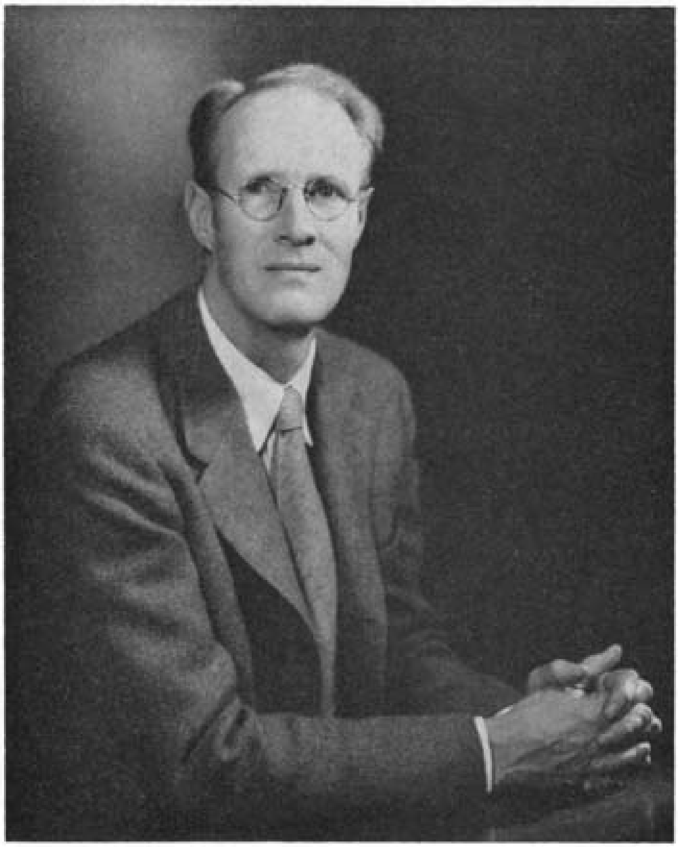
NATIONAL ACADEMY OF SCIENCES

ROBERT EMERSON

1903—1959

A Biographical Memoir by
EUGENE RABINOWITCH



Robert Emerson

ROBERT EMERSON

November 4, 1903–February 4, 1959

BY EUGENE RABINOWITCH

ROBERT EMERSON was born on November 4, 1903, in New York City, into a distinguished New England family. (He was a great-grandson of Ralph Waldo Emerson's brother.) Bob was a typical Yankee—light-haired, blue-eyed, spare, longheaded and long-striding. The family strain was so strong that his brothers and sisters, as well as his three sons, could be easily recognized as members of the Emerson family. The fact that Bob's wife, Claire Garrison, also came from a distinguished Boston family, must have helped to preserve the Yankee type.

Robert Emerson's father, Dr. Haven Emerson, was a pioneer in public health; for many years, he headed the New York City Public Health Service. He was a dedicated, strong-willed, hard-working, stern man; however far his children got away from him in life, or even rebelled against his influence, he left his imprint on them. Bob Emerson used to say that to understand him, one should have known his father. In his eighties, his father not only kept up with his professional work, but spent every moment of his leisure working in the garden of his estate on Long Island. Bob Emerson, too, was a dedicated, hard-working man of strong convictions. After spending a long day reading manometers in the darkness of his laboratory, and walking home, as he always did, Bob would throw himself into digging, weeding and pruning in his garden, until darkness forced him indoors. (Emerson's backyard must have been the most intensely cultivated plot of land in Champaign County, resembling Japanese gardens in the careful utilization of every square foot of ground.) The Emerson family lived to a large extent from the produce of their backyard, despising store-bought fruit, chicken and vegetables.

Bob was a teetotaller (except for an occasional glass of beer), non-smoker, and frowned even on cakes and candies; and his family followed his lead. They were early risers and early to retire. The only recreation in which Emerson indulged was ice-skating. He was the animator of the University of Illinois skating rink and chairman of its figure-skating club. He and his wife—an even more skillful figure-skater than Bob—made a handsome couple on ice; and his whole family joined in this pastime.

