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HISTORY AND BIOGRAPHY

A life in light – in honor of David Mauzerall on his 95th birthday

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Abstract

David Mauzerall was born on July 22, 1929 to a working-class family in the small, inland textile town of Sanford, Maine. Those humble origins instilled a lifelong frugality and an innovative spirit. After earning his PhD degree in 1954 in physical organic chemistry with Frank Westheimer at the University of Chicago, he joined The Rockefeller Institute for Medical Research (now University) as a postdoctoral fellow that summer, rose to the rank of professor, and remained there for the rest of his career. His work over more than 60 years encompassed porphyrin biosynthesis, photoinduced electron-transfer reactions in diverse architectures (solutions, bilayer lipid membranes, reaction centers, chromatophores, and intact leaves), the light-saturation curve of photosynthesis, statistical treatments of photoreactions, and "all-things porphyrins." His research culminated in studies he poetically referred to as "listening to leaves" through the use of pulsed photoacoustic spectroscopy to probe the course and thermodynamics of photosynthesis in its native state. His research group was always small; indeed, of 185 total publications, 39 were singly authored. In brief, David Mauzerall has blended a deep knowledge of distinct disciplines of physical organic chemistry, photochemistry, spectroscopy and biophysics with ingenious experimental methods, incisive mathematical analysis, pristine personal integrity, and unyielding love of science to deepen our understanding of photosynthesis in its broadest context. He thought creatively – and always independently. His work helped systematize the fields of photosynthesis and the origin of life and made them more quantitative. The present article highlights a number of salient scientific discoveries and includes comments from members of his family, friends, and collaborators (Gary Brudvig, Greg Edens, Paul Falkowski, Alzatta Fogg, G. Govindjee, Nancy Greenbaum, Marilyn Gunner, Harvey Hou, Denise and Michele Mauzerall, Thomas Moore, and William Parson) as part of a celebration of his 95th birthday.

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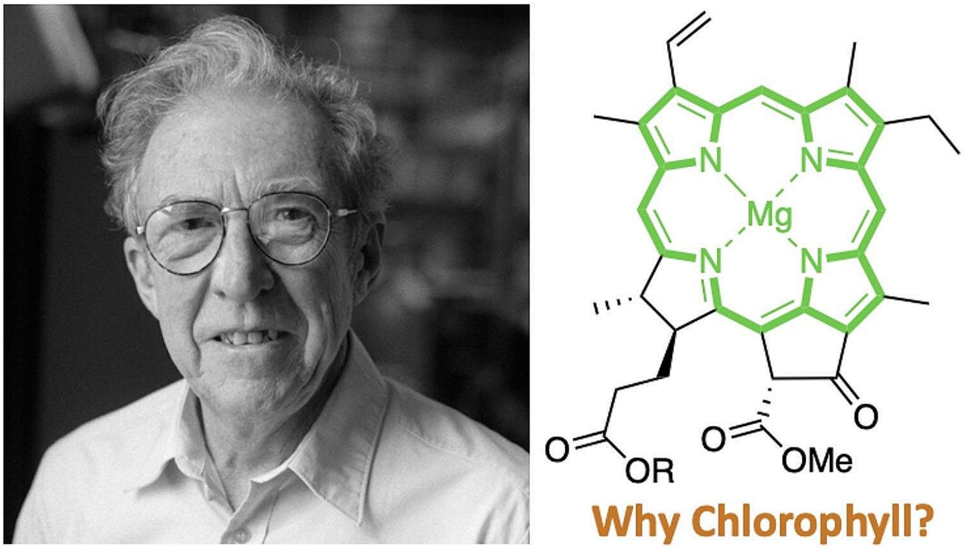
Graphical Abstract



Keywords Chlorophyll · Electron-transfer reactions · Photoacoustic spectroscopy · Photophysics · Photosynthesis · Poisson distribution · Porphyrins · The Rockefeller University

Introduction

> *There is more to photosynthesis than just sunshine and sugar.*

David Charles Mauzerall was born in Sanford, Maine, a textile town some 25 km from the coast. His grandparents had immigrated from New Brunswick and Quebec, Canada to Maine when the textile mills opened there. He grew up in a stigmatized, Francophone underclass community – a 'Petit Canada' (Myall 2000) – speaking Canadian French with his mother and English with his father. His mother had a 4th -grade education and his father was a mill wright, ham radio operator, and a jack-of-all trades; both worked in various jobs at the local mills. His humble beginnings during the Great Depression engendered both generosity towards others as well as general frugality encapsulated in a life motto of "epoxy to the rescue!". It was in small-town Maine where he also developed his affinity for snow, ice and cold winters. Playing pick-up hockey on frozen ponds, with children lined up in late afternoon with buckets of water from holes in the ice to Zamboni the surface, was a highlight of the long Maine winters. He was also a roofer, tarring roofs for spending money in the short Maine summers.

A local librarian pointed him to a shelf of science books while he was in elementary school which he immediately read through, and which spurred his interest in a career in science. While still in middle school, an uncle gave him a blue Gilbert chemistry set that he used to make super gunpowder, replacing potassium nitrate with potassium chlorate, and which led to an alarming explosion in his parent's basement. His father loved being a ham radio operator which led him to make his own radio out of spare parts. When assembled and plugged in one evening it immediately burnt up and blew the fuses in the home, much to the family's consternation.

Mauzerall was Valedictorian (among 13 in the 'boys department') at St. Ignatius High School in 1947 (Sanford Publishing 1947). He also was Valedictorian (Fig. 1) out of 200 students (Jennings 1951) upon receiving his B.S. degree in Chemistry in 1951 at St. Michael's College in Winooski, Vermont. The college yearbook stated (The Shield 1951) *"Red was undisputedly a top ranking student with a 4 year straight A record. He was Doc Quinlan's right hand and the Chem lab was his home. His able assistantship in Chemistry, his presidency of the Honorary Chemistry Society and active membership in other clubs plus his unfailing weekly stroll towards Trinity [the nearby girl's college], gave him a well rounded scholastic and extracurricular stay at SMC."*

Mauzerall moved to Chicago for graduate school at the University of Chicago, where he earned his Ph.D. degree in physical organic chemistry with Prof. Frank Westheimer in 1954. Other faculty in the esteemed Chicago department were Willard Libby and Harold Urey, and of course in Physics there were Enrico Fermi, Robert Mulliken, and John Platt. It was a wonderful place where for the first time he found engaging peers with whom to do and discuss science.

