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BESSEL KOK

1918—1979

A Biographical Memoir by

J. MYERS

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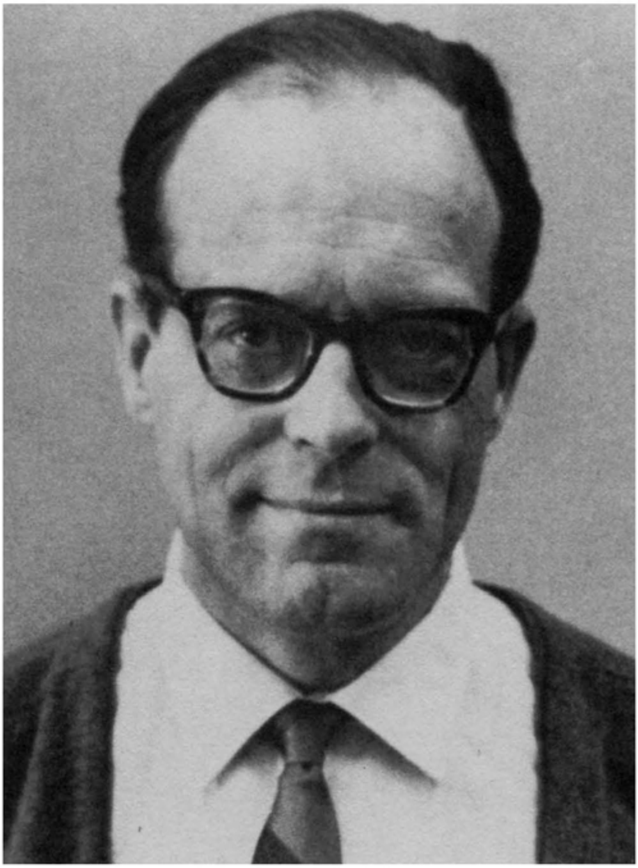
Biographical Memoir



BESSEL KOK

November 7, 1918–April 27, 1979

BY J. MYERS

THE DECADE 1955–1965 was a period of revolution in our thinking about the process of photosynthesis. A key event was the realization that the process, long assumed to require only one photoreaction, actually required two. A key figure in the revolution was Bessel Kok.

In the following years Bessel and his collaborators—in work that bore the stamp of greatness—filled in much of the framework for the Z-scheme model of the energetics of photosynthesis. A predictable result was the recognition that followed. There was a Kettering Research Award in 1963 given by the Charles F. Kettering Foundation and the National Academy of Sciences. There were two awards from the American Society of Plant Physiologists: the Charles F. Kettering Award in 1972 and the Stephen Hales Award in 1978. And there was election to the National Academy of Sciences in 1974.

In composing this memoir for Bessel Kok I shall use freely the thoughts of collaborators, family, and friends, which are recognized only partially in the acknowledgment at the end. I was for almost thirty years a distant colleague, a sometime confidant, a scientific admirer, and a friend—all of which accounts for the highly personal tone of this account. But it would be difficult for anyone to write otherwise because Bessel was a very personal person.

Bessel Kok was born November 7, 1918, in the village of Hardinxveld, The Netherlands. His father, Johannes Evert Kok, was the principal of a local school; he is remembered as a talented man who cast himself in the image of a professor, a puritan Calvinist who lived at the hand of the Bible. His mother, Cornelia Grondys-Kok, is remembered as "the image of Bessel in female form." Bessel was the oldest in a family of six children. He remembered his childhood as happy, although it was interspersed with the many frustrations that must have arisen for an inventive and energetic boy encumbered by a conservative father.

Bessel's own statement about his education was that he "never studied" and that he coasted through his high school and college years. Nevertheless, he assimilated a broad background in science and developed the self-discipline he needed thereafter. His college years began at the University of Leiden in 1934; they led to the undergraduate degree of Candidate of Natural Philosophy in 1938 and the advanced degree of Doctor of Natural Philosophy in 1941. An even more significant event occurred in 1938 when Bessel met Cornelia Hendrika Vogelesang at a Christian Student's Club. Cornelia—or Nell, as she became known to all—had been born and raised in Tandjung Pinang, Indonesia. Her memory of meeting Bessel is one of instantly recognizing him as her future husband.

