Scaling from the Past to the Present
Photosynthesis in a Historical Context

Govindjee
Department of Biochemistry, Department of Plant Biology and Center of Bophysics & Computational Biology, University of Illinois at Urbana-Champaign, Urbana, Illinois, USA
E-mail: gov@illinois.edu
URL: <http://www.life.illinois.edu/govindjee>

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A travel through history

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Selected Nobel laureates

- **Richard Wilstätter (1915)**
- James Franck (1925)
- **Hans Fischer (1930)**
- **Otto Warburg (1931)**
- Paul Karrer (1937)
- Richard Kühn (1938)
- Severo Ochoa (1959)
- **Melvin Calvin (1961)**
- **Robert Woodward (1965)**

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Selected Nobel laureates

- George Porter (1967)
- James Norrish (1967)
- Peter Mitchel (1978)
- Johannes Deisenhofer (1988)
- Hartmut Michel (1988)
- Robert Huber (1988)
- Rudolph Marcus (1992)
- Paul Boyer (1997)
- John Walker (1997)

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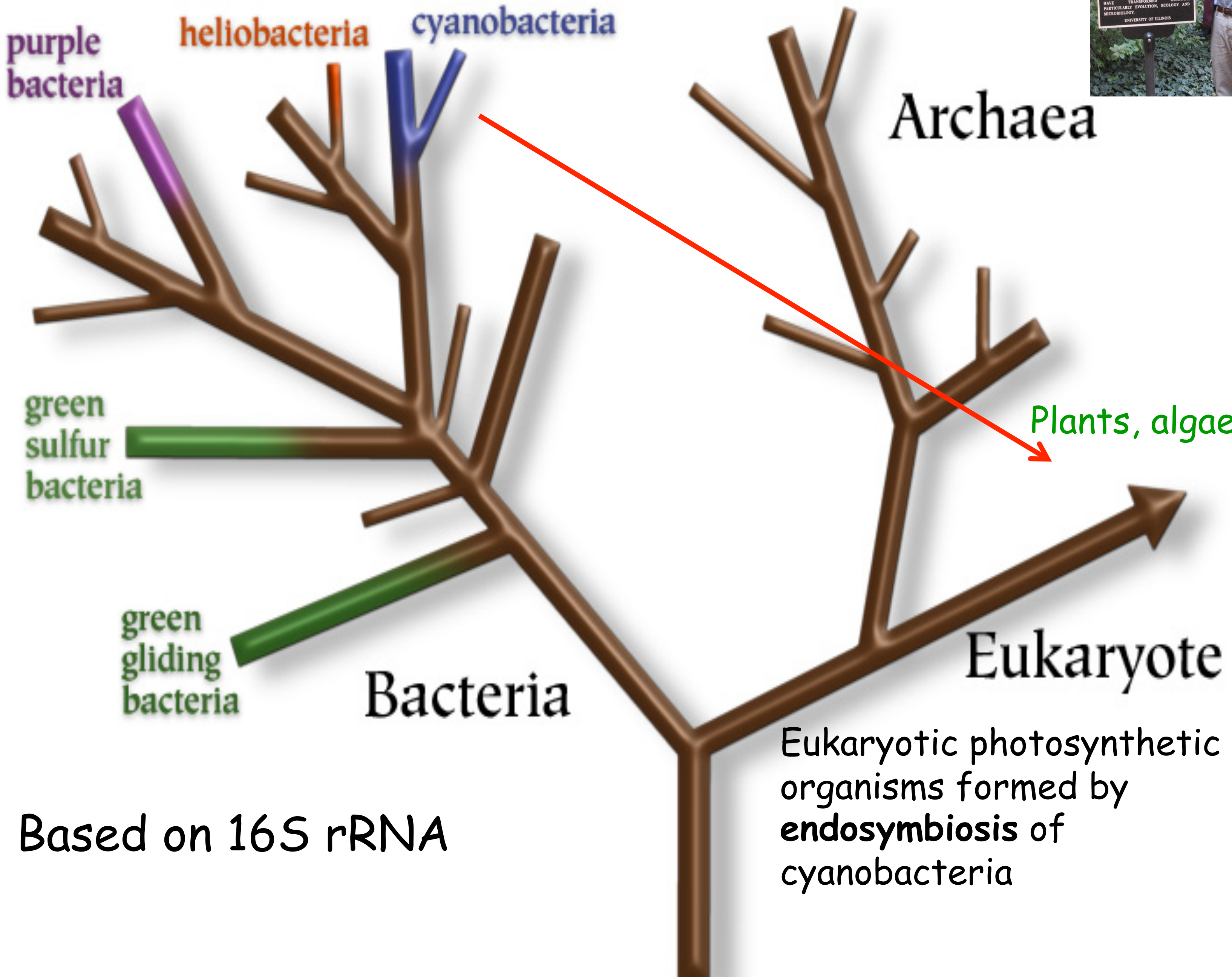
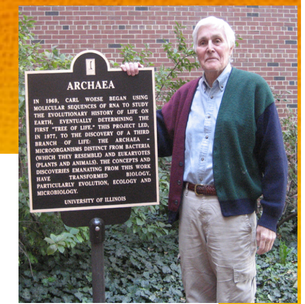
Universal Tree of Life

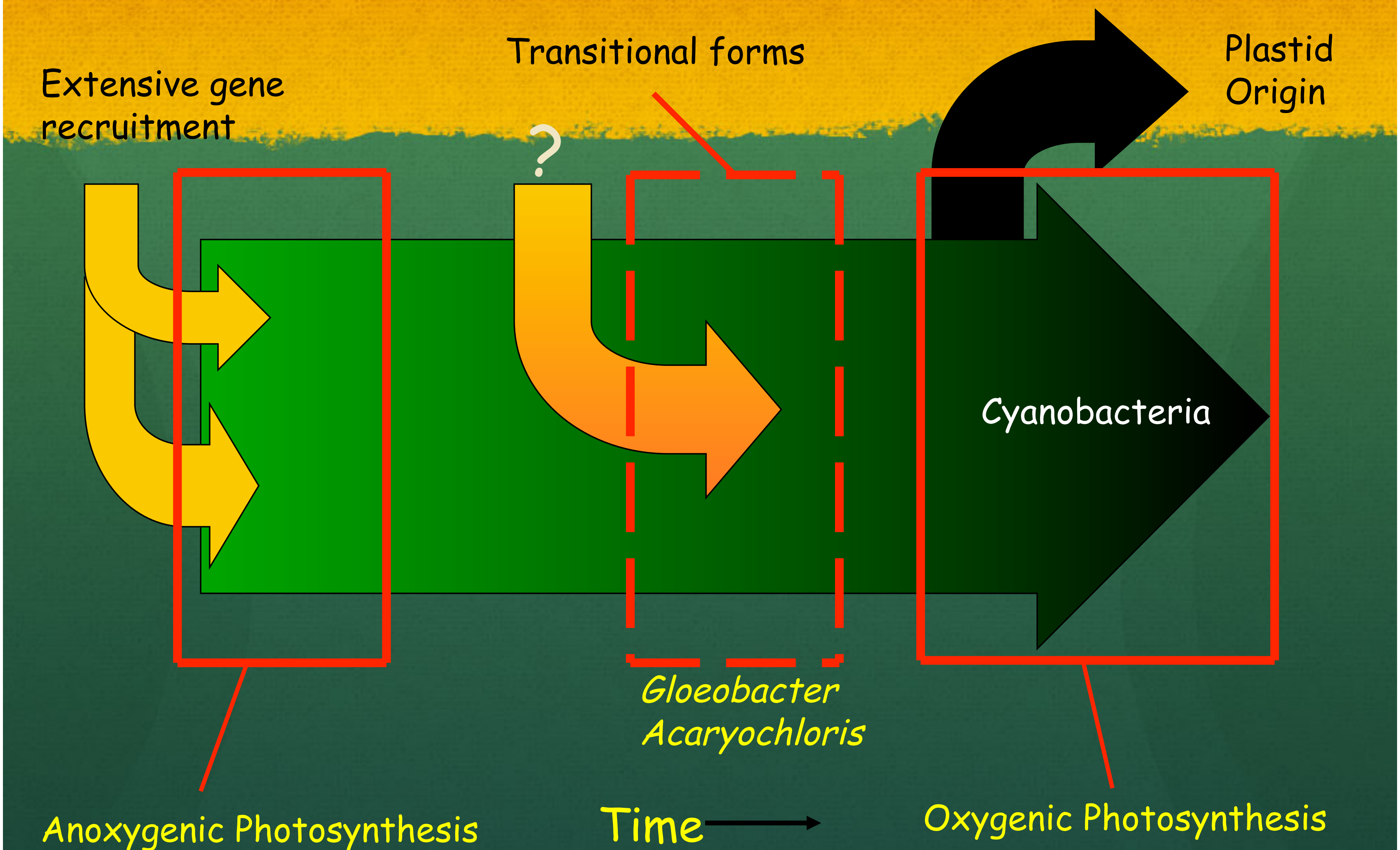




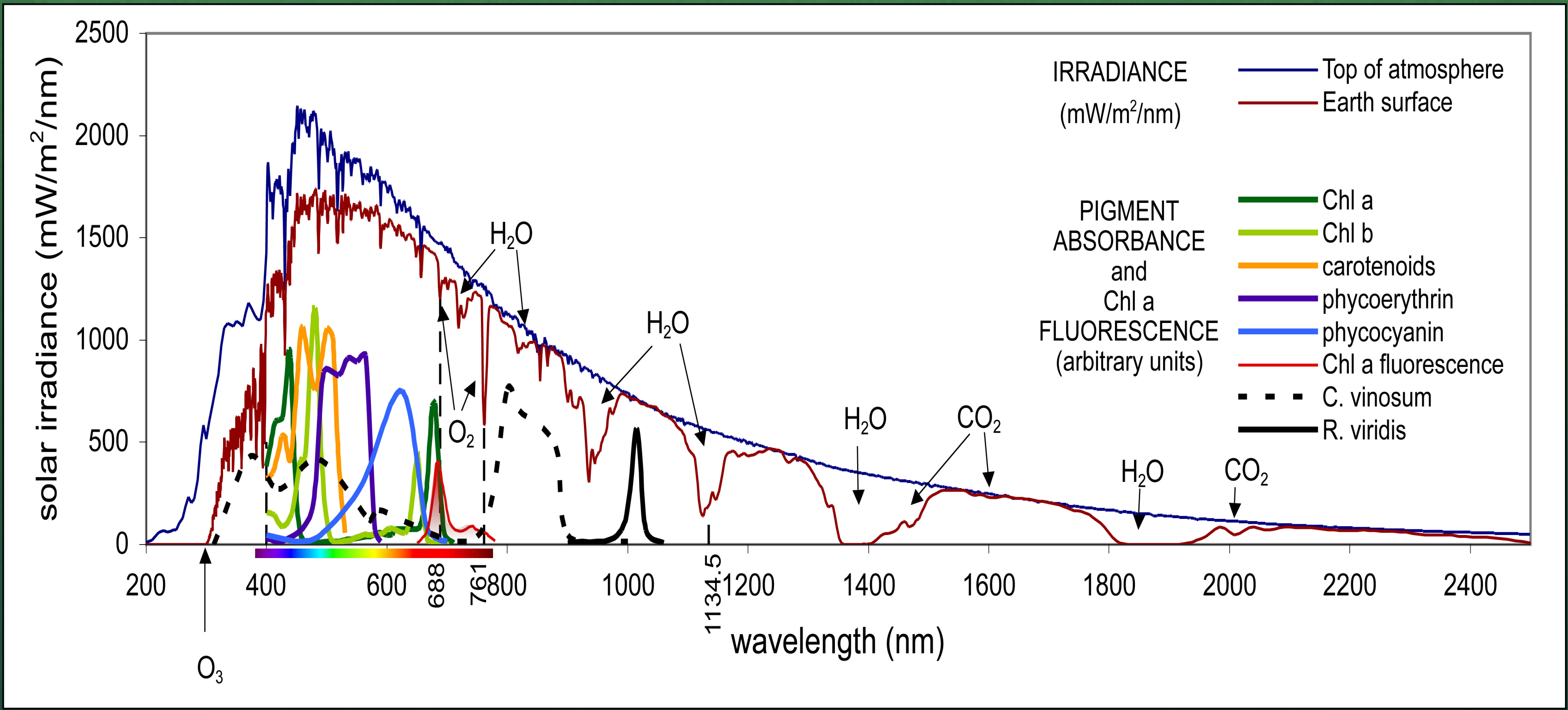
Based on 16S rRNA

Eukaryotic photosynthetic organisms formed by **endosymbiosis** of cyanobacteria

Transition to Oxygenic Photosynthesis



The Color of Light that is Absorbed by Plants, Algae and Photosynthetic Bacteria (Diagram by Nancy Kiang and Govindjee)



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The pts scale of Martin Kamen (1963)

2

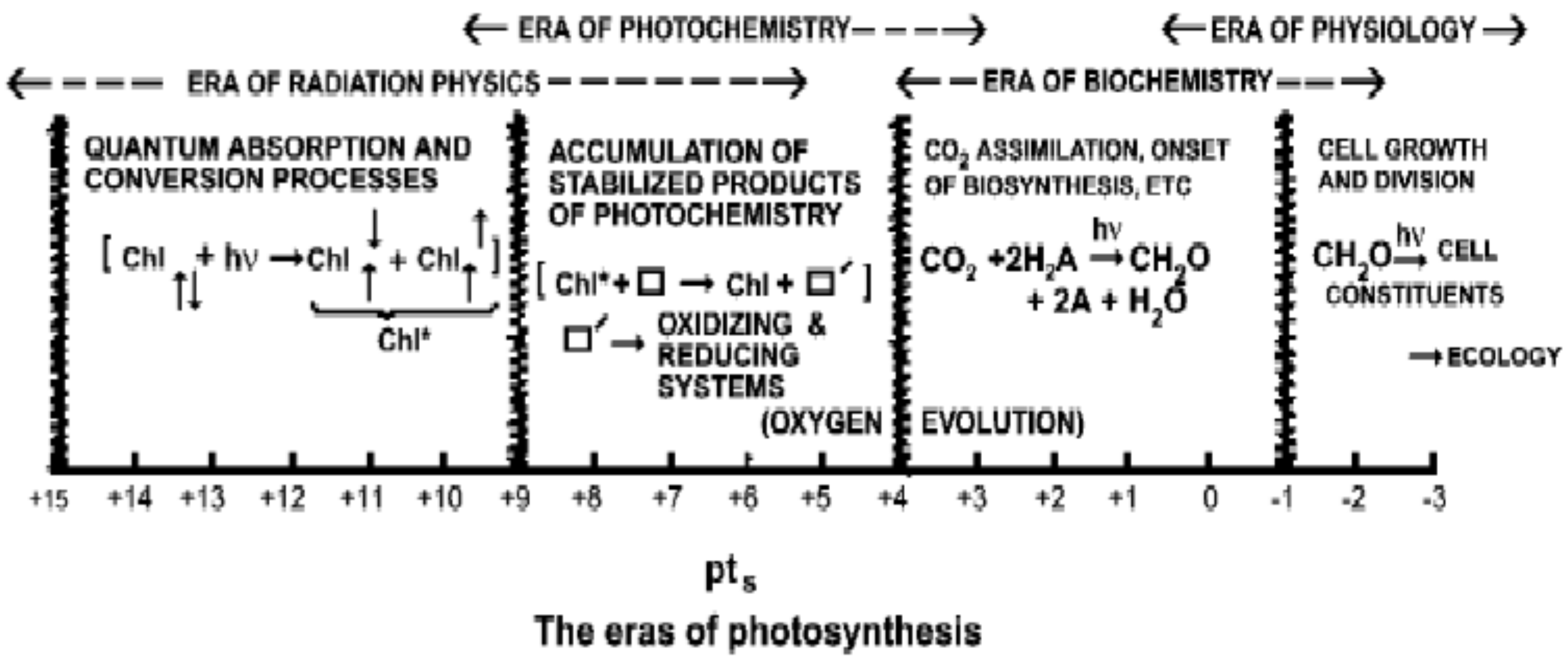

Figure 1. The eras of photosynthesis, according to Martin Kamen (Primary Processes in Photosynthesis. Academic Press, New York, 1963). The term logarithm of the reciprocal of time, expressed in seconds (pts), was suggested by David Gutsche, for which Kamen thanks him.