Fig. 1 Valedictorian of St. Michael's college class of 1951 (Jennings 1951)

In those days a faculty member might have only one or two students in their research group. A classmate was Stanley Miller, of imminent prebiotic chemistry fame, who was a doctoral student of Urey and became a lifelong friend.

Mauzerall's first paper was on a synthetic model with which to understand the hydride donation properties of NADH (Mauzerall and Westheimer 1955), published nearly 2 decades before Ronald Breslow coined the term 'biomimetic' (Breslow 1972) to describe a concept that now pervades the molecular sciences. Westheimer (1912–2007), widely regarded as one of the first to apply physical organic chemistry to understand enzyme mechanisms (Gerlt 2007), was known for *"pushing relentlessly until he got what he wanted"* (personal communication, in 2024, by Mauzerall to the author).

On graduation, Mauzerall traveled back east to join the lab of Prof. Sam Granick at what was then The Rockefeller Institute for Medical Research, located on the upper east side of New York City. Granick, a classical biochemist, was focused on elucidating the biosynthesis of the tetrapyrroles of biology. He did this by subjecting bacteria and algae to X-rays which generated mutants allowing him to deduce the biosynthetic pathways of heme and chlorophyll. Mauzerall jumped in and developed a simple yet reliable assay for δ-aminolevulinic acid, the first committed precursor to all naturally occurring porphyrins and the immediate precursor to the pyrrole porphobilinogen. δ-Aminolevulinic acid appears in the urine in some hereditary hepatic porphyrias (individuals who make excess water-soluble uroporphyrins and are hence highly photosensitive) (Mauzerall and Granick 1956). The simplicity of the assay and the importance of the analyte led the resulting paper to eventually become a Citation Classic (> 1000 citations, Mauzerall 1984) and the water-soluble porphyrin became the basis of much of Mauzerall's early research.

The Rockefeller University lab

The Rockefeller University (Hanson 2000) is a magical oasis for quiet study in the midst of a global city with all the latter conveys – unbridled energy, international dynamism, and teeming humanity. Rockefeller since its inception has been organized around laboratories headed by a principal investigator (PI) rather than academic departments of collections of faculty members (Corner 1964), thereby offering unparalleled individual freedom. In that system a talented ambitious scientist could rise within a PI's group and eventually become an independent PI themselves. Mauzerall was a member of the lab of Prof. Sam Granick (1909–1977) at Rockefeller from 1954 to 1969, rising from his start as a postdoc through the ranks to assistant professor in 1959, associate professor in 1964, and full professor in 1969. Granick himself had joined the lab of Prof. Leonor Michaelis at Rockefeller in 1939 (Kappas 1977). Mauzerall's lab, with legacy items from Michaelis and Granick, spanned the entire second floor of Flexner Hall encompassing ~ 20 rooms (and his daughter Denise loved roller skating up and down the main granite hallway). The inherited facilities included cold rooms, culture facilities for photosynthetic and other organisms, a small library, several chemistry fume hoods, a chemical stockroom, and numerous labs for biological preparations. Mauzerall added laser labs, darkened rooms for optical measurements, and spectroscopy facilities; indeed, he said (personal communication, in 2024, by Mauzerall to the author) *"I saw the ad for the first nitrogen laser and couldn't resist – I bought one immediately and never regretted it."*

Each group member had an independent project. The group size peaked in the early 1980s at ~ 10, but over the years more typically was about 5 or 6 individuals. Most students at Rockefeller, and likely also most postdocs and visitors in the Granick and then Mauzerall labs, probably recall their experiences as halcyon days in an elysian garden of science. There were no limitations in experimental resources. Ultimately, however, building renovations and space reassignments came, and following emeritus status in 2001 the lab moved first to the C level of Theobald Smith Hall, and later to the deepest level beneath the ground-floor cafeteria of the 18-floor Tower Building. Undaunted and always the optimist, Mauzerall perhaps saw a silver lining in the profound quiet in such subterranean zones. Some of his experiments on 'listening to leaves' were done in the total silence and darkness (save for the illumination sources) deep in the hidden bowels of the Rockefeller buildings.

Notable academic activities include the following:

- Guggenheim Fellowship to study electron spin resonance of photosynthetic systems with Professor George Feher at University of California at San Diego (UCSD), where he was Visiting Professor (1965–1966).
- *"Provocateur"* (a title he was terrifically proud of!) at the Jindabyne Conference on the Origin of Life in Canberra, Australia (1981).
- Invited lecturer at the International Congress on Photochemistry in Beijing, China (1985), at an early point in the opening of China.
- Chairman of the Biophysics section of the New York Academy of Sciences (1988–1990).

