a way into research in the biochemistry of chloroplast components and reactions. Later, many scholars pursued research in this direction by expanding the work on the Hill reaction.

Another major breakthrough was the introduction of the radio-isotope ^{14}C and much progress was made in the analysis of carbon assimilation in photosynthesis. Sam Ruben and coworkers had pioneered research in this direction (1939-1940; IV.30). They added CO_2 labeled with carbon isotope ^{11}C (half-life: 20.38 min.) to barley and found that plants have the ability to perform CO_2 fixation without light. After Ruben, Martin Kamen and others utillized the carbon isotope ^{14}C which has a long half-life (*ca.* 5730 years), remarkable progress was made in the analysis of the path of carbon in photosynthesis. The two major research groups in this field were the Berkeley group (Melvin Calvin, Andy Benson, James Bassham, and others; see IV.31) and the Chicago group (Hans Gaffron, Al Fager, and others; see IV.32).

During this period, the research areas opened up by Warburg became increasingly active. Robert Emerson and his group determined the relationship between the quantum yield of photosynthesis and the wavelength of light used (1943; IV.6); they discovered the "red drop" in photosynthesis: far red light, by itself, was ineffective in photosynthesis. This discovery was followed by Emerson's discovery, in Period V, of the "Enhancement effect" that led to the concept of two-light reactions in photosynthesis.

2.5. Period V (*ca.* 1954 - *ca.* 1968)

From about 1950, photosynthesis research methods became increasingly precise, and collaboration by plant physiologists and physicists with chemists became a commonplace. Biophysics and biochemistry led to an analysis of the mechanism of photosynthesis at the molecular level. This was a golden period for photosynthesis research.

A major achievement concerned the area of biophysics: the use of rapid light-induced difference absorption spectroscopy, *i.e.* through the introduction of improved experimental instruments utilizing the concepts of flash photolysis pioneered by Porter and Norris (Witt and coworkers [1955; V.31]; Kok and coworkers [1959; V.32]) and those dealing with steady-state light (Duysens 1952; IV.10). With these techniques, it became possible to trace small absorption changes of reacting species and to explore primary changes in reaction-center chlorophylls or bacteriochlorophylls (the discovery of P870 by Duysens [1952; IV.10] and Clayton [1963; VI.19]; and that of P700 by Kok and coworkers [1956;V.33]). Essentially, all intermediates (*e.g.*, cytochromes, quinones, etc.) could be fingerprinted by this difference absorption method.

Another major achievement concerned with biophysics was the introduction of the electron-paramagnetic-resonance technique which enables the detection of unpaired electrons produced by light excitation (Commoner and coworkers [1956; V.34]; Calvin and coworkers [1957-1962; V.20]). This technique, like absorption spectrophotometry, has many advantages: it is a non-invasive technique; it is possible to analyze organelles *in vivo*, without destructive effects. It demonstrated an absolute advantage in exploring a majority of intermediates (*e.g.*, reaction-center chlorophylls, semiquinones, iron-sulfur centers, *etc.*).

On the other hand, classical methods (*e.g.*, manometry) led to the discovery of the Emerson enhancement effect by Emerson and his group (1957; V.7). Hill and Bendall proposed the momentous Z-scheme of photosynthesis. The concept of the two photochemical systems was born, and the two-photosystem concept was immediately confirmed experimentally by several groups (Kok and Hoch [1959-1961; V.14]; Duysens *et al.* [1961; V.15]; and Witt *et al.* [1961; V.16]). Subsequently other explorations of the two photosystems, both by biochemical and biophysical methods, expanded photosynthesis research tremendously. Many important papers were published one after another: discovery of plastocyanin (Katoh, 1960; V.48); photosynthetic NADP$^+$ reduction (Arnon and coworkers (1951; IV.29); study of the rôle of cytochrome in photosynthesis (Duysens, [1955; V.49]; Chance and Nishimura [1960; V.50]); and the discovery of electron tunneling in bacterial cytochrome oxidation (DeVault and Chance, 1966; V.51).

Another pioneering contribution during this period was that by Al Frenkel (1954; V.44) and by Dan Arnon and coworkers (1954; V45), who independently discovered photophosphorylation. These findings were pivotal in the later studies on the mechanism of energy conversion in photosynthesis. A few years later, Mitchell proposed the "chemiosmotic hypothesis" (1961; V.46) to explain ATP formation in mitochondria and chloroplasts.

The field of fluorescence of chlorophyll prospered during this period. Following the discovery of quenching of photosystem-II fluorescence by photosystem-I light (Govindjee *et al.*, 1960; V.42), Duysens and Sweers (1963; V.43) proposed that electron acceptor Q, located between the two photosystems, was a quencher in its oxidized state, but not in its reduced state. The non-Q related chlorophyll-*a* fluorescence change was discovered in several laboratories during this period. Furthermore, the temperature dependence of emission spectra down to 4° K, analyzed by Cho and Govindjee (1966-1970; V.30), revealed the validity of Förster's theory (1948; IV.15) on resonance excitation energy transfer in photosynthesis.

