Plant Biology Departmental Colloquium Bringing the department together to highlight research, maintain cohesiveness & collaboration

> March 20, 2015 1103 Plant Sciences Laboratory, Dorner Drive

#### Govindjee

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The Midwest photosynthesis gang: Robert Emerson and Eugene Rabinowitch

## I begin my talk by remembering Colin Wraight for being a great friend and dear to all of us



For fear that no one will be here, I brought my own audience













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#### UNDERSTANDING PHOTOSYNTHESIS

DESCRIPTION OF BLINDLY





## The Newest Midwest Photosynthesis Gang, 2015 Watch out !

#### Lisa Ainsworth; Andrew Leakey; & Carl Bernacchi



I will focus on Emerson since I have only 25 minutes--

Photosynthetic Unit (at Cal Tech,1932); The Red Drop (at Carnegie, 1943); and the Enhancement Effect (at UIUC, 1957)

Rabinowitch E (1961) Robert Emerson. Natl Acad Sci USA Biographical Memoirs, XXXV: 112-131

Rabinowitch E (1959) Robert Emerson 1903-1959. Plant Phys 34 (3): 179-184

French CS (1959) Robert Emerson, Investigator of Photosynthesis. Science 130: 437-438.



# There is a small little book written for your pleasure and fun

Kärin Nickelsen Govindjee

The Maximum Quantum Yield Controversy Otto Warburg and the «Midwest-Gang»





Bern Studies in the History and Philosophy of Science Kaerin Nickelsen and Govindjee(2012) The Maximum Quantum Yield Controversy Otto Warburg and the <<MidWest- Gang>>

Bern Studies in the History and Philosophy of Science, Switzerland, 138 pp This is the story: A minimum of 2.5 to 4 photons or 8-12 photons per oxygen molecule evolved ? Hill, J.F. and Govindjee (2014) The controversy over the minimum quantum requirement for oxygen evolution. Photosynth Res 112:97-112.

The midwest gang members : Bob Emerson (Head) Eugene Rabinowitch James Franck HansGaffron and students













Bob Emerson's grand uncle was Ralph Waldo Emerson (Lincoln, Mass). Bob lived in Urbana, Illinois, at 801 W. Main Street



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

#### Über die Wirkung von Blausäure, Schwelelwassersloff und Kohlenoxyd auf die Atmung verschiedener Algen

TOVINDJEE

Ph.D. thesis of

Robert Emerson

#### Inaugural-Dissertation

Erlangung der Doktorwürde

Genehmigt von der Philosophischen Fakultät der Friedrich-Wilhelms-Universität zu Berlin von

aus New-York, U.S.A.

Tag der Promotion 11. Oktober 1927

32 pages

Druck von Paul Pank, Bortle SW 48

Born in New York City, 1903

- Father: Haven Emerson, Head of NY City Public Health Service
- Hobby: Ice skating/figure skating
- Pacifist and Democratic socialist;
   Quaker; worked in Japanese
   concentration camp on Guyayule
- MS Advisor: W.J.V. Osterhout
- PhD Advisor: OttoWarburg

## Robert Emerson was a skilled glassblower, and an artistic carpenter







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



- Discovery of Photosynthetic Unit (1932)
- Minimum quanta needed per oxygen molecule are 8-12 (1941-1958), not 3-4
- The Red Drop (1943); Enhancement Effect and two light reaction/two photosystem concept (1957-1959)

## 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"

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



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

Robert Emerson and William Archibald Arnold (1932) 280 × per flash elashtryso BIOLOGICAL SCIENCES 4000 300 20045 DOM 115 Tenths of a second. The "Blackman reaction" (as used by Otto Warburg)

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  $\sim 400$  ms; it is much faster than 30 ms at 25 C as it already reaches the maximum by 30 ms. •*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.



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



- 1931 Nobel Prize in Physiology or Medicine: respiratory enzymes
- The minimum quantum requirement for 1 molecule of  $O_2$  in photosynthesis is 3-4 (1923-1969); the photolyte hypothesis
- Discoverer of many phenomena in photosynthesis (including "lightinduced respiration"; role of chloride and bicarbonate in Hill reaction).