Thrift was one of the virtues instilled in Emerson in his upbringing. He would buy expensive things if they were truly worth it, but he hated unnecessary spending. He would rather house and feed out-of-town visitors in his own hospitable home than let them pay what he considered outrageous prices in hotels and restaurants.

Bob Emerson admired perfection in human labor; and he sought perfection in his own work, be it experimentation in photosynthesis, writing a paper, building an instrument, wood carving or fruit growing. (He had great respect for workers with pride in their handiwork, and deplored the loss of this pride in the American drive for speed and quantity production, at the expense of attention to detail and quality.) True to his New England tradition—reinforced by his experience as student in Germany—he believed in the unhurried, self-sufficient European scholarship respected for its own sake, as contrasted with the constant pressure for rapid results and external recognition in modern American academic life. He disagreed with the development of American universities into what he saw as department stores of education, offering for sale every educational good for which there was a demand (and granting an assortment of degrees in the most trivial, as well as in truly scholarly subjects). In this as in other fields, he made no secret of his opinions, however much they would antagonize some of his colleagues. In University Senate meetings, when many of us felt unhappy about this or that proposal, but hesitated to start an argument, it was Bob Emerson who stood up and said aloud what we thought in silence, without mincing his words, and yet with a disarming modesty and a smile that made more friends than his frankness made enemies.

Emerson saw little value in new technical gadgets, intended to free people from the need of doing what he considered an honest day's work. He distrusted new cars with lots of chrome and hundreds of gadgets, and much preferred old, simple, solid touring cars, built to survive hundreds of thousands of miles on hard roads. He preferred the sterner New England climate, and the more puritan New England way of life, to the leisurely ways and soft climate of California where he missed the change of seasons, in particular the cold winters of his Eastern childhood.

Emerson considered it one of his missions in life to teach the virtues of integrity, hard work, solid craftsmanship and thrift to his children, as well as to his students. Some of the latter resented his didactic and often sharp reprimands; they complained about his "old-fashioned" views and paternalistic methods; but those who were willing to learn, could—and many did—learn from him not only the fine art of precise experimentation, but also devotion to science, respect for true scholarship, and disdain for external success.

Emerson would not use a University three-cent stamp for a letter not strictly on University business, and expected the same uncompromising integrity from everybody around him. He would argue before the University Senate that professors should not strive for higher salaries, because raises in wages and salaries are bound to defeat themselves by bringing about inflation; and professors, knowing this, should give other classes an example of proper behavior. Some were angry, and some shrugged their shoulders at such quixotic views; but they also brought him much respect and warm friendship.

Emerson was a pacifist, and a democratic socialist, a friend and admirer of Norman Thomas. He taught his children not to fight back when attacked in school or on the street. He felt strongly about economic and racial injustice, and was always on the side of the underdog. He believed that World War II was brought about by economic injustices of the Versailles Treaty, and the post-Versailles policies of the Allies. In the autobiographic note he supplied to the 25th anniversary reunion of his Harvard graduating class, he wrote, "I have seen the strife and violence resulting from economic forces in California during the Grapes of Wrath years. I felt sure that economic forces were driving us into war, and that resort to war could not be expected to correct economic world injustice." He continued, "When the war came, I was not inclined to work as a scientist in support of the war effort. Early in the war, I became interested in rubber research, because of the importance of rubber to the United States, and also because I felt that our exploitation of Southeast Asia, where rubber and similarly important products were produced, may have played a large part in stimulating Japan to attack us." This feeling, and his indignation over the attacks of Californians on the civil rights of American citizens of Japanese parentage, led Emerson to his most important venture outside academic life. "I spent the war fostering a program of rubber research in the concentration camps to which the Japanese-Americans were banished. Our aim was to develop the desert shrub, guayule, as a source of rubber which could be produced under American living standards, without resort to the exploitation of native labor in Southeast Asia."

That this work was successful, both as a scientific project, and as a means to give content and purpose to the lives of a number of deportees, was a great source of satisfaction to Emerson. He was greatly distressed when, at the end of the war, the attempts of Japanese to continue the production of guayule rubber on a commercial scale, failed—in his belief—because of the opposition of vested interests in the rubber industry. (He did not live to see the resumption of this work by one of his original co-workers in Australia.)