Much progress was also made in the analysis of the carbon cycle, and, around 1954 Calvin and Benson established a general principle of the cycle (V.57). There followed the discovery of a new carbon pathway in C4 plants by Kortschak and coworkers (1965; V.60) and by Hatch, Slack, and Johnson (1967; V.61), and research in this area made excellent progress.

Although research using electron microscopy began in the early 1940's, continued refinements (Steinmann, [1952; IV.3], Frey-Wyssling [1953; IV.4], and Menke [1962, 1965; V.6]) and development of new techniques such as negative staining (Brenner and Horne, 1959; V.4), and the freeze-etch technique (Moor, Mühlethaler, Waldner and Frey-Wyssling (1961; V.5) provided a detailed and beautiful picture of what we know today about the structure of thylakoids from higher plants, cyanobacteria and photosynthetic bacteria.

2.6. Period VI (*ca.* 1968 - *ca.* 1980)

After going over the various periods, we notice a rather interesting point. As the years pass, the intervals of the development junctures spanning the periods in this history chart that follows become increasingly shorter. This means the progress of learning has become faster and at the same time it suggests that the events marking the development junctures are inevitable. Viewed from the juncture around 1968, it is also clear that photosynthesis research has stepped into the molecular domain.

An example of the effect of the development of the techniques of flash-kinetic spectrophotometry and the EPR spectroscopy is the remarkable results produced in this period. This started with the discovery of P680 [1969; VI.28] and X320 (Q_A) [1968; VI.29] by Witt and coworkers, followed by the discovery of P430 (Hiyama and Ke [1971; VI.35]), the discovery of photosystem-I iron-sulfur centers (Malkin and Bearden [1971; VI.36]); and the discovery of electron acceptor A_2 (FeS-X) by McIntosh *et al.* (1975; VI.37). Thus the molecular species involved in the photochemical reactions in photosynthesis became clear.

As mentioned earlier, the discovery of the Emerson enhancement effect led to the idea of the existence of two photochemical systems in photosynthesis. Combining this idea with the concept of the "photosynthetic unit," another major progress was seen in the substantive analysis of the relationship between the structure and function in photosynthetic systems. The "photosynthetic unit," a rather statistical and vague concept, could now be looked upon as real pigment-protein complexes. The research in this direction includes: the attempt to separate subchloroplast particles representing the two photosystems (Wessels [1962; V.10]; Boardman and Anderson [1964; V.11]; and Vernon and coworkers [1965; V.12]); the electrophoretic separation of the pigment-protein complexes by Ogawa, Obata and Shibata (1966; V.17) and by Thornber and coworkers (1966; V.18); separation and reconstitution of photosystem-I and -II particles (Huzisige and coworkers [1969; VI.8]; Briantais [1969; VI.9]; and later by Ke and Shaw [1972]; and by Lam and Malkin [1982] (see under VI.9).

The pioneering work on the isolation and characterization of the bacterial reaction center by Reed and Clayton [1969; VI.19] ushered in a new period of new and exciting developments.

In the field of analysis of photosynthetic oxygen evolution, which had been lagging in progress, new advances also began to appear. The important achievements were the discovery of a period-of-four change in oxygen evolution, in a series of light flashes, and the advocacy of the linear four-step mechanism for photosynthetic oxygen evolution (Joliot and coworkers [1968-1969; VI.40]; Kok and coworkers [1970; VI.41]). It became clear that four oxidizing equivalents accumulate on a charge accumulator before water is oxidized to O_2 and protons. Later, this accumulator was shown to be in a manganese complex.

The mechanism of energy transformation was analyzed in depth during this period and spectacular results were obtained: manifestation of membrane potential as electrochromic band shifts (Junge and Witt [1968; VI.50]; Jackson and Crofts [1969; V.51]); the role of ubiquinone in cyclic photophosphorylation in photosynthetic bacteria was observed (Horio and coworkers [1968; VI.49]). Another important development was the discovery of the two-electron gate at the quinone site, first in photosystem II (Bouges-Bocquet [1973; VI.44]; Velthuys and Amesz [1974 VI.45]) and then in photosynthetic bacteria (Vermeglio and Clayton [1977; VI.46] and Wraight [1977; VI.47]).