In 1941 Bessel began work toward a Ph.D. in biophysics at the University of Utrecht. In that era the road toward a degree was tortuous and at times must have seemed impossible. Following the German occupation in 1940, young men were conscripted for labor camps in Germany. But for all it was a time of struggling merely to survive. To provide some protection against conscription, Nell and Bessel were married in 1943. And although she was seldom successful, Nell did her best to hide Bessel. He, on the other hand, was more inclined to trust to his luck and the weak support of a passport with a falsely increased statement of age. Bessel had become assistant manager of a distilling company, Johan Koster. He also improvised a small distillery at home to produce gin from rye and beets; the gin was readily bartered for food. Their first child, Lily, was born in March of 1945, two months before the end of the war. Nell remembers it as the "worst time" for an impoverished and starving people.

With the end of the German occupation, Bessel was free to turn his efforts from survival to science. The firm of Johan Koster provided him both with employment and some direct support of the research for his dissertation, which was presented early in 1948. In the foreword of the dissertation, Bessel recognizes with thanks his professors Bungenberg de Jong and Baas Becking at Leiden. Professor Koningsberger is named as the *Hooggeachte Promotor,* but it is also made clear that E. C. Wassink was the real supervisor. Hence, Bessel's "scientific genealogy" traces to the Biophysical Research Group under the direction of A. J. Kluyver and J. M. W. Milatz.

Bessel's dissertation was a study of the quantum yield of photosynthesis in the alga *Chlorella.* It is not now, and was not then, a very exciting document. One difficulty was that the subject itself, which had been hot in the early 1940s, was only smoldering in 1948. A second difficulty was that a quantum yield, usually expressed as the reciprocal or quantum number (quanta absorbed per oxygen molecules evolved), is actually no more than a number. Its validity hinges only on the nitty-gritty details of measurement.

It must be a source of amazement to much of the scientific world that the quantum yield of photosynthesis should have engendered so many man-hours of work and yet so much controversy. Certainly one of the many aspects of an explanation of this circumstance is historical. In 1923 Otto Warburg had reported a minimum quantum number of 4.3, naturally interpreted as 4. In its time this was an heroic accomplishment. Warburg had invented a manometric method for the measurement of gas exchange. And he had introduced a convenient plant material, the alga *Chlorella*. There were several additional features of experimental protocol that turned out to be important. The first was the use of optically dense cell suspensions that absorbed virtually all the light. Hence quanta absorbed from a monochromatic light beam could be counted simply as incident quanta. The second feature was an assumption that oxygen evolution of photosynthesis was properly evaluated from pressure changes observed in short light periods minus those observed in alternating short dark periods.

Considering the theoretical significance of the quantum number, it is remarkable that Warburg's value went unchallenged for some fifteen years. By the early 1940s, however, other measurements had been made. The number 4 was in doubt as being too low, and the special experimental protocol was being questioned.

Bessel's choice of experimental conditions shows his insight and understanding of the problem. First, he maintained conditions of steady-state photosynthesis and measured oxygen evolution over a long time period (an hour). Second, to ensure steady-state conditions in all cells, he used optically thin suspensions. (Otherwise, cells in a shaken suspension would alternate between periods of light and virtual darkness.) This required mastery of the technology of the Ulbricht sphere, a device for measuring fractional absorption by a light-scattering cell suspension. A third important choice was that for each cell preparation he measured rates of oxygen evolution at several different light intensities. Then the slope of the expected linear plot of oxygen per second versus absorbed quanta per second would give the quantum yield. The quantum numbers obtained from forty-two sets of measurements fell within the range 6.5 to 10.0. Bessel deduced that 7.5 was "the most favorable value."