With such strong feelings about economic and racial injustices of the capitalist system, Emerson's attitude towards the Russian experiment at first was one of sympathetic tolerance. He hated violence from whatever side it came, but it took some time, and reports of his personal friends in Eastern Europe, to make him realize that the violence of Communist totalitarianism was no less inhuman than that of its worst adversaries.

Emerson's work at the Japanese concentration camp in Owen's Valley during World War II was the most ambitious excursion away from academic life; but in a more private way, he kept helping those he considered oppressed or unfairly treated, during his whole life. His thrift notwithstanding, he quietly loaned considerable amounts of money to individuals who, he believed, deserved it for a start in life—and not always was it repaid. In the last years of his life, he devoted much time to the fight against housing discrimination in his own community. He was always ready to help foreign students, particularly those whose race made it difficult to find acceptance and adjust themselves to life in an American community. Perhaps, the strong feeling for the weak and helpless has something to do also with his love for children. I did not know him when his own children (or mine) were small, but I've seen the smile that lit his face when he was permitted to fondle the children of his friends or co-workers. Probably the happiest days of his last year were when he met his first grandson.

Robert Emerson's striving for integrity, reliability, and precision deeply influenced his scientific career. He started studying animal physiology at Harvard, in 1920, with the intention of following his father and becoming a doctor. Under the influence of W. J. V. Osterhout's lectures on plant physiology, his interest turned from animals to plants; after receiving a master's degree in zoology in 1925 and spending a summer at the Harvard tropical laboratory in Cuba, he went to Germany with the intention of studying the formation of chlorophyll in plants. He went to Munich to Richard Willstätter, who had received the Nobel prize for his work on chlorophyll and photosynthesis, but found him in conflict with the University because of anti-Semitic activities of students and faculty, and was advised to go to the Kaiser Wilhelm Institute of Biochemistry in Berlin-Dahlem, where another Nobel prize winner, Dr. Otto Warburg, was doing pioneer work on quantitative study of photosynthesis. In Warburg's laboratory in Berlin-Dahlem Emerson learned, to use his own words, "the techniques which I have continued to use," and which, "I have taught to those few students who have been so misguided as to subject themselves to my instruction." After two years in Warburg's laboratory, Emerson obtained a Ph.D. degree in botany at the University of Berlin. Botany was a subject which he did not study extensively in his undergraduate years, and he wrote, "I have not been able to live down my embarrassment at obtaining a Ph.D. degree in a subject about which I know almost nothing." (That was written shortly after he received the Stephen Hale Prize of the American Society of Plant Physiologists in 1949, and shortly before he was elected to membership in the National Academy of Sciences (1953) upon nomination by the Section of Botany.)

Emerson returned to Harvard in 1927 as a National Research Council fellow and began to put his newly acquired knowledge of manometric techniques to use—first, in the study of the effects of artificial variations of the chlorophyll content in the green alga *Chlorella* (brought about by iron, magnesium or nitrogen deficiency in the nutrient solution), on its capacity for photosynthesis. It was at that time that he married Claire Garrison, who soon became, and has remained, affectionately known as "Tita" to all his colleagues and friends. In 1930, Emerson joined the Biology Division, newly organized by T. H. Morgan, at the California Institute of Technology. He stayed in Pasadena for seven years, and his three sons—Kenneth, Stephen and David—were born there.

