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HISTORY & BIOGRAPHY

Contributions of David Mauzerall to photosynthesis research – celebrating his 95th birthday

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Abstract

We honor here Professor David Mauzerall, a pioneer in the fields of photochemistry and photobiology of porphyrins and chlorophylls *in vitro* and *in vivo*, on the occasion of his 95th birthday. Throughout his career at The Rockefeller University, he refined our understanding of how chlorophyll converts light energy into chemical energy. He exploited top-of-the-line laser technology in developing photoacoustics and a variety of other innovative experimental approaches. His experimental work and conceptual insights contributed greatly to our understanding of photosynthesis and the possible role of photosynthesis in the origin of life. His contributions include many landmark single-authored and collaborative papers, and his legacy includes the training of others who have become authorities themselves. After providing a brief description of his research accomplishments, we include tributes from several of his coworkers and his daughters highlighting their valuable experiences with David Mauzerall on this milestone birthday.

Keywords: chlorophyll; chlorophyll *a* fluorescence; cyanobacteria; excitation energy transfer; Frank Henry Westheimer; photoacoustics; photosynthetic bacteria; porphyrins; Samuel Granick; The Rockefeller University; University of Chicago.

Highlights

- Studied the function of porphyrins and chlorophylls *in vitro* and *in vivo*
- Pioneered the use of fluorescence measurements and photoacoustics in photosynthesis
- Instilled independence among coworkers

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Conflict of interest: The authors declare that they have no conflict of interest.

Introduction

David Charles Mauzerall (born 22 July 1929) grew up under humble circumstances in the French-speaking section of a small, textile town (Sanford) in Maine, USA. His early life, high school and college education, and extracurricular activities are recounted in depth in a recent article (Lindsey 2024). He attended graduate school at the University of Chicago where he did novel research on the physical organic chemistry of NADPH (Mauzerall and Westheimer 1955) in the laboratory of Professor Frank Henry Westheimer (1912–2007; *see*: https://en.m.wikipedia.org/wiki/Frank_Westheimer). After completing his PhD in 1954, he joined the lab of Professor Sam Granick (1909–1977; *see*: https://en.m.wikipedia.org/wiki/Sam_Granick) at The Rockefeller Institute for Medical Research. In the Granick lab, he began research on the fundamental reactivity of molecules in the tetrapyrrole biosynthetic pathway. He rose through the ranks there, becoming a full professor at The Rockefeller University in 1969. Fig. 1 shows a photo of David (Dave) Mauzerall.

Given his physical organic background and research in enzyme-mimetic chemistry, the question arises when did Mauzerall's interest in photosynthesis begin? His first paper on photochemistry, concerning the photoreduction of porphyrins with amines, was in 1960 (Mauzerall 1960). In the 1950s, the Granick lab was routinely generating mutants of photosynthetic bacteria for studies of tetrapyrrole biosynthesis. A further spark appears to have come from Mauzerall's first graduate student, Richard Cellarius, who arrived with a physics background, having done studies on photosynthesis as a solid-state phenomenon; Cellarius and Mauzerall (1966) published together on a model light-harvesting system. From the 1960s on, David's studies were centered on questions about the mechanisms of photosynthesis, and the role of photosynthesis in the origin of life. For a broad overview of Mauzerall's life and far-reaching scientific contributions, *see* Lindsey (2024). In his personal life, Dave was married to Dr. Miriam Jacob (1924–2023; a summary of her life is included in Appendix 1), a cell physiologist and scientific writer, for 64 years. They have two daughters, Denise and Michele. Below, we present some selected contributions of Professor David C. Mauzerall to the field of photosynthesis and related processes.

Fig. 1. A photograph of David C. Mauzerall, January 2020. Source: Family archives.

Appendix 2 provides URLs for websites about Dave Mauzerall.

Research contributions of David Mauzerall

David was first trained in chemistry, but soon thereafter enlarged his horizons to include all areas of science to understand the basics of photosynthesis. Further, he excelled in developing not only new instruments but biophysical methods for these studies, as we summarize below.

On the evolution of photosynthesis and beyond: Early in his career at The Rockefeller Institute for Medical Research, Mauzerall was influenced by the ideas of Sam Granick (1909–1977; Kappas and Levere 1977), who was a biochemist, interested in the areas of iron and ferritin metabolism, chloroplast structure, as well as heme and chlorophyll biosynthesis. Granick had already advanced the hypothesis that the biosynthetic pathway of a biochemical molecule recapitulates its evolutionary sequence (Granick 1965; also *see* Blankenship 2010). Granick applied his theory to heme and chlorophyll (Chl), which are fundamental molecules supporting life by enabling oxygen transport in blood cells and the conversion of light energy into chemical energy in photosynthetic organisms, respectively; furthermore, both are derived from protoporphyrin IX. For the earlier work of Mauzerall on this topic, *see* Mauzerall and Granick (1956), Granick and Mauzerall (1958a,b); Mauzerall and Granick (1958). Based on Granick's hypothesis, Mauzerall suggested that (*1*) the biosynthetic pathway to Chl recapitulates the evolutionary history of photosynthesis (*see* Mauzerall 1973, 1976a,b), and (*2*) the proto-photosynthetic function of the primary porphyrins, when in the photoexcited state, must have been to oxidize organic molecules, with the release of hydrogen gas (Mercer-Smith and Mauzerall 1984). To support these views, Mauzerall and his collaborators published a large number of studies on the photoreactions of various porphyrins and metalloporphyrins on a solid support, dissolved in solvents, or embedded in thin lipid membranes. *See* for example: (*1*) Mauzerall and Feher (1964), which is a study of a photoinduced porphyrin

Contributions: G. Govindjee initiated the idea of honoring Professor Emeritus Dr. David Mauzerall, who turned 95 on 22 July 2024, in "*Photosynthetica*"; he invited others to participate, and then organized and edited the text. In alphabetical order, additional contributors are Ora Canaani, Richard Cellarius, Bruce Diner, Elias Greenbaum, Harvey Hou, Nancy Y. Kiang, Jonathan S. Lindsey, Denise L. Mauzerall, Michele E. Mauzerall, and Michael Seibert. All have presented their reminiscences, and several have included their research with David – the most important part of this tribute. Finally, Alexandrina (Sandra) Stirbet has, together with Govindjee, written the section on David Mauzerall's overall research contributions.

free radical using Electron Spin Resonance (ESR); (*2*) Cellarius and Mauzerall (1966), which describes photochemical spectral analysis of pheophytin *a* adsorbed onto small particles, as a model of the photosynthetic unit; (*3*) Fuhrhop and Mauzerall (1969), which is a study of the one-electron oxidation of metalloporphyrins; (*4*) Hong and Mauzerall (1974), which concerns chemical capacitance and interfacial photoreactions in lipid bilayers; (*5*) Mercer-Smith and Mauzerall (1981), which provides information on molecular hydrogen production by uroporphyrin and coproporphyrin, as a model for the origin of photosynthetic function; (*6*) Lindsey *et al.* (1983), which provides new information on excited-state porphyrin–quinone interactions when the chromophores are 10 Å apart; (*7*) Delaney *et al.* (1990), which presents data on electron tunneling in a cofacial zinc porphyrin–quinone cage molecule; and (*8*) Feitelson and Mauzerall (1993), which concerns a photoacoustic study of electron-transfer reactions of photoexcited magnesium porphyrin and quinones.

In addition to the above, Dave Mauzerall and his collaborators have published a series of reviews on the above-mentioned topics: *e.g.*, Carapellucci and Mauzerall (1975), Mauzerall and Hong (1975), Mauzerall and Ballard (1982), Mercer-Smith and Mauzerall (1984), Mauzerall (1990a, 1992), Hsiao *et al.* (1996), Mauzerall and Sun (2003), and Mauzerall (2007). We note that such studies are also connected to the domain of artificial photosynthesis (*see* Lindsey 2024).

On the process of photosynthesis and more: Around the 1970s, Mauzerall started to publish papers on photosynthesis *in vivo*, working especially on aquatic algae and cyanobacteria. He was mainly interested in the photochemical processes taking place in photosynthesis, which, we know, begin with light harvesting by pigments in the antenna, transfer of the excitation energy from the antenna to the reaction centers (where the primary photochemistry takes place), which is followed by the electron (and proton) transport from water to NADP$^+$; for details, *see* Blankenship (2021). Further, Mauzerall, with H.A. Herron, went beyond all this: Herron and Mauzerall (1970, 1972) studied the greening process in a yellow mutant of *Chlorella* by analyzing the light saturation curves of photosynthesis (*i.e.*, the rate of photosynthesis *vs.* light intensity). They found that the light-saturation curves were strongly dependent on the degree of greening and that Chl molecules first accumulated in the active reaction centers, and only later in the antenna. Furthermore, Herron and Mauzerall (1972) showed that the efficiency of the excitation energy transfer as well as the rate-determining electron-transfer step (designated as α) were constant during the greening process. It is somewhat remarkable that the light-saturation curve of photosynthesis could provide a portal into developmental biology.