On another front, there was much progress in the direction of genetic analysis of photosynthetic systems: namely, the identification of the nuclear gene for LHCII (Kung, Thornber and Wildman [1972]; VI.1); isolation and sequencing, respectively, of the psbA gene for the Q_B (D1) protein by Bedbrook *et al.* (1978; VI.2) and Zurawski et al. (1982; VI.3), and sequencing of the RuBPCase gene by McIntosh *et al.* (1980; VI.4).

2.7. Period VII (ca. 1980 - present)

In 1985, Fish, Kück and Bogorad found two genes (psaA and psaB) which encode the high-molecular-weight polypeptides in the P700-containing heterodimer of photosystem I (VII.1). Similar discoveries soon followed for a number of higher plants, eukaryotic algae and cyanobacteria (VII.2). The knowledge thus derived on the amino acid sequences of the psaA and psaB gene products had a tremendous impact on the studies of structure and function of the P700 complex. The recent avalanche of works on the structure and function of various systems (*e.g.*, see VII.25-28) through site-directed mutagenesis have added truly exciting new areas of research in photosynthesis.

Another trigger for explosive advances was a major breakthrough in the structure of the reaction center by X-ray crystallography, using crystals obtained from the purple non-sulfur bacterium *Rhodopseudomonas viridis*, by Deisenhofer, Michel, Huber and coworkers [1983; VII.13]; and subsequently by Norris, Schiffer and coworkers [1986]; and by Feher and coworkers [1986] for *Rhodobacter sphaeroides* (see under VII.13). Stimulated by this work, active research on similar structural analysis followed with other photosynthetic complexes: Kühlbrandt and Wang

(1991; VII.12) on the electron crystallographic analysis of the light-harvesting Chl *a/b* protein; and Witt and coworkers (1987; VII.14) and Ford and coworkers (1987; VII.15) and more recently by Almog *et al.* (1991; see under VII.15) on the photosystem-I reaction-center complex. Exciting new results on the crystal structure of photosystem-II reaction-center complexes have already begun to appear (VII.43). It is apparent that results from crystal-structure analysis and molecular biology have a huge synergistic impact on our understanding of the structure-function relationship in the photosynthetic apparatus.

Another development is the progress in the analysis of photosystem II: the field was renewed by the isolation of the oxygen-evolving photosystem-II subchloroplast particles by Berthold, Babcock and Yocum in 1981 [VII.5], followed by the isolation of the photosystem-II core complex (Tang and Ki. Satoh [1985;VII.6]; Ka. Satoh, Ohno and Katoh [1985; VII.7], and finally the isolation of the photosystem-II reaction-center complex D1-D2-cyt-*b559* (Nanba and Satoh [1987; VII.8]), and the demonstration of a similarity as well as differences in structure between photosystem-II and purple photosynthetic bacteria. An extension of this work will greatly advance our understanding of the mechanism of photosynthesis.

The analysis of the charge accumulator in oxygen evolution, mentioned above, also has made progress: EPR signal of the S_2-state (Dismukes and Siderer [1980; VII.23] and others [see under VII.23]) and the S_3-state (Boussac and coworkers [1989; VII.24]); absorbance changes associated with the S-state changes (Brettel, Schlodder, Witt and coworkers [1984; VII.29]; Dekker, van Gorkom and coworkers [1984; VII.30]); involvement of amino acids in the oxygen evolution enzyme (Barry, Babcock *et al.* [1987; VII.25]; Debus and coworkers [VII.26]; Boussac, Rutherford and coworkers [1989; VII.24]).

At the present moment, the following seven areas form the goal of future photosynthesis research:

(1) Genetic information and its relevance to the biosynthesis, structure, and function of the photosynthetic apparatus;
(2) Structure and function of the reaction centers;
(3) Regulation and mechanism of energy transfer;
(4) Regulation and mechanism of electron transfer;
(5) Regulation and mechanism of oxygen evolution;
(6) Mechanism of photophosphorylation; and
(7) Regulation and mechanism of carbon dioxide assimilation.

Towards these goals, various research workers, trained in diverse areas, are collaborating with each other and proceeding to form a huge network world wide, aiming at the final target of integrating information so that the mechanism of photosynthesis may be understood at the molecular as well as organismic levels.

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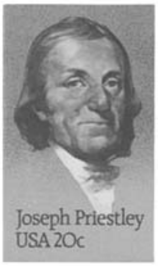
PERIOD I [- *ca.* 1880]