Emerson's work at Cal Tech led to the first of his important contributions to the science of photosynthesis. In collaboration with William Arnold—then an undergraduate student—he carried out experiments on photosynthesis in flashing light, which have by now become classic. Brown and Escombe in England, and Warburg in Germany, had made earlier experiments on the yield of photosynthesis in alternating light with equal light and dark periods, and showed that very short dark periods can contribute to photosynthesis almost as much as equal periods of illumination. Emerson and Arnold achieved decisive progress by substituting flashing for alternating light. They used intense light flashes from condenser discharges, lasting only a few microseconds, and varied the length of the dark periods after each flash. This avoided the complications caused by simultaneous change in both light and dark period. The experiments of Emerson and Arnold led to two fundamental conclusions: (1) that the maximum amount of oxygen produced by a single practically instantaneous flash is—in "normal" green cells—about one molecule oxygen for 2000 molecules of chlorophyll, and (2) that this oxygen production occurred, during the dark period, at an exponentially declining rate, with a decay constant of about 100^{-1} sec. Both results remain of fundamental importance for speculations on the kinetic mechanism of photosynthesis; however, the first one has preserved its validity better than the second one. Despite contradictory results by Tamiya and co-workers in Japan (who found up to three times greater oxygen yields per flash), Emerson and Arnold's value of the maximum yield still appears correct for practically instantaneous flashes (the duration of Tamiya's flashes was of the order of a millisecond). The second conclusion, on the other hand, has since proved to be oversimplified—the decay of oxygen production occurs by a more complicated than a simple first-order law, suggesting a sequence of reactions of different orders, with the first-order reaction observed by Emerson and Arnold being but one of them. This complexity probably accounts for the possibility of obtaining higher flash yields in experiments with longer flashes.

The generally accepted interpretation of the findings of Emerson and Arnold is that photosynthesis requires for its completion an enzyme which is present in the cell in a concentration much lower than that of chlorophyll (the ratio may be 1 : 2000, or a small multiple of it, depending upon how many molecules of the primary photochemical product are involved in the liberation of a single molecule of oxygen). A more specific interpretation, first suggested by Gaffron and Wohl, postulates that 2000 (or a simple fraction of 2000) chlorophyll molecules are combined in the chloroplast with a single enzyme molecule in a so-called photosynthetic unit. Even more specifically, it was suggested that this cooperation may be achieved by resonance migration of excitation energy from numerous chlorophyll molecules to a single reaction center. The hypothesis plays an important part in modern discussions of the mechanism of photosynthesis, but as yet its correctness could not be either proved or disproved by direct experimental evidence.

In the 1930's, doubts had arisen about the correctness of the maximum efficiency (quantum yield) measurements of photosynthesis by Warburg and Negelein in 1921–1922. This classical work—the first application of quantum concepts to biology—led to the conclusion that four quanta are needed to produce one molecule of oxygen. This seemed highly plausible because four hydrogen atoms must be transferred from water to carbon dioxide to reduce the latter to the carbohydrate level. This plausibility, and the great authority of Warburg as an experimenter, caused general acceptance of his results, and James Franck tried hard to find a thermochemically plausible mechanism of photosynthesis which could function with only four quanta. Contrary to Warburg's often expressed opinion, it was *not* the theoretical difficulties encountered by Franck, but the experimental failure of several observers (above all, of Farrington Daniels and co-workers at the University of Wisconsin) to confirm Warburg's and Negelein's findings, using the same biological material (*Chlorella pyrenoidosa*) that first cast doubt on the validity of Warburg's findings, and led to the feeling that a thorough reinvestigation of the important subject of the maximum efficiency of photosynthesis was needed. Emerson undertook this reinvestigation taking for this purpose a leave of absence from Cal Tech and spending three-and-one-half years, beginning in 1937, at the laboratory of Plant Physiology of the Carnegie Institution of Washington, on the campus of Stanford University. He enjoyed there the sympathetic hospitality of the late Herman A. Spoehr, then director of the laboratory, and the skillful collaboration of Charleton Lewis, his second important collaborator after Arnold. Emerson's daughter, Ruth, was born during this happy period of his life.

Emerson and Lewis developed much improved manometric techniques; in particular, they first applied to the study of photosynthesis the method (originated by Warburg) of parallel measurements of gas exchange in two manometric vessels containing the same quantity of identical algal suspensions, but with a different gas : liquid volume ratio. This procedure permitted them to calculate independently the production (or consumption) of the two gases, oxygen and carbon dioxide, involved in photosynthesis, instead of relying on the equality of the two gas exchanges, derived from the over-all stoichiometry of this process (which is what one is forced to do in the simple "one-vessel" method). After long studies, Emerson and Lewis concluded that Warburg and Negelein's results were significantly affected by failure to recognize a gush of carbon dioxide, expelled by cells in the first few minutes of illumination, before steady photosynthesis has set in ("first Emerson effect"). When readings made during this transitional period were omitted, the quantum requirements turned out to be between 8 and 12 quanta per molecule oxygen, instead of 4. These results were published in 1938–1941; the quantum yield problem seemed to be solved, and Emerson turned his attention to the action spectra of photosynthesis in algae of different families, containing different assortments of pigments.