Experimental finesse – use of short laser flashes in the study of early reactions in photosynthesis: In several of his key studies on photosynthesis, Mauzerall used short (nanosecond or sub-microsecond) saturating laser flashes, and then analyzed the changes in the quantum yield of Chl *a* fluorescence. Earlier, Duysens and Sweers (1963) had proposed that the Chl *a* fluorescence yield increase is due to the reduction of an electron acceptor Q (now known as plastoquinone, Q_A, the first stable electron acceptor of the PSII), which in its oxidized state quenches Chl *a* fluorescence of PSII. Thus, in addition to oxygen measurements, Chl *a* fluorescence can be used as a measure of PSII activity in photosynthetic systems. Since Q_A was assumed to be the primary electron acceptor in the photochemical reaction in PSII, Mauzerall and Malley (1971) decided to verify this hypothesis experimentally, by measuring changes in the Chl fluorescence yield after a single turnover saturating laser flash of 10 nanoseconds applied to dark-adapted suspensions of *Chlorella* cells. Their results showed that light-induced increases in the effective fluorescence yield are too slow for a primary photochemical reaction, as the rise time of the Chl *a* fluorescence yield (now known to be due to reduction of P680$^+$ by Y_z) was only 25 ns, while a primary photochemical reaction occurs in the sub-nanosecond or picosecond time scale (*see e.g.*, a recent review by Mirkovic *et al.* 2017). Based on the Chl *a* fluorescence data of Mauzerall and Malley (1971), the optical cross-section for the photosynthetic unit was determined to be 180 Å^2, corresponding to ~350 Chl molecules (Mauzerall 1972).

Soon thereafter, Mauzerall (1972) measured Chl *a* fluorescence changes over an extended period (*see* Fig. 2). Following the illumination of *Chlorella* cells with a single turnover saturating flash, the Chl *a* fluorescence quantum yield undergoes a series of changes in the dark; the slower ones (from the microsecond to millisecond domain) were attributed to the dark reactions leading to oxygen evolution. (Note that in this time domain, it is known to be due to the reoxidation of Q_A^-.) Then, Mauzerall (1976c) and Mauzerall (1978) analyzed the decrease in Chl *a*

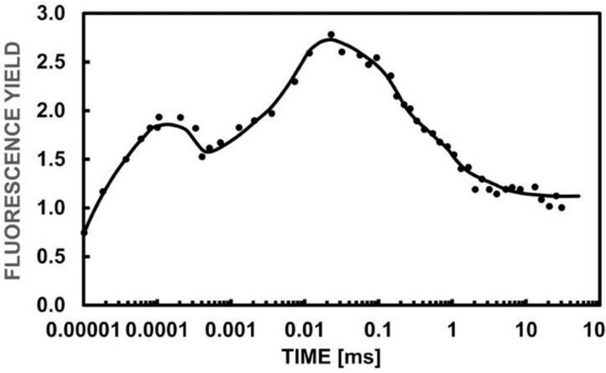

Fig. 2. Chlorophyll *a* fluorescence kinetics (at 685 nm: F$_{685}$), after a 10-nanosecond single saturating light flash (λ = 337 nm), from a *Chlorella* suspension (at 25°C), dark-adapted for 5 min; fluorescence was measured with weak measuring blue light flashes. After an increase to a maximum (~25 nanoseconds), fluorescence yield decreases to a minimum after ~500 ns, and then rises to a maximum after about 10 microseconds, followed by a decrease in the millisecond(s) time range. Modified from Fig. 1 in Mauzerall (1972).

fluorescence yield as a function of the number of hits on the photosynthetic units and concluded that multiple excitations on multi-trapping sites can explain the fivefold decrease in the fluorescence quantum yield. Moreover, Mauzerall (1978) suggested that, after the second hit, photogenerated carotenoid triplets near the funnel or antenna-trap junction must quench the fluorescence of the singlet excited-state Chl (Chl*) during the first few microseconds of the measurement.

On the absorption cross-section: Ley and Mauzerall (1982) determined the absolute absorption cross-sections for oxygen production (σ_{O2}) from the light-saturation behavior of the oxygen flash yields from whole cells of *Chlorella* illuminated with sub-microsecond laser flashes. Further, Greenbaum *et al*. (1987) used transient O_2 uptake measurements – following single-turnover laser flashes of varying energy, which was attributed to PSI activity, to measure its optical cross-section. Since the conditions of measurement in Greenbaum *et al*. (1987) were the same as those used by Ley and Mauzerall (1982) for the determination of the PSII cross-section, it is possible to measure simultaneously the cross-section of both photosystems *in vivo* in cell suspensions, without the use of inhibitors or artificial electron-transport mediators (*see e.g*., Greenbaum and Mauzerall 1991). In another study, Ley and Mauzerall (1986) exposed *Chlorella* cells, kept under continuous background light, to saturating single-turnover flashes, to study the energy-transfer process among PSII reaction centers during the light-adapted state. From this study, they concluded that the probability for the escape of excitation energy, away from the reaction centers, is under 0.25, for both the open and the closed PSII centers (*see* also Mauzerall 1986); however, these conclusions are in contradiction with the idea of PSII excitonic connectivity (*see* Joliot and Joliot 1964, 2003). Thus, we need to wait for future experiments and interpretations. Further, at that time, Falkowski *et al*. (1986) had developed the so-called "pump and probe" fluorescence technique (mainly used on aquatic photosynthetic samples), which was based on fluorescence measurements initiated by Mauzerall (1972) (*see* also Kolber and Falkowski 1993, Falkowski *et al*. 1994). [Also, *see* the 'Message' of Paul Falkowski in Lindsey (2024).] Further, David Mauzerall has extensively reviewed Chl *a* fluorescence studies on photosynthesis using short light flashes (*see*: Mauzerall 1978, 1980, 1981, 1986, 1987).

More on instrumentation – the pulsed photoacoustic technique in the study of photosynthesis: At the end of the 1980s, Mauzerall started to use the pulsed time-resolved photoacoustic (PA) technique to study, *in situ*, different oxidation-reduction reactions in photosynthesis and their thermodynamics (*e.g*., *see* reviews by Boichenko *et al*. 2001, Mauzerall 2006, Hou and Mauzerall 2011); this was an excellent way for Mauzerall to make use of his outstanding expertise in the domain of physical chemistry. For example, Canaani *et al*. (1988) showed that the PA method could be used to study O_2 evolution in leaves, under physiological conditions. [*See* the message of Ora Canaani, in this tribute.] With Ora, Mauzerall measured the PA signals after giving a series of single 10-µs saturating light flashes to leaf discs from tobacco (or wheat) (*see* Fig. 3); the positive part of the signal is due to the gas pressure pulse generated by the dissipated heat during the conversion of light energy in the PSII reaction centers, while the negative part is due to the dissipation of the pressure pulse in the cell. After the first light flash, the following successive PA signals were time-shifted and had increased amplitudes. Since the third PA signal had a large time-shifted (≈ 2 milliseconds) component and was inhibited by DCMU [3-(3,4-dichlorophenyl)-1,1-dimethylurea], heat treatment, or water infiltration, Canaani *et al*. (1988) concluded that this signal originates from the pulsed O_2 evolution. Furthermore, the difference between PA signals following the nth and the first flash as a function of the flash number (*see* Fig. 3*B*) shows a similar pattern to that obtained with polarographic measurements of O_2, which is another indication for the above characterization of the third PA signal.

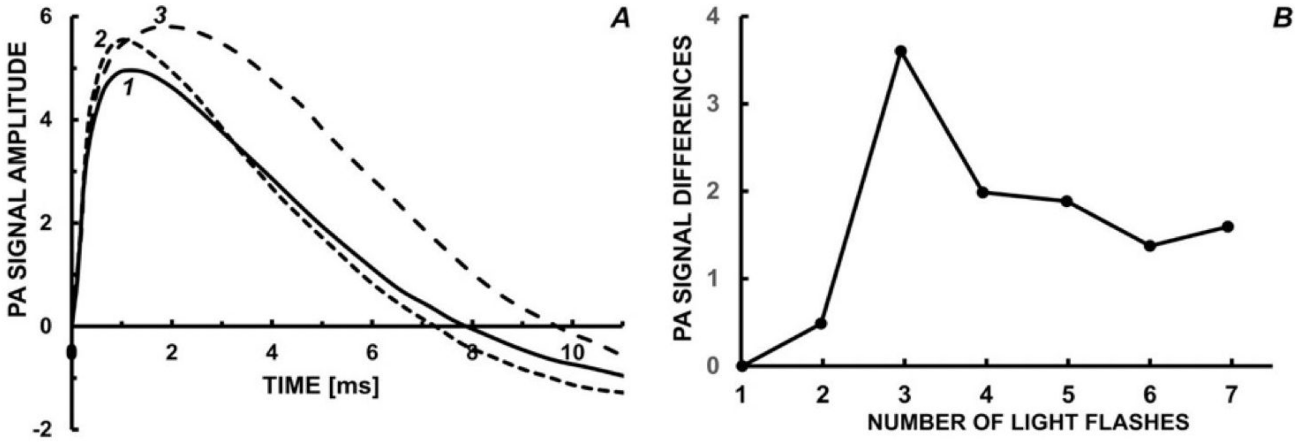

Fig. 3. (*A*) Amplitude(s) of photoacoustic (PA) signals, as a function of time (in milliseconds) from dark-adapted tobacco leaves after exposure to 10 microsecond light flashes (1, 2, and 3), given 0.3 seconds apart. (*B*) The PA signal difference between the nth and the first flash, measured in a tobacco leaf disc as a function of flash number (1 second apart); the resulting flash-number dependent oscillation is similar to that in the O_2-evolution pattern. Data are reproduced from Fig. 1(b) and Fig. 2 in Canaani *et al*. (1988).