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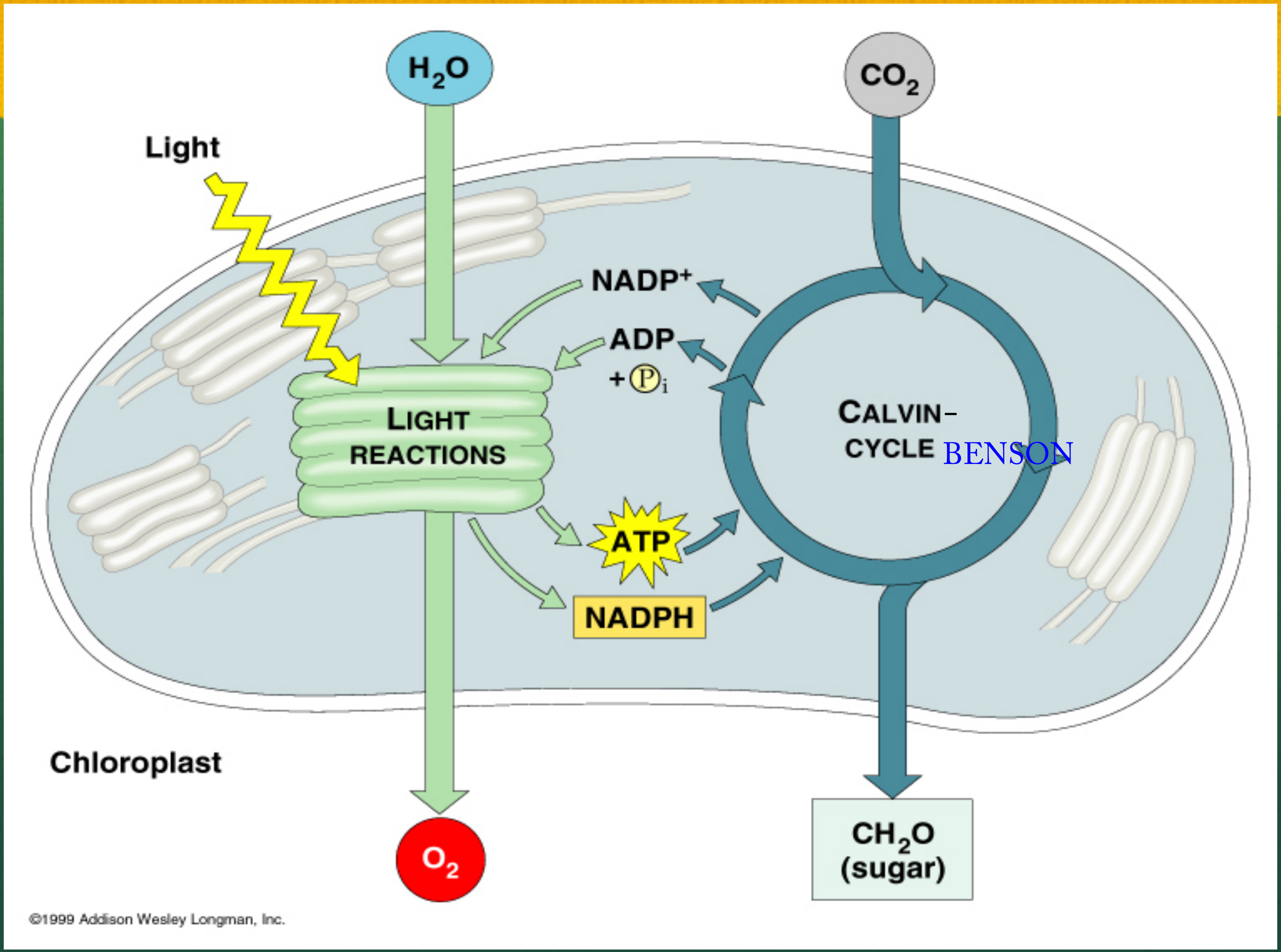
The "Light" and the so-called "Dark" Reactions of Photosynthesis:
The Hill Reaction and the Blackman Reaction (Calvin-Benson Cycle)



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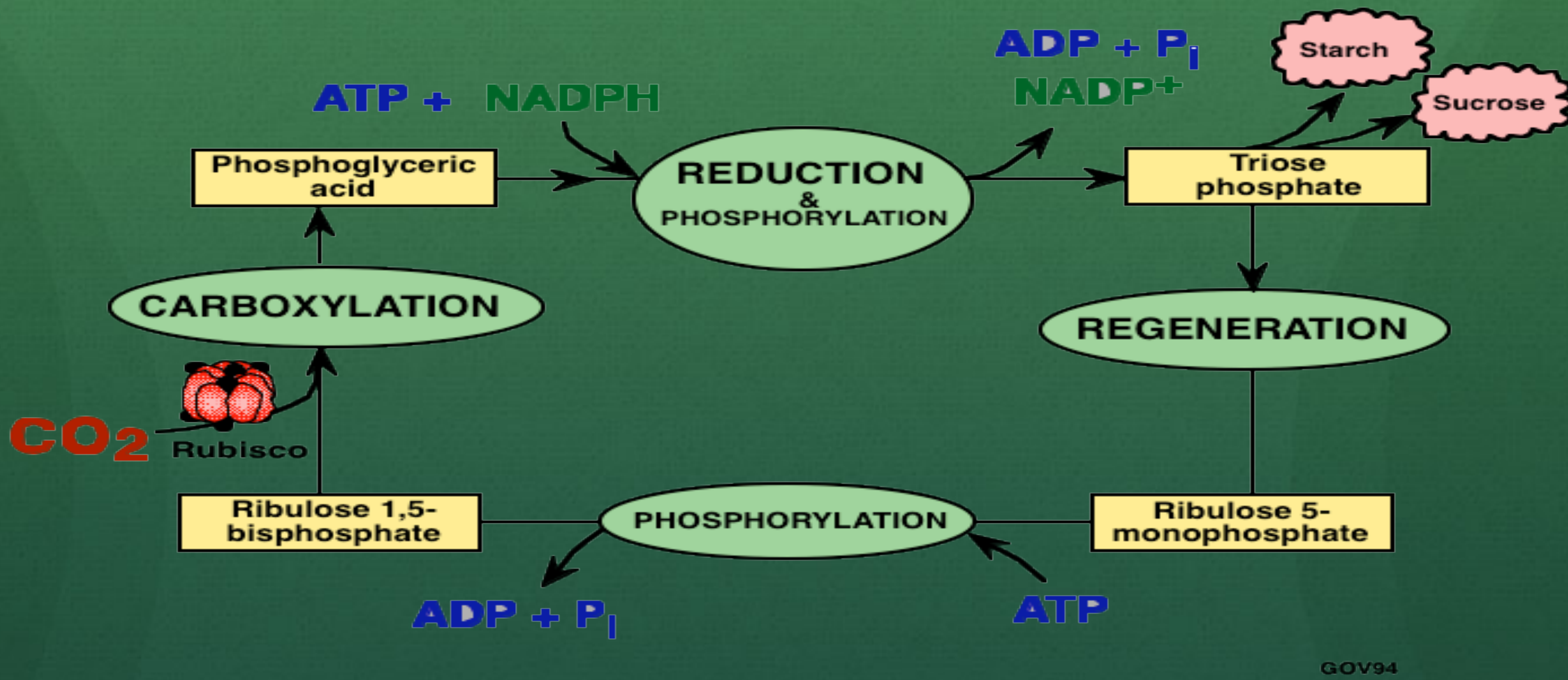
The Calvin-Benson Cycle



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Martin Kamen (1913-2002)

- 1940: Discovery of radiocarbon-14 (with Sam Ruben): story the day C-14 was discovered?
- 1941: Oxygen-18 experiment showing that oxygen comes from water (with Sam Ruben)
- 1949: Nitrogen fixation by photosynthetic bacteria (with Howard Gest)
- Discoverer of several cytochromes in photosynthetic bacteria
- Received Fermi Award in 1996

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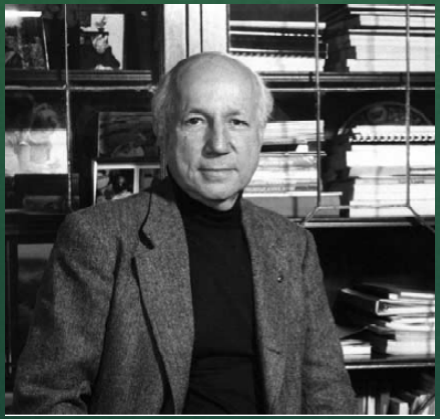
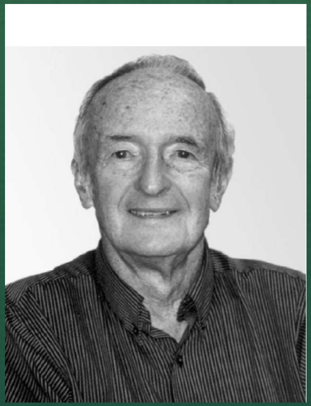
Melvin Calvin (1912-1997), Andy Benson and James Al Bassham





- The discoverers of the path of carbon in C-3 plants were : Andy Benson; James Al Bassham; Melvin Calvin and many others ***(Calvin-Benson Cycle)***

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Andrew Alm Benson

(see Photosynth Res, 2010,Online:
DOI 10.1007/s11120-010-9591-3; DOI 10.1007/s11120-010-9592-2)

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Scaling from the Past to the Present

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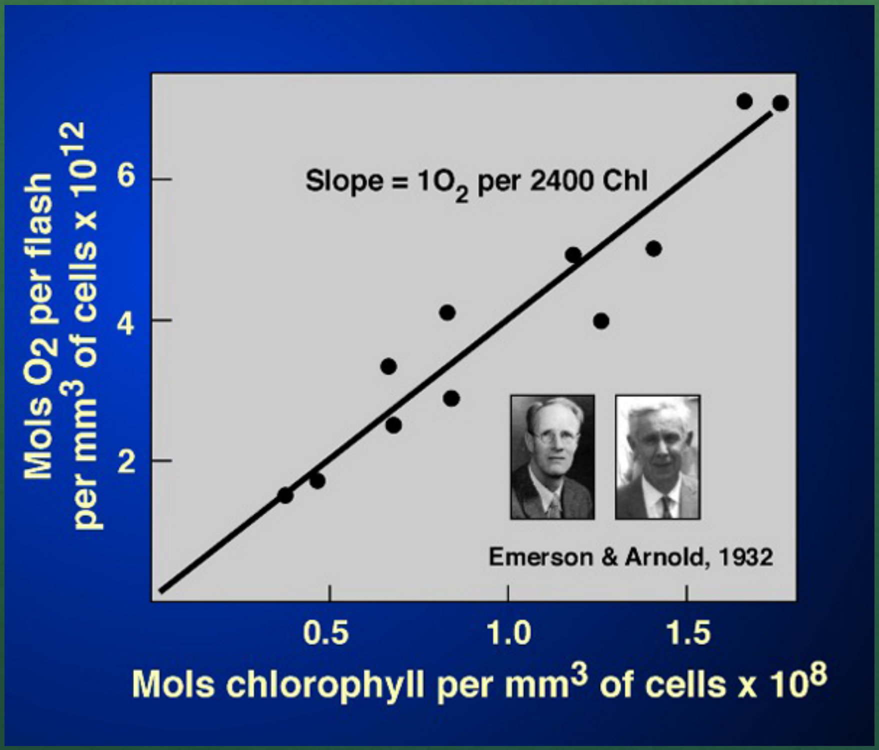
1. The Photosynthetic Unit, 1932
2. The Minimum Quantum Requirement for Oxygen Evolution, 1920s—1960s
3. The Very First Ideas on Two Light Reactions, 1945
4. Action Spectra of Photosynthesis, 1943
5. The Red Drop in Photosynthesis, 1943
6. The Emerson Enhancement Effect, 1957
7. The Blinks Effect: Chromatic Transients, 1957, 1960
8. The Two Light Reactions and Two Photosynthesis: Chlorophyll a in both systems, 1960

The Photosynthetic Unit (1932)



- *"We need only suppose that for every 2480 molecules of chlorophyll there is present in the cell one unit capable of reducing one molecule of carbon dioxide each time it is suitably activated by light."*