Emerson returned to Pasadena in January, 1941, and resumed work there; but in December of that year his work was interrupted by America's entry into the war, and soon, all his attention was transferred to the guayule rubber project. This involved not only growing of the guayule shrub, but also the production of rubber from its juice, carried out by Emerson at the American Rubber Company laboratories in Los Angeles. In this enterprise, Emerson's closest collaborator was Shimpe Nishimura, who brought to this work a combined experience in professional gardening and in the study of physics at Cal Tech—both brutally interrupted by internment.

Soon after his return to Cal Tech after the end of the war, Emerson was approached by Neil Stevens, the late head of the Botany Department of the University of Illinois, with a proposal to organize there a research laboratory on photosynthesis. He took Nishimura with him as his assistant, and also asked the University to appoint a physical chemist with an interest in photosynthesis, so that the project could be properly guided both in its plant-physiological and its physico-chemical aspects. Thus began twelve years of our most harmonious collaboration, which Warburg has mockingly described as the "Emerson-Rabinowitch photosynthetic unit."

Emerson's relation to theory was ambivalent. On the one hand, he was always conscious of his own lack of training in theoretical physics and physical chemistry and had inordinate respect for all who could operate in these fields. On the other hand, he was fully aware of the poor quantitative reliability of most of the experimental data in biological literature, including even his own measurements (since he was always his own severest critic); and he felt that theoretical speculation in biology tends to run away from solid experimental foundations. It was difficult, if not impossible to persuade him that even an inexact measurement must have a certain value—a plausible maximum error—which permits one to use it for theoretical speculations, at least within certain limits. If an experiment was not carried out with the greatest attention to the consistency of biological material and the precision of all measurements, it was "n.g."—no good—to him, and that was that. This was a constant source of friendly arguments between the two of us, and even more, between him and James Franck, who has brought over from physics into plant physiology the conviction that every measurement must mean *something.*

In 1948, after Emerson and Lewis' quantum yield results were widely accepted, and confirmed by independent studies in several countries, which used less precise methods, but were impressive in their consensus, Warburg published a paper in which he reasserted the correctness of his earlier findings, this time on the basis of two-vessel measurements, not subject to Emerson's original criticisms.

Following my suggestion (which I had occasion later to regret) Emerson arranged for Warburg (whose laboratory at Dahlem was inactive at that time due to war losses) to come to the University of Illinois and to attempt the resolution of the discrepancy by cooperative study. Like so many best-laid plans, it all went wrong. Warburg arrived in the summer of 1949, in the midst of the heaviest thunderstorm I have experienced in my fifteen years in Urbana, and this proved to be an augury of his stormy stay in Urbana. Warburg had been accustomed to work with highly trained technical assistants and only rarely with colleagues or even graduate students with independent opinions. He was Warburg and he was right. Emerson, at first modest and helpful in his usual way, and full of respect for his famous teacher and guest, also was a stubborn man, particularly when it came to devising experiments, a matter in which he felt he also had great experience and sound judgment. After several months of fitful attempts at collaboration, and an unsuccessful attempt for a third person's arbitration, Warburg left in anger, without saying good-by.