We end our discussion on the research of Dave Mauzerall by mentioning other studies of photosynthesis by use of pulsed PA methods that he and coworkers carried out: (*1*) Cha and Mauzerall (1992) on energy storage of linear and cyclic electron flows in photosynthesis; (*2*) Mauzerall *et al.* (1995a) on contraction of the system upon photoexcitation of the reaction center of *Rhodobacter sphaeroides* R-26; (*3*) Berges *et al*. (1996) on the effects of nitrogen limitation in microalgae on the efficiency of PSI as well as of PSII; (*4*) Dubinsky *et al*. (1998) on measuring photosynthesis and the biomass of phytoplankton; (*5*) Charlebois and Mauzerall (1999) on the energy storage and optical cross-section of PSI in the cyanobacterium *Synechococcus* PCC 7002 and its psaE-mutant; (*6*) Edens *et al*. (2000) on the enthalpy and entropy of $P^+Q_A^-$ formation in the reaction centers of *Rhodobacter sphaeroides*; and (*7*) Hou and Mauzerall (2006) on the electron-transfer step from A-Fx to F(A/B) in PSI of *Synechocystis* 6803 (*see* the messages of Harvey Hou in Lindsey (2024) and in this paper).

Finally, we recommend that readers read and enjoy the wonderful reviews by Mauzerall (1990b), Canaani *et al*. (1990), Feitelson and Mauzerall (1993), Mauzerall (2006), Liu *et al*. (2008), Mauzerall (2013), and Hou and Mauzerall (2021).

Messages

1. Ora Canaani (e-mail: ora12340@gmail.com)

The very first measurement of flash-induced oxygen evolution and its oscillations by photoacoustics from intact leaves

I first met Prof. David C. Mauzerall in 1988 when he came to Israel for a Sabbatical year at the Weizmann Institute of Science. At that time, I was working in the Biochemistry Department as an Associate Researcher in the laboratory of the late Prof. Shmuel Malkin (for Malkin (1934–2017), *see*: Herbert *et al*. 2018). Prof. Mauzerall proposed that we use photoacoustics to investigate the S-states of the oxygen-evolving complex (OEC) of photosynthesis. In the very first experiment, we experienced a huge surprise. We encountered a large photoacoustic signal which turned out to be a background noise! However, this observation did not make Prof. Mauzerall give up his idea. I had never seen a person like him with such great perseverance and strong will. He immediately suggested that we should get a car tire that acts like a shock absorber. We got that and placed our working table on top of it. Then, we arranged our laser, optical system, photoacoustic cell, and amplifiers again there. *Lo and behold*, we managed to get a nice photoacoustic signal, this time, from oxygen evolution from a leaf inserted in a photoacoustic cell. Thus, oxygen evolution by leaf tissue could be measured by photoacoustics, and that too with a time resolution that cannot be matched by another method (*see* Canaani *et al*. 1988; also *see* Fig. 3).

With the above message, I am sending here my heartfelt best wishes to Professor Mauzerall, with lots of smiles and happiness, on his 95th birthday – all the way from Israel.

2. Richard A. Cellarius (e-mail: richard@cellarius.org)

From the first PhD student of Dave Mauzerall

I was Dave Mauzerall's first PhD student at what was then The Rockefeller Institute for Medical Research. I was introduced to him by Sam Granick, whom I had first approached because of my interest in the early stages of the photosynthetic process, including the role of chlorophyll. Dr. Granick immediately said I should talk to this young postdoc – Mauzerall. To make a long story short, I indeed finished, in 1965, my PhD thesis "A model for the chloroplast: A study of the photochemical and spectral properties of pheophytin *a* adsorbed to the surface of small particles", under the mentorship of David C. Mauzerall (*see* https://digitalcommons.rockefeller.edu/student_theses_and_dissertations/571), and I wrote the following acknowledgment in the preface of my thesis: *This work would be much poorer if it were not for the patient tutelage of Dr. Mauzerall. In addition to teaching the tangible, such as organic and photochemistry, and the "semi-tangible", such as the art and science of designing and performing experiments, he has also demonstrated the great importance of intangible, critical scientific thinking*.

The Cellarius and Mauzerall (1966) paper was the result of my thesis; it dealt with "Photochemical spectral analysis of pheophytin adsorbed onto small particles, as a model of the photosynthetic unit". In introducing me at my graduation, Dave made two comments with metaphors that to me demonstrated his "classical" thinking: "Now, whereas models or analogs are well defined in theoretical studies, in experimental work such model building is somewhat more ambiguous. One must steer between the simplicity of the Scylla and the complexity of the Charybdis…" and "This may sound complicated, but Richard's good understanding of physical processes and measurements allowed him to glide smoothly by those technical and electronic whirlpools that continually threaten the modern molecular Argonauts".

Fig. 4 (*left*) shows a photograph with Dave Mauzerall at my graduation from Rockefeller University, whereas Fig. 4 (*right*) shows me in David's Lab. I thank Professor Mauzerall for the excellent training he gave me that led me to a successful academic career, and I retired as Emeritus Faculty from the Evergreen State College, Columbia, Washington State. With these photographs, and this brief message, I am, with great pleasure and total respect, sending Professor Emeritus David C. Mauzerall my heartfelt special wishes on his 95th birthday.

3. Bruce Diner (e-mail: bdiner7406@aol.com)

Reminiscences on time spent as a graduate student in David Mauzerall's laboratory

Beginning in 1969, I spent three years as a graduate student in David Mauzerall's lab at Rockefeller University. Dave guided my entry into the world of photosynthesis research, a fascinating field at the interface of chemistry, physics,

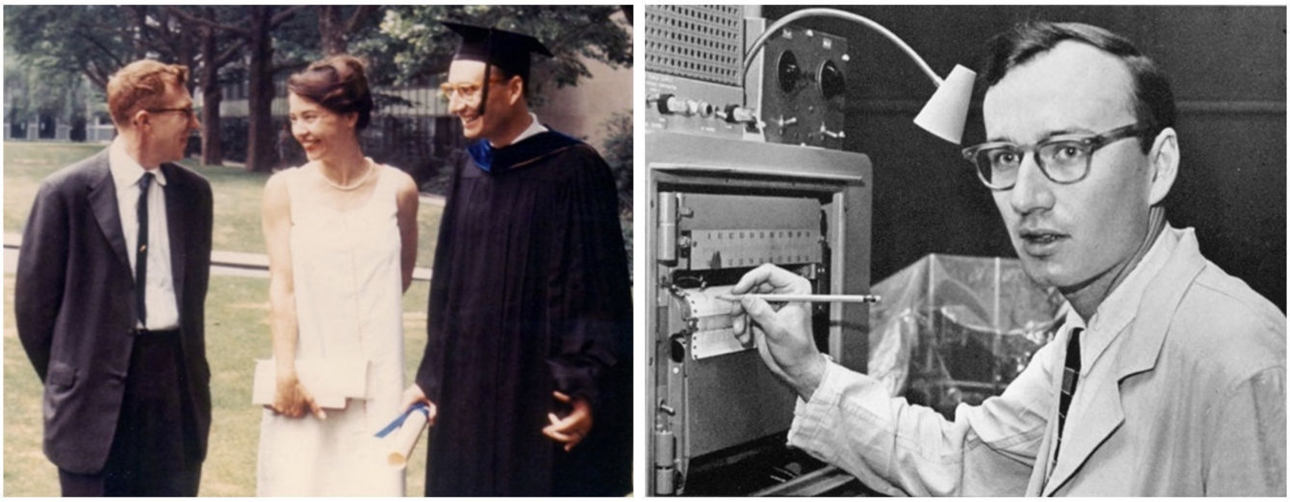

Fig. 4. *Left*: A 1965 photograph at the graduation of Richard Cellarius: (*from left to right*) David Mauzerall, Doris Cellarius, and Richard Cellarius. *Right*: A photograph of Richard Cellarius at the Cary Spectrophotometer, at Rockefeller University. Source: Archives of Cellarius family.

and biology, in which I would continue to work hands-on until 2006. Dave's interests were an eclectic mix, including the identity of, the lifetime of, and the thermodynamics of formation of primary electron donor-acceptor pairs in photosynthesis and in model systems; porphyrin photochemistry; light absorption and excitation energy transfer in the photosynthetic light-harvesting antenna; the mechanism and kinetics of oxygen evolution; and even the origin of life.

