A Journey for Photosynthesis in Urbana with a focus on Robert Emerson

By Govindjee Govindjee (e-mail: gov@Illinois.edu)

I am grateful to

Christoph Benning and many others at MSU (including Tom Sharkey; Dave Kramer; Astsuko Kanazawa; and Josh Vermaas) for invitation to me so that I can be with you today by zoom (without leaving my home in Urbana) and share some stories with you in East Lansing, Michigan

April , 25, 2022

My focus for the 2022 Anton Lang lecture was to be on:

"A retrospective on photosynthesis research that highlights some historic moments I have witnessed or was involved in "

but I decided to focus mostly on my first professor Robert Emerson

(known to me from September 4, 1956-February 4, 1959)

Yes, I will talk about
life and discoveries of Robert Emerson (1903-1959)
with whom I never published anything since he died too young ; it was on February 4, 1959 , when a tragic plane crash in the East River took his life, before my real experiments had even begun! (Emerson was on his way to attend theBoard of Trustees meeting at Harvard)
Further, the research problem Emerson had me working for my PhD thesis was " Two light effect in Polyhedriella helvetica"; but I had become totally disinterested in it since this alga grew just too slowly , but Emerson kept telling me to do "this and that" and have patience! [I learned recently that Emerson had failed to find "two-light" effect in it]

*My interest in "Photosynthesis" had begun when as "Secretary" of the Botanical Society, at Allahabad University, I had organized a "mock symposium" where we students played the role of discoverers of "Photosynthesis"; I acted as Jan Ingenhousz ; we had included Nobel laureate Otto Warburg, and even mentioned his student Robert Emerson. We dressed up as what we thought those early discoverers may be wearing. – and this fun event remains alive in my mind even today!.

*In my MSc (final), at Allahabad, Prof. Shri Ranjan, who had been a student of F.F. Blackman of UK, asked the students to give " a seminar" in the" Advanced Plant Physiology" class on a topic of interest to us; I chose "Role of Chlorophyll in Photosynthesis", and included Emerson's 1943 paper that baffled me since he showed that photosynthesis was inefficient in the far-red light (where chlorophyll a still absorbed light): This was "The Red drop"

* Right after my MSc., I was appointed "Lecturer", and taught "Plant Physiology" to MSc students and when I lectured – Emerson's 1943 experiment and his unconvincing explanations would crop up…it would constantly haunt me!

**During 1955, I wrote a letter (using an aerogramme) to Professor Robert (Bob) Emerson. After about 2 months, I received an encouraging reply –asking me to apply for admission for PhD, fellowship and a Fulbright travel grant. He wrote that he was solving the "The Red Drop" problem; I received the UIUC fellowship and the Fulbright Travel grant. Yes, Emerson had already discovered the "Two Light Effect", solving the dilemma of the "Red drop" (Emerson et al. , 1957, PNAS).*

The trip

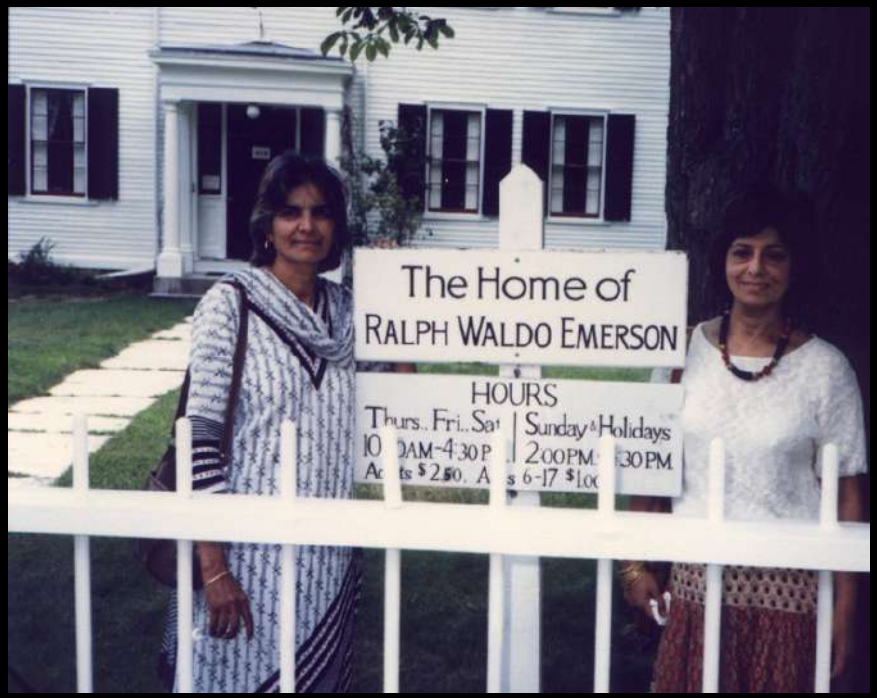
From Allahabad to Urbana, September 1956—by train to Bombay; by plane to London; and. by boat (Queen Elizabeth) from Southampton to New York; then by train to Urbana; and finally in Emerson's Mercedes Benz to the UIUC campus

On the Discoveries of Robert Emerson

Govindjee (e-mail: gov@Illinois.edu) and Rajni Govindjee (govindje@Illinois.edu)
Department of Plant Biology, Department of Biochemistry and Center of Biophysics, University of Illinois at Urbana-Champaign, Urbana, IL , USA..

Christmas, 2020

Robert (Bob)Emerson's grand uncle was the famous Ralph Waldo Emerson (1803--1888), Concord,MA. Bob lived in Urbana at 806 W. Main Street, in Urbana, Illinois; this is still there



From the Archives of the University of Illinois at Urbana-Champaign

- **Dr. Robert Emerson Running Photosynthesis Experiments |**
- **(Dec. 1948)**

1932…….1943……..1957

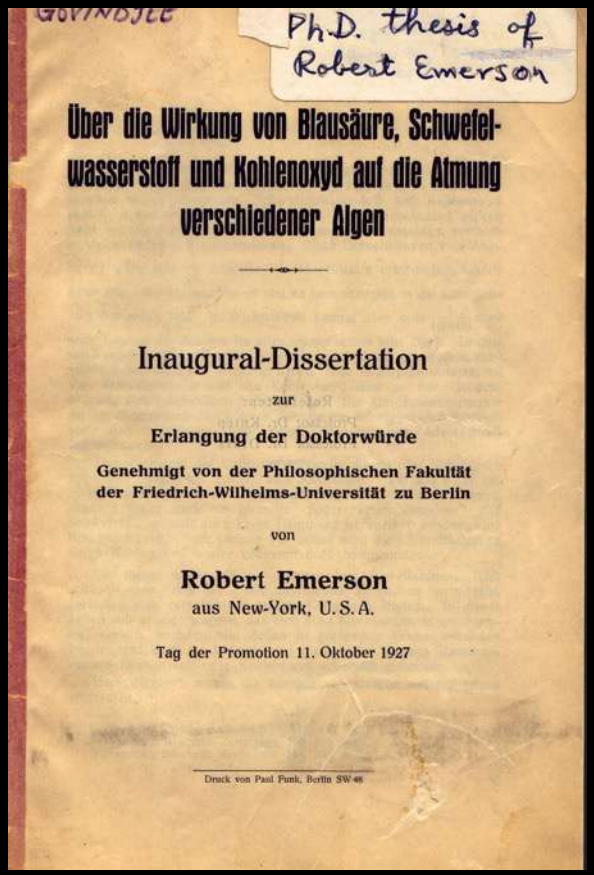
Robert Emerson's Discoveries in Photosynthesis included

*Photosynthetic Unit: hundreds of chlorophyll molecules per reaction center

*Minimum quantum requirement: 8-12 quanta per oxygen molecule

* The "Red Drop" ; "Enhancement" Effect: Two Light Reactions and Two Pigment Systems in Oxygenic Photosynthesis

Robert Emerson: MS in Zoology (1925, Harvard); PhD in Botany (1927, Berlin)



- ***Born in New York City, 1903**
- ***His father was Haven Emerson, Head of NY City Public Health Service**
- ***Hobby: Ice skating/figure skating**
- ***Pacifist and Democratic socialist; Quacker; worked in Japanese Concentration camp on Guyayule**
- ***PhD Advisor: OttoWarburg/ ~32 page thesis on Cyanide -insensitive respiration in Chlorella**
- ***[English translation by Lichtenthaler and Bjorn (2020) Journal of Plant Science Research 36(1-2): 5-24]**

Robert Emerson was not only a major discoverer in photosynthesis, but he was a skilled glassblower, and an artistic carpenter and wore a tie while working

Robert Emerson (1903-1959): at his desk in 157 Natural History Building, Urbana,IL

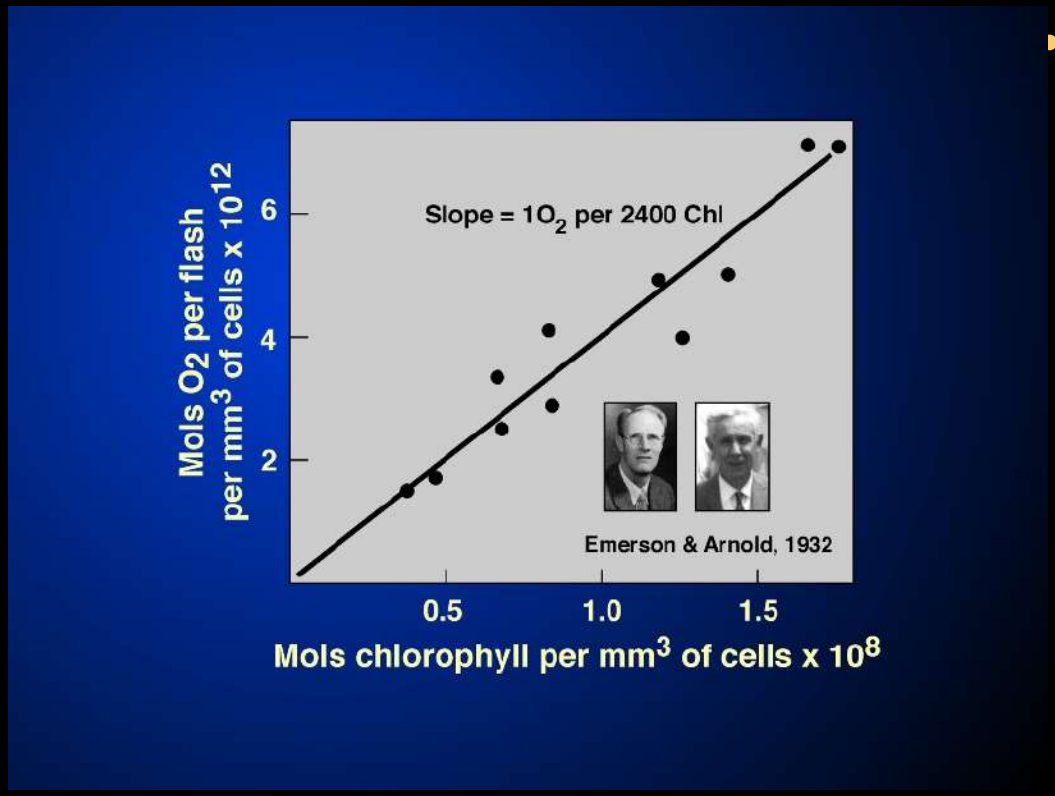
- **Repeat and Remind was his way of teaching; so, I follow him by telling you again about his discoveries: He was the discoverer of**
- *** "Photosynthetic Unit" (1932)**
- ***Minimum quanta needed per oxygen molecule being 8-12 (1941-1958), not 3-4**
- ***The Red Drop(1943)**
- **&**
- ***The Enhancement Effect and the two-light reaction/two photosystem concept (1957-1959)**