This interlude was hard on Emerson. He was completely convinced of the correctness of his measurements, but his reputation was at stake and everybody expected from him a new study of the quantum yield problem, and interpretation of Warburg's new results. For several subsequent years, Emerson's experimental work in Urbana was devoted mainly to this task. Together with Nishimura, and later with other assistants, he went into a detailed study of the manometric techniques. Several interesting findings were obtained, particularly in the demonstration of the complexity of the transitional phenomena in the first minutes of exposure to light and darkness. These results explained some of the discrepancies between

Emerson's and Warburg's results. However, the aim of finding a complete explanation of Warburg's results proved elusive, because Warburg, rather than investigating thoroughly the conditions under which the alleged high quantum yields could be obtained, kept publishing increasingly startling new observations, whose relation to his own earlier findings was not always clear, and which made Emerson's control experiments obsolete faster than they could be performed. The minimum quantum requirement of 4 (which had a certain plausibility) was replaced, by Warburg, by one of 3 and finally by one of 2.7—the minimum number of quanta needed to conform to the law of conservation of energy. This conclusion was greeted by Warburg as confirmation of his belief that (to use his words) "in a perfect world, photosynthesis must be perfect," but seemed entirely implausible to all those with some respect for the general tenets of modern reaction kinetics. Furthermore, the high quantum yield, previously described as obtainable only in short experiments in weak light (and which Franck has therefore attempted to attribute to the involvement of respiration intermediates in photosynthesis), was now said to have been obtained also in hour-long runs in strong light, far above the compensation point. For a while, the presence of a respiration-compensating background illumination was said by Warburg to be of decisive importance; then this was changed to an alleged need for a "catalytic" amount of blue light. A very high carbon dioxide concentration—of the order of 10 percent and thus far above the physiological range—was once announced to be indispensable for obtaining high quantum yields (although these were supposed to be evidence of physiological perfection of the plant cell!). Later, photosynthesis was stated to require only a single quantum of light, the rest of the needed energy being provided by respiration, which, according to Warburg, was enormously enhanced during the illumination. Many of these results were directly contradicted, not only by Emerson's experience, but also by the experiments of other observers; none was confirmed. It was this kaleidoscopic change of claims that convinced Emerson that he should leave the problem, confidently, to the judgment of time, and turn to research subjects of his own choosing.

Beginning with the work of his student, Tanada, on the action spectrum of photosynthesis in diatoms published in 1951, Emerson resumed the studies he had begun in California with Lewis on the action spectra of green and blue-green algae (*Chlorella* and *Chroococcus*). For this work, a large monochromator was used, with optical parts originally lent by the Mount Wilson Observatory, which permitted working with much narrower spectral regions than were used by earlier investigators, particularly those employing color filters. Much more precise action spectra could now be obtained, revealing many important details; and the relative efficiency of the quanta absorbed by the different pigments, contained in various photosynthetic cells, could now be established with a far improved reliability. The relatively low efficiency of the carotenoids in green and red cells, contrasted with the high efficiency of fucoxanthol and chlorophyll *c* in diatoms (already indicated by earlier measurements of Warburg, Montfort, and particularly by Daniels, Dutton and Manning in Minneapolis), were among the early findings; but perhaps the most important results, obtained in a recent study with M. Brody, concerned the efficiency of the phycobilins in the red alga *Porphyridium*. Previous studies of such algae by Blinks, Haxo and Yocum had led to the paradoxical conclusion that chlorophyll *a* in these organisms was much less effective as sensitizer of photosynthesis than the red pigment, phycoerythrin. Even more paradoxical, a similar result was obtained (by French, and also by Duysens) in the study of the action spectrum for the excitation of chlorophyll fluorescence; in other words, chlorophyll *a* in red algae seemed less effective than phycoerythrin in the excitation of its own fluorescence! At the same time, the apparent parallelism of the action spectra of photosynthesis and chlorophyll fluorescence confirmed the widespread conviction that energy absorbed by other pigments had to be transferred to chlorophyll *a* in order to become active in photosynthesis. Several more or less implausible hypotheses were advanced to explain these peculiar findings; but Emerson believed that the time for speculation would come when the experimental results had been made more reliable and systematic. In fact, the results of Emerson's studies with M. Brody suggested a shift in the experimental basis of speculation. The low efficiency of chlorophyll *a* in red algae was found by them to be characteristic not of this pigment as such, but only of light absorbed by it above 650 mμ; light of shorter wavelengths, also absorbed by chlorophyll *a,* proved to be even more effective than that absorbed by phycoerythrin; in the limiting case—that of algae adapted to green light—both were equally effective. The puzzle was not solved, but shifted to a different plane.