The mechanism by which oxygenic photosynthesis evolves O_2 was one of the key problems of biology, and I was keen to work on PSII both in detergent-extracted, but still functional, complexes and in whole algal cells. The Mauzerall laboratory had a one-of-a-kind technique for detecting O_2, the "luminometer", developed by Burr and Mauzerall (1968), in which photosynthetically produced O_2 was transported, *via* an argon gas flow system, from a cuvette containing illuminated algae to a pool of luminol in DMSO (dimethyl sulfoxide) that would emit light on contact with O_2. A photomultiplier detected the emitted light, and the instrument was calibrated by *in-line* electrochemical generation of O_2 from water. To have an acceptable signal/noise and lifetime of the luminol solution, the carrier gas needed to contain low contents of O_2 (several ppm). A puzzling observation under these conditions, however, was a non-linearity in the light intensity dependence of O_2 production at low light intensities (Allen 1955, Herron and Mauzerall 1970). To better understand this non-linearity, we replaced the luminol detector with an O_2 polarograph, containing the algal cells, where the background O_2 concentration could be varied over orders of magnitude. We found (Diner and Mauzerall 1973a,b) that in both green algal and cyanobacterial cells this non-linear light dependence in the light-saturation curves for O_2 production was replaced by a linear dependence as the background O_2 concentration was increased. Similarly, in repetitive saturating single turnover light flash experiments, the decline in the O_2 flash yield with decreasing flash frequency (10 to 0.25 Hz) was much more pronounced the lower the background O_2 concentration. However, at low background O_2 concentration, the O_2 flash yields, in this flash frequency range, remained high and constant in the presence of benzoquinone, expected to maintain the plastoquinone pool in an oxidized state. These observations were mathematically simulated, with help from Felix Hong, using a model (*see* Fig. 5) in which the redox state of the plastoquinone (PQ) pool was determined by both a light-dependent (PSII – PQ – PSI) and a light-independent (R – PQ – O_2) electron-transport chain; in the latter case, there is a respiratory pathway where oxidation by molecular O_2 offsets reduction by an endogenous reductant, R (presumed to be NADPH).

I performed follow-up studies (Diner 1975, 1977), while a post-doc in Pierre Joliot's laboratory, on spinach chloroplasts lacking both endogenous reductant and a PSI acceptor. These experiments, using chlorophyll *a* fluorescence induction to monitor the plastoquinone pool redox state, showed that the rate of reoxidation of the plastoquinone (PQ) pool in the dark, following full photoreduction by PSII, increased as the background O_2 concentration was increased. The lifetime of the S2 state of the oxygen-evolving complex (OEC) of PSII (determined by PSII donor-acceptor side charge recombination), was shown to increase with increased oxidation of the PQ pool as the background O_2 concentration increased, consistent

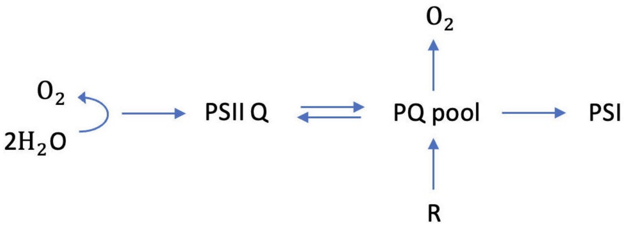

Fig. 5. Model of electron flux in the plastoquinone pool.

with this model, proposed while a graduate student with Dave Mauzerall.

Subsequently, Pierre Bennoun initiated studies to establish the enzymatic identity of the oxidative and reductive components of this light-independent respiratory pathway, for which he coined the term "chlororespiration". Bennoun (1982), using whole cells of *Chlamydomonas reinhardtii*, showed that the oxidative pathway was sensitive to inhibitors of terminal oxidases, resulting in PQ pool reduction, even under aerobic conditions, and that, in open-cell preparations, added NADH and NADPH could act as reductants, reducing the PQ pool. This work triggered an extensive research effort on "chlororespiration" and its role in regulating the redox state of the plastoquinone pool, which was shown to have implications for poising state transitions and PSI cyclic electron transfer, and for carotenoid biosynthesis and photoprotection. NAD(P)H dehydrogenase (NDA2) (Jans *et al.* 2008) plus NAD(P)H and plastid terminal oxidases, PTOX and its isozymes (Houille-Vernes *et al.* 2011) plus O_2, have now been shown to be responsible for electron inflow and outflow, respectively, in this light-independent "chlororespiratory" pathway (for a review, *see* Nawrocki *et al.* 2015).

Dave Mauzerall insisted on clarity of thought in his students. For him, success in research depended upon the clarity with which a problem is stated at the start and how clearly the goal is perceived as the research progresses. I learned, however, in working in Dave's lab, that the arrow of research rarely travels in a straight line. Clear thinking needs to be accompanied by vigilance to those observations that do not comply with one's theories as to how things work. Sometimes those theories need to be modified or even laid aside to head off in new directions. The students in Dave's lab were granted a great deal of independence. While we were encouraged to find our own way, Dave was always available, generously sharing his wealth of knowledge. He provided a welcoming atmosphere in his lab, and I am deeply indebted to him for my time spent there at a formative time in my research career.

I end my message by showing a photograph with Dave, at my graduation in 1972 (*see* Fig. 6, *top*) and at his 95th birthday party (Fig. 6, *bottom*). I join the photosynthesis community in wishing Dave all the best on the occasion of his 95th birthday. Good health, Dave, and wishing you many more birthdays to celebrate.

4. Govindjee Govindjee (e-mail: gov@illinois.edu)

Dave Mauzerall: A contemporary from the 1960s, but my senior – a bit on his unique ideas

I have known David (Dave) Mauzerall for a very long time. He is senior to me by a few years, having received his PhD in 1954 in Chemistry, from the University of Chicago, whereas I had mine in 1960 in Biophysics from the University of Illinois at Urbana-Champaign – but we both attended some of the same conferences, including Gordon Conferences on Photosynthesis. We did not talk much with each other, but I read and appreciated his research. Recently, I re-read the highly original views of Mauzerall (2013) on the thermodynamics of photosynthesis, where he stated, among other key observations, that (*1*) considerations of thermal machines are irrelevant to the efficiency of photosynthetic reactions since these are essentially isothermal photochemical processes; and (*2*) since the observed overall maximal efficiency is 35%, it may be difficult to improve on evolution. What personally delighted me was that he had extremely nice words for my 80th birthday in the footnote to this paper.

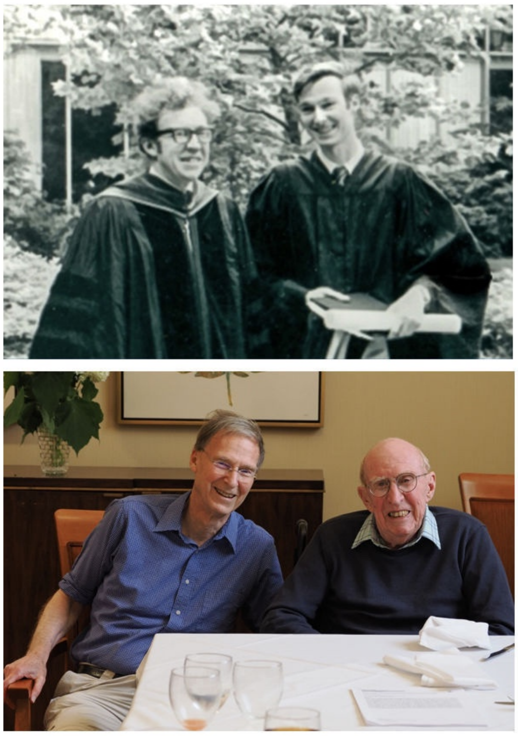

Fig. 6. (*A*) David Mauzerall and Bruce Diner at the latter's graduation from Rockefeller University on 1 June 1972. Source: Bruce Diner. (*B*) Bruce Diner and David Mauzerall at David's 95th birthday celebration. Source: Ken Duell.

I have read almost all of Dave's papers (and there are many) – what is important to note is that, in many of these papers, he had unique ideas – whether they agreed or disagreed with what others thought. I will mention here only one example. Mauzerall and Chivvis (1973) asked: Can oxygen be produced directly through chlorophyll photochemistry? He bravely discussed his very imaginative idea of how oxygen can, in principle, be produced directly by using chlorophyll itself. For this, he proposed a cyclic mechanism involving a "dioxylium" cation intermediate, which was considered a precursor to oxygen! Although nothing like that had been shown experimentally, Dave still considered it a reasonable possibility. He cited Rabinowitch (1945) who had suggested that some form of organic peroxide is made photochemically which then disproportionates to make oxygen! Despite negative results, thus far, we must keep his unusual thoughts alive on a "back burner" since they may help those who are currently in the field of "artificial photosynthesis".

5. Elias Greenbaum (e-mail: greenbaum@gtah2.com)

How I met Professor David Mauzerall: Teacher, Mentor, Colleague, Friend

I received a PhD in Physics from Columbia University, New York, in 1970. My thesis advisor was Professor Chien-Shiung Wu (1912–1997), who directed a highly respected nuclear physics research group. While sitting in her office and talking about my next options, the phone rang. University of Illinois physics professor Hans Frauenfelder (1922–2022) was on the line. He was looking for a post-doc to work on a biophysics project that involved flash spectroscopy and enzyme kinetics. Was I interested, and would I be willing to come to the UIUC (University of Illinois at Urbana-Champaign) for a job interview and give a seminar? My answer was: Yes, and Yes. Two weeks later I was in Urbana for the interview and offered a research position at the end of the day. The research was a joint project between Hans's physics group and the biochemistry group of Professor I.C. "Gunny" Gunsalus (1912–2008). The project involved triggering a normally dark biochemical reaction with a flash of light. The photochemical reducing system was EDTA (ethylene diamine tetra acetic acid) + proflavine + methyl viologen (MV). I spent a lot of time in the library reading. I learned that MV was an electron accepter for Photosystem I in oxygenic photosynthesis. During a discussion with Gunny, he said "you should speak with Professor Govindjee (Gov)". I did, and Gov said "you should speak with my graduate student Prasanna K. Mohanty". I did and had a new friend and colleague in the area of photosynthesis (unfortunately, Prasanna passed away in 2013).