William Arnold (1904-2001) was Emerson's first student (as an undergraduate)

- ***Photosynthetic Unit, with his Professor, Emerson (1932)**
- ***Dicoverer of Delayed Light Emission in plants (with Bernie Strehler) (1951)**
- ***Excitation energy migration (with Meek, 1956)**
- ***Thermoluminescence in plants (1957)**
- ***Solid -state picture of Photosynthesis (with Rod Clayton: first charge sep. at 1K, 1960)**

Choules L & Govindjee (2014) Stories and photographs of William Arnold (1904-2001): A pioneer of photosynthesis. Photosynth. Res. 122:87–95

The 1932 discovery of "Photosynthetic Unit" (2400 Chlorophylls per Oxygen)

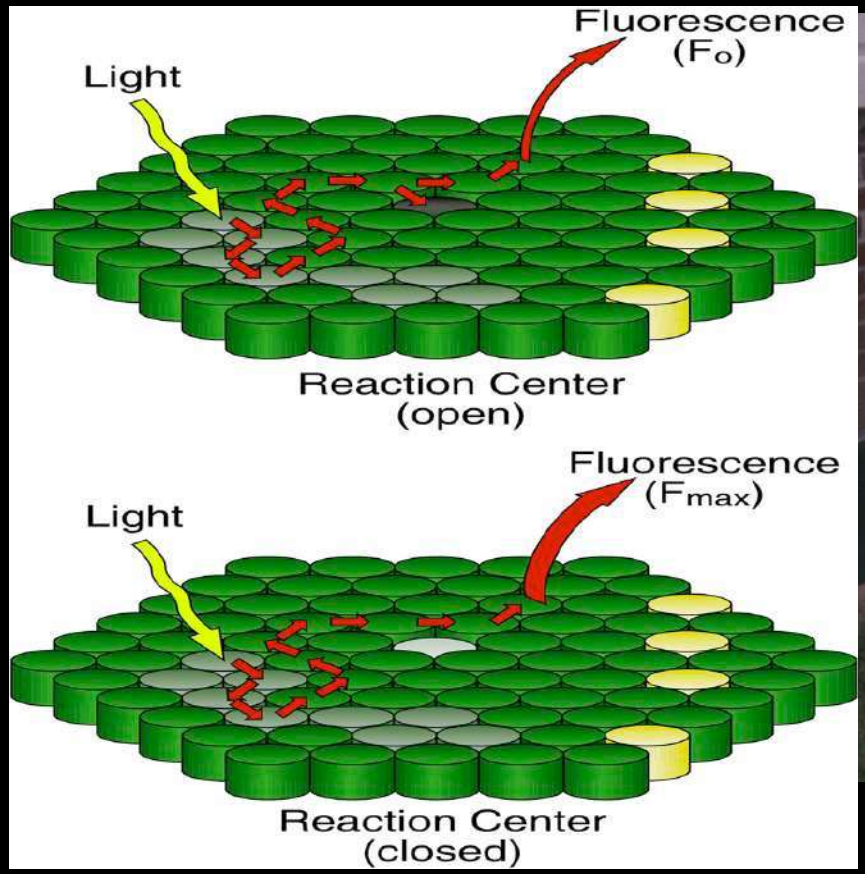


- We need only suppose that for every 2480 molecules of chlorophyll there is present in the cell one unit capable of reducing one molecule of carbon dioxide each time it is suitably activated by light"

These experiments were done at CalTech

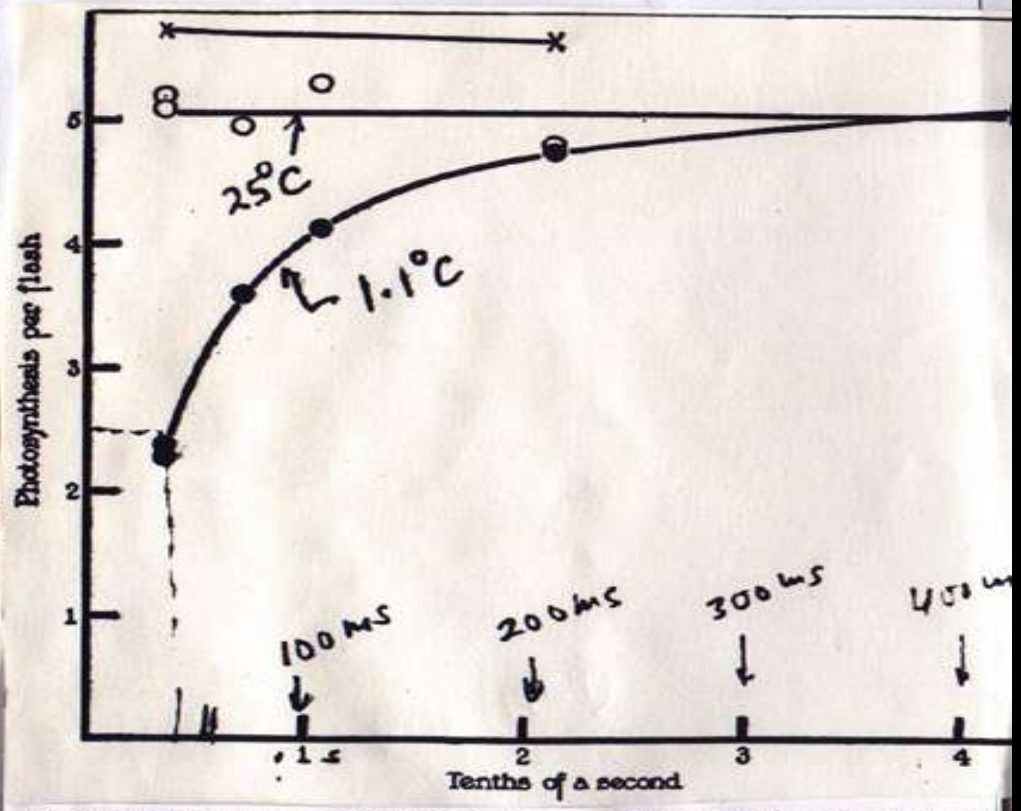
William Kerckhoff Labs of the Biological Sciences, CalTech. The trio is Bill Arnold; Stacy French (had worked with Emerson and Warburg) and Hans Gaffron(had also worked with Warburg)

- ***Hans Gaffron (1902-1979):*** **The 1936 "Concept of Excitation Energy Transfer" and a "Photoenzyme"-explaining Emerson and Arnold (1932) ; later in the 1940s, he discovered hydrogen evolution and hydrogen uptake by algae**



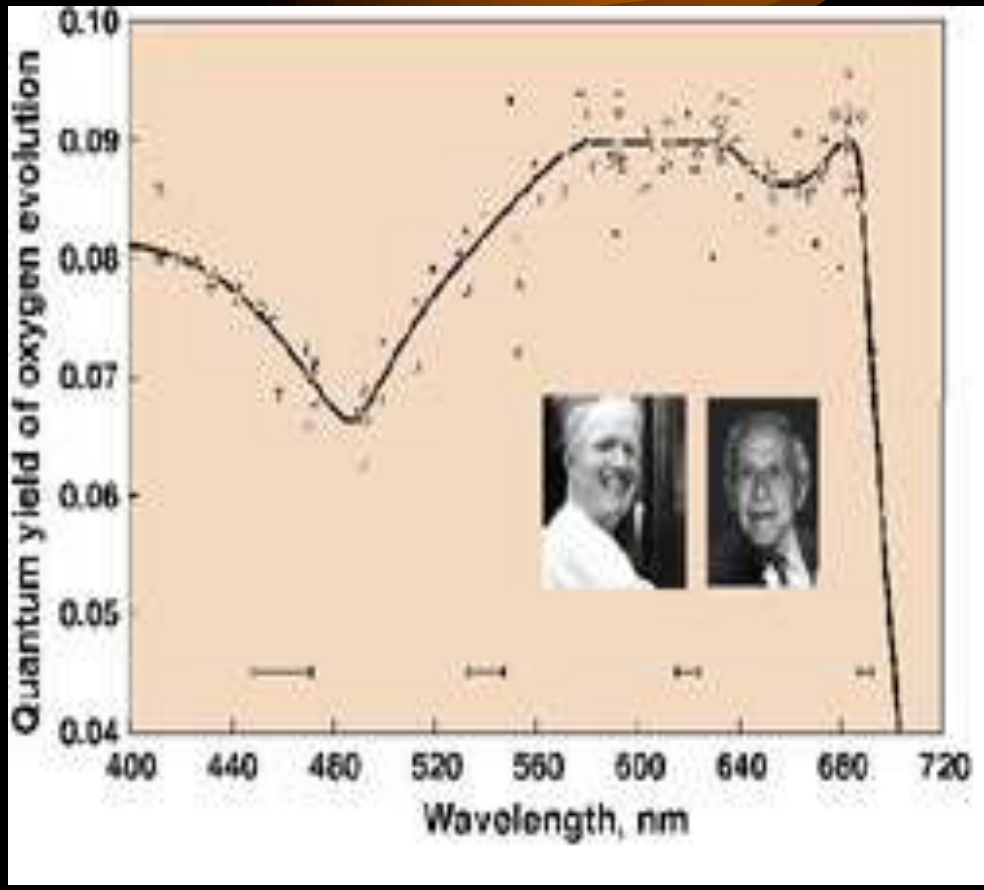
Light and Dark Reactions (halftime, ~30ms at ~1C)

Robert Emerson and William Archibald Arnold (1932)



The "Blackman reaction" (as used by Otto Warburg) has a half time of about 30 ms at 1.1 C, and reaches the maximum at ~ 400 ms; it is much faster than 30 ms at 25 C as it already reaches the maximum by 30 ms.