- Rejection of the Aristotelian dogma that plants derive nourishment from the soil - van Helmont (1648) [1]
- Recognition that plants obtain nourishment from the atmosphere through the leaves - Mariotte (1679) [2]; Hales (1727) [3]
- Observation of the emission of gas bubbles by a submerged illuminated leaf - Bonnet (1754) [4]
- Discovery of the evolution of oxygen by plants - Priestley (1772) [5]
- Discovery of the rôle of light and green color in plant photosynthesis - Ingenhousz (1779) [6]
- "Fixed air" (CO_2) is involved in photosynthesis - Ingenhousz (1798) [7]; Senebier (1782) [8]
- Naming the green-plant pigment "chlorophyll" - Pelletier-Caventou (1818) [9]
- Recognition of the need for chlorophyll in plant photosynthesis - Dutrochet (1837) [10]
- Discovery of chloroplasts in plant cells - von Mohl (1844) [11]
- Proposal that plants convert light energy into chemical energy - Mayer (1845) [12]
- Rejection of the idea that plants are nourished by absorbing humus and water from the soil - De Saussure (1804) [13]; Liebig (1840) [14]
- Development of methods for growing plants in sand with nutrient solutions - Sachs (1853) [15]; Knop (1860-1865) [16]
- Measurement of the "photosynthetic quotient" - Boussingault (1864) [17]

Joseph Priestley



1733-1804

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- Conclusion on the basic factors in photosynthesis;
- Recognition of the essential function of chlorophyll;
- Verification that starch is a product formed by photosynthesis;
- Sachs (1859-1862) [18]; Pfeffer (1874-1892) [19]
- Proposed the use of the term "photosynthesis" - Barnes (1893) [20]

PERIOD II [1880-1910]	PERIOD III [*ca.* 1910 - *ca.* 1938]

Observation of the chloroplast grana - Meyer (1882) [1]

Isolation of chloroplasts - Granick (1938) [1]

Recognition of the interrelationship between various parameters; Concept of limiting factors - Blackman (1905) [2]

- Quantitative manometry;
- Utilization of new experimental material (*Chlorella*);
- Use of inhibitors;
- Confirmation of light and dark reactions;
- Utilization of photochemical apparatus - Warburg (1911-1920) [2]

First determination of the quantum yield of photosynthesis - Warburg-Negelein (1922-1923) [3]

First flash experiments - Warburg (1919-1920) [2]

Concept of photosynthetic unit - Emerson-Arnold (1932) [4]

Structure of chlorophyll and identity of chlorophyll from different species - Willstätter-Stoll (1906-1926) [3]

First attempt on chlorophyll synthesis - Fischer (1926-1945) [5]

Concept of a chlorophyll-protein complex - "Chloroplastinsymplex - Stoll (1936) [6]

Parallel measurement of fluorescence and carbon dioxide assimilation - Kautsky *et al.* (1931) [7]

Richard Martin Willstätter

1872-1942

Otto Heinrich Warburg

1883-1970

Cornelis Bernardus van Niel

1897-1985

Discovery of photosynthetic bacteria - Engelmann (1883) [4]; Winogradsky (1887) [5]

Interpretation of the primary photochemistry of photosynthesis as a light-induced oxido-reduction process - Wurmser (1925, 1930) [8]; van Niel (1929) [9]

Recognition that photosynthesis occurs inside the chloroplasts; confirmation of the effectiveness of light absorbed by chlorophyll - Engelmann (1881-1882) [6]

Molisch reaction - Molisch (1896) [7]

PERIOD IV [*ca.* 1938 - *ca.* 1954]

Early electron-microscope study of chloroplasts - Kausche-Ruska (1940) [1]; Granick-Porter (1947) [2]

Electron microscopy of chloroplast structure - Steinmann (1952) [3]; Frey-Wyssling - Steinmann (1953) [4]

The quantum-yield controversy - Warburg-Emerson (1939-1951) [5]

Dependence of quantum yield on wavelength; discovery of "red drop" - Emerson-Lewis (1943) [6]

Chlorophyll-containing photosynthetic unit - Arnold-Kohn (1934) [7]; Gaffron-Wohl (1936-1941) [8]

Size limit for active chloroplasts - Thomas-Blaauw-Duysens (1953) [9]

Discovery of P870 - Duysens (1952) [10]

Evidence that chlorophyll was bound to proteins - Smith (1938) [11]

Crystallization of chlorophyll lipoprotein - Takashima (1952) [12]

Crystallization of chlorophylls - Jacobs *et al.* (1953) [13]

Parallel measurement of fluorescence and photosynthesis - McAlister-Myers (1940) [14]

Energy transfer between pigment molecules - Förster (1948) [15]; Dutton *et al.* (1943) [16]; Duysens (1952) [10]; French-Young (1952) [17]

Discovery of delayed light emission - Strehler-Arnold (1951) [18]

Robert (Robin) Hill

1899-1991

Robert Emerson

1903-1959

Introduced difference spectrophotometry - Duysens (1952) [10]

Rôle of Mn in photosynthesis - Pirson (1937) [19]

Hydrogen adaptation in photosynthesis - Gaffron (1940) [20]

Oxygen in photosynthesis originates in water - Ruben *et al.* (1941) [21]