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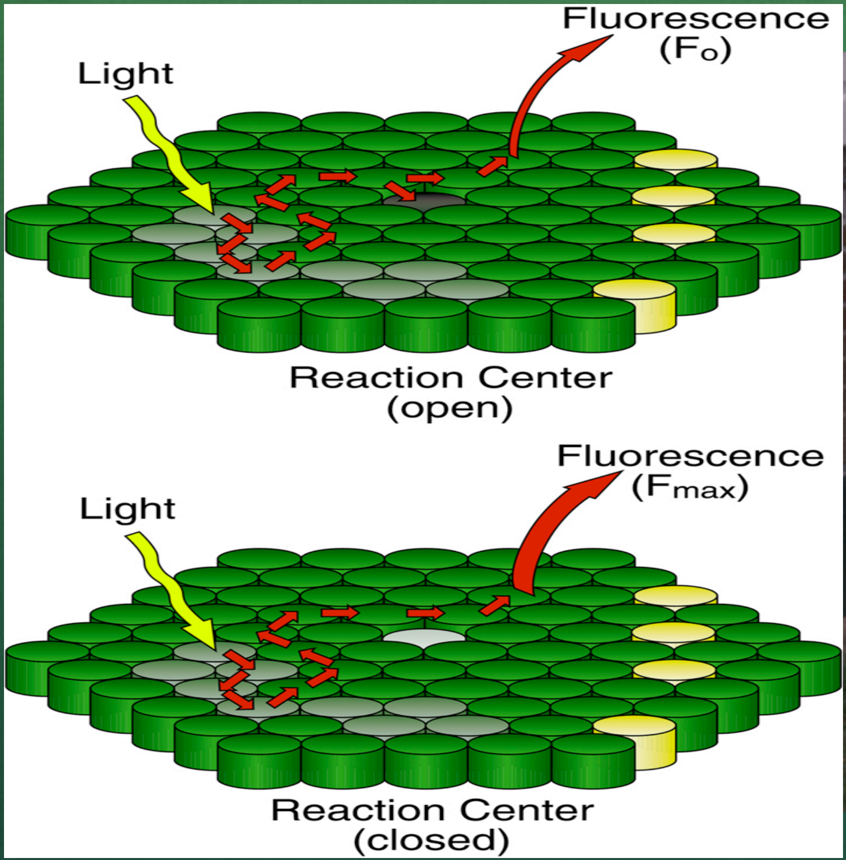
• Hans Gaffron (1902-1979): The 1936 "Concept of Excitation Energy Transfer" and a "photoenzyme; discovery of hydrogen evolution and hydrogen uptake by algae in the 1940s.



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On the question of:

the Maximum Quantum Yield or the Minimum Quantum Requirement of oxygen evolution

The 1931 Nobel-laureate in Physiology or Medicine

Otto Warburg (1883-1970) reported, for more than 40 years (1923—1969), that the minimum number of photons needed to evolve one molecule of oxygen, at low light intensities, was 2.8—4!

And, he was wrong, as proved by his own PhD student Robert Emerson (1941-1958) who obtained a value in the range of 10 to 12

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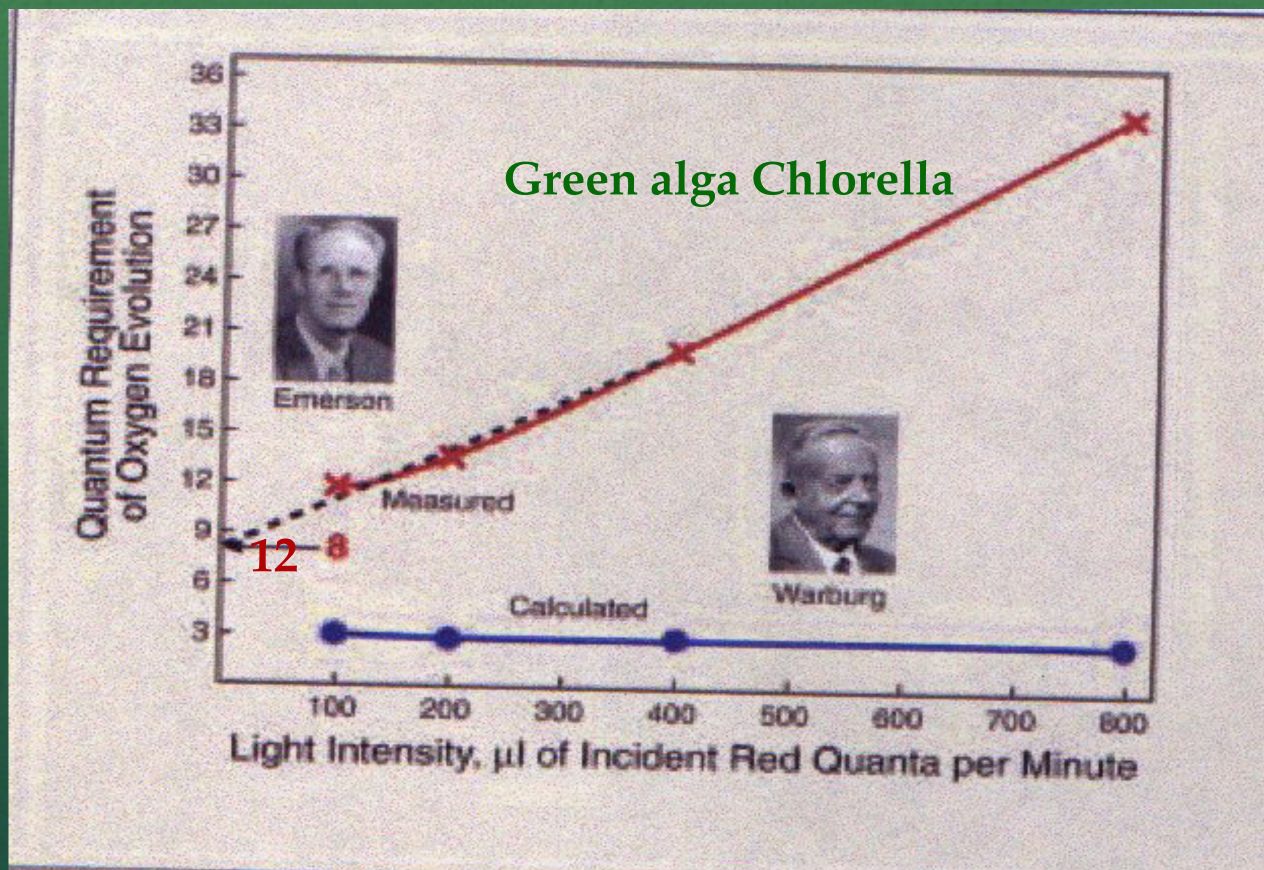
The battle on minimum quantum requirement per oxygen has been over for some time (see Govindjee (1999) Photosynth Res 59:249-254); Rajni Govindjee, Govindjee and Eugene Rabinowitch (1968) confirmed Emerson under the precise experimental conditions of Otto Warburg: young synchronous cells, with blue catalytic light and 10% CO_2



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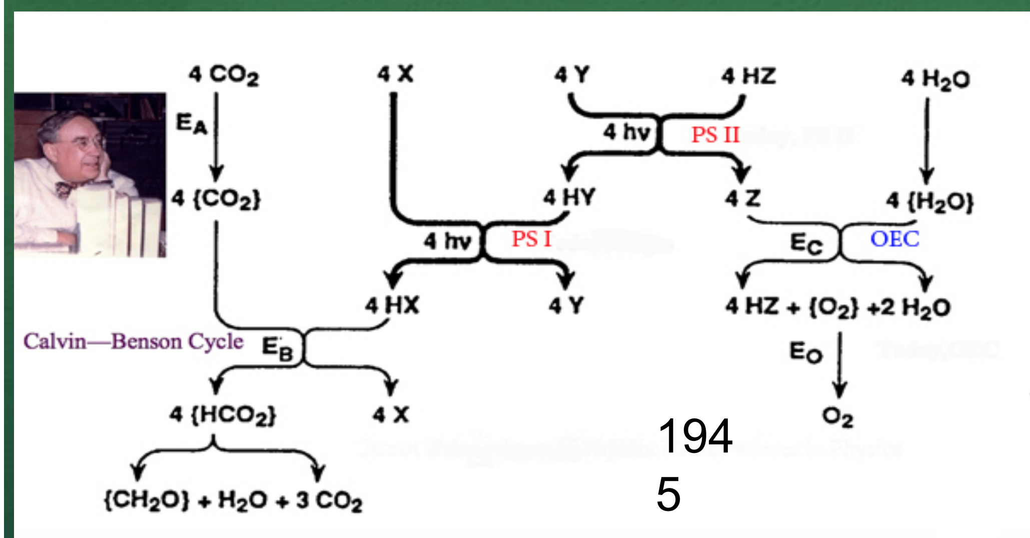
Eugene Rabinowitch (1945,1956)



- *"….two quanta will be needed to transfer each of the four required H atoms (or electrons), first from water to the cytochrome, and then from the cytochrome to the final acceptor." ---1956*

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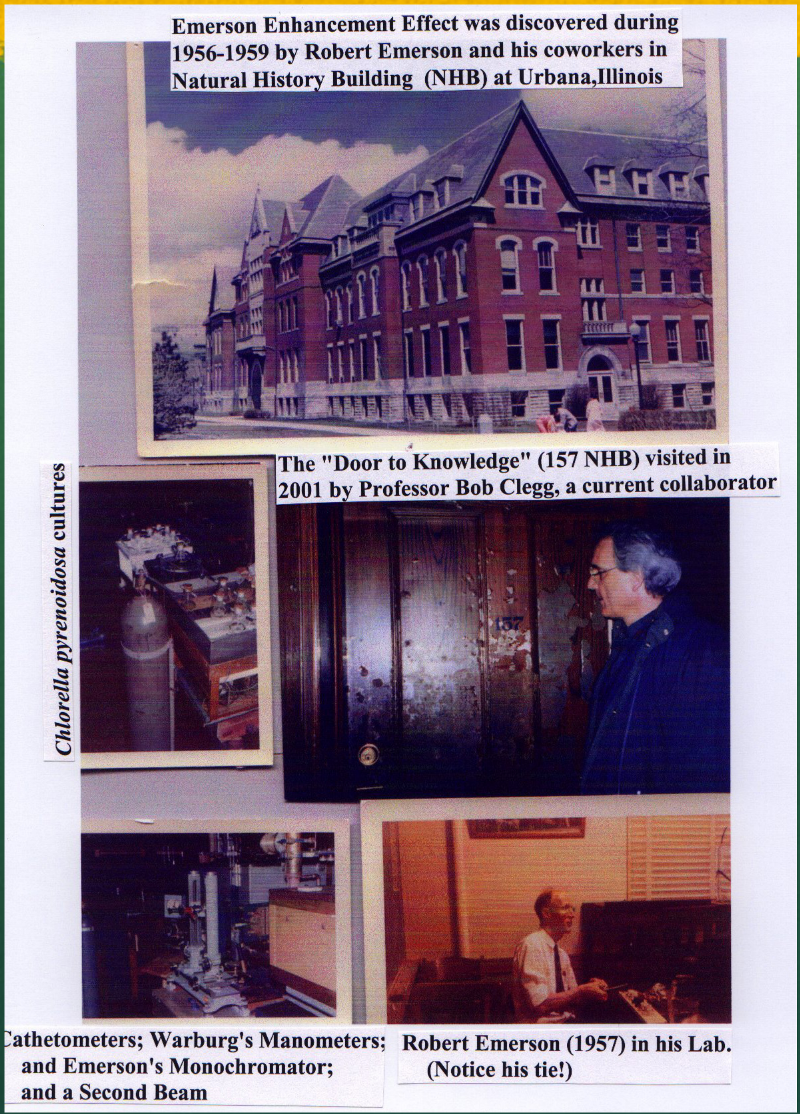
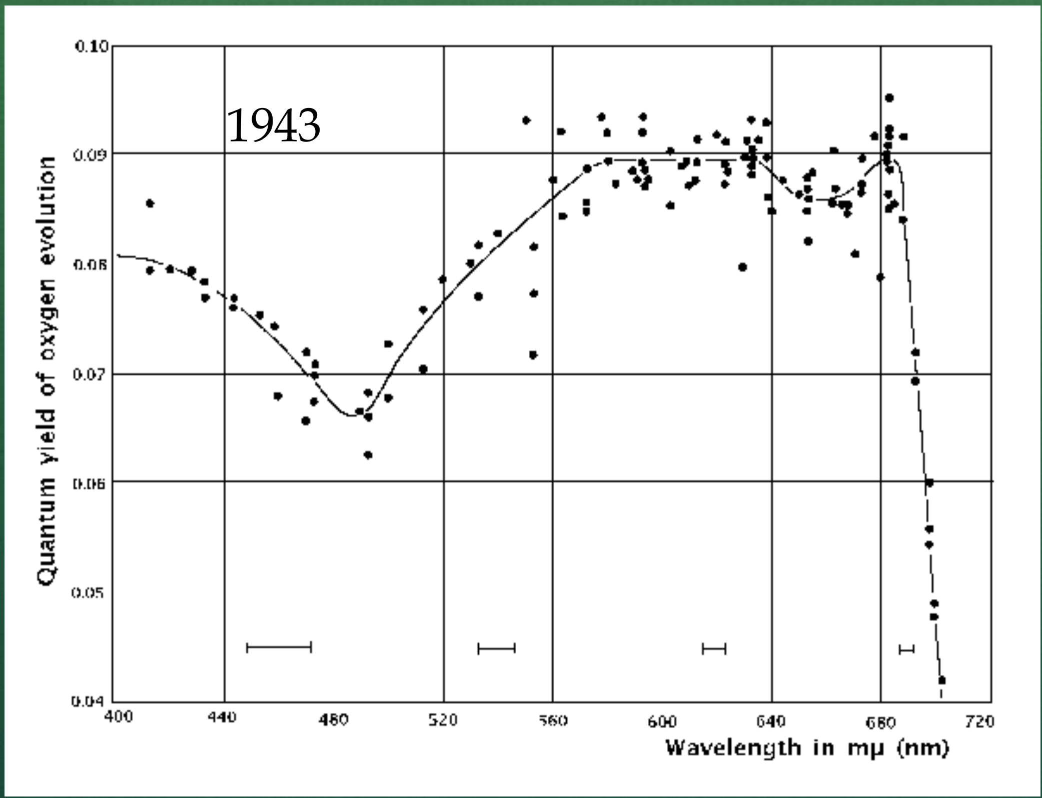
Natural History Building, Mathews Avenue, Urbana

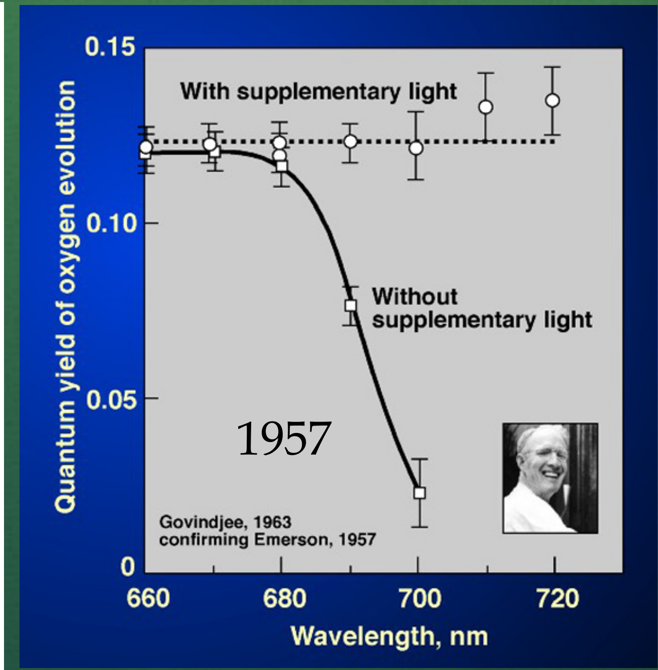


- Experiments with manometers were carried out in a room that we entered from 157 Natural History Building
- Algae were grown in a tiny culture room
- Cathetometers were used to read pressure changes with 0.01 mm precision.
- Emerson always wore a red tie and an old apron in the lab.