The first time I saw the name "D. Mauzerall" was in one of my marathon reading sessions in 1970 in the UIUC library. It was the Mauzerall (1962) paper: "The Photoreduction of Porphyrins: Structure of the Products" in JACS (Journal of American Chemical Society). Paul Loach and Joseph Katz (1912–2008) organized the "Conference on the Primary Photochemistry of Photosynthesis" at Argonne National Laboratory, in November 1971. Hans sent me to the conference to learn more about photophysics and photochemistry. At the evening reception, I saw a badge with the name "David Mauzerall". I introduced myself and told David (Dave) that I had read his 1962 JACS paper and described to him the photobiochemistry project in Hans's group. Dave was pleased that I had read and learned from his work. I was pleased with how he fully understood my project and started making helpful suggestions. That was the start of a mutual admiration society. About three months later, Dave called and said he had an opening in his lab at Rockefeller University for a research assistant professor. Was I interested and would I be willing to travel to New York and interview for the position? Yes, and Yes.

It was Dave Mauzerall who launched my career in photosynthesis by starting me to read the 1932 landmark papers of Emerson and Arnold on the 'photosynthetic unit' and more (*see* Mauzerall (1996) for what he wrote later on this topic). Following the concept of 'photosynthetic unit', which evolved in 1932, I extended it, with Dave, to *Chlorella* cells under anaerobic conditions, and by using chemical oxidants (*see* Greenbaum and Mauzerall 1976).

Dave wrote many great papers. One of my favorites is "Light-induced fluorescence changes in *Chlorella* and the primary photoreactions for the production of oxygen" (Mauzerall 1972). The paper is directly related to the subject of the 1971 Argonne conference. Dave showed that the light-induced increases of the effective chlorophyll fluorescence yield in *Chlorella* are too slow to be primary processes in photosynthesis.

The U.S. Department of Energy and National Science Foundation started major research programs in renewable energy in response to the 1973 Arab oil embargo. Dave said "yes" to my idea for an experiment that measured the photosynthetic unit of hydrogen evolution (Greenbaum 1977). This work led to an invitation to speak at the 1976 Conference on Biological Solar Energy Conversion (Mitsui *et al*. 1977), which led to a staff appointment in the Union Carbide Corporate Research Laboratory, and then to a staff appointment and 30+ years of career at Oak Ridge National Laboratory. I'm now President of GTA Inc., a prototype R&D engineering company focused on subsea electrolytic hydrogen production powered by offshore wind and ocean energies. Thank you, Dave!

Working in different divisions and on different projects at Oak Ridge National Laboratory, William (Bill) Arnold and I had, for a short time, overlapping careers there. Helen Arnold Herron is Bill's daughter and one of Dave's graduate students. (*See* a tribute to Bill Arnold by his granddaughter, coauthored with Govindjee: Choules and Govindjee 2014). Before I end my message, I show a photograph at my wedding reception where David and members of his research group were present (*see* Fig. 7). There was camaraderie in the entire group of Dave Mauzerall.

I end the message on Dave Mauzerall's 95th birthday by emphasizing that, to me, he is not only a great teacher, and an outstanding mentor, but a wonderful colleague, and a lifelong friend.

6. Harvey Hou (e-mail: hhou@alasu.edu)

Significant entropy changes of electron-transfer reactions in chemical and biological systems revealed by pulsed photoacoustics

First, I present my academic background before I went to work with Dave Mauzerall. In 1993, I received my PhD in chemistry, studying the electrochemistry of Co- and Ni-porphyrins in aqueous solutions, and this was under the mentorship of Xiaoxia Gao at Peking University, Beijing, China. Then, I did research on the structure and the function of PSII reaction center, with Pei-sung Tang and Ting-Yun Kuang at the Institute of Botany, Chinese Academy of Sciences, in Beijing. This was followed by research, in 1997, on the orientation of pigments in PSII, using linear dichroism in the laboratory of Paul Mathis and Jacques Breton, at Service de Bioénergétique, CEA

Fig. 7. Professor David Mauzerall's 1973 research group. *Back row* (*left to right*): Cheryl Hong, graduate student Felix Hong, Dr. Olaf S. Andersen (Olaf was a post-doc in Alex Mauro's lab, but a regular participant in Dave's weekly group meetings), Johanne Andersen, graduate student S. Gwyn Ballard, Dr. Joel Lee Groves (Joel was a physics postdoc in Professor C.S. Wu's lab at Columbia University). *Front row*: David Mauzerall, Miriam Mauzerall, graduate student Richard Piccione, Barry Masters, Mary Ann Groves. Photo taken at the Lincoln Square Synagogue, New York, NY, 4 November 1973, at the wedding reception of Anne and Elias Greenbaum. Source: Elias Greenbaum.

(Commissariat à l'Energie Atomique et aux Energies Alternatives), Saclay, France. After this, I moved to the USA, where I worked, in 1998, under the guidance of Parag Chitnis, at Iowa State University, Ames, Iowa, probing the organization of PSI. It was then that I joined David Mauzerall's laboratory and worked with him for four years (1998 to 2002).

I am delighted to share here my excitement and happiness that I experienced in working with Dave on the thermodynamics of electron transfer in photosynthesis. When I came to Rockefeller University in 1998, I knew that Dave and his team were passionate about studying the thermodynamics of photochemistry using pulsed photoacoustics. Dave and Jehuda Feitelson, a visiting professor, in his lab, from the Hebrew University (*see* Feitelson and Mauzerall 1996), had already provided information on the entropy change of electron-transfer reactions of triplet-state zinc uroporphyrin, in aqueous solution, using pulsed photoacoustics. The large value of the entropy change ($T\Delta S$ = +0.58 eV), which they had observed, for the recombination of the ions, already indicated that entropy cannot be neglected in explaining electron-transfer reactions. The value of the entropy of ion recombination in aqueous solution was, indeed, as expected for the liberation of solvent molecules (because the ions that cause the organization of the solvent molecules are no longer present). This study was a prelude to studies of the more complex natural systems, of which four examples follow.

(*1*) In collaboration with Marilyn Gunner, at the City College of New York, Dave and his postdoc, Greg Edens, discovered that there was a significant entropy change ($T\Delta S$) of +0.42 eV for the formation of $P_{870}^{+}\ Q_{A}^{-}$ from excited P_{870} in the purple bacterium *Rhodobacter sphaeroides* (Edens *et al.* 2000). This unexpected value of the entropy was assigned to the release of counterions from the reaction center surface when the charge transfer cancels the dominant opposite charges at the interfaces.

(*2*) In collaboration with Vlad Boichenko, a visiting scientist from the Russian Academy of Sciences, we studied the thermodynamics of electron-transfer reactions in both PSI and PSII from the cyanobacterium *Synechochocystis* sp. PCC 6803 both *in vitro* and *in vivo* (Boichenko *et al.* 2001, Hou *et al.* 2001a,b). For this project, Parag Chitnis at Iowa State University and Bruce Diner at Dupont provided the PSI and PSII complexes. Here, the light-induced charge separation forming $P_{700}^{+}F_{A}/F_{B}^{-}$ from the excited state P_{700}^{*} in PSI trimer complexes proceeded with entropy change ($T\Delta S$) of +0.35 eV, about half of the free energy of the overall reaction (Hou *et al.* 2001a).

(*3*) By examination of the photoacoustic waves on the nanosecond and microsecond time scales, we were able to time resolve the entropy changes of two different kinetic steps in *Synechocystis* 6803 (Hou and Mauzerall 2006): (i) P_{700}^{*} leading to the formation of $P700^{+}\ A^{-}_{1}$ (<10 ns) and then (ii) A_{1}^{-} transferring an electron to $F_{A/B}^{-}$ (20–200 ns). The first reaction proceeded with a small negative entropy ($T\Delta S$), –0.2 eV, whereas the second reaction proceeded with a large positive entropy of +0.54 eV (although the overall free energy was –0.14 eV).

(*4*) In collaboration with John Golbeck, we then determined the thermodynamic parameters of electron transfer in *menA* and *menB* null mutants of *Synechocystis* 6803 (Hou *et al.* 2009). In these mutants, plastoquinone-9 (A_{P}) occupies the A_{1} site. Our pulsed photoacoustic data (Hou *et al.* 2009) showed that the apparent entropy change ($T\Delta S$) for the reaction $P_{700}^{+}A_{P}^{-}F_{A/B} \rightarrow P_{700}^{+}A_{P}F_{A/B}^{-}$ is +0.40 eV. As the free energy of the reaction in the mutants is close to zero (–0.07 eV), the reaction is almost completely entropy-driven.

The discovery of entropy-driven reactions is often surprising because enthalpy changes are generally regarded as the driving force in chemical reactions. To find a large entropy change in photosynthetic processes is even more surprising and implies a change in the energy distribution or disorder of the systems. The pulsed photoacoustics developed in Dave Mauzerall's laboratory has uncovered the importance of apparent entropy change (TΔS) in systems encompassing both chemistry and biology (Mauzerall *et al.* 1995b, Feitelson and Mauzerall 1996, 2002; Edens *et al.* 2000, Boichenko *et al.* 2001, Hou *et al.* 2001a,b; 2009; Hou and Mauzerall 2006, 2021). An emerging view from the aforementioned studies is that understanding entropy changes is important to completely understand the molecular mechanisms of electron transfer and/or proton transfer in condensed phases.