Now back to *"The Red Drop" in the Quantum Yield of Photosynthesis, which was discovered at the Carnegie Inst, Stanford (1943, with Charleton Lewis)- remember my problem understanding it in 1954*



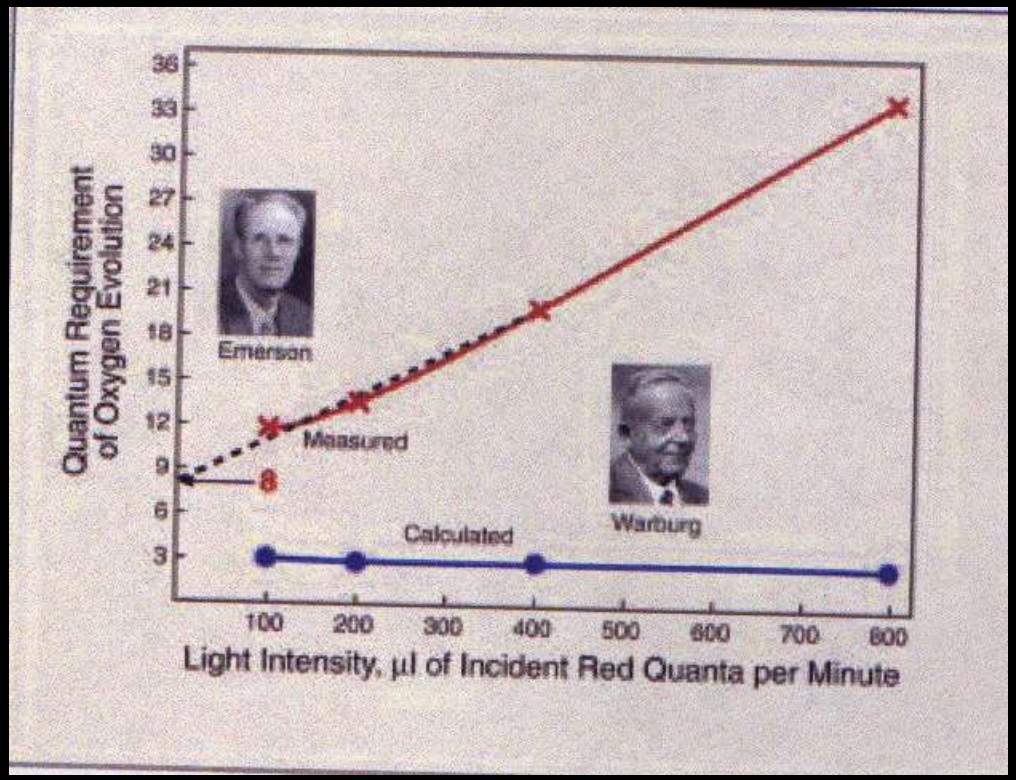
Otto Warburg (1883-1970):Emerson's "Professor"

- 1931 Nobel Prize in Physiology and Medicine: respiratory enzymes
- The minimum quantum requirement for 1molecule of O_2 in photosynthesis is 3-4 (1923-1969); the photolyte hypothesis (Warburg was wrong; see K. Nickelsen and Govindjee's 2011 book: The Max Quantum Yield Controversy: Otto Warburg and the Midwest Gang, Bern)
- Discoverer of many phenomena in photosynthesis (including "light-induced respiration"; roles of chloride and bicarbonate in Hill reaction; we, however, showed that he was misguided in his interpretation of " bicarbonate" effect).

Otto Warburg(publications in 1949 and 1950)

- **It was at NIH that Warburg did experiments confirming (but not accepting) Emerson's 8-10 quanta for cells in carbonate-bicarbonate buffer (statement is hidden in the "appendix"), but not in acid culture medium where they obtained a value of 4. Emerson showed these, in 1955, to be due to " transient artifacts"**

Was the battle over in1969? Warburg passed away in 1970

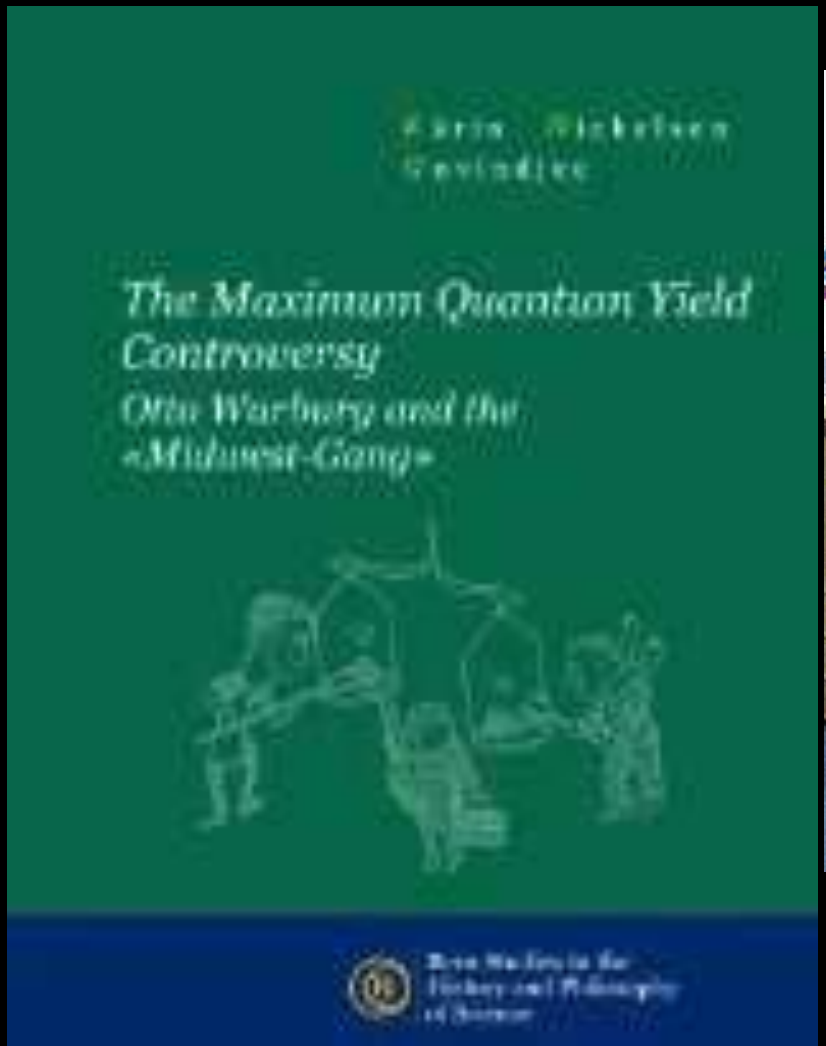


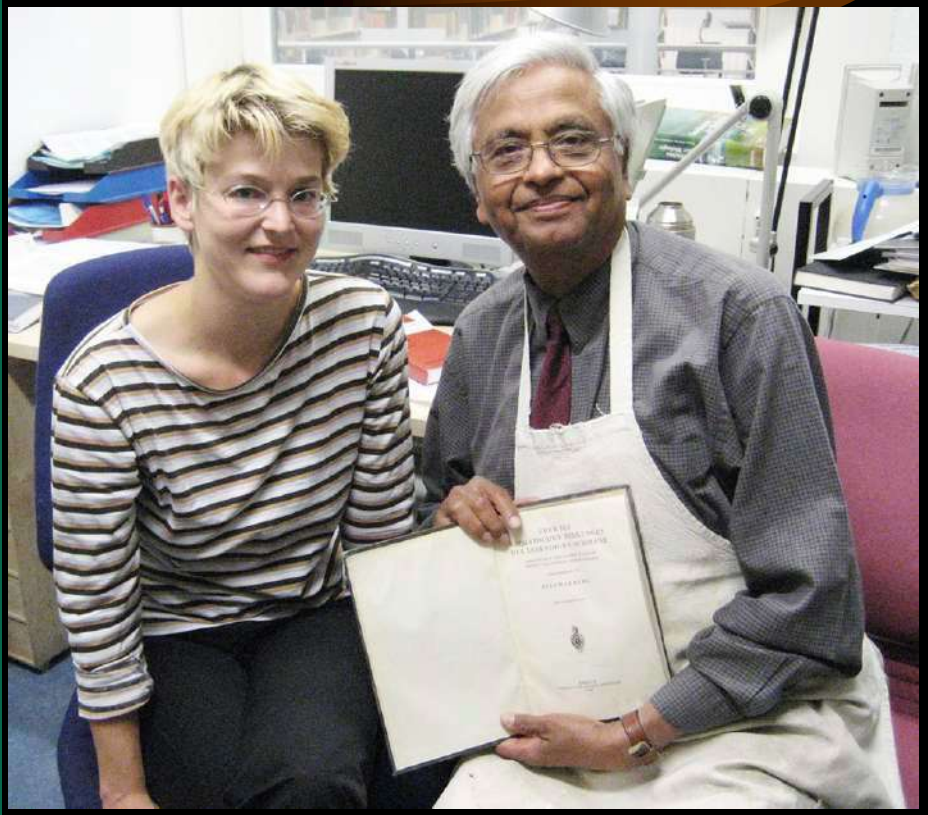
- Warburg,Krippahl and Lehman (1969) measured a minimum quantum requirement of 12 at the lowest intensity they used, but calculated a value of 3 using an ingenious but erroneous "photolyte" intermediate.
- Read about it in Govindjee (1999) Photosynth Res 59: 249-254.

After' Emerson's death in 1959, and at meetings (once in 1963 in France) and beyond, Warburg was heard saying that "Now, the problem is solved";
"Emerson did not use the right conditions: young synchronous cultures ; 10 % CO_2 ; and blue catalytic light and thus he had the wrong results". Rajni and I finally decided to check it all out and in 1968 showed , under these conditions, that the minimum quantum requirement (per oxygen molecule) is TWELVE, NOT FOUR.. Warburg did NOT cite this paper in his 1969 paper….

R. Govindjee, E. Rabinowitch, and Govindjee (1968)Maximum Quantum Yield and Action Spectra of Photosynthesis and Fluorescence in Chlorella.Biochim. Biophys. Acta 162: 530-544.

I request you to read the 2011 book of Nickelsen and Govindjee to know all about the controversy betweenEmerson and Warburg