Robert Emerson

Red Drop (1943) and Enhancement Effect (1957)





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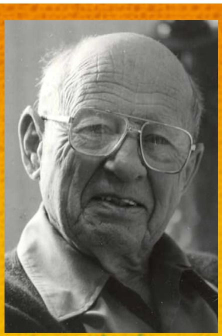
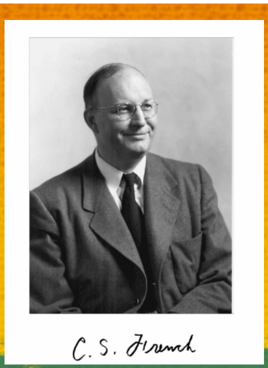
The Emerson Enhancement phenomenon, explained

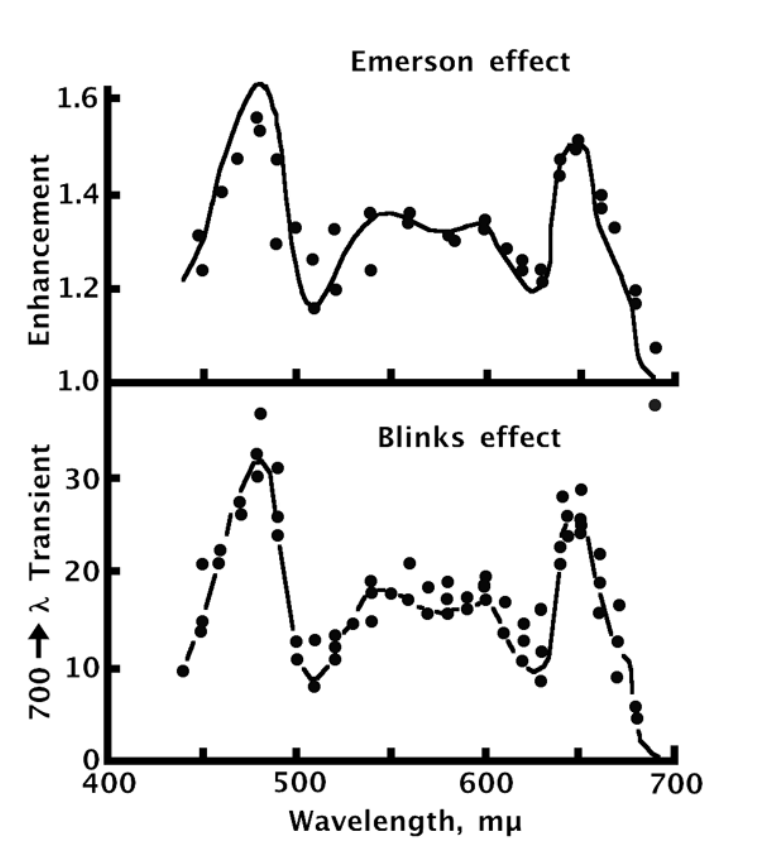
with fictitious numbers

- Let us say, the rate of oxygen evolution, at a low intensity of far-red light, was 10 molecules per second.
- And the rate of oxygen evolution, at a low intensity of supplementary light, was 40 molecules per second.
- Emerson discovered that when the same two beams of light were given together, the rate was, e.g., 70 , instead of the expected 50.
- Thus, there was an Enhancement of 20 oxygen molecules; for the rate of oxygen evolution in far-red light (in the presence of the supplementary light), enhancement would have a ratio of 2 : 70 minus 50 , divided by 10 !





Action Spectra of the Emerson Enhancement Effect and the Blinks Chromatic Transient Effect (Myers and French, 1960)



- Myers and French (1960) concluded, as Emerson had done, that one light reaction was run by Chlorophyll a and the other by Chlorophyll b, but they added that the chromatic transient discovered by Blinks was related to the same basic phenomenon.

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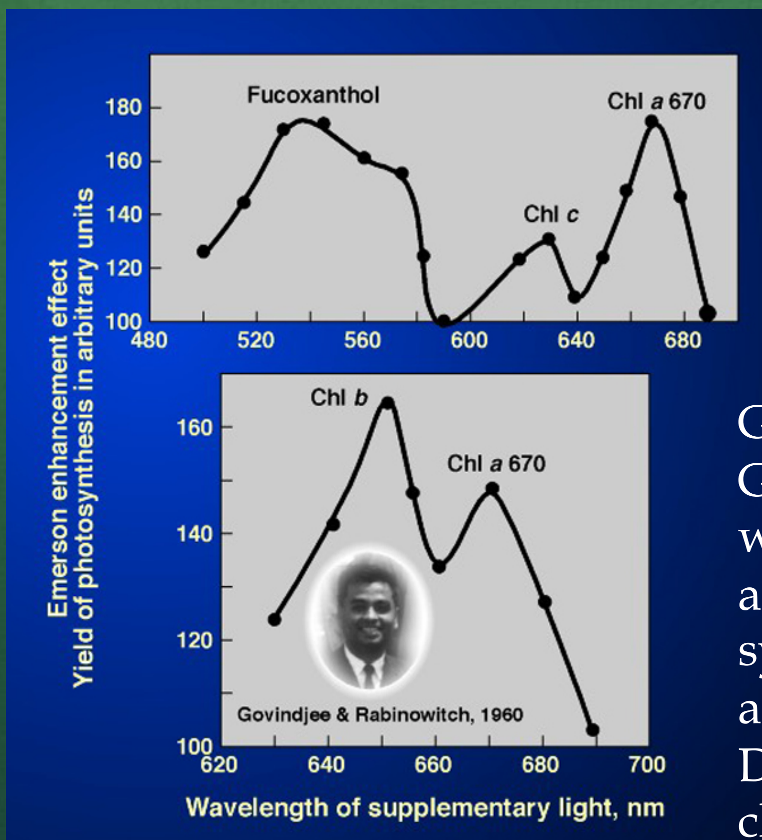
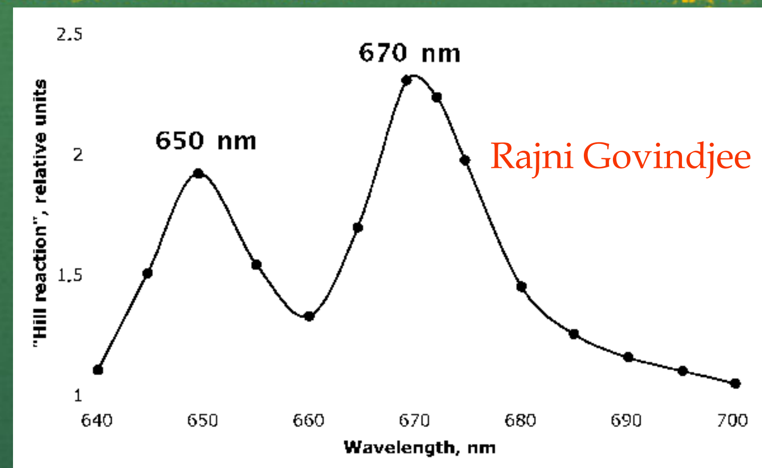
Govindjee and Rajni look back at their experiments done 50 years ago..





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Govindjee and Rabinowitch (1960) and R. Govindjee et al. (1960) showed that a short wavelength absorbing form of chlorophyll a (Chl a 670) was present in the same system that used chlorophyll *b* (or other accessory pigments) . This agreed with Duysens (1952) that all energy absorbed by chlorophyll *b* is transferred to chlorophyll *a*. Also Rajni's work showed that the effect was in photosynthesis , not respiration

Scaling from the Past to the Present

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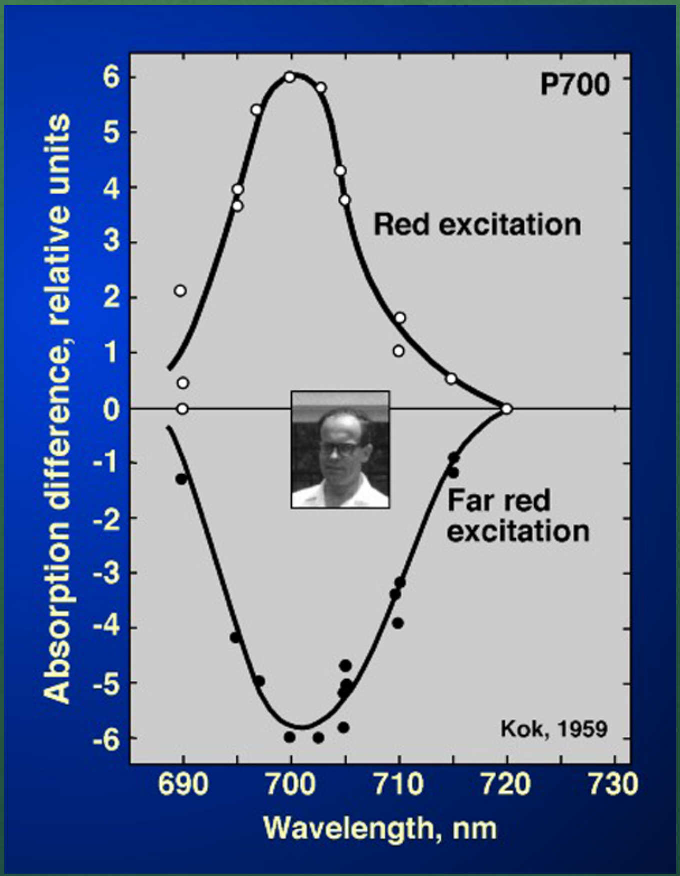
7. Antagonistic Effect of Two Lights on P700: Bessel Kok, 1959
8. Robin Hill's Concepts (Hill and Fay Bendall, 1960)
9. Lou Duysens and Jan Amesz's Key Experiments on Cytochrome f: Naming of the System 1 and System 2; The Push and Pull Experiments; Evidence for the Series Scheme, 1961
10. Experiments by Horst Witt and coworkers with Light Flashes, 1961

Bessel Kok, discoverer of P700, had the first two light effect on an intermediate of photosynthesis

- Kok (1959), in the Robert Emerson Memorial issue of *Plant Physiology*, showed a two-light effect, in a cyanobacterium *Anacystis nidulans*, on the redox state of the reaction center chlorophyll "P700", and discussed his observations in the context of the discovery of the Emerson Enhancement Effect.



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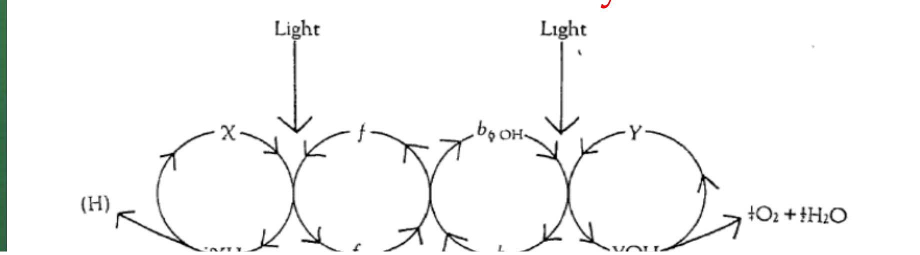
Hill and Bendall (1960) and Hill (1965)