A very important point to emphasize is the freedom that Dave gave to his students in the lab. As encouraged by Dave, Kai Sun (a postdoc) published his paper as the sole author on the development of a molecular mechanoelectric sensor, with Dave's name in the acknowledgment (Sun 1997). What a remarkable advisor Dave is! Fig. 8 shows Dave Mauzerall and me at a conference in 2002 and again at his 95th birthday party.

Congratulations to Dave Mauzerall on his 95th birthday!

7. Nancy Y. Kiang (e-mail: nancy.y.kiang@nasa.gov)

From "Why chlorophyll?" to probing far-red absorbing chlorophyll *d* with photoacoustics

Review papers that ponder the unique capabilities of chlorophyll pigments for light harvesting are few and far between. Back in 1973, David Mauzerall, who turned 95 in 2024, asked the question "Why chlorophyll?" delineating its origins *via* the biosynthetic pathway of the porphyrins and selection pressures leading to the structure of chlorophyll (Mauzerall 1973). Then Mauzerall (1976a) laid out in exquisite detail how chlorophyll meets the electronic requirements for a photopigment successfully to perform oxygenic photosynthesis and how its integration into cellular membranes achieves great efficiency in charge transfers. The same year, Lars Olof Björn asked "Why are plants green?" (Björn 1976), taking the approach of optimizing the efficiency of the conversion of solar energy, with similar explorations by others that were done a decade and more later. In Mauzerall (1992), David then merged these three angles of solar radiation, the hypothesis of Samuel Granick on the evolutionary path, and the molecular energetics of chlorophyll in a beautiful review of origins. There were no attempts for another 15-plus years to explain the primacy of chlorophyll *a* in oxygenic photosynthesis. It was great luck, for me, then to have David Mauzerall, just across Manhattan on the East Side at The Rockefeller University, to consult regarding questions about a novel chlorophyll: Chl *d*.

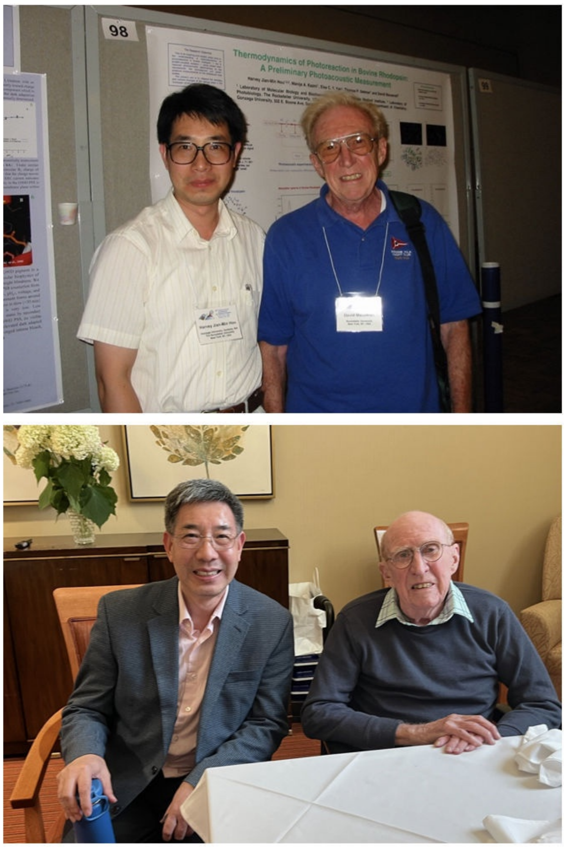

Fig. 8. *Top*: Harvey Hou (*left*) and David Mauzerall (*right*), in front of their poster at the 10th International Conference on Retinal Proteins, in Seattle, Washington, in 2002: "Thermodynamics of a photoreaction in bovine rhodopsin: A preliminary photoacoustic measurement". Source: Harvey Hou. *Bottom*: At David Mauzerall's 95th birthday celebration in Skillman, NJ, June 2024. Source: Denise Mauzerall.

Back in 2007, I was a budding astrobiologist at the NASA Goddard Institute for Space Studies (GISS) in New York City, having just published my first couple of papers (Kiang *et al.* 2007a,b) that year on "Spectral signatures of photosynthesis" (on Earth and potentially around other stars), with somewhat simplistic conclusions then about photosynthetic pigment peak absorbance wavelengths related to the incident radiation spectra. A young biophysicist, Stephen Mielke, contacted me seeking a postdoctoral position. Seeing his biophysics background, I immediately introduced him to the question of the long wavelength limit of oxygenic photosynthesis, as an important constraint in the search for life on other planets. Chl *d* was discovered by Miyashita *et al.* (1996), which replaced nearly all of Chl *a* in PSII in the cyanobacterium dubbed *Acaryochloris marina*, with clear evidence that it was able to evolve oxygen by absorbing at wavelengths as long as 714–718 nm. This changed the textbooks on the photon energy requirements for oxygenic photosynthesis and raised the question of the uniqueness of Chl *a*. And it gave the search for life beyond the Solar System a potential basis to extrapolate alternative "biosignatures" of photosynthetic pigments on planets orbiting different kinds of stars from our Sun.

When *A. marina* was discovered, questions immediately swirled as to what was the precise PSII trap wavelength, whether this organism's efficiency might be subject to back reactions, whether uphill energy transfer might be happening, what modifications to the photosynthetic apparatus might be enabling electron transfers with the lower potentials from the longer wavelength photons, among other unknowns, such as whether the active branch of the special pair uses Chl *a* or Chl *d*. Was *A. marina* struggling at the long wavelength limit for oxygenic photosynthesis, or did it demonstrate yet untapped potential for the use of photons in the far-red and near-infrared?

We thus began a collaboration with David Mauzerall to conduct photoacoustic measurements of the spectral thermodynamic efficiency of photon energy storage in *A. marina*. (Also *see* the message from Ora Canaani, in this paper, concerning David's earlier work on photo-acoustics.) Photoacoustics (PA) refers to how photons striking a surface have their energy dissipated as heat, which can be detected as sound (pressure changes) with a microphone, a principle first discovered by Alexander Graham Bell (Bell 1880). David had developed highly advanced PA spectroscopy methods in which light from millisecond timescale laser pulses aimed at a target material can be used to measure enthalpy and volume changes for different photoreaction steps (Mauzerall and Mielke 2014). This allowed fast and accurate direct measurement of the energy-storage efficiency of photons that are used in photochemical reactions. David took Steve Mielke under his wing, training him in the rigors of precise alignment and calibration of a Nd:YAG laser and measuring the pulse energies, down in the stable basement environment of David's lab away from other noise and electronic disturbances. Robert (Bob) Blankenship, then at Washington University in St. Louis supplied purified PSII complexes and cultures of *A. marina*, strain MBIC11017. We were ever grateful to the steadfastly capable lab technician Irene Zielinski for ensuring the integrity of the cultures.

During Steve and David's meticulous efforts, retuning the laser, overcoming a damaged mirror, developing a method to fit the saturation curves, experimenting with diuron (which blocks electron transport), comparing efficiencies of cultures at different growth stages, and more, Björn *et al.* (2009) came out with a follow-up to Mauzerall (1973) and Mauzerall (1976b), this time asking "Why chlorophyll *a*?" They revisited David's itemization of the properties of chlorophyll and concluded that Chl *a* remains unchallenged by Chl *d* for dominance of oxygenic photosynthesis, at least empirically to date, while it remained (and remains) unresolved whether the special pair P_{D1}/P_{D2} in *A. marina* is a homodimer of Chl *d*. In 2011, the work in David's lab confirmed unequivocally that PSII in *A. marina* is not subject to back reactions with the longer wavelength photons, and, in fact, given the lower energy input, the efficiency of photon energy storage is comparable to or higher than that of a Chl *a*-containing cyanobacterium, *Synechococcus leopoliensis* – UTEX 625 (Mielke *et al.* 2011). Finally, through a beautiful series of careful measurements stepping through wavelength increments, Steve Mielke provided the spectral characterization of the thermodynamic energy storage efficiency and found the PSII trap in *A. marina* to be at 723 ± 3 nm (Mielke *et al.* 2013). Thus, oxygenic photosynthesis can indeed operate quite well at a trap wavelength ~40 nm longer than that of P_{680}, the reaction center of Chl *a*-dominated PSII.

A definitive rule is still elusive for the molecular energetic and environmental limits to oxygenic photosynthesis that could help constrain the search for life elsewhere, but studies are proliferating on far-red absorbing cyanobacteria, and we are making progress. It was such a privilege and pleasure to work with David on this journey – all the discussions to puzzle over the data and model to account for the dip in efficiency between PSI and PSII, David's frequent praises for Steve Mielke, his precise identification of "bullshit", and his and his wife Miriam's cheerful, enlightened hospitality and beach forays at their home in Woods Hole, with its view of thick seagrasses on the shore. Miriam always kept a lookout for us women scientists, herself a pioneer as a PhD in cell biology in 1954. It is with wonder that I regard having the opportunity to work with and get to know David Mauzerall, who first laid out "Why chlorophyll?" back in the 1970s, updating to answer a critical part of "How chlorophyll *d*?" nearly 40 years later.