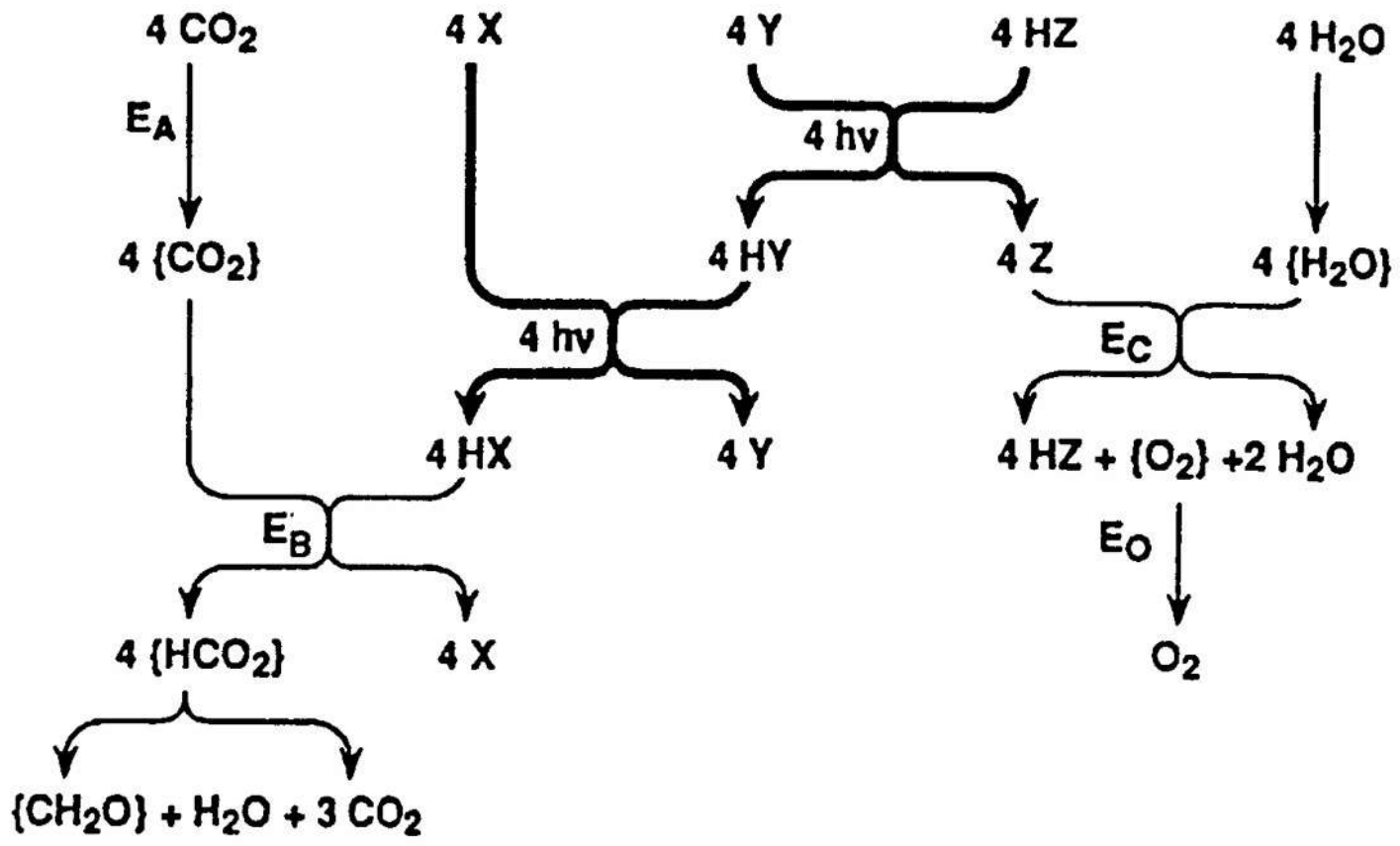




A Great Mentor ***Eugene Rabinowitch (1901-1973): in 277 Morrill Hall, Urbana, 1967 (see: G.Govindjee, G.Papageorgiou and R. Govinndjee (2019) Photosynth Res 141 (2): 143-150.***

- ***He wrote the masterpiece treatise on Photosynthesis (1945-1956)**
- ***Discovered Photogalvanic Effect(1940s)**
- ***First quantitative measurements on lifetime, and quantum yield of Chl fluorescence (1956-1958)**
- **Messiah of Peace, & Science & Society in the World**
- **"His contributions to scientific progress, and to our very culture have been so deep, so broad, so prolific that it is impossible for any one person to appraise them all".**

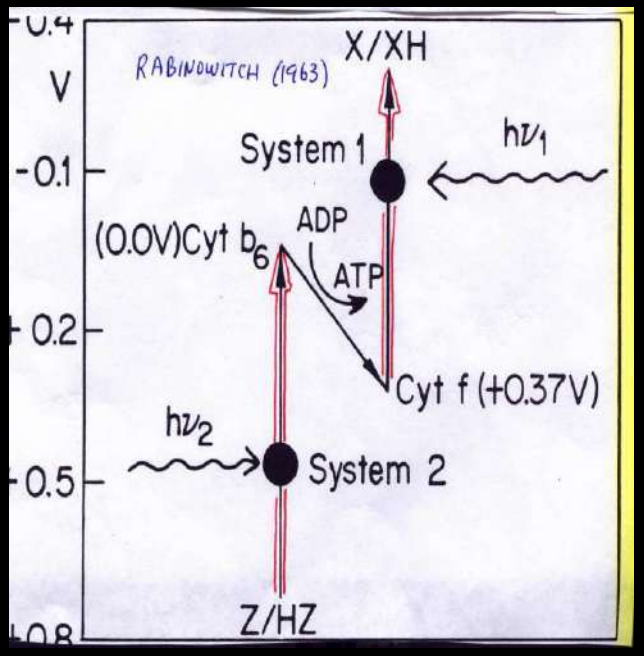
Scheme # 7.V on p. 162 (Rabinowitch, 1945) to explain 8 quanta/oxygen (based on Franck&Herzfeld,1941) The Basic Idea of Two Light Reaction Scheme



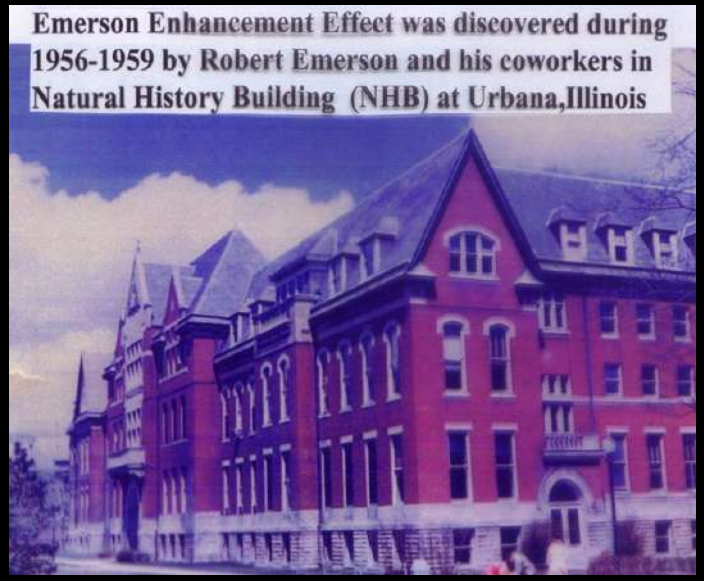
Eugene Rabinowitch (1956)

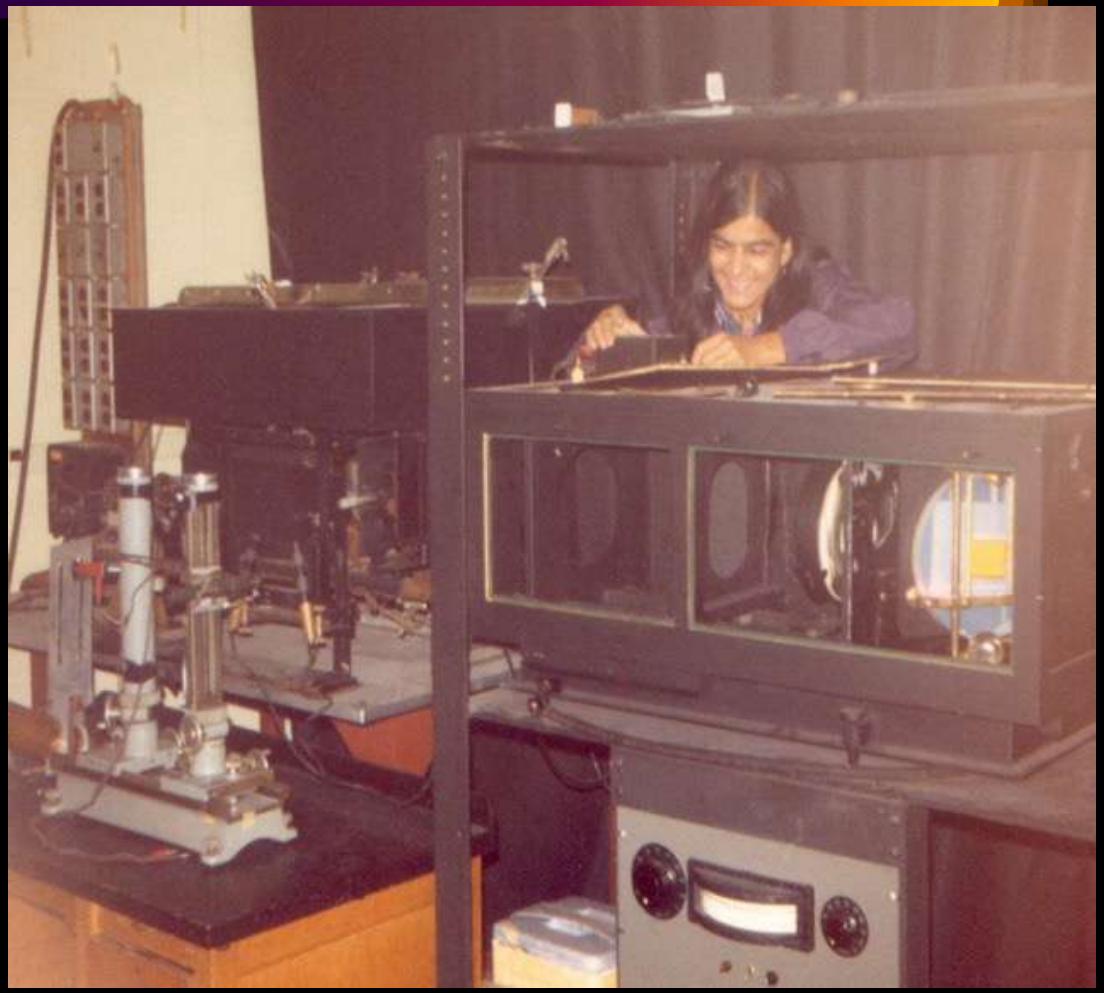
- **"…two quanta will be needed to transfer each of the four required H atoms (or electrons), first from water to the cytochrome, and then from the cytochrome to the final acceptor.**

(p.1862,Vol.II,part 1,para 2, lines 15-19, 1956)



Where was Emerson Enhancement Effect discovered? 155-157 NHB--And what instrument was used?