#### 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) as well as by 'grand students" Govindjee and Rajni Govindjee (1960—1968) who obtained values in the range of 8 to 12 even under Warburg's conditions!



## Otto Warburg arrives in Urbana in the summer of 1948

- July 30, 1948, issue of "Science" announced that Warburg had recently come from Germany to serve as visiting professor at the University of Illinois.
- On November 12, 1948, Science published his photograph doing experiments at the University of Illinois (it was the Natural History Bldg)



## Otto Warburg (publications in 1949 and 1950)



It was at NIH that Warburg did experiments confirming 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"

# The battle was over (1969): 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 "photolyte" intermediate.
- Read all about it in Govindjee (1999) Photosynth Res 59: 249-254.

The Red Drop in the Quantum Yield of Photosynthsis was discovered at Carnegie Inst, Stanford (1943)



## Eugene Rabinowitch (1901-1973): in 277 Morrill Hall, Urbana, 1967



- He wrote the masterpiece treatise on Photosynthesis (1945-56)
- 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)



## Eugene Rabinowitch (1956, 1963)



Eugene wrote...."since 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? What instrument was used?



## The first paper on the Enhancement Effect: a 1957 PNAS paper



• The photo that is added on the cover of this paper is that of Carl Cederstrand (a Physics student); Ruth Chalmers (trusted research/laboratory assistant) and Emerson himself (Photo, 1958)

## The Emerson Enhancement Effect (1957)



The Action Spectrum of the Emerson Enhancement Effect (1958; right): Rajni and I were Emerson's last PhD students; Emerson passed away on Feb. 4, 1959 after a plane crash in the East river



#### 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.



# Lou Duysens chatting with Eugene Rabinowitch



- Duysens' 1952 thesis on excitation energy transfer is a classic of all times:"P870"; two forms of Chl a (active and inactive); energy transfer efficiencies from accessory pigments to Chl a.
- When Eugene wrote, Lou read;
   When Eugene spoke, Lou listened (here is the proof).

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



Rajni Govindjee showed (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 enhancement in NADP reduction.





#### R. Govindjee et al. (1968) Biochim Biophys Acta 162: 539-544

- After Emerson had passed away on Feb. 4, 1959, Warburg was heard saying even in 1963:
- "Now, the problem is solved; Emerson did not use young cells and did not add 10 percent CO<sub>2</sub> and thus he got poor results.." Well, he did not know that the gang now had Govindjees --still there!

Minimum quantum requirement/ oxygen

- 1) Young cells, 2 h in light: 8
- 2) Young cells, 6 h in light: 9
- 3) Mature cells, 14 h in light: 12
- 4) Mature cells, 14 h in light,
- 1 h in dark: **14**

# Robin Hill (1899-1991)



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

## This short talk is dedicated to my professors: Robert Emerson (1956-1958) and Eugene Rabinowitch (1959-1960)



- The left picture shows Robert Emerson with his students on a Saturday noon after lunch (1957-1958, Urbana,ILL).
- The right picture shows Eugene Rabinowitch with us after we had our PhDs and we were requested then to call him "Eugene" (1961, Stockholm, Sweden)



- Govindjee (2004) Robert Emerson, and Eugene Rabinowitch:
   Understanding Photosynthesis. Lillian Hoddeson (editor). "No
   Boundaries: University of Illinois Vignettes", Chapter 12, pp.
   181-194.University of Illinois Press, Urbana and Chicago.
- Govindjee and Björn, L.O. (2012) Dissecting Oxygenic
  Photosynthesis: The Evolution of the "Z"-Scheme for Thylakoid
  Reactions. In : Photosynthesis: Overviews on Recent Progress
  and Future Perspective, edited by S. Itoh, P. Mohanty, and K. N.
  Guruprasad (I.K. Publishers, New Delhi, India), pp. 1–27.