I end my message with photographs of cyanobacteria cultures, photoacoustic instruments, and a signal output from Mauzerall's laboratory (*see* Fig. 9; for details *see* its legend).

Thank you, David, for the years of elegant science, your blunt, quiet-spoken challenges to our understanding, the warm welcome to your photobiology lab, and for keeping in touch in the years since. Thank you and best wishes on your 95th birthday!

8. Jonathan Lindsey (e-mail: jlindsey@ncsu.edu)

Inspiration for a lifetime

I first met David Mauzerall in the fall of 1979 as a second-year graduate student while casting around for a PhD project with a suitable chemistry and biology combination. Shortly after entering his office and hearing my interests and background, he promptly suggested the synthesis of a molecule containing a porphyrin and a quinone held in a sandwich configuration, but at 10 Å apart, which he illustrated with his hands separated by 15–20 cm of air. Mauzerall had been formulating concepts about electron tunneling since his early studies on porphyrin photoreduction (Mauzerall 1962) and charge separation in the bacterial photosynthetic reaction centers (McElroy *et al.* 1974). He explained to me how this "simple" chemical model could provide a valuable counterpart for more complex processes in photosynthetic systems. I wasn't sure I wanted to do *that much* chemistry, particularly organic synthesis, but (*1*) it seemed like a really big mountain to climb, (*2*) as with each project in his group, this would be entirely my own, (*3*) there was somehow

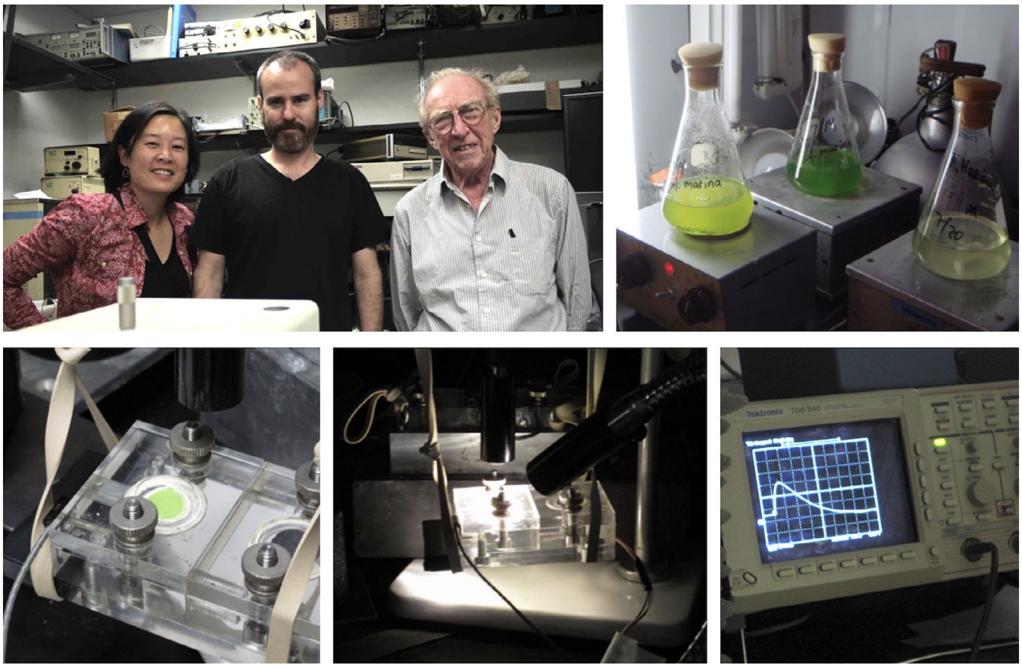

Fig. 9. *Top left* (*left to right*) Nancy Y. Kiang, postdoc Steven P. Mielke, and David Mauzerall, in David's Photobiology Lab at Rockefeller University, in 2010. *Top right*: Culture flask of suspensions of cyanobacteria, *Acaryochloris marina* and *Synechococcus leopoliensis*. *Bottom* (*left*) Whole cells of *A. marina* on filter paper on a photoacoustic cell, suspended with rubber bands to avoid vibrations; (*middle*) a setup with microphone in the light; (*right*) a photoacoustic signal, showing a rise and a decay of a pressure wave after a light pulse flash. Source: Nancy Y. Kiang.

an attractive all-or-nothing risk because making the target compound was only a prelude to carrying out the meaningful science, the photochemistry studies, and (*4*) his intellect and exuberance were enthralling – so as green as the mutant *Chlorella* down the hall, I signed on right away to a project I regarded then (and now) as immensely thrilling. He provided no further guidance as to how such a synthetic compound could be prepared, or what molecular entities would bridge that vast 10 Å chasm of empty space – that was all to be figured out on my own. To the extent I have accomplished anything scientifically meaningful in the 45 years since it all started with the above conversation with Dave Mauzerall.

With the porphyrin–quinone compound in hand a seeming eon (but actually ~2½ years) later, studies shifted from the synthesis hood to the spectroscopy lab. We did experiments together in the laser lab on Monday and Thursday evenings beginning after dinner and often ending around 1:30 a.m. In that dark lab, quiet except for the pulse of the nitrogen laser, we made initial studies concerning the effects of metal, charges, temperature, and solvent polarity on the electron-transfer process as inferred by time-resolved fluorescence spectroscopy. Dave always emphasized the importance of signal-averaging of the fluorescence from repetitive weak laser pulses to get high-quality data with good signal/noise ratio and to limit sample bleaching and multiphoton effects. For time-resolved absorption spectroscopy, Dave turned to his longtime friend and kindred spirit, Henry Linschitz at Brandeis University (about Henry Linschitz (1919–2014), *see*: https://www.bostonglobe.com/metro/obituaries/2014/12/19/henry-linschitz-waltham-manhattan-project-scientist-became-antinuclear-activist-and-brandeis-professor/2iPHL7Qd8XK3OnlcSzwjxH/story.html). The spirited conversations between Dave and Henry were an education in photochemistry, biophysics, and topics far beyond science. Both were dedicated to the highest scientific integrity – that no page should be left unturned in obtaining accurate results and appropriate interpretation.

Dave was always patient about publishing – in this case, several years of work yielded two communications (Lindsey and Mauzerall 1982, Lindsey *et al.* 1983). While time eventually lapsed on my graduate days and 1-year postdoc there (1984), the gods of science smiled broadly and beneficently by sending John K. Delaney, a new graduate student, to the Mauzerall group. It was Delaney, through patient and meticulous work, who vastly expanded the scope of photophysical studies and unequivocally established the electron-tunneling phenomena in the porphyrin–quinone compound (Lindsey *et al.* 1988, Delaney *et al.* 1990). Through experiment and theory, John Delaney over time was able to balance Dave's tenaciously held ideas on this topic; in so doing, they together developed deep new insights into how biological systems might tune the tunneling process (Delaney and Mauzerall 1989).

I have always regarded Dave Mauzerall as a scientific icon; and, I have always felt beyond privileged to count him as both a mentor and a lifelong friend (*see* Fig. 10).

Fig. 10. Jonathan Lindsey discussing the paper he wrote as a tribute to Dave Mauzerall at Mauzerall's 95th birthday celebration (Lindsey 2024). Source: Ken Duell.

9. Denise and Michele Mauzerall (e-mail: mauzerall@princeton.edu; mem.amber@gmail.com)

Dad has always been a constant source of support, encouragement, and endless optimism. Even today, as he celebrates his 95th birthday, legally blind and struggling with his gait, he cheerfully answers "can't complain" in his soft Maine accent when asked how he's feeling. His days are now filled with listening to NPR, podcasts, and audiobooks, with as much scientific content as we can find.

Dad inspired us to have confidence in our abilities to accomplish anything we set our minds to if we were willing to put in the effort. He challenged us to think critically and not blithely accept widely held views without reflection. He set high standards and maintained interest in what we were doing and confidence that we would succeed. His love of science, joy in conducting his own experiments in the laboratory, and delight in understanding the world around him continue to inspire us. We are delighted to know that he has similarly inspired his students and colleagues.

Happy 95th birthday Dad! We are so lucky to still have you with us. *See* Fig. 11. For family photos from recent years, *see* Fig. 12.

10. Michael Seibert (e-mail: mike.seibert@nrel.gov; mseibert71@gmail.com)

How and when I met David (Dave) Mauzerall

Although I never worked directly in his laboratory, Professor David (Dave) Mauzerall was an important early career mentor during the year that I was in the New York City area. In the way of background, I had moved to New York in the fall of 1971 after completing my PhD, in Biophysics and Molecular Biology, in Britton Chance's lab at the Johnson Research Foundation (University of Pennsylvania). [For Chance (1913–2010), *see* https://en.wikipedia.org/wiki/Britton_Chance; and https://www.nytimes.com/2010/11/29/us/29chance.html.] My new work at the former GTE (General Telephone & Electronics Corporation) Laboratories in Bayside, Queens, emphasized

Fig. 11. Group photograph taken at the 95th birthday celebration of David Mauzerall on 23 June 2024 in Skillman, NJ. *Sitting* (*left to right*): Denise Mauzerall (daughter), David Mauzerall, and Jonathan Lindsey (former PhD student). *Standing* (*left to right*): Silas Duell Mauzerall (grandchild), Ken Duell (son-in-law), Nancy Greenbaum (former post-doc), Marilyn Gunner (former collaborator), Bruce Diner (former PhD student), Judy Diner, and Michele Mauzerall (daughter). Source: Ken Duell.