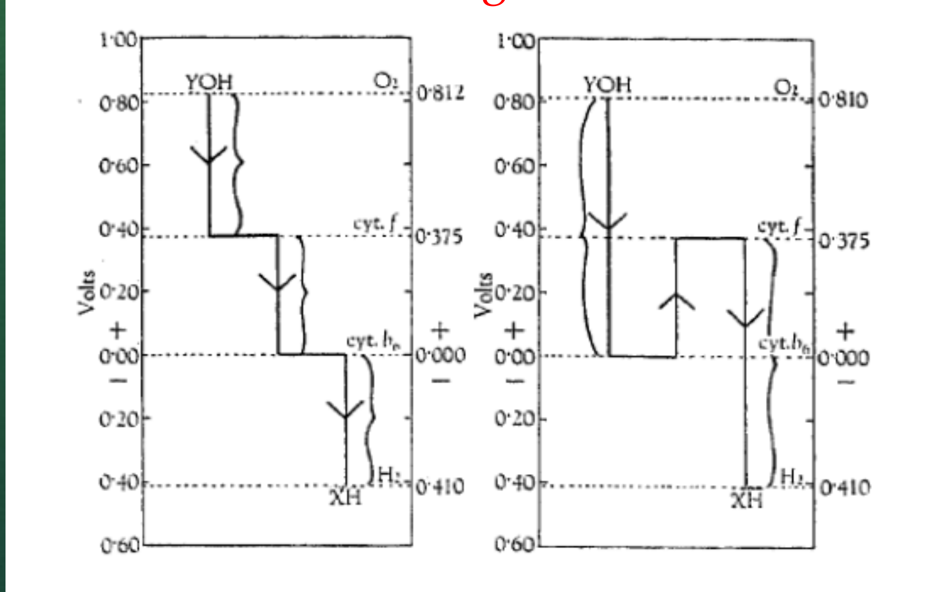
Hill

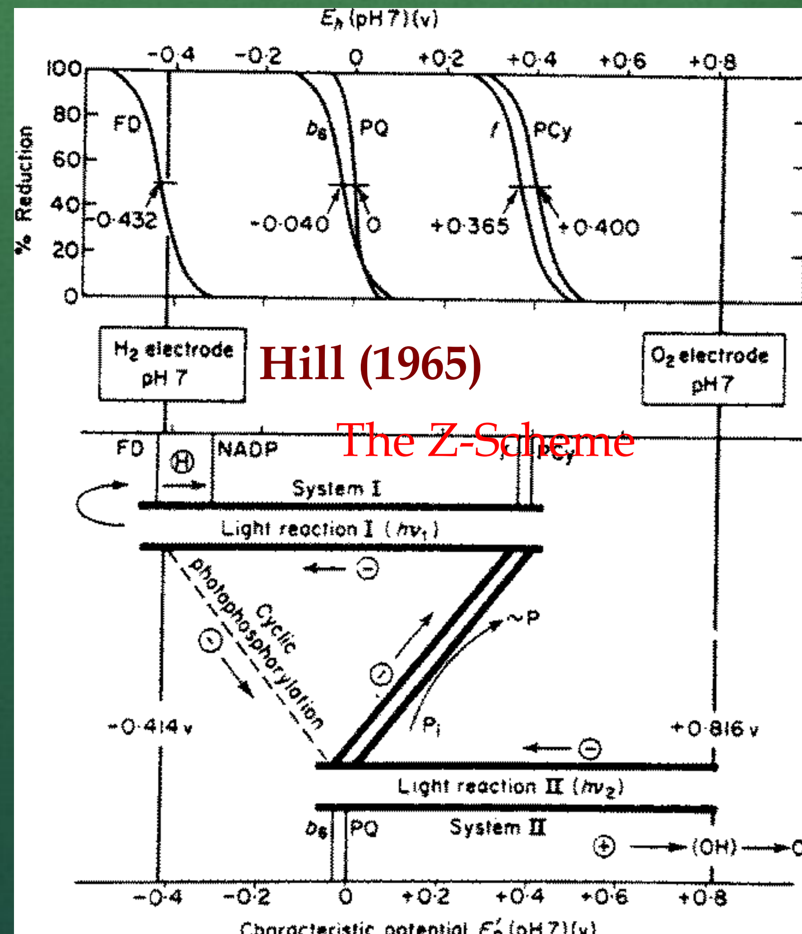
Forti

The bicycle model



Three or two light reactions?





Hill (1965)

The Z-Scheme

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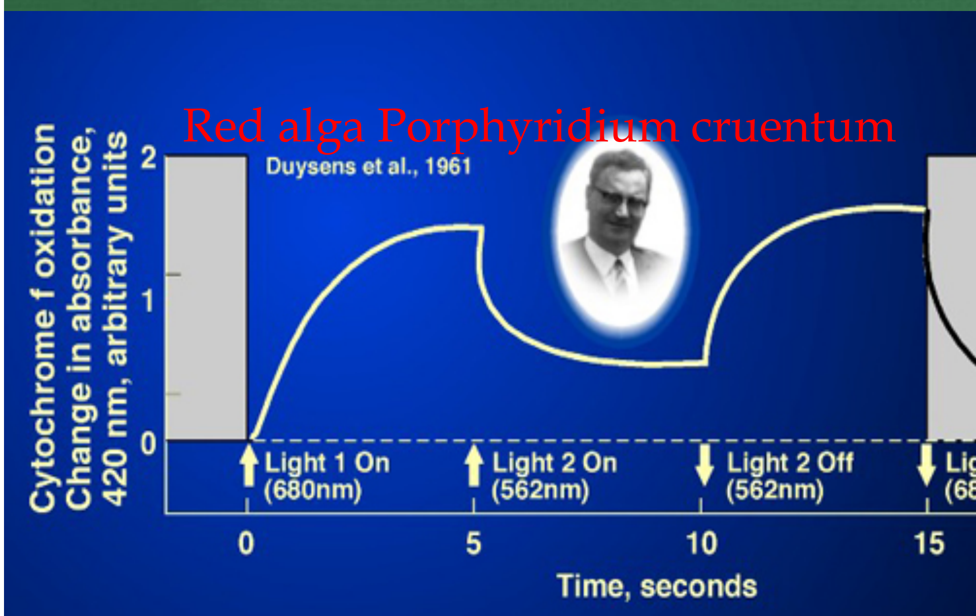
Louis N. M. Duysens et al. (1961) and Duysens and Amesz (1962)

Light 1 (red light) oxidized cytochrome f (called Light Reaction 1 and its Photosystem,PS 1) ; whereas, Light 2 (green light) reduced it (called Light Reaction 2, and its photosystem, PS 2). This push-pull antagonistic effect on a redox intermediate is the crux of the Series Z-Scheme.



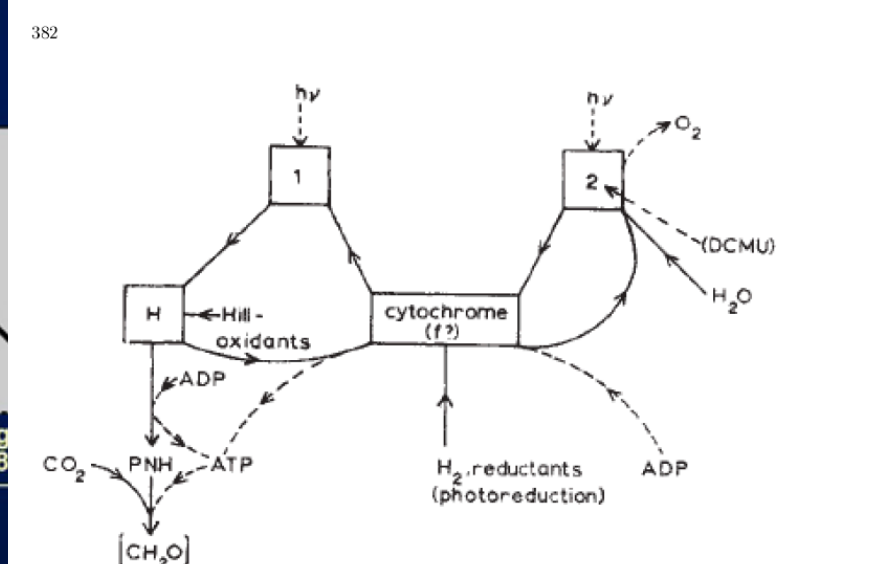


Fig. 3. Hypothetical scheme showing functions of systems 1 and 2 in photosynthesis

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Horst Witt et al. (1961); E. Rabinowitch (1963)

We note that Horst Witt had the intermediates X,Y and Z different from what Rabinowitch had in 1945.

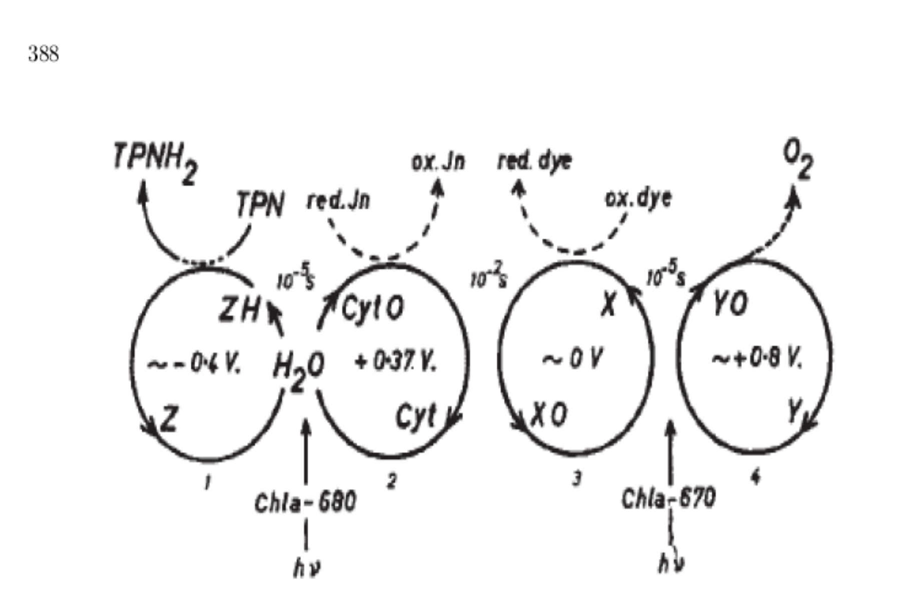
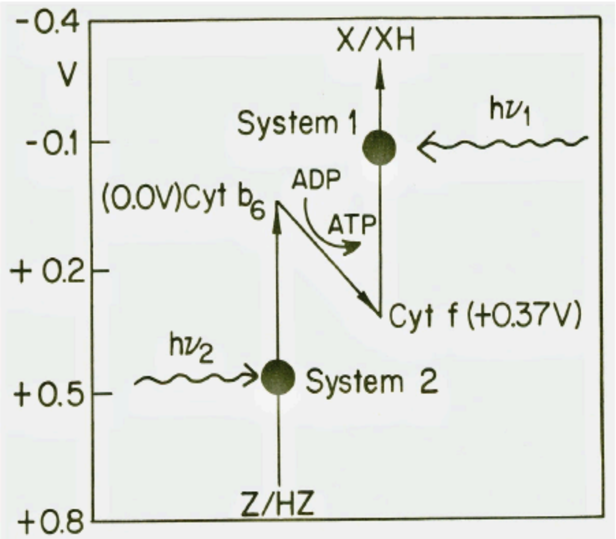


Fig. 2. Reaction pattern of photosynthesis



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Scaling from the Past to the Present

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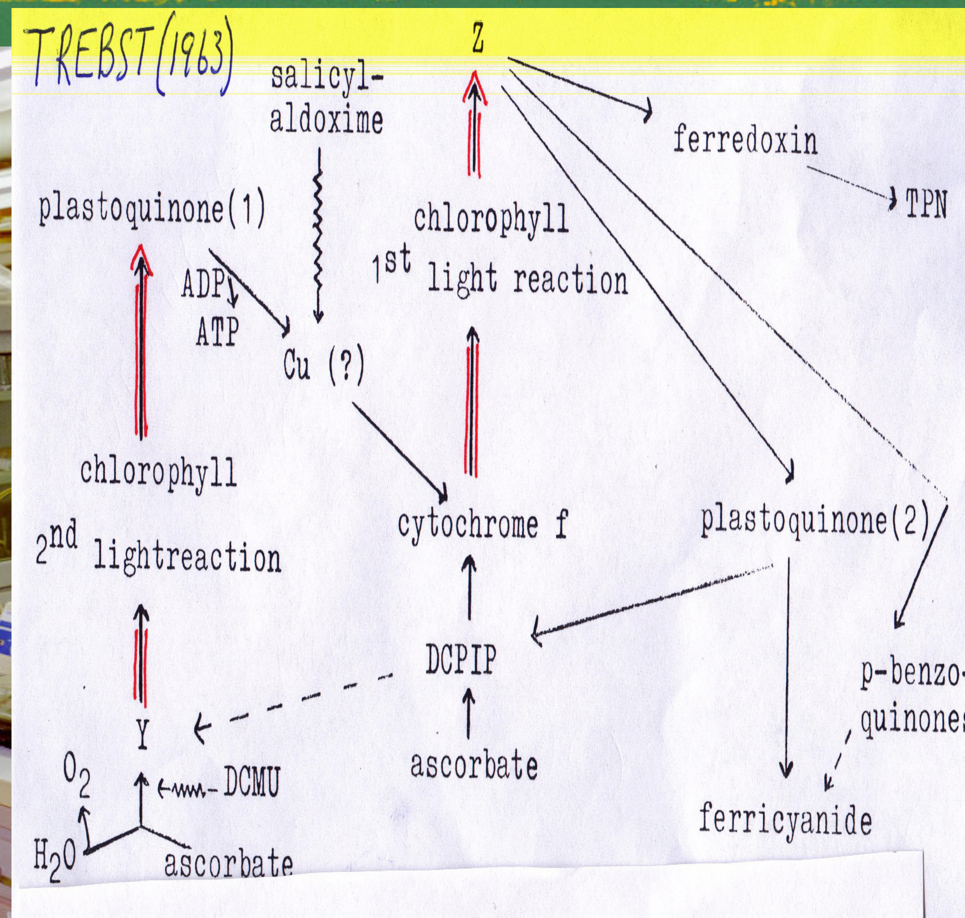
11. Biochemists Began to Contribute Through Use of Chemicals, Inhibitors, Electron Donors and Acceptors, 1962 et seq
12. Physical Separation of Pigment Systems ; Keith Boardman and Jan Anderson, 1964
13. Geneticists (e.g.,Paul Levine) Began to Provide Key Confirmation of the Steps Through the Use of Mutants

By 1963, the Picture was Clear

Two-light reaction scheme was also studied by many biochemists (Leo Vernon/Mordhay Avron/Daniel Arnon/ Achim Trebst, among others)