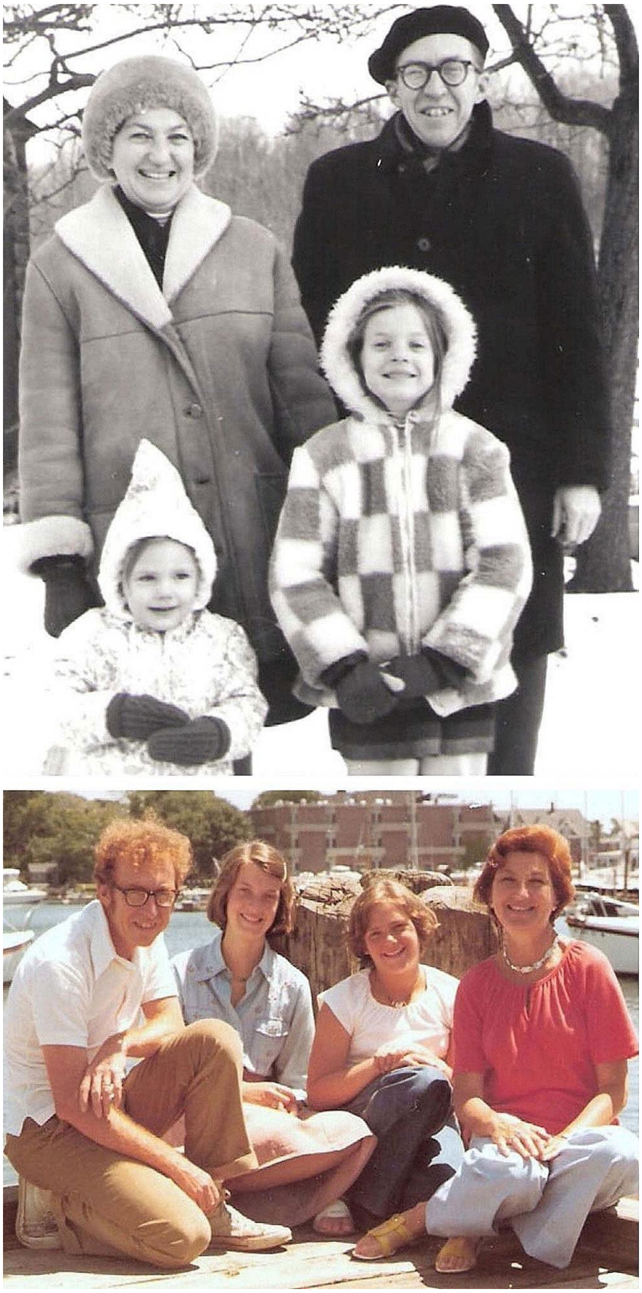


Fig. 2 Top: Miriam, Dave, Denise, and Michele (clockwise), in March 1969. Bottom: Dave, Denise, Michele, and Miriam (left to right) in Woods Hole, MA in summer 1977

A symposium in honor of Mauzerall's 60th birthday was held at The Rockefeller University (June, 1989) entitled 'Biological Charge Transfer: Photosynthesis to Physiology' with speakers including Britton Chance, George Feher, Felix T. Hong, Jonathan Lindsey, Stanley Miller, and Shigeru Sassa.

Visitors were common – some for a few days, others for months or years, or for repeat visits in the summers. International visitors who came and enriched the group with seminars and sparkle included Jack Barrett from Australia; Jurgen Fuhrhop from Germany; Zvi Dubinsky, Jehuda Feitelson, and Asher Ilani from Israel; and Anatoly Losev from Russia. Visiting scientists who came and stayed for years included Tong Ming Liu from China.

Notable external collaborators (who were not postdocs, students, or visitors) include Robert Alfano, Samuel Beale, Robert (Bob) Blankenship, Ora Canaani, Roderick (Rod) Clayton, Paul Falkowski, George Feher, Alan Finkelstein, John Golbeck, Marilyn Gunner, Henry Linschitz, Shmuel Malkin, William (Bill) Parson, Roger Prince, Joseph Ramus, and Gordon Tollin. Internal collaborators at Rockefeller were Brian Chait, Eddie Cohen, Attallah Kappas, Alex Mauro, Bruce Merrifield, and Mo Schreiber.

The family

Mauzerall and his wife Dr. Miriam Jacob, a cell physiologist, were married in 1959 at The Rockefeller University and were later joined by two daughters, Denise and Michele (Fig. 2). Miriam was a PhD scientist in her own right, and in later years worked as a scientific writer. They lived near The Rockefeller University on the upper east side of New York City until 1973, when the family moved to Dobbs Ferry, a small town on the Hudson river about 45 min by train from Manhattan. Mauzerall typically commuted in on Monday mornings, slept over in the lab, returned home late on Tuesdays, worked at home on Wednesday, and repeated the commute cycle on Thursday–Friday. He invariably did experiments in the laser lab on Monday and Thursday evenings until the wee hours.

Summers away

To escape the New York summer, from 1962 to 1972 Dave and Miriam and their two daughters would drive from NY to La Jolla, California, where Dave worked at UCSD with George Feher (Okamura et al. 2018), *"each time taking a different route to give the girls a view of more of the country"* (personal communication, in 2024, by Mauzerall to the author). In 1974, the focus shifted to the Marine Biological Laboratory (MBL) in Woods Hole on Cape Cod where both Dave and Miriam had independently spent happy summers as graduate and postdoctoral students. Woods Hole became a second home. They bought a small house there and continued to spend summers associated with the MBL for the rest of their lives. Transcripts of oral interviews at the Woods Hole Marine Biological Laboratory for both Dave and Miriam Mauzerall are provided in the Supplementary information (Sects. 1 and 2).

Porphyrinogens

Interest in the properties of the pyrrole porphobilinogen in heme biosynthesis during Mauzerall's postdoctoral work led to fundamental studies of reactivity in that system (Fig. 3). He showed that (1) porphobilinogen is pre-programmed for self-assembly without enzymes to give uroporphyrinogens, (2) uroporphyrinogens are thermodynamically stable, and (3) among the four possible isomers, uroporphyrinogen III is the most abundant and forms naturally. He explained how the greater stability of uroporphyrinogen III is understandable on statistical grounds – the orientation pattern of the acetic acid and propionic acid groups can be formed in more ways relative to any of the other three isomers (Mauzerall 1978). The same pattern is observed in all native tetrapyrroles and in fact provides a telltale signature for biosynthetic proposition of newly discovered tetrapyrrole macrocycles (Nguyen et al. 2023).

Such incisive experiments were fecund in providing a deep conceptual framework for understanding the biosynthesis and perhaps the evolutionary origin of the pigments of life. Uroporphyrinogen III is now known as the last universal precursor of all native tetrapyrrole macrocycles, standing at the nexus of the Fe, Mg, and Co/Ni branches. Granick (1957) had earlier discussed the biosynthesis of tetrapyrroles – heme, chlorophylls, and cobalamin – in an evolutionary context, but Mauzerall's studies deepened the concepts and added essential molecular granularity. Mauzerall first coined the term *"window looking back on evolution"* (Mauzerall 1976a). In total, his pioneering experiments cast light in darkness, enabling one to imagine how the great aromatic macrocycles of Nature could be formed under remarkably simple conditions.

Photoreactions of porphyrins and reaction centers

Next came studies of porphyrin photoreactions. Mauzerall learned photochemistry on his own, fascinated that *"you can shine light on molecules, and 'bang' something happens!"* (personal communication, in 2024, by Mauzerall to the author). Indeed, free base porphyrins in the presence of amines undergo photoreduction, affording the phlorin (i.e., a dihydroporphyrin upon addition to the meso-carbon) and more highly saturated macrocycles (Mauzerall 1962). The likely process of photoreaction via presumed radical intermediates provided a segue into studies concerning the intermediates in the primary process of photosynthesis.