Fig. 12. *Top*: David and Miriam Mauzerall, Rockefeller University Graduation, June 2006. *Bottom*: Miriam Mauzerall, Michele Mauzerall, Denise Mauzerall, Ken Duell, Silas Duell Mauzerall, David Mauzerall, 2014. Source: Family archives.

artificial lighting effects on ornamental and crop plants (GTE at the time owned the lighting company, Sylvania), but my real interest was in basic photosynthesis. There I met up with two laser physicists, Drs. Robert Alfano and Stanley Shapiro, who had developed an ingenious way of directly measuring the kinetics of fluorescence emission on a picosecond time scale. At that time, fluorescence lifetimes were measured indirectly by phase techniques. These two physicists had set up a mode-locked laser actinic system in combination with an optical Kerr cell (*see* Seibert 1978, for a description of the gating method) that could record the intensity of fluorescence emission on a point-by-point basis at set times after a picosecond laser pulse. I approached them to use their system to measure chlorophyll fluorescence in a thylakoid membrane system.

For my PhD research, I measured microsecond domain transient absorption changes in bacterial chromatophore membranes. However, I lacked experience with plant systems. Thus, I contacted Dave Mauzerall at Rockefeller University in Manhattan. This was done at the recommendation of Professor Don C. DeVault, my PhD advisor [for DeVault (1915–1990), *see* Seibert 1991]. My plan was to start discussions with Dave on our recent GTE fluorescence studies of chloroplast membranes, which I had isolated from spinach and endive leaves. Dave had extensive experience in (*1*) porphyrin and chlorophyll chemistry/metabolism (Granick and Mauzerall 1958a,b; 1961; Mauzerall and Granick 1958, Mauzerall 1964), (*2*) light-induced fluorescence changes in algae (Mauzerall and Malley 1971, Mauzerall 1972), and (*3*) primary photoreactions of Photosystem II (Mauzerall 1972). I was very happy when he invited me to visit his lab. We had several exciting discussions about our fluorescence data, and his advice helped us get the work published (Seibert *et al*. 1973, Seibert and Alfano 1974). In both these papers, we specifically acknowledged Dave's contributions to critical discussions of our results. Dave provided the motivation for me to get into Photosystem II, reaction center charge separation, and oxygen-evolution studies years later after I had joined the National Renewable Energy Laboratory (NREL) in 1977.

At the time that I first visited Dave's laboratory, he was the chairperson of the New York Area Photosynthesis Seminar Series, and he invited me to attend several of the lectures at Rockefeller (which occurred every couple of months on Wednesday evenings). Before long, he invited me to be the co-chair of the Seminar Series, giving me the responsibility for inviting the speakers (using the minimal amount of travel funds that we were able to procure). During this time, I had invited several from the University of Pennsylvania (Britton Chance, Don C. DeVault, P. Leslie Dutton, and David F. Wilson) to come up and give talks at Rockefeller. However, GTE labs moved me to their Boston area facility (Waltham) in late 1972; thus, I was not able to help Dave out for very long. Nevertheless, I really benefitted from his mentoring, kindness, and the opportunity of getting to know other photosynthesis experts in the New York City area. In any case, we corresponded and talked by phone for at least 25 years after I left New York. I also provided Mauzerall's lab with PSII-enriched spinach membrane fragments (since we made them routinely as part of the procedure to isolate PSII reaction centers) as late as 1997!

During 1971–1972, when I was interacting with Mauzerall's research group, I met Bruce Diner and Elias (Eli) Greenbaum. I visited Bruce years later in Paris (France) during a sabbatical in Jean Lavorel's laboratory at Gif-sur-Yvette (close to Paris), and he visited my lab several times at NREL (*see* the message from Bruce Diner). I have had extensive interactions and collaborations with Eli throughout the rest of my career, while at NREL in Golden, Colorado, a sister DOE laboratory of Oak Ridge National Laboratory, where Eli has spent most of his working career after leaving Rockefeller (*see* the message from Eli Greenbaum). For these contacts, I am also indebted to Dave Mauzerall and congratulate him on the important occasion of his 95th birthday!

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Appendix 1. **Obituary of Miriam I. J. Mauzerall:** https://www.facebook.com/denise.mauzerall/posts/10229729128995584

Miriam Isabelle Jacob Mauzerall, 19 April 1924–7 July 2023

It is with sadness that we announce the passing of Miriam Isabelle Jacob Mauzerall on 7 July 2023 at the age of 99. She died peacefully in Skillman, NJ where she had moved with her husband David nearly 6 years ago to be closer to her children. Miriam is survived by her loving husband of 64 years, David Charles Mauzerall, her two daughters, Denise Mauzerall (Kenneth Duell) of Princeton, NJ and Michele Mauzerall of Gulfport, FL, her grandchild, Silas Duell Mauzerall also of Princeton, NJ, and by special friends all over the world.

Miriam was born on 19 April 1924 in New York City, the child of Minnie (Rosen) and Isadore Jacob. Minnie was a Russian Jewish refugee who designed and made clothing for Milgram's Department Store and Isadore was an accountant who managed the business. Miriam adored her mother and grew up helping in the store. Miriam's aunt Lena (Singer) kept a kosher kitchen and Miriam was close friends with her children and fondly remembered "stealing cookies by the light of fireflies in jam jars with them". Her favorite aunt Nadine (Nan) Rosen was a linguist who introduced Miriam to a wide-range of new ideas, books, opera, and theatre.

From a young age, Miriam enjoyed learning. She graduated early from high school, received a scholarship to New York University (NYU) for college and a master's degree, and a fellowship for her PhD which she received in cell physiology from NYU in 1954. At a time when few women obtained college degrees, Miriam was committed to a career in science. She was pleased to have been a part of the newly emerging women in science who were starting to be remembered for the work they did and the intellect they contributed to the world of science. From 1948 to 1951 she worked as a research assistant for Dr. W.J. Osterhout at the Rockefeller Institute for Medical Research in New York. Dr. Osterhout spent his summers at the Marine Biological Laboratory (MBL) in Woods Hole, MA. Miriam's work with him extended to summers in Woods Hole where she took the MBL physiology course and enjoyed spending hours in informal discussions with various eminent scientists of the time. This began a lifelong connection to the MBL and the Woods Hole scientific community which she considered her 'home away from home'. From 1951 to 1953 Miriam worked as a teaching assistant at the NYU Dental School. She also worked as a research associate at Columbia University Medical School from 1953 to 1954. Following her PhD, Miriam became a post-doctoral research fellow at the Enzyme Institute at the University of Wisconsin–Madison (1954–1956) and then an instructor at the Western Reserve University School of Medicine in Cleveland Ohio (1956–1958).

While an instructor at the medical school in Cleveland, Miriam was invited to attend a biochemistry conference in Vienna, Austria. A plane was chartered for the trip, and she was introduced to David Mauzerall as they boarded. Sitting next to each other on the plane they were so engaged in conversation that a stranger seated in front of them asked them if they were married. When they both responded with a surprised "No!" the stranger said, "You will be!"

In 1959, Miriam married David Mauzerall in a ceremony held at Rockefeller University where David was then an assistant professor. They lived on the east side of Manhattan for ten years where they raised their family until moving to Dobbs Ferry, NY where they lived until 2016, spending summers first in La Jolla, CA, and then in Woods Hole. Miriam left laboratory research to focus on raising her children but became involved with local politics as well as with the League of Women Voters where she led study groups on nuclear disarmament. After her children left home, Miriam returned to her love of science and became a freelance science writer, publishing early reports on research on AIDS in Genetic Engineering News under her maiden name of Miriam I. Jacob, PhD. She enjoyed being a science reporter and traveled to conferences around the world interviewing and writing about current research in molecular biology.

Miriam loved sailing, art, music, dance, and gardening. Any opportunity to sail was enthusiastically welcomed, all museums and art studios (regardless of size or reputation) were happily visited, few Rockefeller concerts were ever missed, and season tickets to The Joyce Dance Theatre were thoroughly enjoyed. Miriam was especially proud of a massive rhododendron in front of the Dobbs Ferry, NY house that she nurtured from a small cutting she received to a towering cascade of flowers every spring.

None of us likely know exactly how many people we have touched in our lives. Miriam as a student, as a scientist, as a teacher, as a writer, as a daughter, as a wife, as a mother, as a friend, as an audience, as an activist, as an environmentalist, as a gardener, as nature lover, as philanthropist, as all the things that made her unique and unconventional… Miriam will be missed. All those who have been lucky enough to be touched by Miriam can share in the joy of having known her and smile at what was truly a remarkable and well-lived life.

Kindest Regards,
The Mauzerall Family

Appendix 2. Websites related to David Mauzerall

(*1*) Interview about the Marine Biological Laboratory:
https://history.archives.mbl.edu/browse/video-audio/david-mauzerall

(*2*) Webpages at The Rockefeller University:
https://www.rockefeller.edu/our-scientists/emeritus-faculty/917-david-mauzerall/
https://lab.rockefeller.edu/emeriti/mauzerall/

(*3*) List of publications:
https://www.researchgate.net/profile/David-Mauzerall
https://academictree.org/chemistry/publications.php?pid=76562