Nickelsen, K., Govindjee: The Maximum Quantum Yield Controversy. Otto Warburg and the Midwestern Gang. – Bern Studies in the History and Philosophy of Science, Bern 2011. ISBN: 978-3-9523421-9-0, paperback, 138 pp., € 10.00.

What is the minimum number of light quanta, a plant needs to absorb, in order to reduce one molecule of carbon dioxide (CO_2) to carbohydrate? Or, said otherwise, what is the maximum number of oxygen molecules (O_2) a plant sets free to the atmosphere after it absorbs one quantum of light? These were the fundamental questions about the *minimum quantum requirement* (*m*-QR), or the *maximum quantum yield* (*M*-QY) of plant photosynthesis that the German scientist and future Nobel laureate in medicine (1931) Otto Warburg and his associate Erwin Negelein did ask and answer in the early 1920s. The book by Kärin Nickelsen, a Professor of History of Science at the University of Münich, and Govindjee, Ph.D. student of Robert Emerson and Eugene Rabinowitch and presently Professor Emeritus of the University of Illinois at Champaign-Urbana, relates the course of the controversy that erupted between Otto Warburg and his associates who favored a *m*-QR ≈ 4–5, on one side, and Robert Emerson and other American scientists who favored a *m*-QR twice as large. The controversy lasted nearly 30 years (to the late 1950s), and it involved a number of influential scientists of that time. It was finally settled in favor of the Americans, not because Warburg conceded that he erred, but because the explosive progress in the science of photosynthesis made his position untenable.

In 1922, the *m*-QR ≈ 4–5 light quanta per O_2 released of Warburg and Negelein was seemingly in harmony with the *law of photochemical equivalence* that Johannes Stark and Albert Einstein independently formulated around 1908–1913, as well as with the photosynthetic CO_2 assimilation model that Richard Wilstätter (1915 Nobel laureate in chemistry) and Arthur Stoll proposed in their 1918 monograph[1]. The central feature of this model was a Chl.carbonate adduct, formed in darkness, which upon light absorption dismutates CO_2 to free O_2 and to reduced C. The model was actually an elaboration of the earlier Adolph von Baeyer's model[2], minus it's pitfalls. Warburg adopted the Chl.carbonate adduct concept (which he named a *photolyte*) while his *m*-QR of 4–5 light quanta was consistent with the stoichiometric fact that 4 electrons are necessary to reduce 1 C atom. These two conjectures, however, were purely hypothetical, since the photolyte model provided no convincing reaction scheme to account for the provenance of the hydrogen needed to reduce the C atom, and there was no indication for the 4 primary photoacts needed to move the 4 electrons. In fact, lower or higher than 4 *m*-QR values could easily be interpreted as satisfying the photochemical equivalence law.

Despite its deep roots in the prevailing physicochemical concepts of its time, Warburg's photolyte model did not fare well in the subsequent years. Not only the *m*-QR = 4 came under dispute, but also its very foundation, the Willstätter and Stoll model. Already in the early 1930s, these two concepts began to be seriously contested in the USA. The American side included a number of influential scientists, including W. Arnold, F. Daniels, R. Emerson, J. Franck, C. S. French, H. Gaffron, W. M. Manning, E. Rabinowitch, and others. Most outspoken was Robert Emerson, Warburg's Ph.D. student in Germany and leader of what Warburg nicknamed the "Midwest Gang".

In 1932, Emerson and Arnold established, beyond doubt, that the Chl:CO_2:O_2 stoichiometry for photosynthetic O_2 evolution is not 1:1:1, as the photolyte model prescribed, but 2400:1:1. This preposterous stoichiometry made also the application of the law of photochemical equivalence even more enigmatic. Through it, however, the photosynthetic unit concept, which visualizes the majority of Chls to engage in light harvesting and few Chls in photochemistry, made its entrance. Then, in 1939–1943, Emerson and Lewis measured accurately *m*-QR to be 10–12 and explained the lower values of Warburg to be caused by the "CO_2 burst" (the so-called *1st Emerson effect*). Both *m*-QRs, however, were equally unexplainable in terms of the photosynthetic unit stoichiometry. In 1949, the Dutch microbiologist Cornelis van Niel formalized his hypothesis (based on his comparative studies on photosynthetic bacteria since the 1930s) that H_2O, not CO_2, is the source of the O_2 that oxygenic photosynthetic organisms release. In 1943, Emerson and Lewis discovered, also, the "red drop" paradox in the green alga *Chlorella*, namely that the quantum yield of photosynthesis drops beyond 685 nm, *i.e.*, within the red absorption band of Chl *a*. And finally, in 1957, Emerson discovered the so-called "enhancement effect" according to which supplemental short-wavelength light shifts the red drop to longer wavelengths. This discovery lead subsequently to the concept of the two photoreactions and two pigment systems mechanism of oxygenic photosynthesis.

The controversy was enacted in a series of episodes, beginning with each side disputing the accuracy of the other's measurements, and ending with unreserved mutual suspicion of intentional wrongdoing. Characteristic are the exchanged ironies and verbal accusations. More inventive, Warburg accused Emerson of *strewing sand in the mills of science*, of *muddying the waters without any new experiments*, as *philistine,* as member of *the Midwest Gang*, and the dyad Emerson and Rabinowitch as the *photosynthetic unit*. Emerson, on his part, tired of Warburg's evasions of direct scientific challenges, inventing instead novel experimental conditions to be tested (a defensive tactics analogous to soccer's *catenaccio*) described him as the *crafty* and *deceitful old poker player*, implying obviously some kind of bluffing on Warburg's part.