Working with George Feher at UCSD, they measured the absorption spectrum and electron paramagnetic resonance spectrum of a porphyrin free radical which was stable in air due to its high redox potential (Mauzerall and Feher 1964a,1964b). They then extended the studies to photosynthetic organisms and newly available photosynthetic reaction centers. While now a routine part of undergraduate biochemistry textbooks, reaction centers were completely

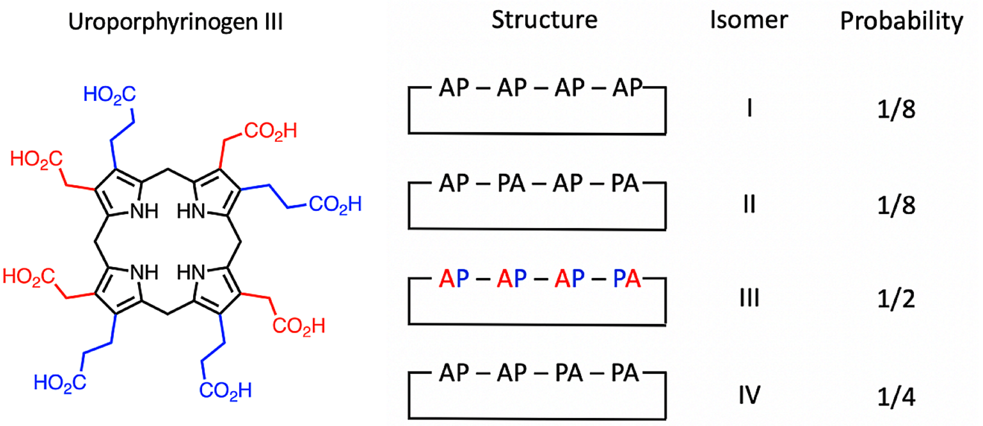


Fig. 3 Uroporphyrinogen III is the most probable among possible isomers (A = acetic acid, P = propionic acid)

novel then, and the constituents and molecular structure were not yet delineated.

The decay of the photoinduced charge-separated state in *Rhodobacter spheroides* R-26 and four other organisms was found to occur with $(k_d)^{-1} \sim 30$ ms and to be temperature independent in the range of 1.5–80 K. The results implied electron tunneling (McElroy et al. 1974). The importance of electron tunneling is not the absence of temperature dependence at physiologically irrelevant temperatures, but the structure–performance implications: as the authors pointed out (McElroy et al. 1974), *"A remarkable consequence of tunneling is the extreme sensitivity of the tunneling time on the width of the barrier. A 3% change in d (i.e., 1 Å) would approximately triple the value of* k_d*. A 50% increase in d (or an approximate doubling of (V–E)) would result in a decay time of about* 10^5*s (approximately one day!)."*

Consideration of electron tunneling in that era (and perhaps still today?) may have been a type of Rorschach test for scientists:

- Biologists, who would accept it without understanding it yet put it in the 'mechanistically who-cares' category;
- Physicists, who knew it to be obvious and put it in the 'no novelty' category;
- Organic chemists, who have always been wedded to rigid-edged molecular models and put it in the 'physically impossible' category; and
- Physical chemists/biophysicists, who could understand it, see the profound mechanistic relevance, and put it in the 'truly fascinating and centrally important' category.

Mauzerall was clearly in the very last camp comprised of a small band of fellow tunnelers. Studies of photoinduced electron-transfer reactions and electron tunneling were a mainstay of his research for decades.

Photoreactions in diverse model systems

Mauzerall investigated diverse model systems for studies of electron-transfer. The scope is too large to treat comprehensively here; hence only two systems will be mentioned.

(1) Transient conductimetry to measure ionogenesis upon photoreactions. While transient absorption spectroscopy has been a go-to method for decades to probe photoreactions in solution, the similarity in spectra of transient neutrals and transient ions of porphyrins complicated quantitative delineation of ion yields. The excited triplet state of zinc octaethylporphyrin ($^3P^*$) was found to react with a ground-state molecule (P) to give the separated cation radical ($P^{\bullet+}$) and the anion radical ($P^{\bullet-}$). At higher light intensity, the geminate recombination of two triplet molecules was observed with an encounter-limited rate constant depending only on the viscosity, and no other parameters, of the solvent. The electron-transfer radii for both reactions (~21 Å) exceeded twice the radius of the porphyrin π-electron system by ~7 Å. The observed results showed that the electron transfer could occur without molecular contact and were consistent with a mechanism of electron tunneling (Mauzerall and Ballard 1982).

(2) Interfacial photoreactions with bilayer lipid membranes (BLMs). The BLMs provide distinct advantages for the study of interfacial photoreactions: first, donors and acceptors can be separated across the lipid–aqueous interface in a self-assembled nanoscale architecture; and second, fast electrical measurements can be used to assess the ions formed upon light and dark electron-transfer reactions. *"BLMs were magical – one had to get them stretched and stable across a 1-mm orifice"* (personal communication, in 2024, by Mauzerall to the author). This line of inquiry, begun in collaboration with Alan Finkelstein, an established expert in BLMs, showed an increase of conductance upon illumination of polyiodide ions (e.g., I_5^-) in the BLM (Mauzerall and Finkelstein 1969). This allowed, for the first time, rapid measurements of photoinduced electron transfer across the less than 20 Å thick BLM.

Mauzerall immediately pivoted to studies of more biologically relevant chromophores, namely porphyrins. A classic system was magnesium octaethylporphyrin in the BLM and potassium ferricyanide in the aqueous solution. Electron transfer from the photoexcited porphyrin triplet state was close to the encounter limit, recombination was 100-fold slower, and the diffusion of the porphyrin cation radical across the BLM was orders-of-magnitude slower still. Inclusion of hydrophobic ions along with a donor on one side resulted in photogating of current flow across the membrane – a nanoscale photo field-effect transistor (Drain and Mauzerall 1990). The presence of an electron acceptor on one side and donor on the other resulted in light-induced pumping, via electric-field effects, of lipophilic anions across the BLM (Sun and Mauzerall 1996a,b). Mauzerall and coworkers ultimately published more than 30 field-defining papers on the topic of BLMs over the period 1969–2003 (Mauzerall and Sun 2003).

Why chlorophyll?

Mauzerall posed this simple question about the majestic molecular centerpiece of photosynthesis in 1973 (Mauzerall 1973), ~150 years after the first definitive isolation of chlorophyll (Govindjee et al. 2024). He considered the biosynthetic pathway, possible prebiotic origins of porphyrin analogues, the electronic properties that underpin spectral, photochemical and excited-state properties, self-assembly features in a BLM, and the perfect match of such properties for photosynthetic function – namely a light-trapping system for electron transfer. All taken together, this posited porphyrins as emerging upon selection from a universe of possibilities as the ideal molecule for photosynthesis – a system to capture sunlight and power the global biosphere based on perfectly logical physical and chemical principles. The same question revisited 35 years later emphasized chlorophyll *a* as the *sine qua non* for oxygenic photosynthesis given its features as a reductant (–1 V), oxidant (+1 V), and redox-silent energy-transfer partner (Björn et al. 2009). An intellectually rich cottage industry has arisen to pursue Mauzerall's 50-year old question in myriad directions, ranging from agricultural productivity, biofuels, and ecology to exoplanetary signatures and habitable venues in the cosmos.