Concept of the high-energy phosphate bond - Lipmann (1941) [22]

First idea of a proton gradient - Lundegårdh (1946) [23]

Discovery of the Hill reaction - Hill (1937-1939) [24]

Discovery of cytochrome *f* - Hill *et al.* (1951-1952) [25]

Discovery of the Mehler reaction - Mehler (1951) [26]

Photochemical reaction of NADP$^+$- Vishniac-Ochoa; Tolmach; Arnon *et al.* (1951) [27,28,29]

Tracing the path of carbon in photosynthesis using radio carbon - Ruben-Kamen-Hassid-DeVault (1939-1940) [30]

The path of carbon in photosynthesis - Calvin-Benson et al. (1945-1954) [31]; Gaffron et al. (1945-1951) [32]

PERIOD V [*ca.* 1954 - *ca.* 1968]

Development of negative staining - Brenner-Horne (1959) [4]

Development of the freeze-etch technique - Moor-Mühlethaler-Waldner - Frey-Wyssling (1961) [5]

Chloroplast structure - Menke *et al.* (1962) [6]

Discovery of chloroplast DNA - Ris-Plout (1962) [1]; Chun *et al.* (1963) [2]; Sager-Ishida (1963) [3]

Discovery of the Emerson enhancement effect - Emerson and coworkers (1956-1960) [7]

Proposal of the Z scheme - Hill-Bendall (1960) [9]

Separation of photosystem-I and -II particles - Wessels (1962) [10]; Boardman-Anderson (1964) [11]; Vernon and coworkers (1965) [12]

Isolation of P700-Chl *a* protein complex - Thornber *et al.* (1969) [13]

Discovery of the "chromatic transient" - Blinks (1957) [8]

Evidence for two-light reactions - Kok-Hoch (1959-1961) [14]; Duysens (1961) [15]; Witt-Müller-Rumberg (1961) [16]

Electrophoretic separation of the pigment-protein complexes - Ogawa-Obata-Shibata (1966) [17]; Thornber-Smith-Bailey (1966) [18]

Crystallization of a BChl *a*-protein - Olson *et al.* (1969) [19]

EPR signal of oxidized P870 Sogo, Calvin *et al.* (1957-1959) [20]

Reversible bleaching of P870 at 1° K - Arnold-Clayton (1960) [21]

Synthesis of chlorophyll *a* - Woodward and coworkers (1956-1960) [22]

Preparation of a water-soluble chlorophyll-protein - Yakushiji *et al.* (1963) [23]

Photochemical reactions of chlorophyll and pheophytin - Krasnovsky-Voynovskaya (1951) [24]; Evstigneev-Gavrilova (1954) [25]

Different "forms" of chlorophyll - Albers-Knorr (1937) [26]; French *et al.* (1957) [27]; Litvin-Krasnovsky (1957) [28]

Relationship between fluorescence and energy transfer - Murata-Nishimura-Takamiya (1966) [29]

Temperature dependence of energy transfer - Cho-Govindjee (1966-1970) [30]

Development of flash kinetic spectrophotometry - Witt (1955) [31]; Kok (1959) [32]

Bessel Kok

1918-1979

Discovery of P700 - Kok (1956) [33]

Application of the EPR technique to photosynthesis studies - Commoner *et al.* (1956) [34]

Analysis of oxygen evolution using flash illumination - Allen-Franck (1955) [35]; Whittingham-Brown (1958) [36]

Mn functions in photosystem II - Kessler *et al* (1957) [37]

Discovery that Hill reaction is influenced by CO_2 - Warburg-Krippahl (1958, 1960) [38]

Discovery of ubiquinone - Morton (1956) [39]; Green *et al.* (1956) [40]

Discovery of plastoquinone - Crane (1959) [41]

Quenching of photosystem-II fluorescence by photosystem-I light - Govindjee *et al.* (1960) [42]

Proposal that Q is the photosystem-II primary electron acceptor - Duysens-Sweers (1963) [43]

Discovery of photophosphorylation in chromatophores - Frenkel (1954) [44]

Photophosphorylation in chloroplasts - Arnon *et al.* (1954) [45]

Chemiosmotic theory - Mitchell (1961) [46]

Peter Denis Mitchell

1920-1992

pH-gradient-induced ATP synthesis - Jagendorf-Uribe (1966) [47]

Discovery of plastocyanin - Katoh (1960) [48]

Analysis of cytochrome photooxidation - Duysens (1955) [49]; Chance-Nishimura (1960) [50]

Discovery of electron tunneling in bacterial cytochrome oxidation - DeVault-Chance (1966) [51]

Discovery of the methemoglobin reducing factor - Davenport *et al.* (1952) [52]

Discovery of PPNR - San Pietro-Lang (1956) [53]