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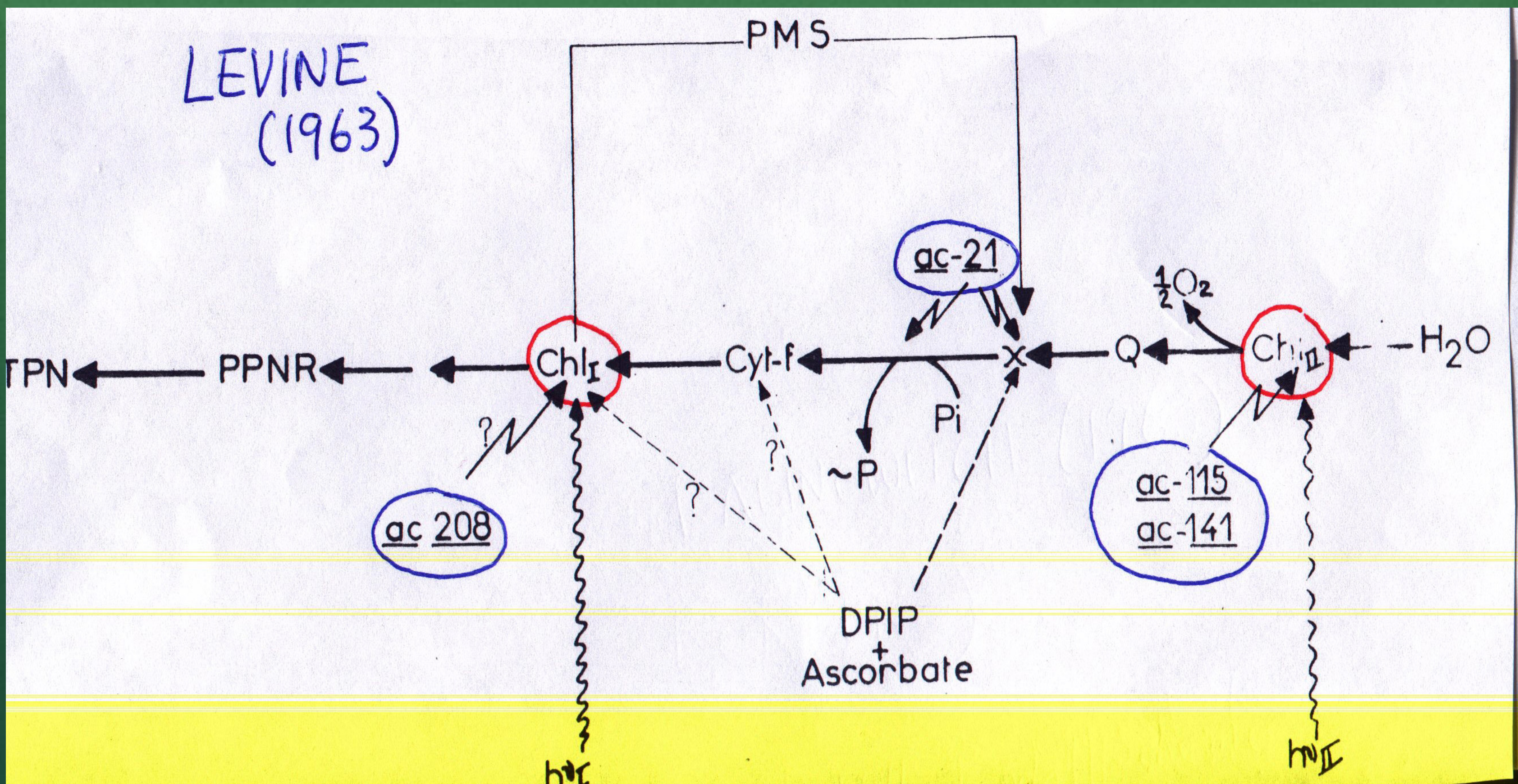
Two-Light Reaction Scheme of Paul Levine, using Chlamydomonas mutants



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Scaling from the Past to the Present

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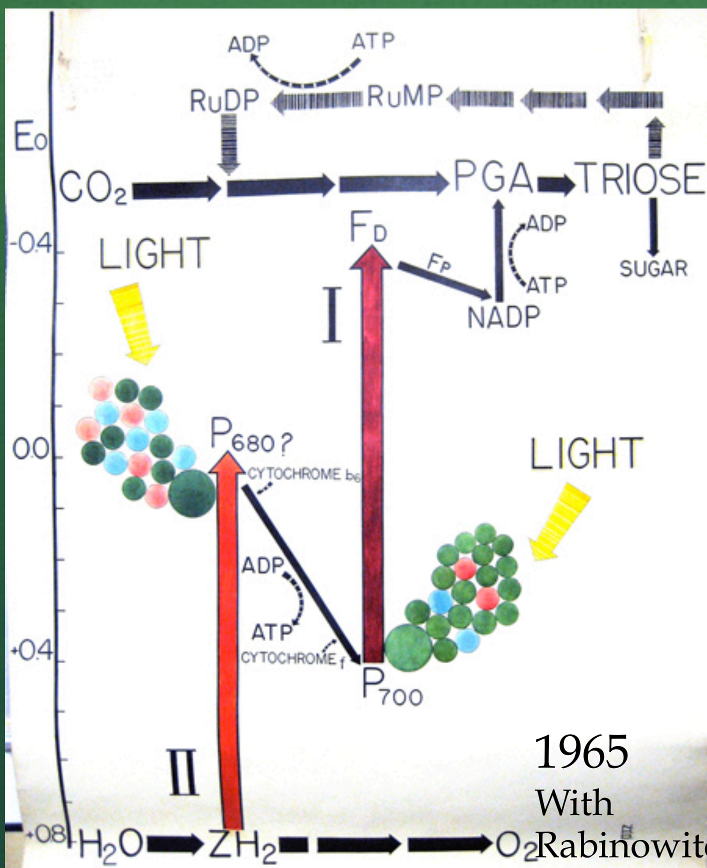
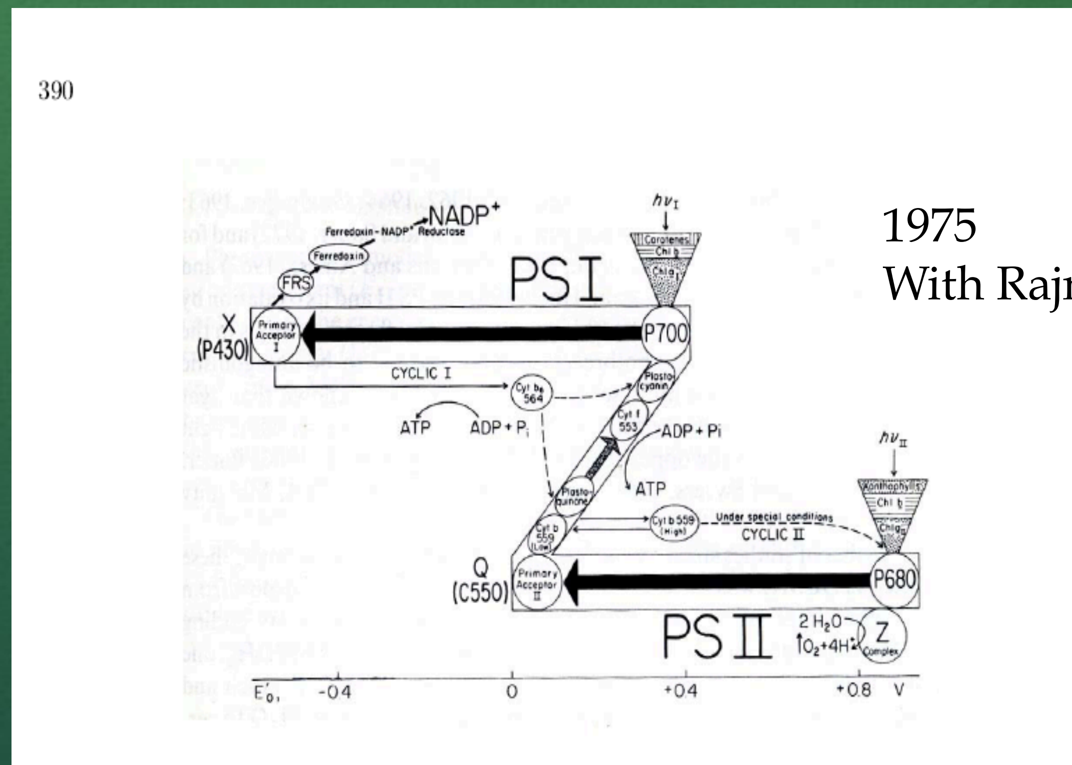
The Various Z-Schemes of Electron Transport in Photosynthesis that We Have Drawn over the Years, 1965--2010

Comments on How Best to Teach The Z-Scheme at Various Levels

Z-Schemes with different characteristics ..1965; 1975



1965
With
Rabinowitch



1975
With Rajni

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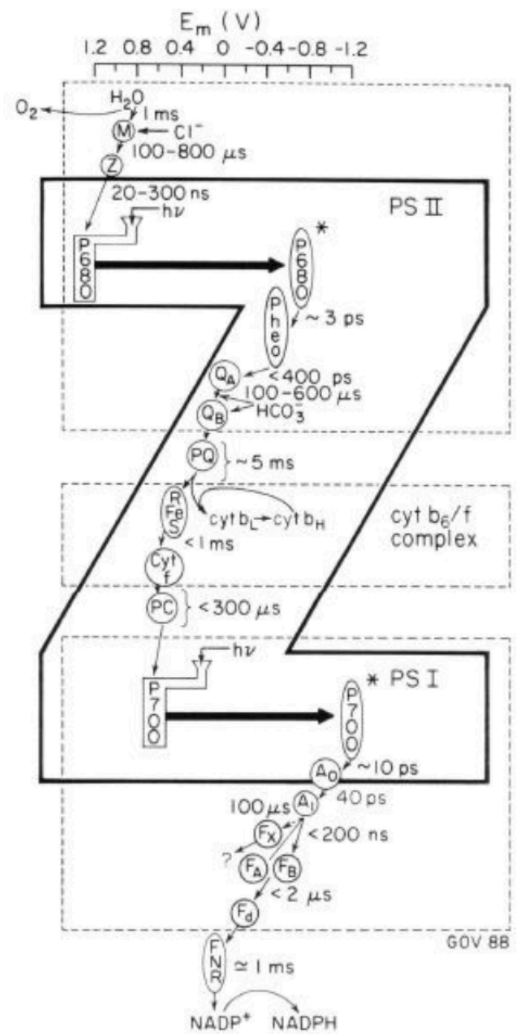
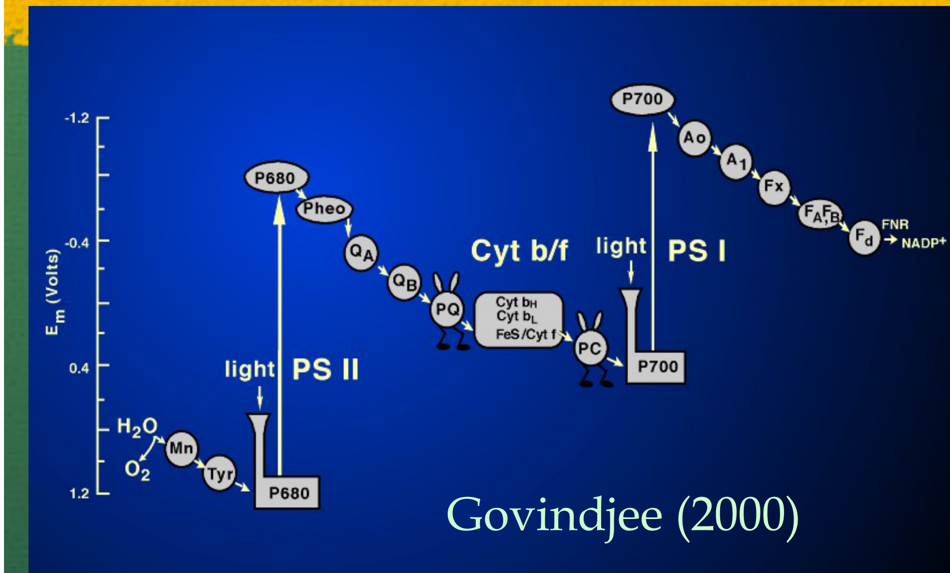
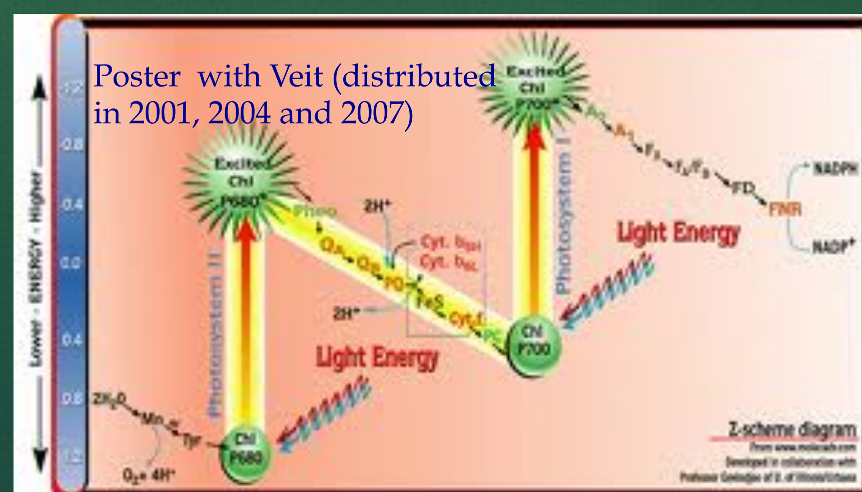
1989; 2000; and 2004

1989, Govindjee with Demeter





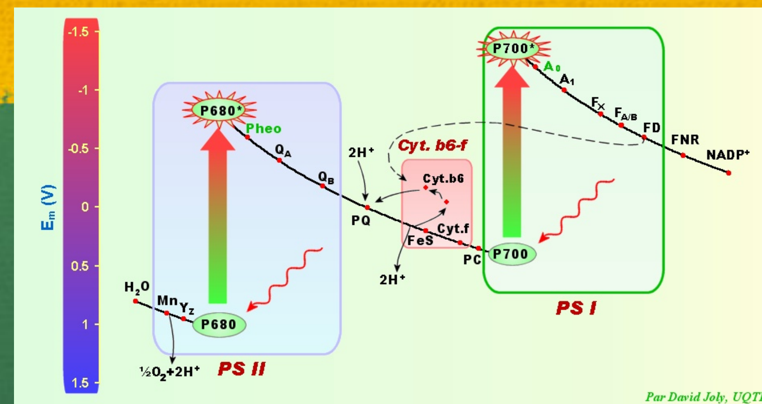
Govindjee (2000)

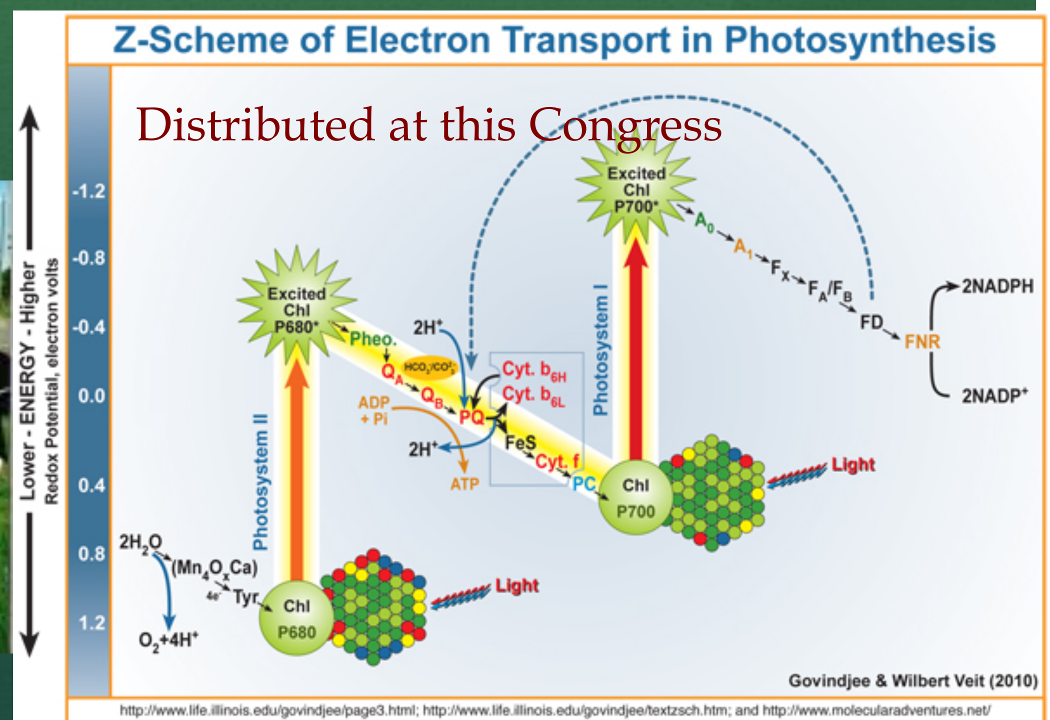


Poster with Veit (distributed in 2001, 2004 and 2007)

There are many schemes on the internet..