Origin of life

Understanding how life may have originated remains one of the most fundamental and perplexing problems in science. Mauzerall made several significant contributions to this topic. While this short article can hardly do justice, a summary is as follows:

- Demonstration of the thermodynamic stability of uroporphyrinogens (Mauzerall 1978). This magnificent finding prompted the realization that the 'great rings' might be formed entirely without enzymes in a prebiological milieu.
- Demonstration of the liberation of hydrogen upon photochemical conversion of uroporphyrinogens to uroporphyrins (Mercer-Smith et al. 1985), showing an unprecedented molecular function of possible relevance in the prebiotic era.
- Demonstration of high quantum yields of photochemical ionogenesis of porphyrins in solution (Mauzerall and Ballard 1982), which indicates that porphyrins alone can yield potent photo-generated oxidants and reductants.
- Demonstration of efficient interfacial photoreactions of porphyrins in a self-assembled BLM, including the remarkable photoinduced ion pumping in a protein-less system, as a model for a prebiological ion pump (Mauzerall and Sun 2003).
- Articulation (argued happily and vigorously) of a photochemical origin of life, owing both to the immense energy needs of a living system, and the far-from-equilibrium nature of living systems that could be produced upon absorption of light. "*Photochemistry, and in particular, photochemical cycles, offer a centralizing principle so characteristic of living organisms. Reactants and photons flow into the photoreactive pigments or reaction center, and products of higher free energy flow out. This is just the gradient of free energy crucial for the stability of organized systems*" (Mauzerall 1992).

Mauzerall was an active participant in the International Society for the Study of the Origin of Life (ISSOL) and for several years had a grant from NASA for studies on the plausible porphyrin photochemistry in the prebiotic era.

Photosynthetic unit

The Emerson-Arnold experiment (Emerson and Arnold 1932) revealed a light-saturation curve in the efficiency of photosynthesis and thereby led to the concept of a photosynthetic unit (PSU). The experiment, the curve, and the concept together have been a polestar for understanding light capture and energy funneling in photosynthetic organisms. Mauzerall probed the light-saturation curve of photosynthetic organisms through the use of (1) single turnover flashes (e.g., ~1 μs) of monochromatic light of various intensities, (2) measurement of oxygen evolution or fluorescence emission (yield, lifetime), and (3) in many cases, analysis of the resulting data by target theory. The latter typically entailed application of (cumulative one-hit) Poisson statistics.

The use of single turnover flashes has been a personal campaign by Mauzerall. Application of this approach to diverse seaweeds showed a turnover time (~0.5 ms) for oxygen production that was similar to that of cyanobacteria and higher plants, suggesting a *"universal mechanism of photosynthesis"* and prompting the statement that *"we hope that this quantitative but holistic approach will increase our knowledge in this field"* (Mishkind and Mauzerall 1980). The approach also provides an unambiguous measurement of the size of the PSU (Mazella et al. 1981).

The use of Poisson statistics for data analysis provided a profoundly new approach for understanding the light saturation curve of photosynthesis as outlined in pioneering papers beginning in 1976 (Mauzerall 1976b,1976c). Studies were chiefly carried out with *Chlorella*. With increasing light intensities, events such as exciton capture in open traps, exciton rejection from closed traps, and exciton–exciton annihilation could all be modeled. This simple strategy coupled with elegant analysis has yielded a wealth of information concerning topology (e.g., the absolute size of the PSU and the number of traps per PSU) as well as dynamics (e.g., rate of energy migration, trapping time). A superb review captures the results published over nearly 20 years (Mauzerall and Greenbaum 1989).

Thermodynamics of photosynthesis and photoacoustic spectroscopy

A question that occupied Mauzerall perhaps since he first began contemplating photosynthesis in the late 1950s concerned the energetics of photoreactions, and ultimately the thermodynamics of the entire photosynthetic process. A seemingly simple question concerning energetics has proved to be rich with confusion. In his last peer-reviewed publication (Mauzerall 2013), entitled "The Thermodynamics of Photosynthesis," Mauzerall made a number of key points:

- *"the free energy of a process can only be defined for the process at equilibrium,"* whereas *"the absorption of a photon – at the intensities and for molecules relevant to photosynthesis – is an irreversible process."* In this regard, *"the efficiency of converting the energy of the absorbed photon to free energy of products is limited only by kinetics."*
- Thermal or Carnot cycle arguments concerning the temperature of the light source are irrelevant; instead, the thermal efficiency depends largely on the trap energy, which is set in oxygenic photosynthesis by the requirement to use water as the source of reducing equivalents.
- *"The methodology of photoacoustics allows direct measurement of trap energies* (Mielke et al. 2011)*,"* that energy at which the photon energy is irreversibly converted to chemical energy. This made it possible to show that *"the thermal efficiency of 54% from a 680 nm (1.8 eV) photon is possible,"* while *"the measured efficiency at the trap is* ~35% (Mielke et al. 2011)*."*

Photoacoustic spectroscopy – where a pulse of light upon absorption has its energy dissipated as heat, which causes the surrounding medium to expand and thereby creates a sound wave that can then be detected with a microphone – has been applied over the years to numerous systems. It is particularly well suited for scattering media where optical methods may be of limited use. Mauzerall was the first to develop and apply pulsed photoacoustic methods to examine photochemical reactions in solution, photosynthetic cells, and whole leaves with an aim to measure the thermodynamics and energy-storage features. This complemented the more extensive information concerning kinetics and structure obtained via other methods. Indeed, *"pulsed photoacoustics is the ideal experimental method for probing the thermodynamics of photosynthesis over an extended time scale"* (Mauzerall and Mielke 2014). Mauzerall referred to photoacoustic spectroscopy as *"calorimetry at the speed of sound"* (Amato 1989). Some of the advantages of photoacoustics are as follows:

- Determining yields of photochemical reactions. Indeed, "*in flash photolysis one requires absolute extinction coefficients of the short-lived species. Photoacoustic measurements provide the yields of the ions formed directly and unambiguously"* (Feitelson and Mauzerall 1993).
- Determining the energy efficiency as opposed to the quantum efficiency. Indeed, *"One determines* _all_ *the energy stored in the system"* including those in the products of photochemistry, the proton gradients, and even protein conformational changes, and this can be achieved in vivo without fractionation or disruption of the elaborate biochemical machinery. In particular, the trap energies of both photosystem I (PSI) and photosystem II (PSII) can be measured directly (Mauzerall and Mielke 2014).
- Measurements of diverse photosynthetic phenomena. For example, both oxygen release and uptake, due to photogenesis and photorespiration, can be measured in intact leaves. The resolution (0.1 ms) suffices to determine S-state oscillations of oxygen formation, revealing the lag time (1 ms) and rise time (5 ms) of oxygen formation in spongy leaves (e.g., spinach, viburnum), as well as oxygen uptake (~7–9 ms), the latter attributed to oxidation of reduction products of PSI (e.g., ferrodoxin) (Mauzerall 1990).