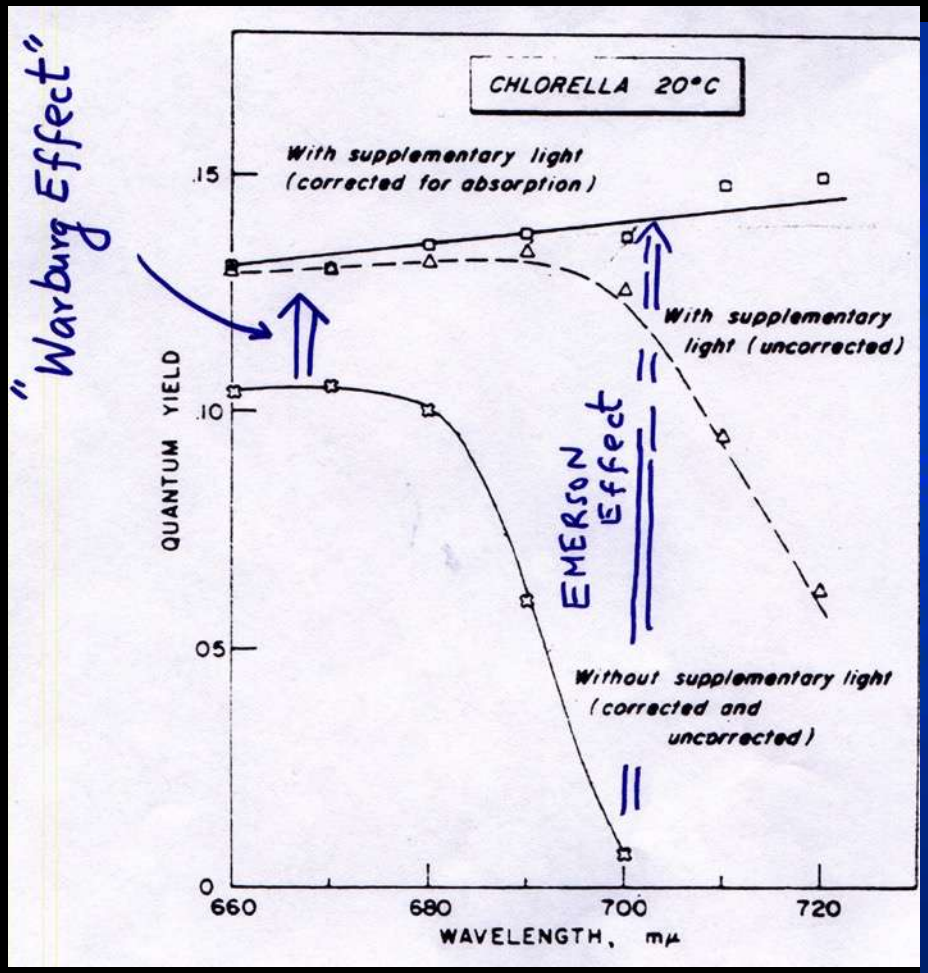


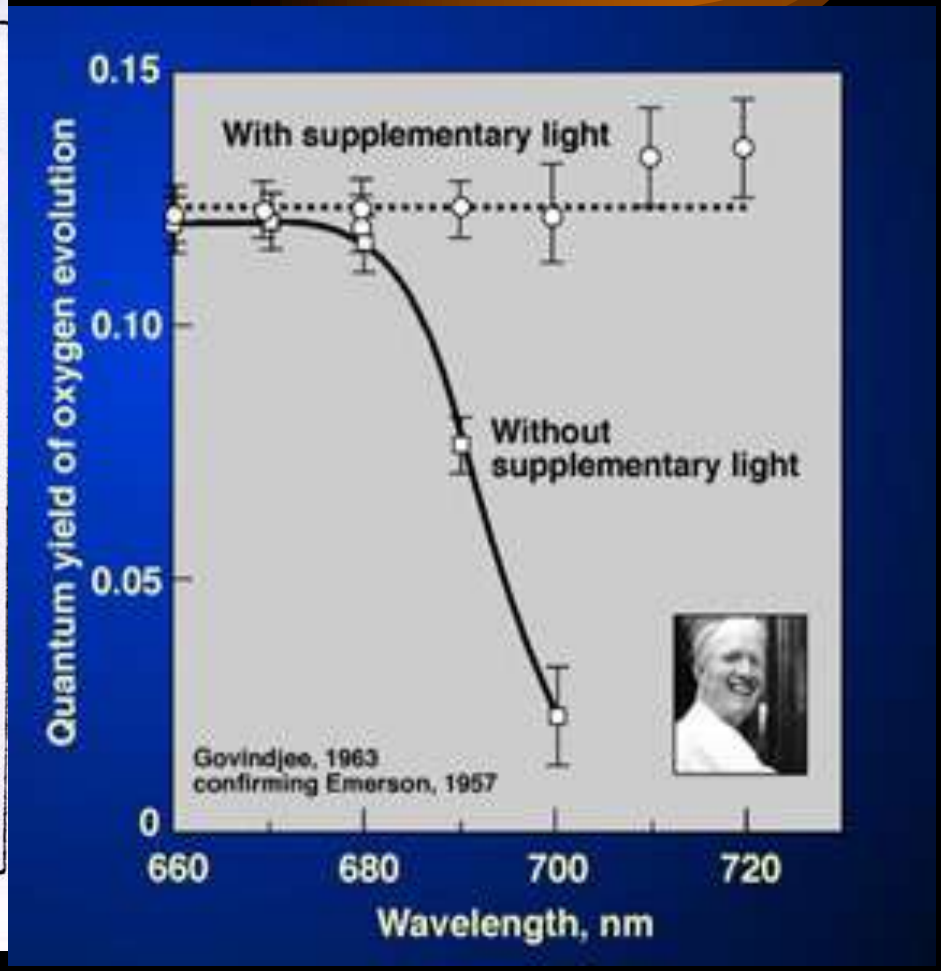


A Glimpse of Bob Emerson's instruments

Setup for giving the second beam of light; Emerson used Hg Cd lamp to get fixed selected wavelengths of light , and he used a monochromator to get "far red" light (the first beam). I will tell you soon what I did!

The Emerson Enhancement Effect (1957): What is it?

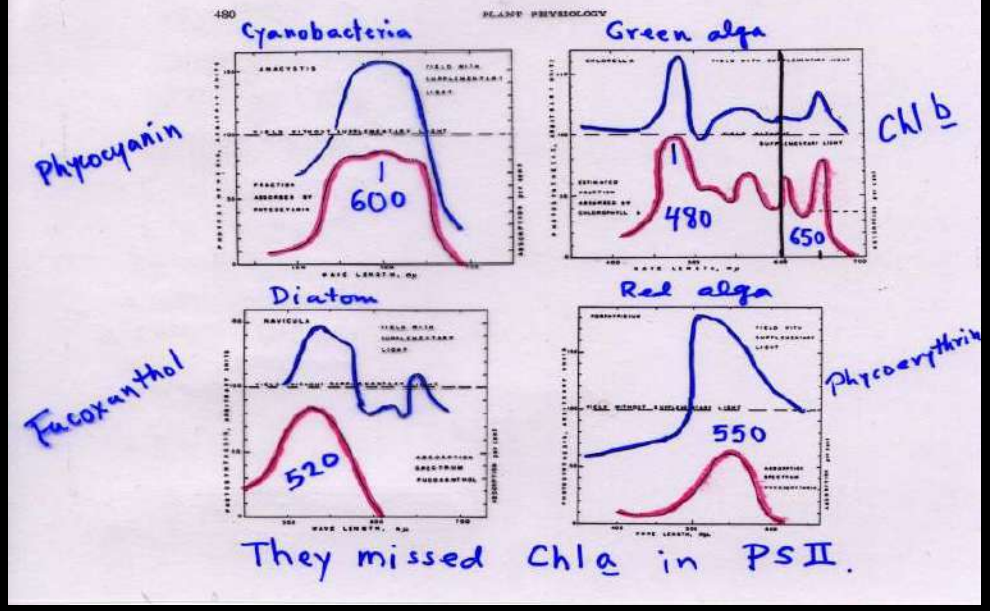




Action Spectra of the Emerson Enhancement Effect (1958;left): Rajni, Emerson and Chalmers-Bloomington, Indiana (right). Photo by Govindjee

THE EMERSON EFFECT

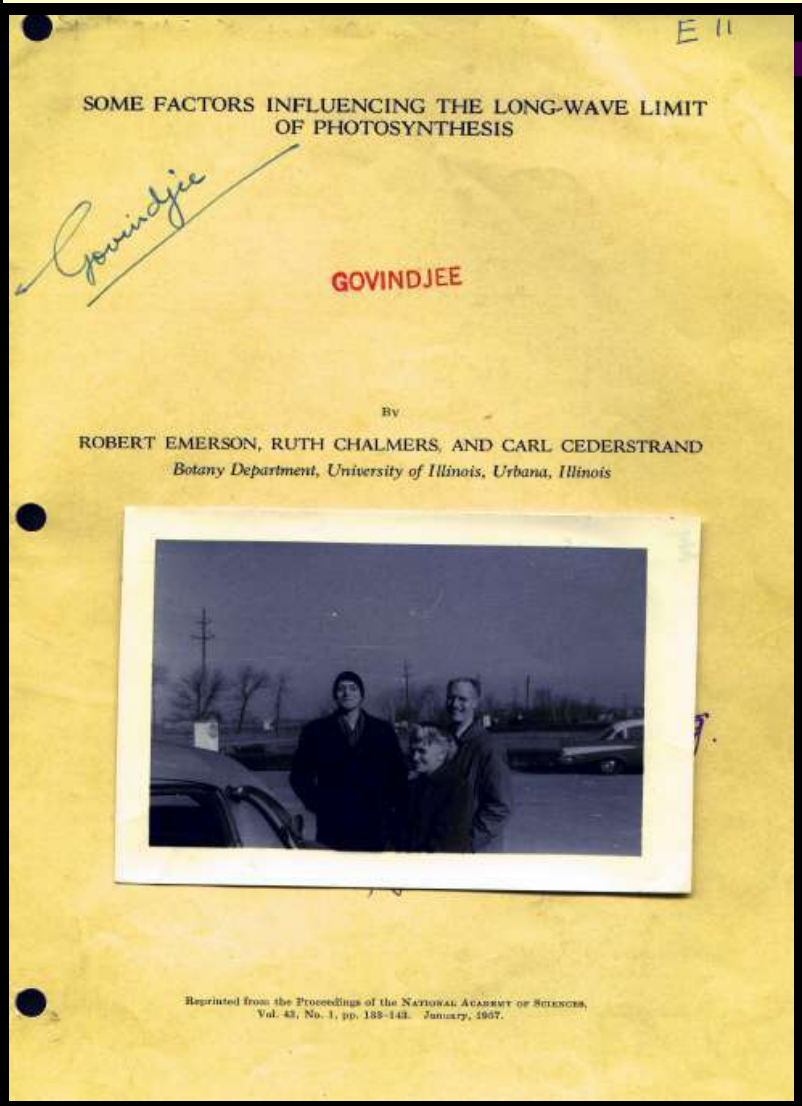
Robert Emerson and Ruth V. Chalmers (1958) "Speculations Concerning the Function and Phylogenetic Significance of the Accessory Pigments of Algae". The Phycological Society of America News Bulletin, Vol.XI, No. 35, 1958, pp. 51-56.



Emerson's 1958 lecture has been just resurrected

Govindjee G (2022) Discovery of auxiliary pigments working in synchrony with chlorophyll *a* in algae, followed by a reprint of: Emerson R and Chalmers RV (1958) "Speculations concerning the function of the accessory pigments of algae" from the News Bulletin of the Phycological Society of America (PSA), X1 (35), November 1958. Phycological Newsletter, a publication of the PSA, 58 (1):11-20, March 2022.

The first paper on the Enhancement Effect: the classical 1957 PNAS paper of Emerson



E 11

SOME FACTORS INFLUENCING THE LONG-WAVE LIMIT OF PHOTOSYNTHESIS

Govindjee

GOVINDJEE

By

ROBERT EMERSON, RUTH CHALMERS, AND CARL CEDERSTRAND

Botany Department, University of Illinois, Urbana, Illinois

Reprinted from the Proceedings of the National Academy of Sciences, Vol. 43, No. 1, pp. 133–143. January, 1957.