The most interesting way to explain the Z-Scheme is to involve students by having them play the role of different intermediates



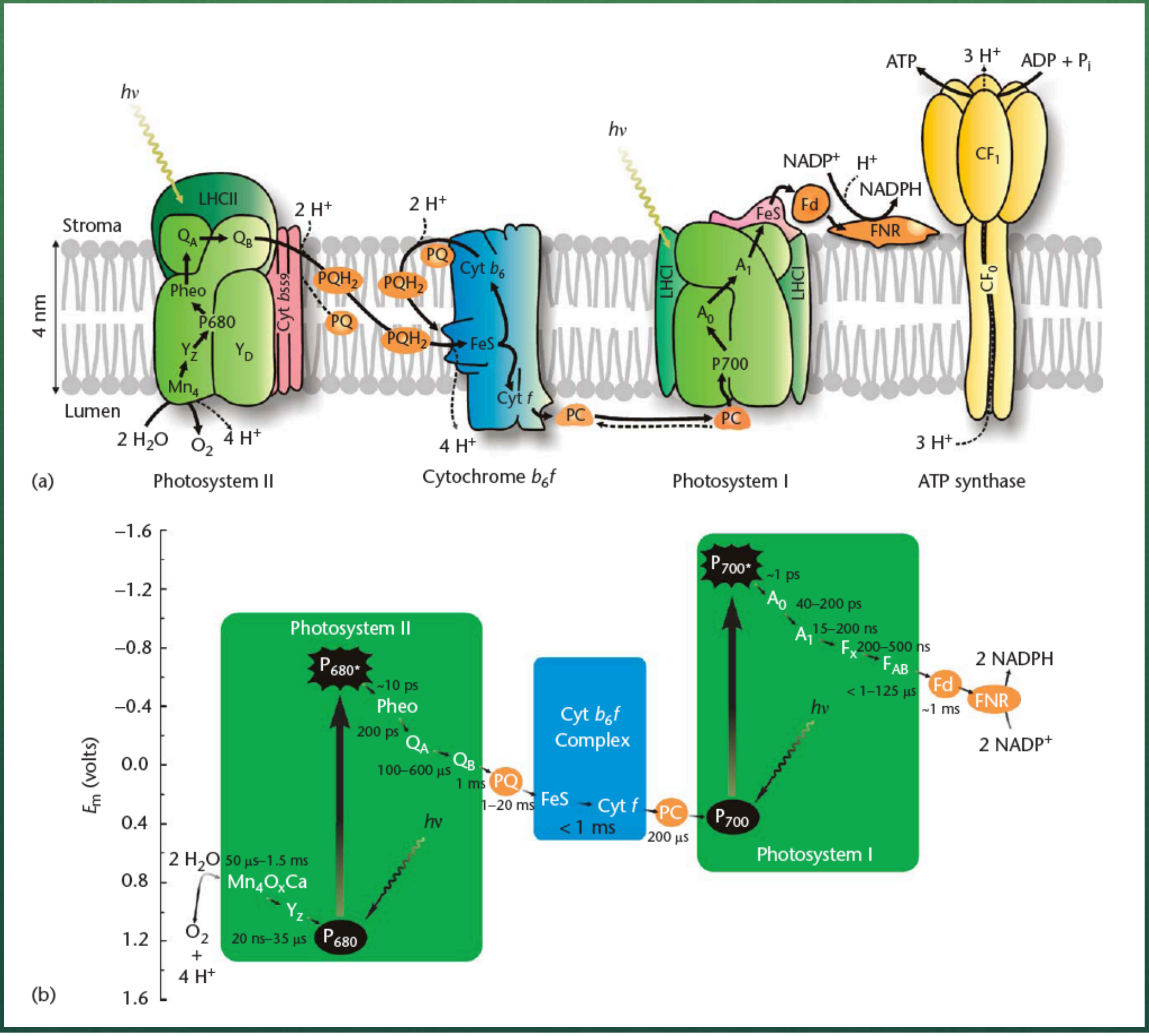


Distributed at this Congress

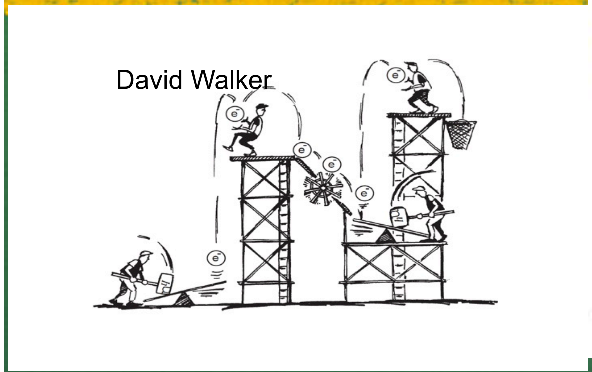
Z-Scheme

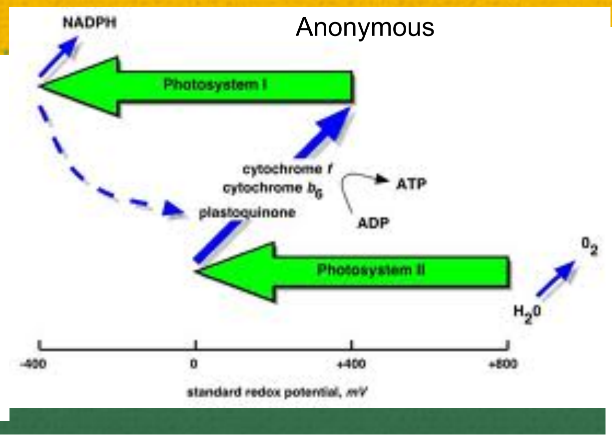
Govindjee,Kern, Messimger and Whitmarsh (2010)

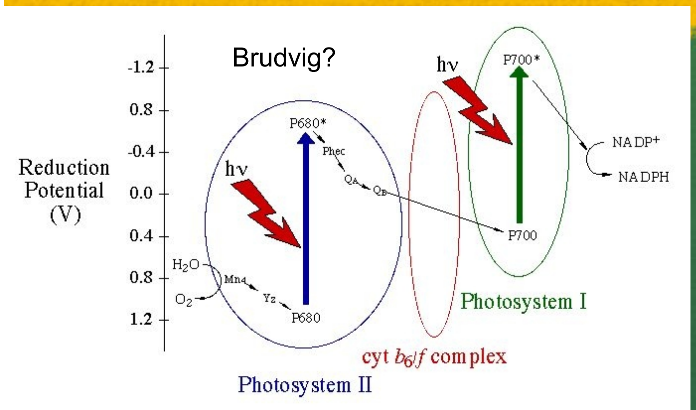
Encyclopedia of Life Sciences (Courtesy:D. Shevela)

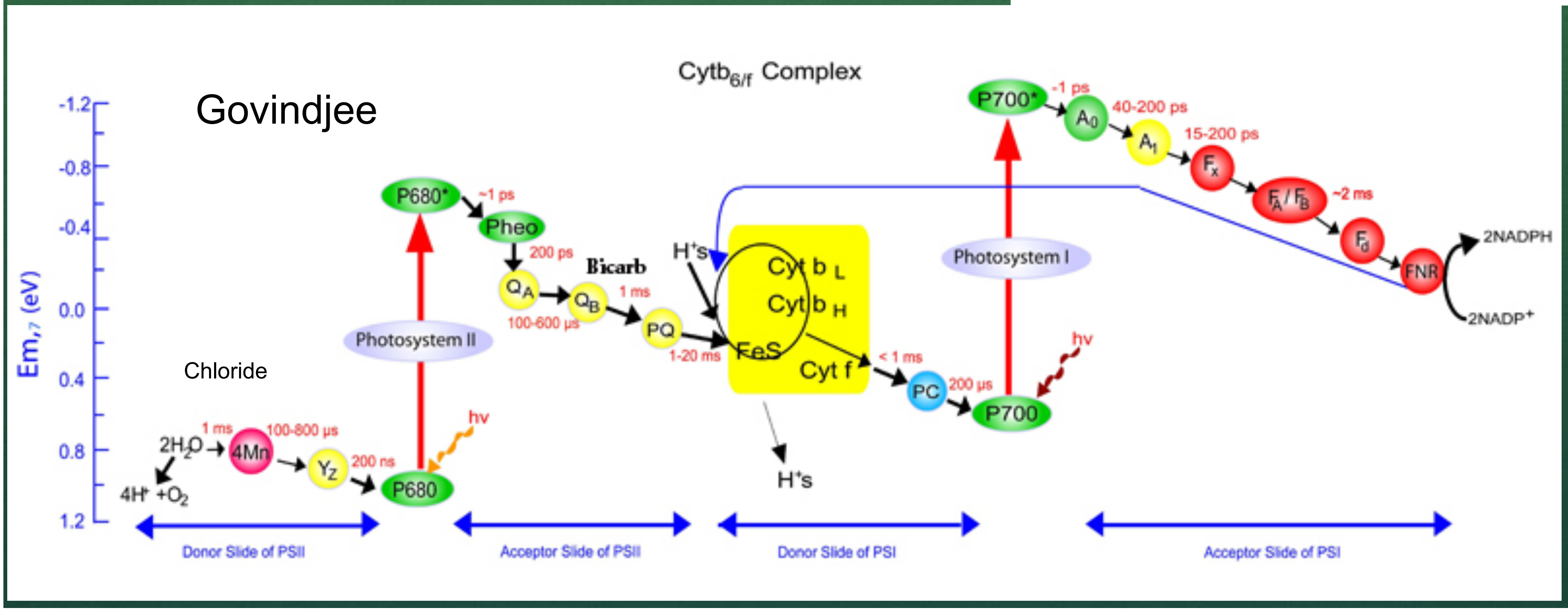


Z-Schemes: Simple (for undergraduate students) to detailed (for graduate students)