Already in his work with Lewis, Emerson had noted that a drop in the quantum yield towards the longer waves did occur also in green algae; only there, the decline began much later—beyond 680 mμ, in a region where the absorption of light by chlorophyll declined rapidly, so that the loss of efficiency was much less obvious. In an attempt to find an explanation of this phenomenon (the "red drop"), Emerson now began to study it systematically with R. V. Chalmers and C. Cederstrand. The first exciting thing he found was that no red drop occurred when a sufficiently strong background illumination with light of shorter wavelengths was provided. This finding is superficially reminiscent of some of Warburg's observations, but is unrelated to them because the background light is effective only in bringing the quantum yield in the far red up to its "normal level" of 0.10 ± 0.02; and a considerable intensity of this light is needed, rather than only "catalytic amounts," as suggested by Warburg.

A study of the action spectrum of the "background light effect" ("second Emerson effect") led to the striking conclusion that it seemed to be identical with the absorption spectrum of certain "accessory pigments" present—chlorophyll *b* in green algae, phycobilins in red or blue algae (thus suggesting an explanation of the earlier beginning of the "red drop" in these organisms), and fucoxanthol and chlorophyll *c* in diatoms. These results suggested that, in contradiction to previous concepts, photosynthesis requires, in addition to red light absorbed *only* by chlorophyll *a,* also light of shorter wavelengths, absorbed by one of the accessory pigments! The interpretation of this highly unexpected result could be sought *either* in different photochemical functions of the several cell pigments, which must be combined to achieve photosynthesis, *or* in the existence of two or more different forms of chlorophyll *a,* only one of which undergoes direct excitation by absorption in the far red part of the spectrum, while the other can be excited either by direct absorption of higher frequency quanta, or by resonance energy transfer of quanta from excited accessory pigments. The problem remains open, and calls for more experimentation, with the skill and patience Emerson would have applied to it; this is being carried on by Emerson's last co-workers, Mr. and Mrs. Govindjee and C. Cederstrand, and the results appear to favor the second hypothesis.

In the midst of these exciting studies, Bob Emerson met sudden death on February 4, 1959, when the plane carrying him to a conference at Harvard University, missed the La Guardia runway and plunged into the East River. As part of his dislike of new gadgets, Emerson distrusted airplanes and always advised me against flying. Only in the last years, when his favorite train from Indianapolis to New York was discontinued, did he grudgingly choose air transportation for his trips to New York. He was booked for another flight, but the lateness of the ill-fated Electra in leaving Chicago made it possible for him to transfer to it at the last moment, hurrying him to his death.

The feelings of his numerous and widely-scattered friends are well expressed in a letter from his Harvard friend, Kenneth Thimann, who wrote:

"Bob is not a man whom you can ever forget. In some way Bob was the very symbol of uprightness; he loved the truth just as much as he loved the underdog, and he scorned the untruthful and could not have anything to do either with it or with the man who promulgated it. I can imagine his students feeling that they have to judge their lives by what Bob would have done in the circumstances. . . . Everyone who has come into contact with Bob must have been inspired by him to some degree; it is impossible not to be, just as it is impossible not to remember with clarity his every gesture, his ready smile—often belying fierce disagreement—his enormous ability for friendship and real tenderness. This is a kind of immortality—at least survival for another lifetime—in the memories and even to some extent in the characters of other people, which it is given to very few men to achieve."

KEY TO ABBREVIATIONS

Amer. J. Bot.=American Journal of Botany
Ann. Rev. of Biochem.=Annual Review of Biochemistry
Ann. Rev. Plant Physiol.=Annual Review of Plant Physiology
Ann. Rept. Carnegie Inst. of Wash.=Annual Report of the Carnegie Institution of Washington
J. Gen. Physiol.=Journal of General Physiology
Phycol. Soc. Amer. News Bull.=Phycological Society of America, News Bulletin
Plant Physiol.=Plant Physiology
Proc. Nat. Acad. Sci.=Proceedings of the National Academy of Sciences

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