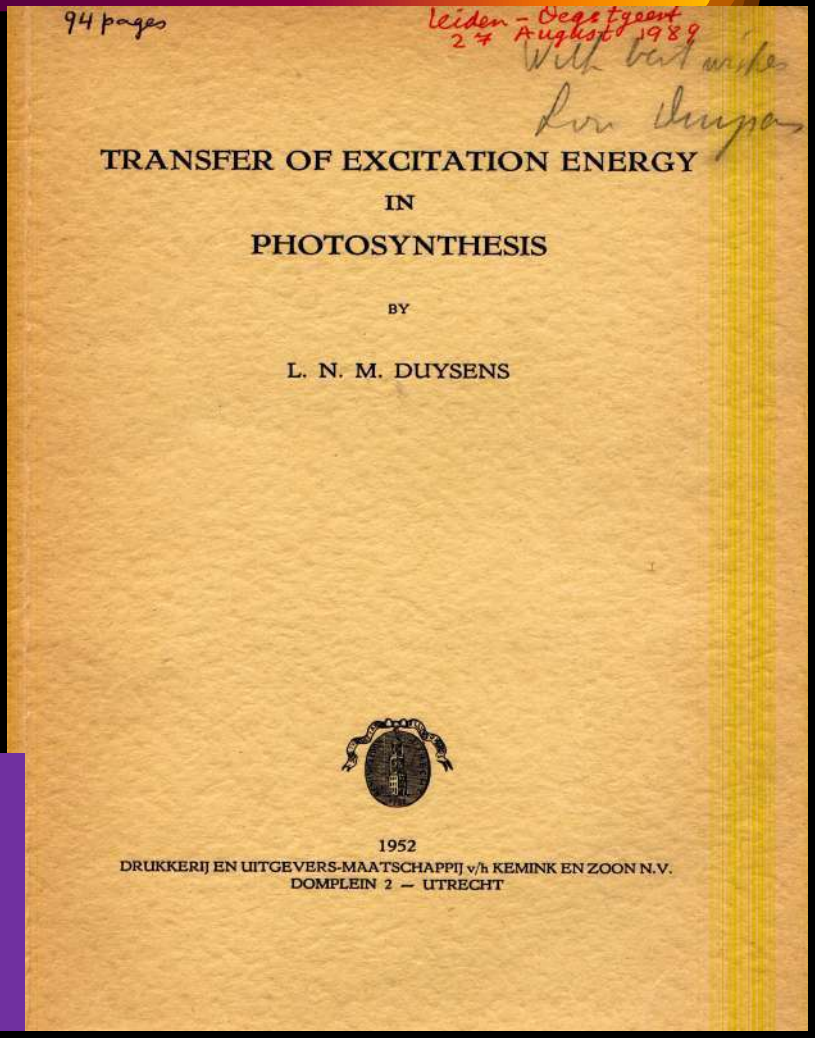
- The photo that I pasted on the cover of this classical paper shows Emerson's coauthors (Carl Cederstrand and Ruth Chalmers) (Photo, 1958)

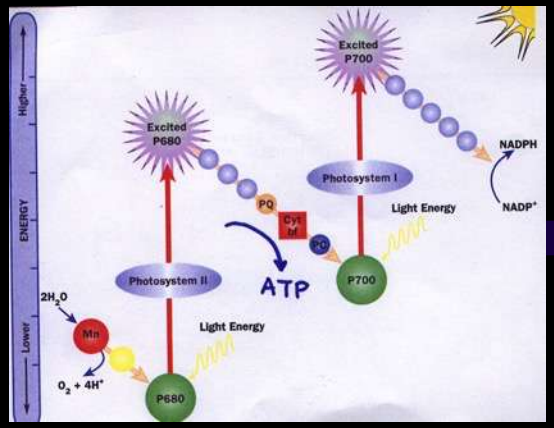
A 1958 Celebration in Urbana:Tom&MaryJeanne Bannister;Ruth Chalmers;Tita Emerson; Eugene Rabinowitch;Rajni Varma -Govindjee; Robert Emerson; Marcia & Steve Brody, Photo by Govindjee

Emerson's conclusion that Chl a runs one system and accessory pigments another made no sense because Lou Duysens had shown in 1952 that the latter transfer energy with high efficiency to Chl a

Photo of Duysens and Rabinowitch

Govindjee, Pulles MPJ (2016) **Louis Nico Marie Duysens (1921-2015)A leading biophysicist of the 20th century.** Photosynth Res 128:223-234



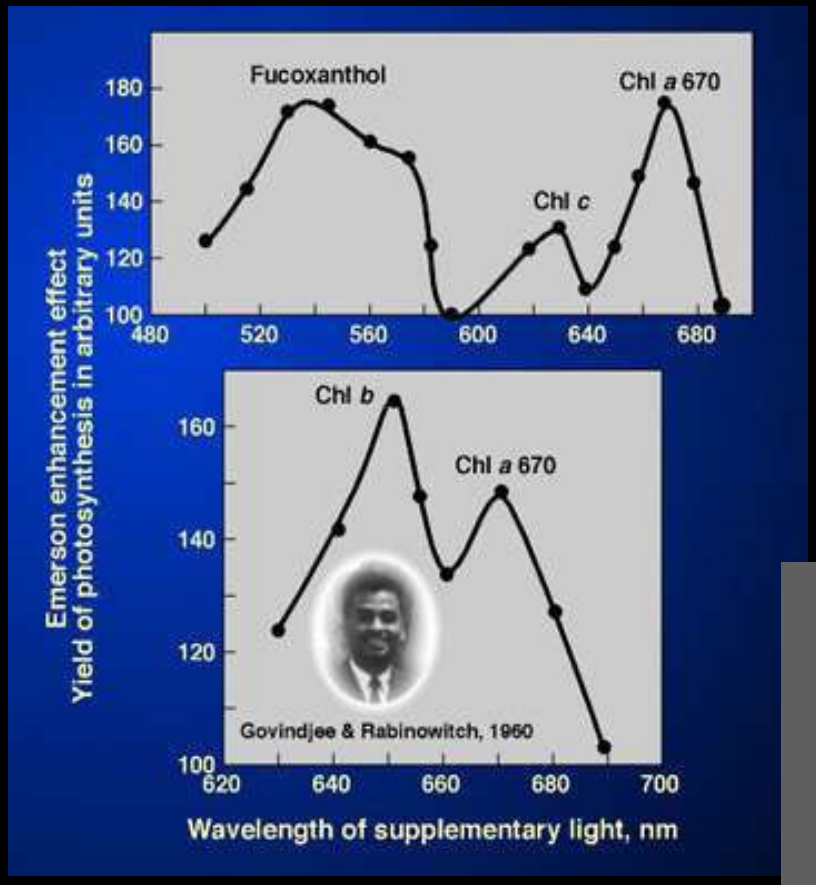


Robin Hill (1899-1991)

Robert (Robin) Hill with Georgiou Forti (Photo by Govindjee, 1969?)

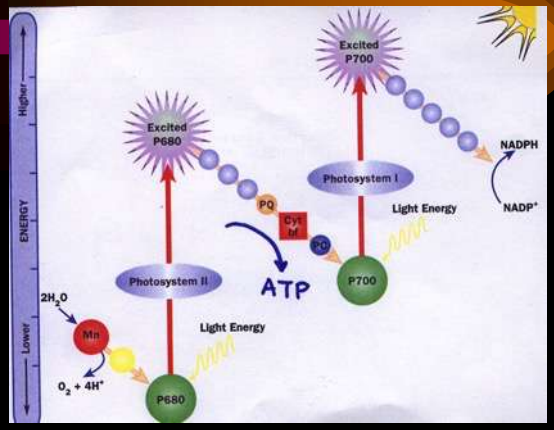
- Discoverer of the "Hill Reaction"; and some cytochromes.
- The famous 1960 "Z" scheme- although the concepts were already there.
- **" In the end, when everything is settled, few of us perhaps will really desire to look back at it at all"**

In 1960, the role of Chlorophyll a in the short-wave system (PSII) was discovered (Govindjee & Rabinowitch, Science). In addition, Govindjee et al. discovered, also in 1960, the quenching of blue- light excited Chl a fluorescence by far-red light (PSI), another evidence of "two-light effect".



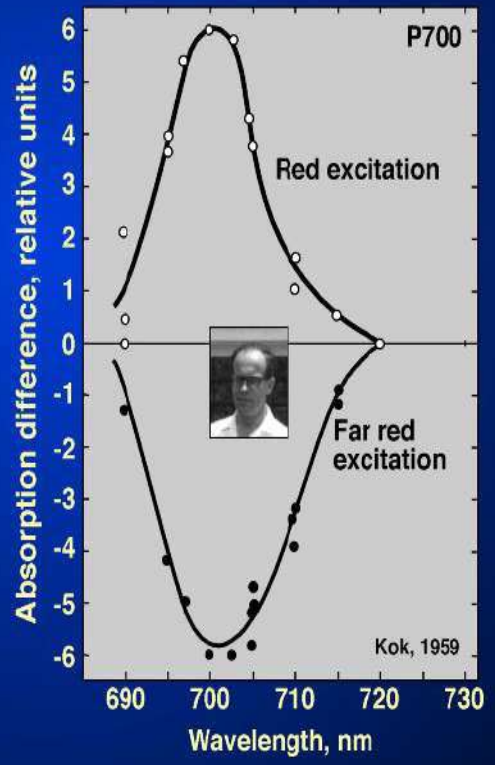
Govindjee at the door that led to the Lab where all discoveries were made in 157 NHB (it is now totally changed- including the room number)

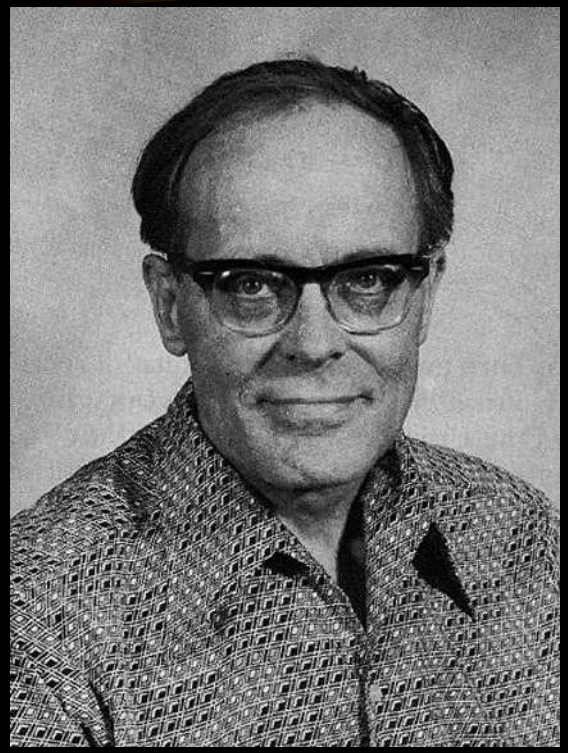
The "creator" of the Z-Scheme: Robin Hill



- ***During 1960, there were several schemes and discussions at a "Light Life" conference ;*Robin Hill, published the first "Z" Scheme (theory) with Fay Bendall (1960); *During 1961, there were schemes by Lou Duysens & Jan Amesz; Horst Witt; and Dan Arnon (who went from 2 light reations, to one and then to three??) : See Govindjee et al. (2017) Photosynth Res 133: 5-15 for the Evolution of the Z-Scheme.**

Bessel Kok (1918-1979) had discovered P700, the reaction center of PSI, in 1956-1957; in 1959, he showed the two-light effect on it