Mauzerall's work on photoacoustic spectroscopy may well be *la cerise sur le gâteau* as it combines instrument building, spectroscopy, photophysics, analysis, and the entire photosynthetic apparatus found in nature, namely in a leaf, all with the objective of meaningful quantitative measurement. His lecture on this topic, 'Listening to Leaves,' perfectly embodies the scientific interests and the spirit of David Mauzerall himself (Fig. 4). To the author's knowledge, no recording of the lecture nor audiofile of the photoacoustic data is available, most unfortunately.

Instrumentation

Mauzerall was inclined to create and build his own instrumentation when needed to solve a scientific problem that extended beyond the typical gear found in a spectroscopy lab. Four examples include the following:

- The oxygen luminometer (Burr and Mauzerall 1968) with detection limit of 10^{-11} M in water was devised and used to (i) identify a cell-free preparation of the oxygen-evolving apparatus from the cyanobacterium *Phormidium luridum* (Diner and Mauzerall 1971) and (ii) characterize the development of photosynthesis in greening organisms (Herron and Mauzerall 1972).

Fig. 4 David Mauzerall in his lab in 1992. Photo by Robert Reichert. (Courtesy of The Rockefeller University)

- A nanosecond-gated photomultiplier was constructed that enabled detection of a signal change of 1 part in 10^4 relative to and following the main pulse (Rossetto and Mauzerall 1972), which was used to decipher energy flow in *Chlorella* through examination of multi-excitation events and analysis by Poisson statistics; this study revealed antenna–trap equilibration times, exciton annihilation processes, and antenna/trap size (Mauzerall 1976c).
- A tunable voltage-clamp apparatus was developed for electrical measurements of photoinduced charge separation, ion movement, and charge recombination in nanoscale BLMs (Hong and Mauzerall 1976).
- A closed-pressure microphone cell was developed that enabled photoacoustic measurements over prolonged times (20 µs to several seconds) with 15 µJ absorbed energy (Mauzerall et al. 2003). In a classic act of frugal ingenuity, one of his air microphones for photoacoustics was *"suspended by a viscoelastic medium"* (i.e., dangled by rubber bands), which resulted in undetectable noise, in lieu of a fancy vibration isolation optical table (Mauzerall and Mielke 2014).

Mauzerall's philosophy concerning lasers and instruments is: *"If you just push the button, you don't learn how it works…. Students should not be deprived of taking it apart – that's how they learn"* (personal communication, in 2024, by Mauzerall to the author).

As an educator

Mauzerall always had a small research group and over 50 years trained 11 (very fortunate) PhD students: Cellarius (1965), Arthur Houghton (Jay) Burr (1966), Helen Herron (1968), Bruce Diner (1972), Felix Tseng-Hsing Hong (1973), S. Gwyn Ballard (1977), Norman Kagan (1977), Richard Piccioni (1977), Jonathan Lindsey (1983), Josef Sedlmair (1985), and John K. Delaney (1991). Comments on the first and last students provide some sense of the scope of projects they were encouraged to pursue.

- The introductory aphorism paraphrases Cellarius, Mauzerall's first PhD student (1958–1965), who wrote *"Photosynthesis is not all sweetness and light"* at the outset of his PhD thesis (Cellarius 1965). Cellarius worked on the development of an artificial photosynthetic antenna by the assembly of tetrapyrrole macrocycles on microscopic spherical beads (Cellarius and Mauzerall 1966). Cellarius went on to become President of the Sierra Club (1988–1990).
- Delaney (1984–1991) studied photoinduced electron-transfer reactions and developed theories of quantum mechanical electron tunneling germane to photosynthesis (Delaney and Mauzerall 1989). Delaney has combined his awe-inspiring knowledge of optics with knowledge of pigments and photochemistry to lead a pioneering program at the US National Gallery of Art concerning hyperspectral imaging of classical works of art (see e.g., Delaney 2020).

Courses were not required at Rockefeller, where the graduate students in residence across the entire university at any time during the latter third of the 20th century numbered in total ~ 100, and there were no undergraduates. Few faculty members, in fact, taught any course. Yet Mauzerall, an outlier, was dedicated to teaching an annual course in Photochemistry and Photobiology from 1966 onwards. The present author took the course and found the depth challenging and the breadth inspiring. Mauzerall also offered seminars and tutorials over the years in physical organic chemistry, biochemistry, chemical kinetics, chemical bonding, and photochemistry.

Mathematics

Mauzerall said *"I studied math with a young professor at Rockefeller who really helped me see that some problems could be formulated in a mathematical manner. I always enjoyed studying mathematics"* (personal communication, in 2024, by Mauzerall to the author). David C. White, MD, who took the advanced math class with Mauzerall while working toward a PhD (1962) in the Granick lab, said 'during the final exam each student had one problem to do, except Dave Mauzerall, who had to do all of them, and he did. He solved them all. One of them was such an elegant solution that the instructor thought seriously of publishing it.' (White DC as interviewed by Kenneth W. Ford (2004). http://davidcwhite.org/professional_advised_mauzerall.html).

Felicitous language

Writing scientific papers did not seem to come easily, but Mauzerall worked hard at it and one can find profound if not poetic expressions deeply embedded in the guts of papers on biophysical chemistry. In some instances, there was text as spare yet as loaded with meaning as that of Hemingway: "*Clearly, cells are little black holes for energy"* (Mauzerall 1992). Other language contains felicitous flights drawn from the classics: *"attempts to evade these Scylla and Charybdis"* is an allusion to how statistical treatments of excitation trapping enable moving beyond the unnecessarily complex Pauli master equation and the too simple Duysens' kinetic approach (Mauzerall 1981). In many other cases there is textbook clarity: *"The porphyrins have been selected by the finecomb of evolutionary processes for two functions in biology. As the iron chelate, heme, they are at the center of the electron transfer reactions in all cells. As the magnesium chelate, and with certain structural modifications known as chlorophyll, they are at the center of photosynthesis."* (Mauzerall 1973).