Discovery of ferredoxin - Mortenson *et al.* (1962) [54]; Tagawa-Arnon (1962) [55]

Study of ferredoxin-$NADP^+$-reductase - Shin-Tagawa-Arnon (1963) [56]

Calvin-Benson-Bassham cycle - Calvin-Bassham (1954) [57]

Photoactivation of RuBPCase- Bassham and coworkers (1966) [58]

Discovery of the Kortschak-Hatch-Slack pathway - Kortschak *et al.* (1965) [60]; Hatch-Slack-Johnson (1966) [61]

Discovery of photorespiration - Decker (1955) [59]

PERIOD VI [*ca.* 1968 - *ca.* 1980]

Nuclear gene for LHCII identified - Kung-Thornber-Wildman (1972) [1]

psbA gene for Q_B protein (D1) isolated - Bedbrook *et al.* (1978) [2]; sequenced - Zurawski *et al.* (1982) [3]

RuBPCase gene sequenced - McIntosh *et al.* (1980) [4]

Model for the photosynthetic membrane - Miller *et al.* ; Staehelin *et al.* (1976-77) [5,6]

Lateral asymmetry in thylakoid membrane - Andersson-Anderson (1980) [7]

Separation and reconstitution of photosystem-I and -II particles - Huzisige *et al.* (1969) [8]; Briantais (1969) [9]

Separation and analysis of photosystem-II subchloroplast particles - Huzisige (1972) [10]; Satoh-Butler (1978) [11]

Isolation of the oxygen-evolving photosystem-II particles from thermophilic cyanobacteria - Stewart-Bendall (1979) [12]; and from red alga - Gantt- Clement-Montral (1983) [13]

Photosystem II heterogeneity - Melis-Homann (1975-1976) [14]

Discovery of phycobilisomes - Gantt (1969) [15]

Isolation of the light-harvesting Chl *a/b* protein - Thornber *et al.* (1971) [16]

X-ray crystallography of a BChl *a*-protein - Fenna-Mathews (1976) [17]

Discovery of chlorosomes - Staehelin *et al.* (1978) [18]

Isolation and analysis of the bacterial reaction center - Reed-Clayton (1969) [19]

Subunit structure of the bacterial reaction center - Okamura-Steiner-Feher (1974) [20]

Discovery of BPheo as the intermediary electron acceptor in photosynthetic bacteria - Dutton *et al.* (1975) [21]; Fajer *et al.* (1975) [22]; Parson and coworkers (1975) [23]; Shuvalov-Klimov (1976) [24]; van Grondelle *et al.* (1976) [25]

Split EPR signal of BPheo·$Fe^{2+}Q_A^-$ Leigh-Dutton (1972) [26]; Feher *et al.* (1974) [27]

Discovery of P680 and X320 - Döring, Witt and coworkers (1969) [28]; Stiehl-Witt (1968) [29]

Discovery that P680 is a quencher of Chl *a* fluorescence - Butler (1972) [30]; Mauzerall (1972) [31]

Discovery of the photosystem-II primary electron acceptor — pheophytin - Klimov *et al.* (1970) [32]

Split EPR signal of Pheo·$Fe^{2+}Q_A^-$ Klimov *et al.* (1980) [33]

Primary electron donor P700 is a "special pair" - Norris-Katz and coworkers (1971-79) [34]

Discovery of P430 (FeS-A/B) - Hiyama-Ke (1971) [35]

Discovery of photosystem-I iron-sulfur centers FeS-A/B - Malkin-Bearden (1971) [36]

Discovery of the electron acceptor FeS-X - McIntosh-Chu-Bolton (1975) [37]

EPR signal II_{vf} attributed to electron donor to $P680^+$ Blankenship-Babcock-Warden-Sauer (1975-1976) [38]

Loss of oxygen-evolution activity correlated with loss of Mn - Cheniae-Martin (1966) [39]

The linear four-step mechanism for photosynthetic oxygen evolution - Joliot *et al.* (1968-1969) [40]; Kok *et al.* (1970) [41]

Relation of thermoluminescence to the "oxygen clock" - Inoue *et al.* (1976) [42]

Tris inactivation of photosystem II and its reactivation - Yamashita-Butler (1968) [43]

Two-electron gate on the acceptor side of photosystem II - Bouges-Bocquet (1973) [44]; Velthuys-Amesz (1974) [45]

Two-electron gate in photosynthetic bacteria - Vermeglio (1977) [46]; Wraight (1977) [47]

CO_2-effect of Warburg is located at the two-electron gate of photosystem II - Govindjee and coworkers (1975, 1976) [48]

Rôle of ubiquinone in cyclic photophosphorylation in photosynthetic bacteria - Horio *et al.* (1968) [49]