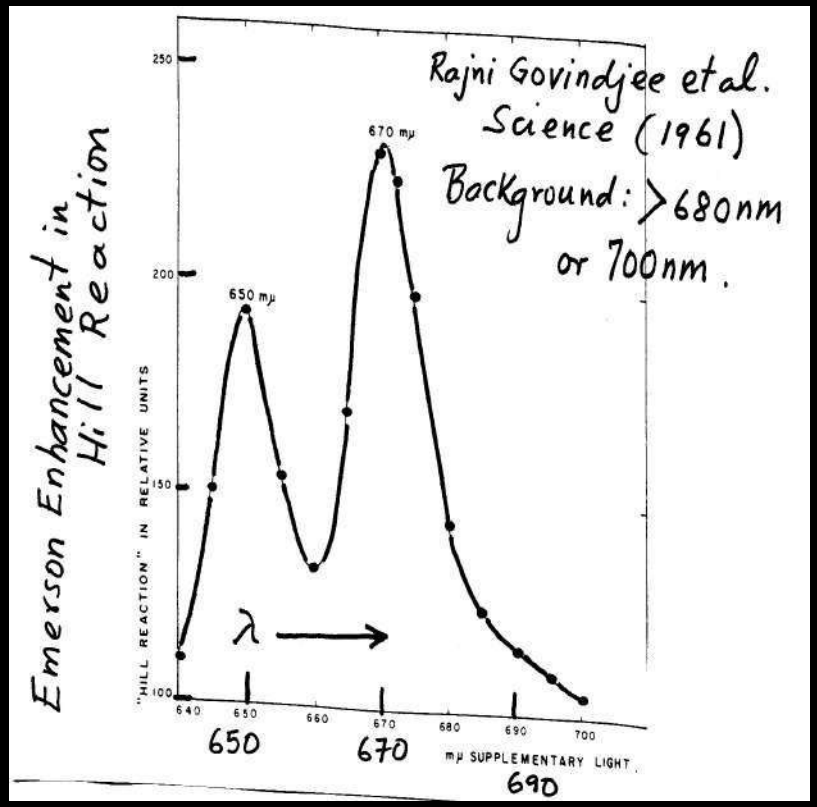


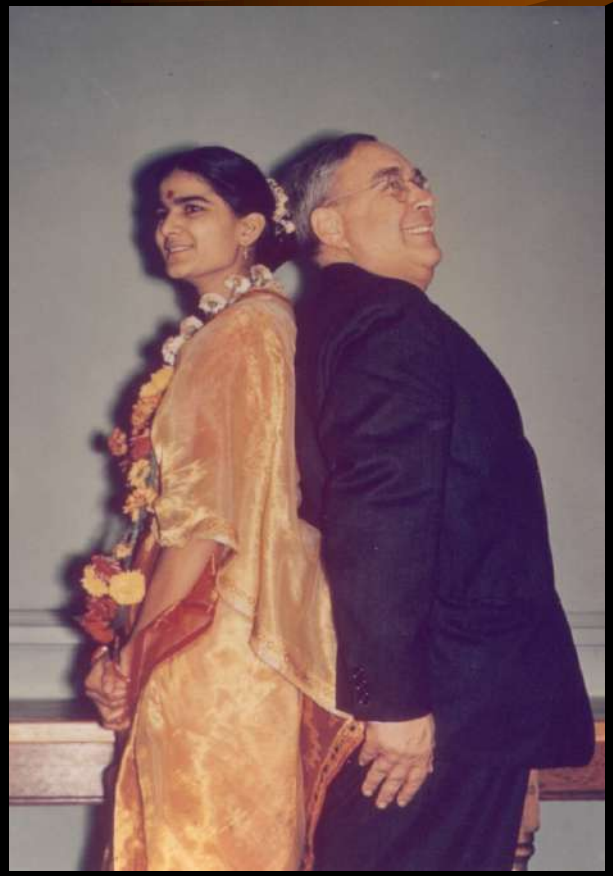
Lawrence Blinks ; a laboratory is named after him at Hopkins Marine Station

Lawrence (Larry) Rogers Blinks (1900- 1989): See Thorhaug et al. (2009), Photosynth Res

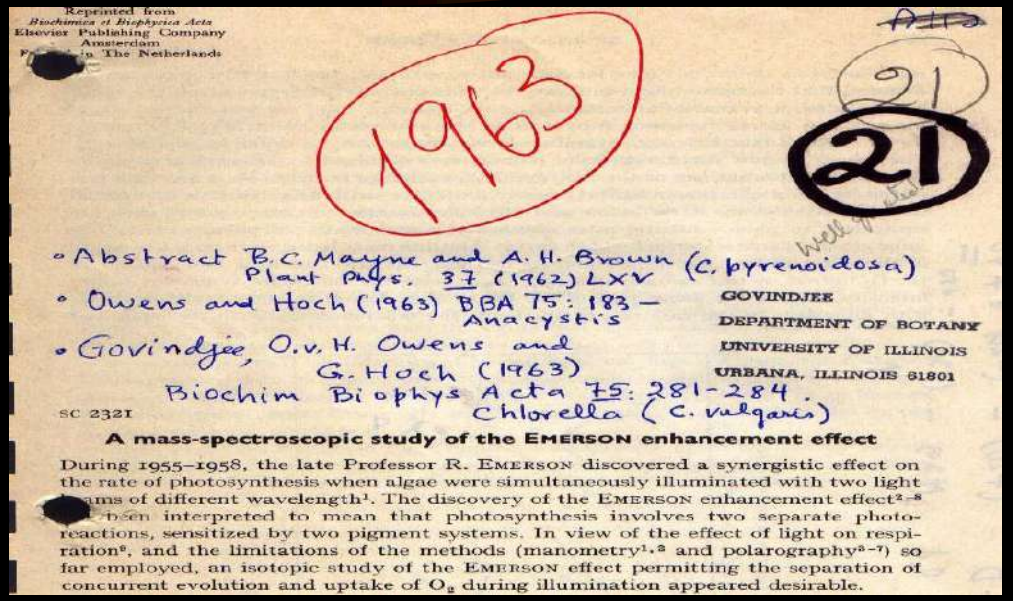
- 1950: Development of Haxo and Blinks Oxygen electrode, and action spectra of photosynthesis
- 1955-1957: Chromatic transients in algae..related it to respiration (citing Emerson 1941)
- Gave a boring lecture at 1972 Gatlinburg conference when Bessel Kok and Govindjee chatted in the back—Hope none of you are doing it for me

Rajni Govindjee showed (in 1961) that the Enhancement Effect was in the Hill Reaction. Thus, it could not be in respiration as Blinks thought. In 1962, with George Hoch, she and I discovered Emerson enhancement in NADP reduction.





During 1962-1963, George Hoch, Olga v.h. Owens, soon joined by Govindjee, showed by oxygen-18 mass spectrometry, that the two-light effect was indeed in photosynthesis.



Reprinted from
Biochimica et Biophysica Acta
Elsevier Publishing Company
Amsterdam
[illegible] The Netherlands

1963

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- Abstract B.C. Mayne and A.H. Brown (C. pyrenoidosa) Plant Phys. 37 (1962) LXV
- Owens and Hoch (1963) BBA 75: 183 – Anacystis
- Govindjee, O.v.H. Owens and G. Hoch (1963) Biochim Biophys Acta 75: 281-284. Chlorella (C. vulgaris)

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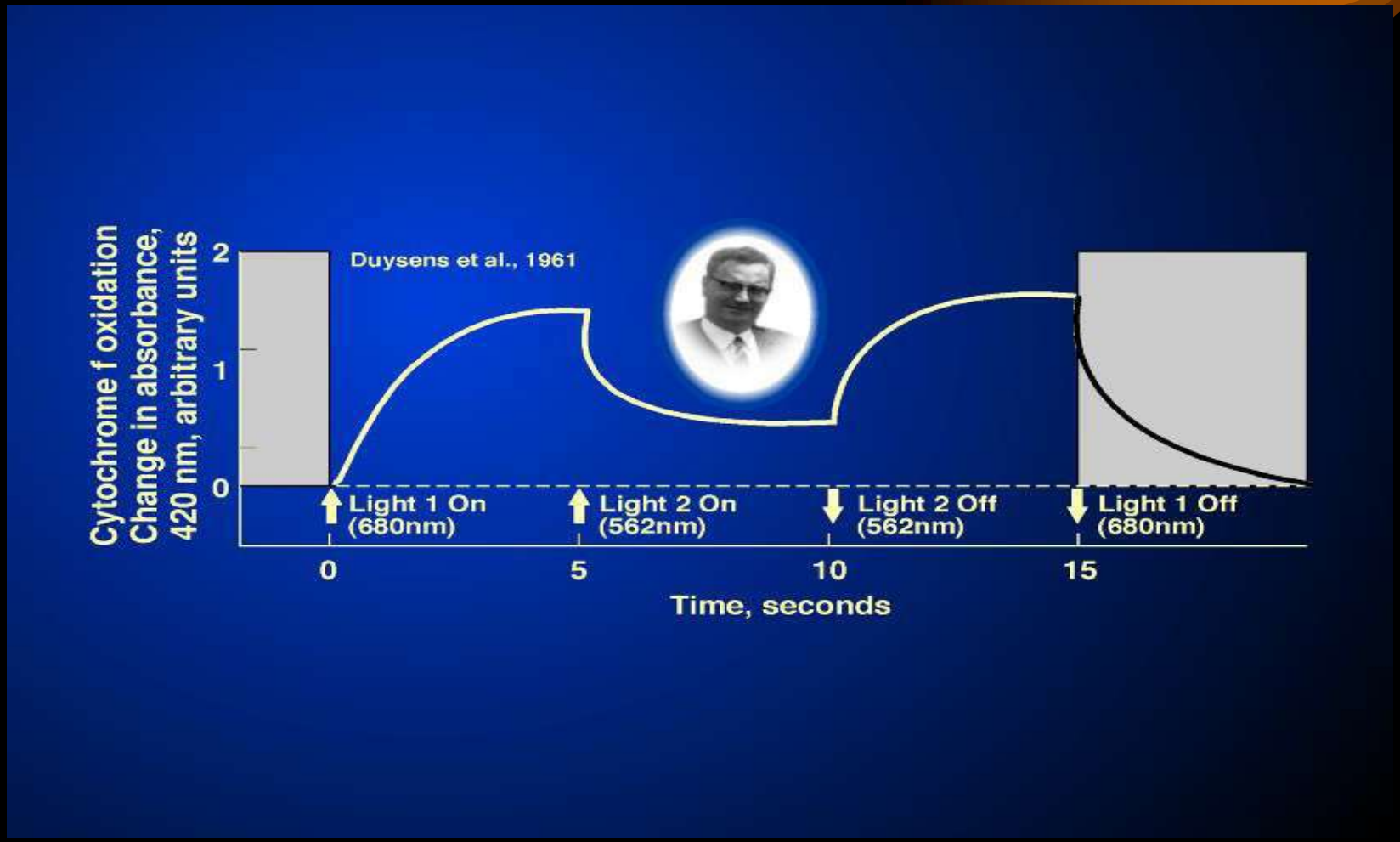
SC 2321

A mass-spectroscopic study of the EMERSON enhancement effect

During 1955–1958, the late Professor R. EMERSON discovered a synergistic effect on the rate of photosynthesis when algae were simultaneously illuminated with two light [illegible]ams of different wavelength[1]. The discovery of the EMERSON enhancement effect[2–8] [illegible]been interpreted to mean that photosynthesis involves two separate photo-reactions, sensitized by two pigment systems. In view of the effect of light on respiration[9], and the limitations of the methods (manometry[1,3] and polarography[3–7]) so far employed, an isotopic study of the EMERSON effect permitting the separation of concurrent evolution and uptake of O_2 during illumination appeared desirable.

Lou Duysens; George Hoch And Warren Butler

Lou Duysens and Jan Amesz's 1961 key experiment in Porphyridium



Reaction Center of PSII, P680 (1965-1969)

Sonderabdruck aus der ZEITSCHRIFT FÜR NATURFORSCHUNG Band 22 b, Heft 6, 1967
Verlag der Zeitschrift für Naturforschung, Tübingen

A Second Chlorophyll Reaction in the Electron Chain of Photosynthesis
— Registration by the Repetitive Excitation Technique —

G. Döring, H. H. Stiehl, and H. T. Witt

Max-Volmer-Institut, I. Institut für Physikalische Chemie der Technischen Universität Berlin

(Z. Naturforschg. 22 b, 639—644 [1967]; eingegangen am 25. April 1967)

New absorption changes with a life time of $2 \cdot 10^{-4}$ sec at ~690 nm probably represent the chlorophyll-a light reaction in photosynthesis which promotes the cleavage of water.