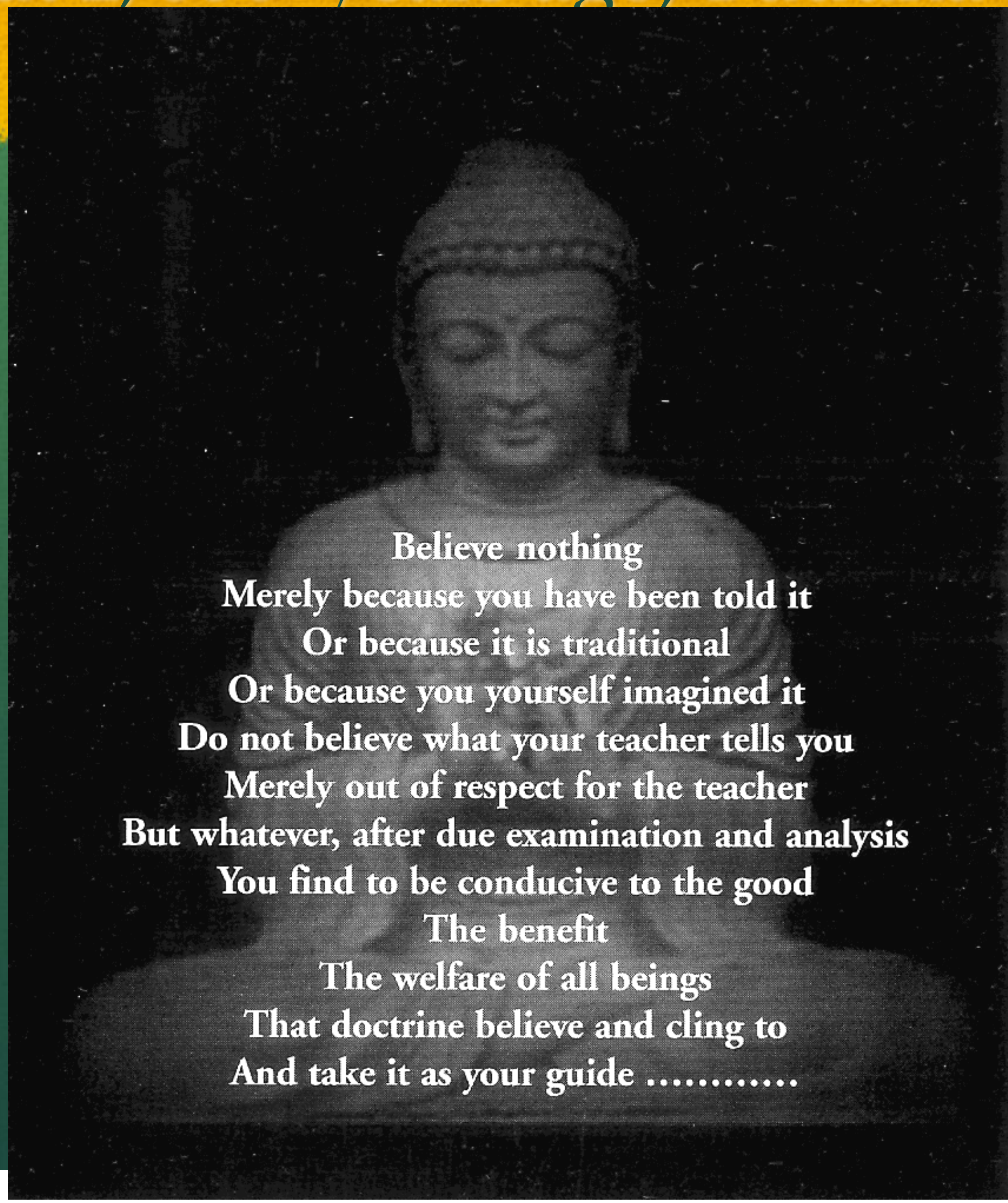


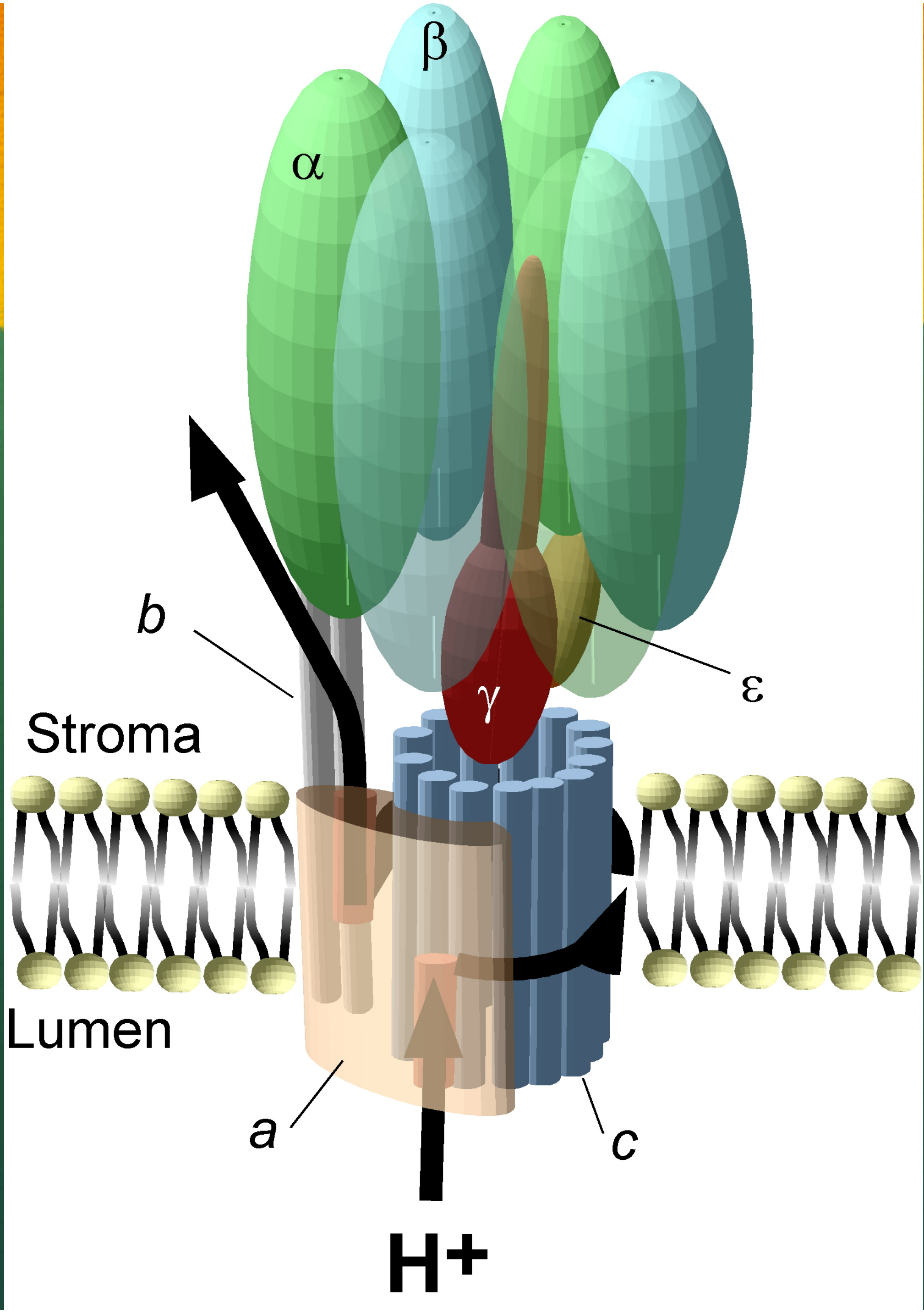






About 2, 550 years ago, Buddha said





ATP Synthesis Rotary Motor: A nonomachine

The energy stored in a pH gradient (and electricpotential)acro-ss the membrane is converted into ATP phosphate energy by coupling mechanical motion to chemical bond formation.

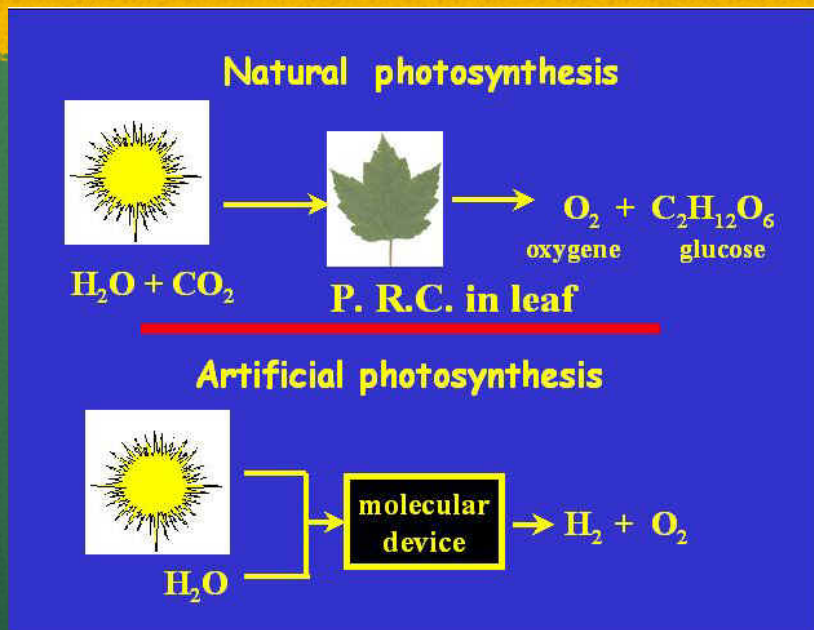
Miscanthus

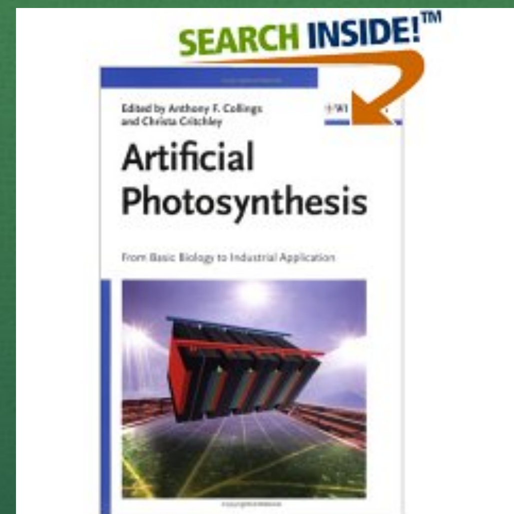
Miscanthus is a perennial grass that has a very high efficiency and a long growing season. Currently used in Europe as a biomass source.
Steve Long and others have begun to exploit this grass for Bioalcohol, the Big British Petroleum grant!

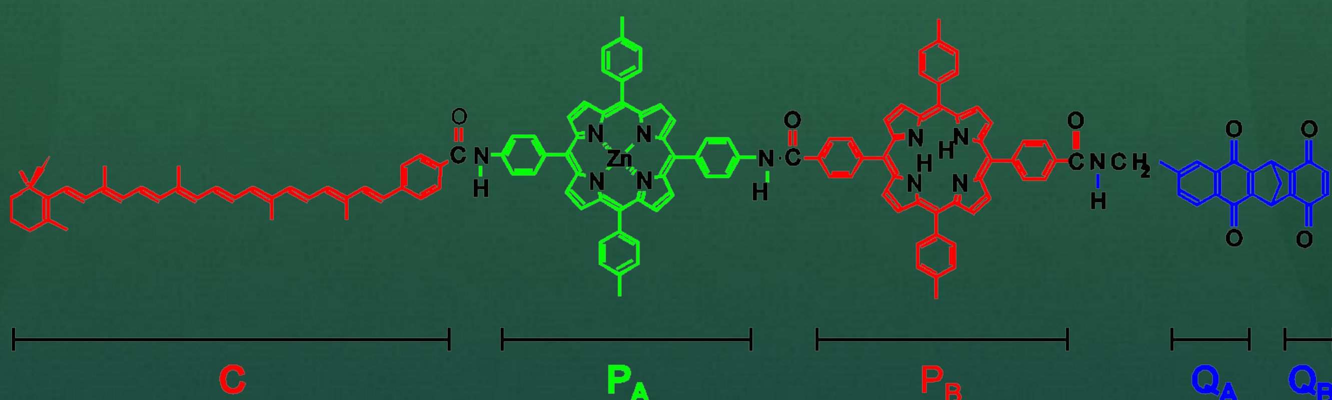
Biodiesel from algae

Algae and cyanobacteria as potential sources of biodiesel

Artificial photosynthesis



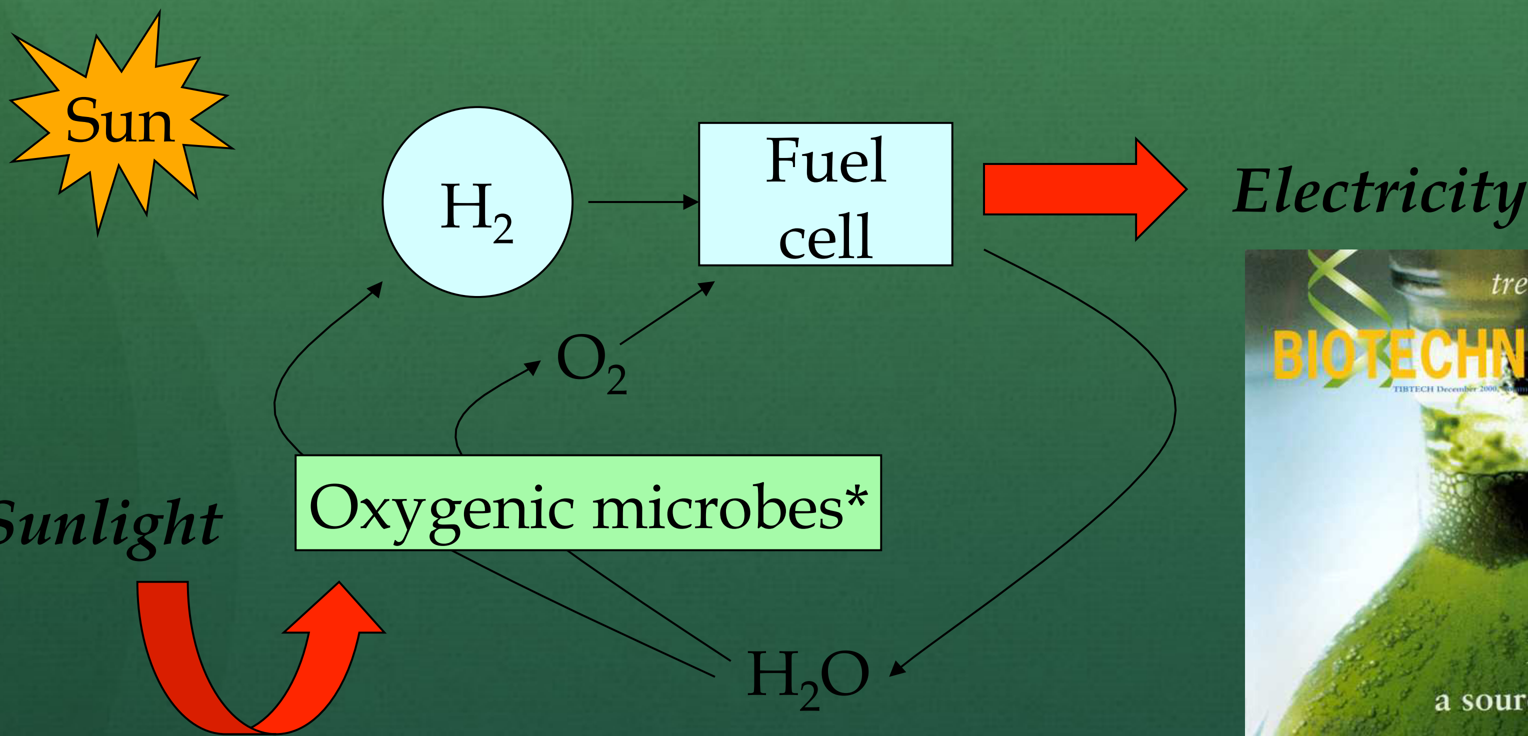


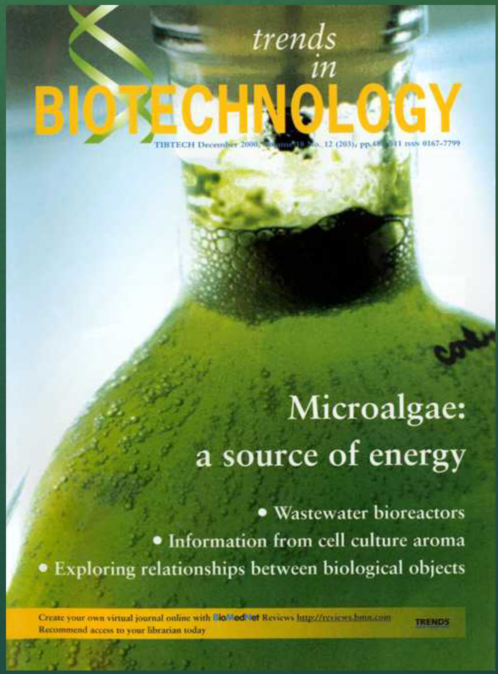


Vision for Renewable Biohydrogen Production/Utilization

Robust and Sustained H_2 Production:

Instead of making food, make hydrogen and thus…





Work being done by Mike Seibert (Colorado) and Tasso Melis (Berkeley)&…

Total solar energy

Conversion efficiency

$$W_h = S\,\varepsilon_i\,\varepsilon_c\,\eta$$

Harvested yield

Interception efficiency

Partitioning efficiency (Harvest index)

I end this discussion by honoring my own professors as well

In the "**City of Photosynthesis**", Urbana, Illinois, once Robert Emerson (1903—1959) and Eugene Rabinowitch (1898—1973) walked on its streets