Membrane potential and the electrochromic band shift - Junge-Witt (1968) [50]; Jackson-Crofts (1969) [51]

Photooxidation of cytochrome *b559* - Knaff-Arnon (1969) [52]

Isolation of cytochrome b_6f complex - Nelson-Neumann (1972) [53]; Hurt-Hauska (1981) [54]

Rieske Fe_2S_2 in photosynthetic bacteria and chloroplasts - Prince *et al.* (1975) [55]; Malkin-Aparicio (1975) [56]

Q-cycle - Mitchell (1976) [57]

Crystal structure of plastocyanin - Colman *et al.* (1978) [58]

Superoxide formation and dismutation - Asada-Kiso (1973) [59]

Rôle of thioredoxin (Td) and Fd-Td-reductase - Buchanan *et al.* (1967-1976) [60]

Crystal structure of thioredoxin - Holmgren *et al.* (1975) [61]

RuBPCase subunit structure and biosynthesis - Kawashima-Wildman (1968) [62]

Regulation of carbon metabolsim - Miyachi and coworkers (1970) [63]

Carboxylase/oxidase functions of Rubisco - Bowes-Ogren-Hageman (1971) [64]

Regulation mechanism of the Kortschak-Hatch-Slack cycle - Hatch-Slack (1969 review) [65]

Carbon isotope discrimination in photosynthesis - Smith-Epstein (1971) [66]

Discovery of the peroxisomes - Tolbert *et al.* (1968) [67]

PERIOD VII [*ca.* 1980 -]

psaA/psaB genes for P700-protein (maize) characterized - Fish-Kück-Bogorad (1985) [1]; and others [2]

Leucine-zipper motif in the psaA/psaB heterodimer - Webber-Malkin (1990) [3]; Kössel *et al.* (1990) [4]

Isolation of oxygen-evolving photosystem-II particles from spinach - Berthold-Babcock-Yocum (1981) [5]

Isolation of the oxygen-evolving photosystem-II core complex - Tang-Satoh (1985) [6]; Satoh-Ohno-Katoh (1985) [7]

Isolation of the *D1-D2-Cyt-b559* complex - Nanba-Satoh (1987) [8]

PSI/PSII stoichiometry - Melis *et al.* (1988) [9]; Graan-Ort-Whitmarsh (1986-1990) [10]

Reversible phosphorylation of LHC and regulation of excitation-energy distribution - Bennett-Arntzen-Steinback-Allen *et al.* (1977-1981) [11]

Electron crystallographic analysis of the light-harvesting Chl *a/b*-protein complex - Kühlbrandt-Wang (1991) [12]

X-ray structural analysis of the bacterial reaction center - Deisenhofer-Michel-Huber (1982) [13]

Crystallization of the photosystem-I reaction-center complex - Witt *et al.* (1987-1993) [14]; Ford *et al.* (1987) [15]

Picosecond measurement of charge separation in photosystem II - Wasielewski and coworkers (1989) [16]

P700 chlorophyll may be chlorophyll a' (?)- Watanabe and coworkers (1985) [17]

Identification of the electron acceptor A_1 - Brettel *et al.* (1986) [18]; Mansfield-Evans (1986) [19]; Ikegami and coworkers (1987) [20]; Biggins-Mathis (1988) [21];

Resolution and reconstitution of PSI protein subunits - Golbeck-Bryant and coworkers (1990-1992) [22]

EPR signal of the S_2-state - Dismukes-Siderer (1980) [23]

EPR of the S_3-state - Bousaac *et al.* (1989) [24]

Tyrosine is the electron donor Z - Barry-Babcock (1987) [25]

Tyr-161 (-160) is Z (D) (electron donor) to $P680^+$ Debus *et al.* (1988) [26]; Metz *et al.* (1989) [27]; Vermaas *et al.* (1988) [28]

Absorbance changes associated with S-state changes - Brettel-Schlodder-Witt (1984) [29]; Dekker-van Gorkom *et al.* (1984) [30]

Manganese involvement in photosynthetic oxygen evolution measured by EXAFS - Klein, Sauer and coworkers (1984) [31]

Interpretation of thermo-luminescence - DeVault *et al.* (1989) [32]

Herbicide inhibits photosystem by displacing Q_B - Velthuys (1981) [33]; Wraight (1981) [34]

Isolation of *Cyt-bc₁* complex - Gabellini *et al.* (1982) [35]

Isolation of genes of the *Cyt-bc₁* and *Cyt-b₆f* complexes - Daldal *et al.* (1987) [36]; Hauska *et al.* (1988) [37]