Contributions from friends and admirers

Comments verbatim are provided below.

Gary Brudvig (Yale University)

I got to know Dave Mauzerall at the Eastern Regional Photosynthesis Conference (ERPC) that has been held each spring at Woods Hole, MA since 1984. Dave and his wife attended the ERPC annually for many years, combining the meeting with spring cleaning of their summer home in Woods Hole, MA. I much enjoyed our discussions about solar water splitting. Dave was especially interested in synthetic catalysts for water oxidation and the oxygen evolution reaction of photosystem II (PSII). He was a stickler for the use of single turnover light pulses and was very critical of researchers who used light pulses that were too long for single turnover reactions. Dave often presented on his research to study the thermodynamics of photosystems by using flash-induced photoacoustic spectroscopy. Among his most interesting contributions was an audio recording of the oxygen evolution cycle of PSII in which we could literally hear the formation of molecular oxygen.

Greg Edens (New Jersey Institute of Technology)

When I joined the lab, Professor Mauzerall told me, "*We are going to use photoacoustics to measure the thermodynamics of Bacteriorhodopsin's photocycle, and we're going to do it right."* I liked that there was ample freedom to try new ways. We began with the air microphone on a floating table. Then we moved on to a hydrophone. I came up with many ideas–I was very persistent and would not give up on the project–some ideas we tried, others were shown to have a fatal flaw without trying. One day Mike Drain came to visit from his lab at Hunter College. When we were walking back from lunch, Mike turned to Dave and me and said, *"Have you considered an HPLC valve, the type used to inject a sample? That should hold the pressure."* We obtained a valve and replaced the sample loop with PEEK (PolyEtherEtherKetone) tubing leading to and from the thermostated one-window pressure cell. I tried our new setup one quiet Wednesday, and it was successful–an answer to prayer! We now had a way to measure enthalpy and volume changes on the timescale of tens of microseconds to multiple milliseconds (Edens et al. 2003). With other workers from the lab joining in we were able to characterize the photocycle and publish a definitive paper (Liu et al. 2008). I am thankful to Dave for passing on to me his technical knowledge, passion for lab work, critical evaluation skills, and desire to explain things clearly and accurately. I wish him happiness on his 95th birthday.

Paul Falkowski (Rutgers University)

I was introduced to Dave Mauzerall in 1978 by Bill Siegelman, who was Chairman of the Biology Department at Brookhaven National Lab, where I had been recently hired. Bill, together with Warren Butler and Sterling Hendricks, discovered phytochrome, the molecule that makes plants tick, literally (Butler et al. 1959).

I was working on how algae photoacclimate to changes in irradiance. At that time, photoacclimation was a descriptive science. I was trying to understand how photosynthetic antenna complexes could change in response to growth irradiance. In that endeavor, I worked on chlorophyll to PSI ratios using an Aminco spectrophotometer, which, at the time, was the best you could buy commercially. André Jagendorf suggested I talk to Dave about PSII/PSI ratios – which, I assumed would be unity. Dave was measuring PSII absorption cross sections. I had no idea what a cross section of a PS was (e.g., Falkowski et al. 1981).

Over the next 15 or so years, I worked for many hours on the 2nd floor of Flexner Hall – where Dave slept two nights a week, in between returning home to a suburb of New York. I took the train back to my home in Stony Brook.

Dave taught me pump and probe fluorescence spectroscopy, how to measure the cross section of PSII, and basic kinetics of electron transfer in photosynthetic organisms. Over the years, we worked on how variable chlorophyll kinetics is related to oxygen evolution and discovered that non-photochemical quenching was probably related to a carotenoid (Falkowski et al. 1986a). More important, by simultaneously measuring oxygen flash yields and variable fluorescence, we understood that there had to be cyclic electron flow around PSII (Falkowski et al. 1986b). The exact process is still not fully understood, but almost surely involves Cyt b559.

I connected Dave with Shmuel Malkin, who was working on photoacoustics. Dave became incredibly interested in that phenomenon, and we built a very high-resolution instrument together (Yan et al. 2011).

In the end, I went on to use PSII fluorescence kinetics (including lifetimes) to elucidate photosynthetic efficiency of marine phytoplankton in the ocean; using the equations of Warren Butler and colleagues (Gorbunov and Falkowski 2022). Later, I discovered Dave's work on origins of life (Mauzerall 1992). I came full circle.

Dave is a hero. He is an inspiration to understanding how life works.

Denise and Michele Mauzerall

Our father always challenged us to observe the world carefully, think scientifically, and figure things out. When asked by friends what our father was like, we would sometimes reply *"you ask him what time it is and he tells you how to build a clock."* In retrospect, we realize how fortunate we were that his enthusiasm to share how things worked would transcend simple responses and help us think more deeply about the world around us. Our father always wanted to understand how things work, as well as why they work, and how we can make sure they continue to work. Throughout his life he made time for us, was eager to discuss both science and world events, and provided a sounding board for professional endeavors as well as thoughtful advice. He set an example of selflessness, honesty, and an endless curiosity and excitement about learning. He was highly egalitarian, deeply believing that ability and hard work defined what was possible, not gender. He instilled in us the confidence and belief that we could do whatever we set our minds to do. His view was that "grades don't matter, what matters is what you accomplish with your life". Although this relieved pressure on schoolwork, it instilled high long-term expectations. His curiosity, and both our parents' adventurous spirits, made travel a constant in family life. As children we spent weeks each summer navigating via different routes from New York to California and back in a 1969 Dodge Dart, stopping at Indian reservations and national parks along the way. Our family excursions inspired an appreciation for different cultures. Conversations inspired a recognition of the fragility of our planet and a desire to help it through its many challenges. Our parents made frequent academic trips around the world including to Russia, China, Japan, Israel, Australia, and Europe, which opened our minds to the rest of the world and likely inspired our mutual passion for world travel.

Alzatta Fogg (Manager of The Rockefeller University Abby Dining Hall for nearly 60 years)

Dave Mauzerall – he was a scientist – but he was always so nice to me. Such a kind man. Always a gentleman.