Readers will enjoy highly interesting details, some offered for the first time, about Warburg's and Emerson's times in Germany and in California, during WWII; and about the looting of Warburg's laboratory by the Red Army and the apology Marshall Zhukov offered. Also, a lengthy and amply commented account of Warburg's yearlong stay (1948–1949) in the United States, first in the University of Illinois at Urbana-Champaign (at the invitation of Emerson) and subsequently in the National Cancer Institute in Bethesda, Md., and in the Marine Biological Station at Woods Hole, Mass. Emerson arranged for Warburg to meet with several influential American scientists and hoped that he and his visitor would resolve the *M*-QY of photosynthesis problem by working together with the same manometric apparatus and the same *Chlorella* culture. For twelve days (26 December 1948 to 6 January 1949) they both worked in Emerson's laboratory at the University of Illinois at Urbana, in the presence of assigned impartial observers, but not together, failing to reach an agreement. Warburg measured a *m*-QR of ~4, and Emerson of ~10–12. Warburg, at the end, declared Emerson's *Chlorella* to be unsuitable for such measurements.

Warburg's postwar visit to the USA earned him an influential American ally in the person of biochemist Dean Burk. Together they reported in 1950 a 1 light quantum per O_2 evolved photosynthetically, the theoretically absolute *m*-QR value, and Warburg repeated it in his 1958 review published in Science. This strengthened the disbelief of Emerson *et al*. for Warburg's experimental results. Authors write in this book that Warburg used to proclaim that he let nature speak for itself through his experiments. Actually, however, he persistently strived to squeeze nature to his own photolyte model, which in its most perfect form was reflected in the 1 Chl:1 CO_2:1 light quantum stoichiometry.

The final and most decisive blow, however, to the low *m*-QR values was the discovery of the *enhancement effect* (or *2nd Emerson effect*) by Emerson in 1957. Emerson was inspired by an earlier (1954) report of Warburg's that catalytic amounts of blue light enhance the quantum yield of photosynthesis. Emerson proved, however, that shorter wavelength light enhanced photosynthesis not catalytically but quantititatively and this led him to postulate that accessory pigments, such as Chl *b*, Chl *c*, phycocyanin, phycoerythrin, and fucoxanthol, which absorb light at shorter wavelengths than Chl *a*, participate in photosynthesis.

After Emerson's tragic death in February 1959, in an airplane crash, Govindjee (this book's author) and Eugene Rabinowitch continued his enhancement work and discovered a near-red absorbing form of Chl *a* (Chl *a* 670) which together with the accessory pigments belonged to one pigment system, while the far-red absorbing Chl *a* (Chl *a* 685-710) belonged to another pigment system. Furthermore, based on the high efficiency with which the accessory pigments sensitized the fluorescence of Chl *a*, they proposed[3] that the accessory pigments were not themselves photoactive but they acted as light harvesters transferring electronic excitation to photoactive Chls *a*. These were the foundations of today's two photoreaction model of oxygenic photosynthesis. In the light of this model, the *m*-QR values of 8–10 quanta/O_2 of Emerson are in perfect agreement with the Stark-Einstein law.

Disregarding the overwhelming evidence flowing from all sides, and in particular the demonstration by M. Calvin (Nobel Laureate in Chemistry, 1961), A.A. Benson and J.A. Bassham that CO_2 adds to a diphosphopentose as carboxylate (and not to Chl *a* as carbonate) Warburg stuck to his photolyte model until his death (1970). Characteristically, however, in a 1969 paper he modified his view about it, stating that only 1 Chl *a* per approx. 1,000 combined with CO_2 to form a photolyte. This novel photolyte approximated the 1932 photosynthetic unit concept of Emerson and Arnold, but not quite, since Warburg saw the remainder Chl *a* as inert. In another 1969 paper, he reported a *m*-QR of ~ 12, which upon extrapolation to zero actinic intensity yields the theoretical *m*-QR value of 8. In spite of all these hard facts, he clung to the end to his dogma of one light quantum enabling one Chl *a* molecule to transfer one electron to one CO_2 molecule.

Authors, K. Nickelsen and Govindjee, are both acknowledged experts on the subject, having published several important papers on it. Their present book, nevertheless, stands out, not only because it gathers scattered information in one place, but also because of its wealth in anecdotal information (from several archival sources, personal correspondence, recorded discussions and reminiscences and photographs) that illuminates personalities and contested issues in the *M*-QY controversy as never done before. As a highly engaging story of a human drama, with several of the most influential photosynthesis personnae of the last century parading through its acts, it is natural to appeal strongly to readers of *Photosynthetica.* Furthermore, as authors make only moderate use of scientific and technical terms, I anticipate that also non-specialists of photosynthesis will find this book intellectually stimulating and pleasant to read.

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[1]Willstätter, R., Stoll, A.: [Untersuchungen über die Assimilation der Kohlensäure.] – Verlag Julius Springer, Berlin 1918. [In German.]
[2]Nickelsen, K., Grasshoff, G.: In pursuit of formaldehyde: Causally explanatory models and falsification. – Studies History Philosophy Biol. Biomed. Sci. **42**: 297-305, 2011.
[3]Govindjee, Rabinowitch, E.: Two forms of chlorophyll *a in vivo* with distinct photochemical functions. – Science **132**: 335-335, 1960.