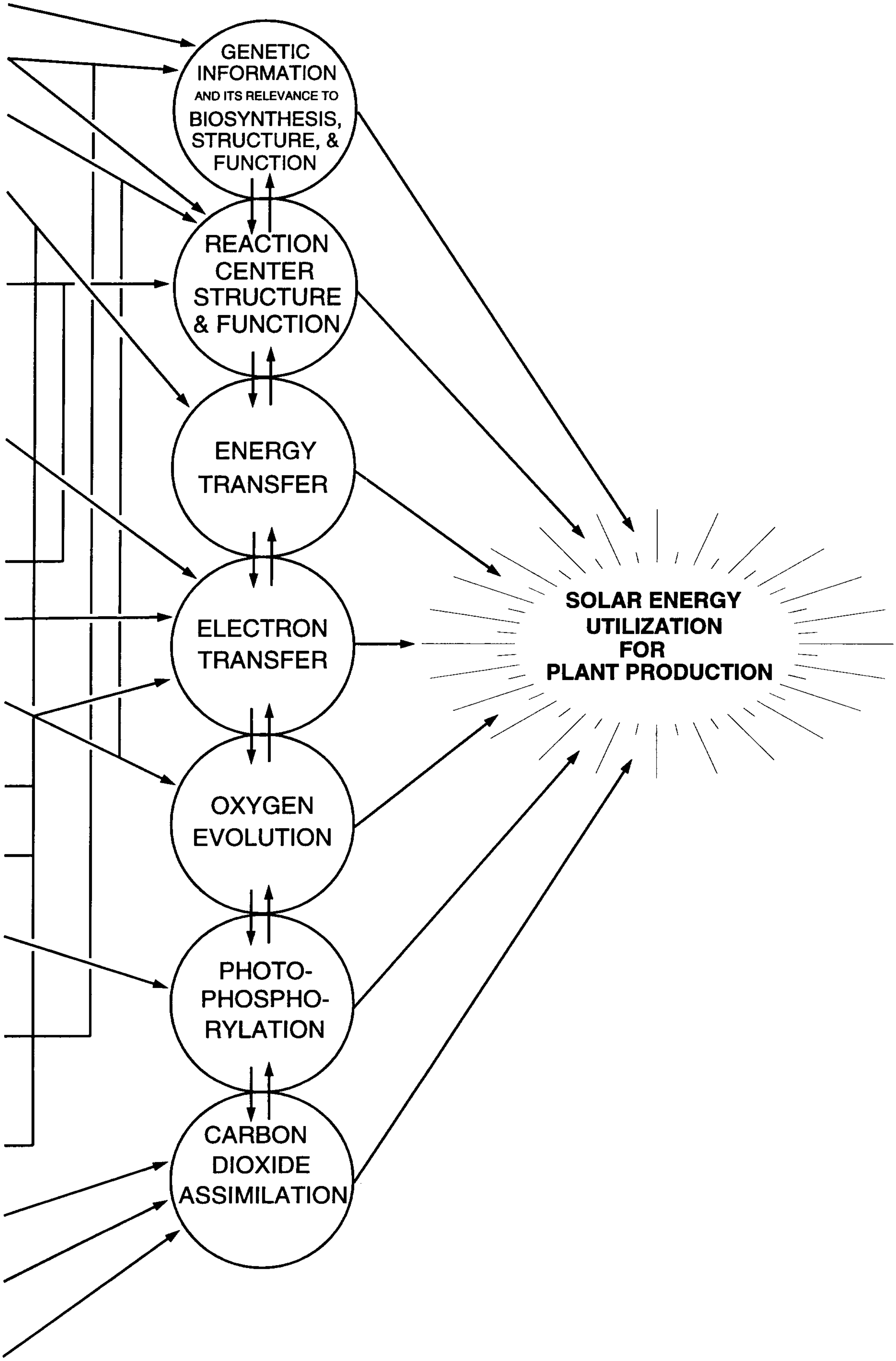
Preparation and characterization of site-directed mutants of the *Cyt-bc₁* complex - Daldal and coworkers (1992) [38]

Crystal structure of Fd-$NADP^+$-reductase - Karplus *et al.* (1988) [39]

Discovery of activase - Salvucci *et al.* (1985) [40]

3-dimensional structure of Rubisco from *Rsp rubrum* - Schneider-Lindqvist-Brändén-Lorimer (1986) [41]

Carbon isotope discrimination correlates with water-use efficiency - Farquhar-Richards (1984) [42]


GENETIC INFORMATION AND ITS RELEVANCE TO BIOSYNTHESIS, STRUCTURE, & FUNCTION
REACTION CENTER STRUCTURE & FUNCTION
ENERGY TRANSFER
ELECTRON TRANSFER
OXYGEN EVOLUTION
PHOTO-PHOSPHORYLATION
CARBON DIOXIDE ASSIMILATION
SOLAR ENERGY UTILIZATION FOR PLANT PRODUCTION

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