G. Govindjee (University of Illinois at Urbana-Champaign)

I have always marveled at Dave Mauzerall's brilliant, and sometimes unusual and novel ideas, on how chlorophyll does wonders for us. I vividly remember and continue to appreciate many of his wonderful single-authored articles including one on the thermodynamics of primary photosynthesis (Mauzerall 2013). I wish Dave a very happy and really enjoyable 95th birthday.

Nancy Greenbaum (Hunter College of the City University of New York)

I was honored to do postdoc research with Dave Mauzerall for four years starting in 1985, studying the optical cross sections of photosynthetic reaction centers. Coming from a background of mitochondrial bioenergetics, I found the world of dye lasers and optical cross sections of photosynthetic units in *Chlorella* very challenging for me – but, with support from Dave and others in the lab and pursuing an observation by my postdoc predecessor Art Ley, gradually overcame my fears and established a new approach to analyze the size of Photosystem I. This work culminated in the writing of a comprehensive (at the time) review of the number of pigments contributing to photosystems II and I in biological systems from multiple photosynthetic organisms under different environmental conditions in which we attempted to correlate existing data from highly disparate approaches to achieve a cohesive and encyclopedic body of information (Mauzerall and Greenbaum 1989) – a truly memorable and, at times, painful experience.

Conversations outside the lab – whether during lunch with the group at Rockefeller or during drives up to Woods Hole for annual meetings – were always an occasion to learn about photosynthesis, electron transfer, or the scientific and humanitarian contributions of other scientists.

Dave was a proponent of learning new things every year – and it was inspiring to be part of the group while he was launching his novel and exciting work in photoacoustics. In addition to new conversations with leaves every day, Dave's passion for his new endeavor, and the importance of lifelong learning, taught me valuable life lessons.

And, very importantly, Dave was always a *mensche* concerned with the wellbeing of lab members and our families (and the entire world). I will always be grateful for these lessons and experiences.

Marilyn Gunner (City College of New York)

I was lucky enough to collaborate with David making use of his photoacoustic techniques to probe the reactions of photosynthesis. We studied the energy storage in *Acaryochloris marina*, the first cyanobacteria known to use photons beyond 700 nm. His techniques showed that these organisms could carry out water oxidation with efficiency comparable to or higher than found in typical, chlorophyll *a*-utilizing oxygenic species (Mielke et al. 2011). Working with David was always an education, and a privilege to benefit from his knowledge and experience.

Harvey Hou (Alabama State University)

It was a privilege and honor to work in Dave's lab for four years at The Rockefeller University on the thermodynamics of electron-transfer reactions in photosynthesis. Dave worked with me in the laboratory hand-by-hand and solved issues in laser operation, revision of his own programs, data collection, and manuscript writing in great detail. Dave is passionate about the thermodynamics of electron-transfer reactions, which is equally important as the kinetics of electron transfer in photosynthesis. Dave and his team using pulsed photoacoustics revealed thermodynamic parameters in photosynthesis. The accessible volume changes of charge separation in PS II could be accurately determined with the remarkable detection limit of +/– 0.1 $Å^3$, which is a parameter indicative of photochemical activity and may be explained by electrostriction (Mauzerall et al. 2002). We further extended the photoacoustic work to cyanobacterium *Synechocystis* sp. PCC 6803 (Hou and Mauzerall 2006) and confirmed the hypothesis that the apparent entropy changes in electron-transfer reactions are significant, not negligible, and play an important role in photosynthesis. I am absolutely lucky to have an advisor and friend like Dave. Happy birthday, Dave!

Thomas Moore (Arizona State University)

I went to Japan with Dave on a science exchange program that he had set up (NSF-sponsored U.S.–Japan Information Exchange Seminar in Photosynthesis and Photoconversion, Lake Biwa, Japan, January 13–17, 1988). It was quite an experience for me to see firsthand his insight and critical questioning, particularly into electron-transfer processes. At one session someone was explaining tunneling in electron-transfer reactions and Dave said, in a friendly way with just a touch of exasperation, *"electrons always tunnel, tell us something we don't already know."* I remember thinking that in this situation that would be a hard thing to do.

William W. Parson (University of Washington)

Reading Dave Mauzerall's papers was always a pleasure. This is partly because of his imaginative and scholarly experimental work, but also because of his clarity of expression and the insightful analogies and sprightly turns of phrase that peppered his writing. I learned a great deal from his papers on the evolution of photosynthetic pigments, and later from his important contributions to porphyrin photochemistry, photoacoustic spectroscopy, and the thermodynamics of photosynthesis. Although we collaborated only on a single paper with Rod Clayton and Susan Straley (Straley et al. 1973) when studies of bacterial reaction centers were just getting started, we had many stimulating discussions of our common interests. Talking with Dave was one of the things that made science fun.

Concluding remarks and summary

David Mauzerall was at The Rockefeller University from 1954 until at least 2014 (Mauzerall and Mielke 2014). Of 185 total publications (~ 1700 pages), 39 were singly authored, and 22 were published after he became professor emeritus in 2001; the publications include 24 book chapters and 1 book review. The full publication list is provided in the Supplementary information (Sect. 3).

As of this writing, Mauzerall resides in a retirement community outside Princeton, New Jersey, close to his daughter Denise. Denise is the William S. Tod professor of environmental engineering and international affairs at Princeton University in a position jointly held between the Civil and Environmental Engineering department and the School of Public and International Affairs. She researches technical and policy options for simultaneously mitigating air

Fig. 5 Dave and Miriam, ca. 2015. Dave always tried to protect his eyesight

pollution and climate change. His second daughter Michele, who visits often, founded a medical device company that has brought new green sterilization technology to market, literally saving one large 60 gallon bag of multi-layer laminated polypropylene blended paper trash with every single use. He and his wife Miriam (1924–2023) of 64 years were devoted to each other (Figs. 5 and 6). He spent a lifetime reading voraciously and boundlessly, especially the *Science* and *Nature* journals which piled high in his home study. His mind is sharp and he has much time on his hands, but in irony worthy of Borges, is legally blind and is no longer able to read. When asked about books on tape, he replied with an irrepressible smile *"they don't have science journals on tape, that's the problem!"*

In summary, Mauzerall has combined a polymathic knowledge of distinct disciplines of physical organic chemistry, photochemistry, spectroscopy, and biophysics with ingenious experimental methods, incisive mathematical analysis, pristine personal integrity, independent thought, and unyielding love of science to deepen our understanding of photosynthesis in its broadest context.

Fig. 6 Dave and Miriam at home in Dobbs Ferry, NY, ca. 2010

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Declarations

Competing interests The author declares no competing interests.

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