THE ROLE OF CHLOROPHYLL IN PHOTOSYNTHESIS

by EUGENE I. RABINOWITCH and GOVINDJEE

SCIENTIFIC AMERICAN
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Properties of the Photoactive Chlorophyll-a_{II} in Photosynthesis

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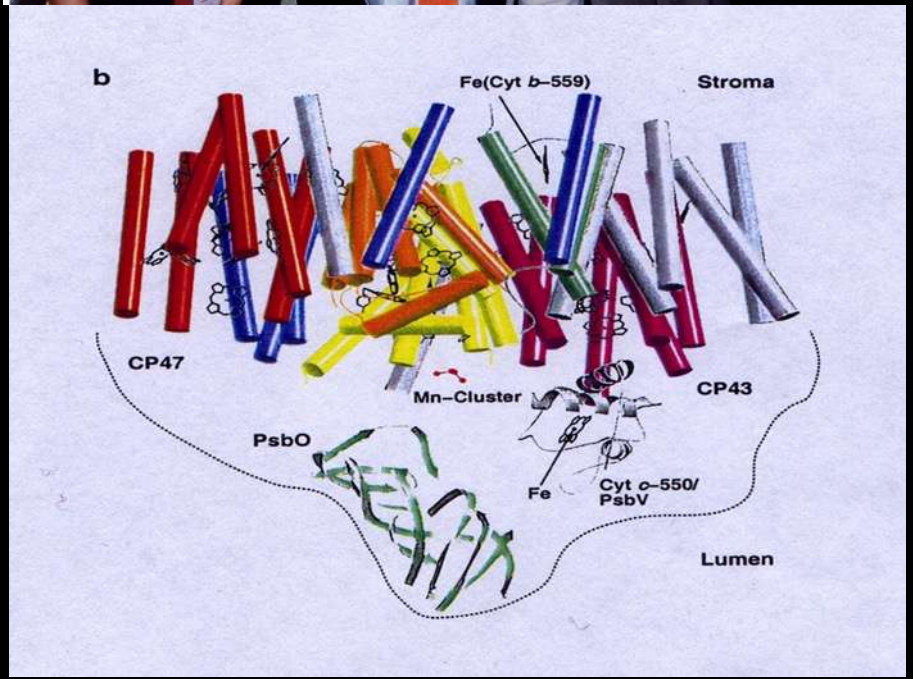
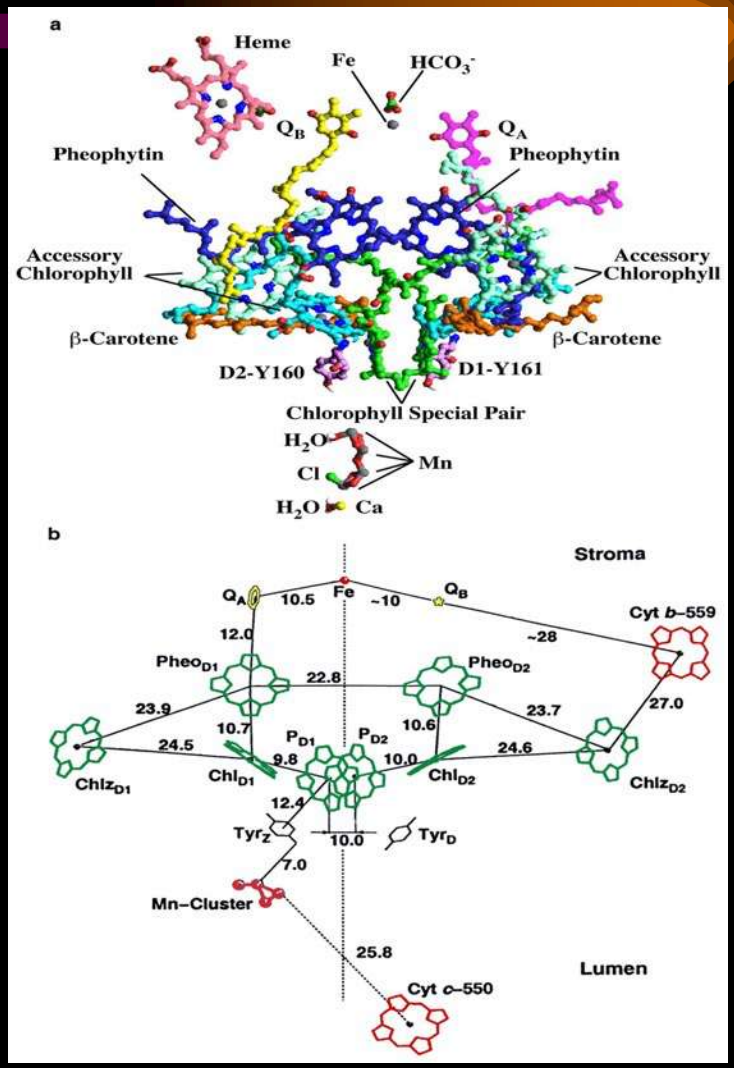
1. The complete difference spectrum of the reaction of the photoactive chlorophyll-a_{II} is presented.
2. The reaction of excited chlorophyll-a_{II} is of the type of a sensitizer. It is not engaged directly in the electron transfers. This is in contrast to the photoactive chlorophyll-a_{I} which is an electron donor in its excited state.
3. The chlorophyll-a_{II}-reaction can be separated from the overall reaction by heating chloroplasts 5 min at 50 °C.
4. Chlorophyll-a_{II} is the reaction center of the well-known poison DCMU.
5. Properties of chlorophyll-a_{II} are depicted in Tab. 1. They are compared with those of chlorophyll-a_{I} and the O_2-evolution system.

The Photosystem II Reaction Center (see Zouni et al., Nature, 2001).For an educational review on Photosystem II, see Shevela et al. (2021), Encyclopedia of Life Sciences: Don't miss "my" bicarbonate"





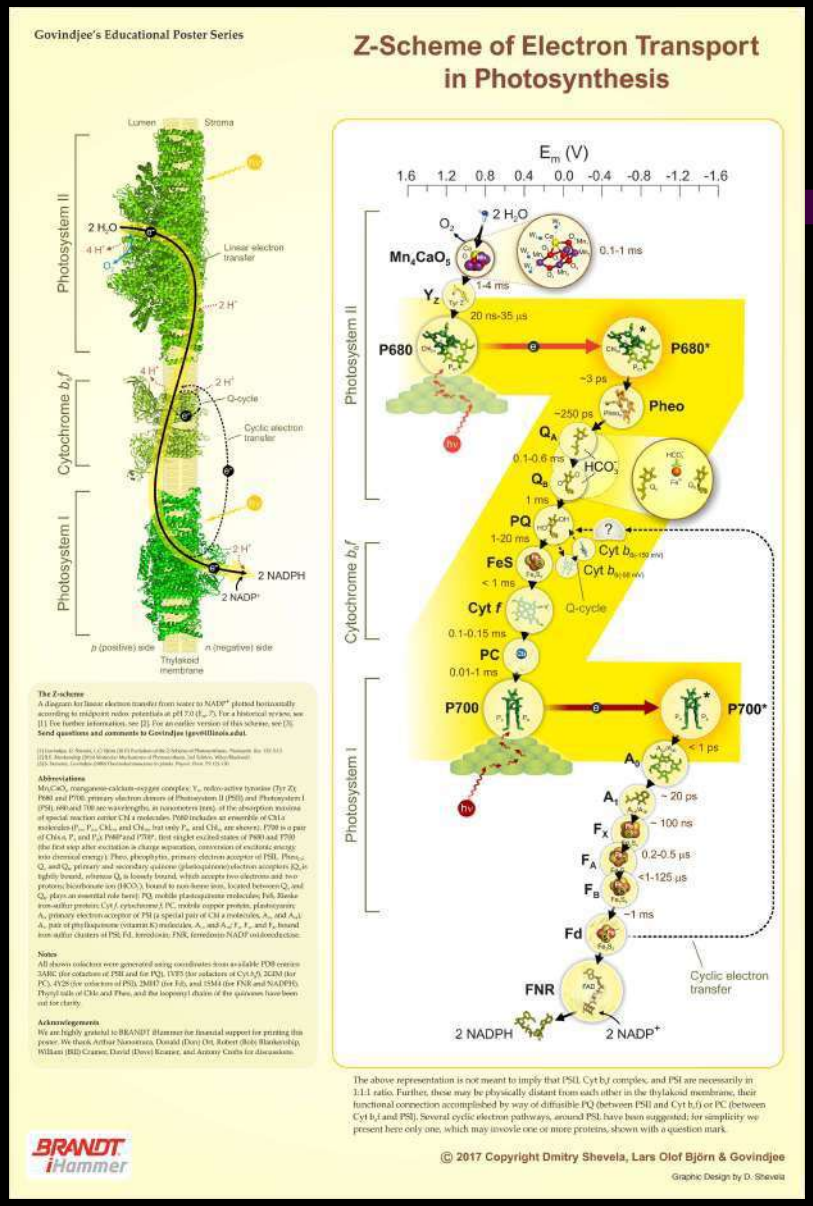
A 1961 photograph in Sweden – where we presented our PhD thesis work at the International Biophysical Society Meeting

Rabinowitch is shown here reading a Swedish newspaper; it was at this meeting that we presented our results showing that the Two Light Reactions are RUN by different spectral forms of chlorophyll and that the two light effect was in photosynthesis, not respiration

Question of P680 being an artifact

- *Warren Butler raised this question
- * In 1970, Rajni and I, with Guenter Doring, proved that it was not an artifact

- Govindjee, G. Doering, and R. Govindjee (1970) The Active Chlorophyll *a* II in Suspensions of Lyophilized and Tris-Washed Chloroplasts. Biochim. Biophys. Acta 205: 303-306.



Govindjee, Shevela D and Björn LO

(2017)

Evolution of the Z-scheme of photosynthesis. Photosynth

Res 133:5-15.

(There has been tremendous progress since Emerson's discoveries, and scientists are focusing on them)

Beyond Photosynthesis, there is Respiration and More

Robert Emerson Memorial Award

Each year a graduate student is chosen, based on academic credentials,and write-up, to get this award; the student chosen in 2019 was Rachel Moran

Robert Emerson Professor of Plant Biology: Donald R. Ort (left)

See his web site: https://sib.illinois.edu/profile/d-ort

During 1999- 2008, another influential professor Steve Long (right) held this professorship; listen to him on a Youtube:

https://youtu.be/XYXJeZdzpZE

This presentation is dedicated to our first professor Robert Emerson (1956-1958) , with whom we have no single publication!

- The picture shows Robert Emerson with his students (from a class he taught in 1957) at a party in Urbana, IL

I am highly thankful to
Jeff Haas; Karl Schlief; Thomas Uebele;
andAndrew Debevec , of UIUC, for their
constant help for my web pages and much more

http://www.life.illinois.edu/govindjee/

And

http://www.life.illinois.edu/govindjee/recent_papers.html