In addition to finding that the quantum number was high (7 to 10) rather than low (4 to 5), Bessel discovered a related phenomenon. The curve for the oxygen rate versus the quantum rate had two linear segments with slopes in the approximate ratio of 2:1 and converging near the compensation point where photosynthesis just balances respiration. The phenomenon, which has come to be called the Kok effect, is commonly thought of as resulting from a "suppression of respiration." It provides a possible explanation for low quantum numbers (as 4 to 5) observed at very low light intensities below the compensation point.

In 1949, Bessel joined the Solar Energy Research Group of the Organization for Applied Scientific Research (T.N.O.) under E. C. Wassink at the Agricultural University in Wageningen. This was an excellent match for his needs. As he later wrote on an employment record, it provided for "full time research, freedom, adequate services." A major mission was the mass culture of algae, a subject that Bessel followed, albeit sporadically, for the rest of his life. An immediate question was the maximum efficiency of *Chlorella* in producing total cell material, the efficiency for growth. Bessel's result was an efficiency of about 20 percent (equivalent to a quantum number of about 10), which still stands as a benchmark. Simply growing algae, however, was too bland for Bessel's taste. Most of his efforts went into attendant basic problems.

There is an ultimate limitation on the yield of algae that can be achieved under sunlight illumination. The problem is that photosynthesis and growth become rate limited at a light intensity far less than that of midday sunlight. Those of us concerned with mass culture naturally sought ways to circumvent the limitation. Of several possibilities the most interesting was to take advantage of the intermittent light effect of photosynthesis. With sufficient turbulence in a dense culture, individual algal cells move rapidly into and out of the illuminated front surface and thereby receive high light only in flashes. It was well known that short flashes could be used with higher efficiency, but the time parameters of the effect were not known. Bessel set out to study photosynthesis in flashing light.

Bessel spent much of 1951–1952 on leave from Wageningen and as a fellow of the Carnegie Institution in the Department of Plant Biology at Stanford under Stacy French. The family—now with two children, Lily and young Bessel—lived in the old barracks-like buildings that later became the Stanford Research Institute. I first met them there and was attracted by the happy self-sufficiency of a family learning the ways of a strange land. Bessel's part of the laboratory became a shambles of equipment-building, and he was frustrated by the slow progress of a machinist who was constructing a sector for light chopping. His work at Stanford was reported in a chapter of the 1953 Carnegie monograph on algal culture, and it provided at least a partial answer: any reasonable turbulence could be expected to give some gains in the yield of an algal culture under sunlight. Large gains, requiring very short flashes, probably would be impractical because of the power cost for the necessary turbulence.

On his return from Stanford, Bessel began extending his work with flashing light to an attack on the kinetics surrounding the photochemical events in photosynthesis. His remarkable experimental talents now came into play. He used a high-intensity projection beam that could be chopped and/or attenuated; there were two coaxial sectors that allowed independent variation of both the light and the dark periods.

As a side effort, he had developed—almost to ultimate limits—the measurement of gas exchange by volumetry. Now he could choose a very small reaction vessel (<5 mm diameter) coupled to a volumeter arrangement that measured oxygen evolution with high sensitivity. The broad scope of the experiments provided an unequivocal answer to a twenty-year controversy about the reality of the "photosynthetic unit." The oxygen yield from short flashes confirmed the earlier finding of R. Emerson and W. A. Arnold: a maximum flash yield independent of temperature and equivalent to about one O_2 per 2,000 chlorophylls. Lengthening the flashes gave a temperature-dependent flash yield approaching the rate observed in continuous saturating light. Bessel again went beyond the immediate and obvious objective in order to obtain an explanation of earlier and apparently conflicting results.

In 1955 Bessel again visited the United States for two meetings: a Gatlinburg conference on photosynthesis followed by a world symposium on applied solar energy at Tucson and Phoenix. E. C. Wassink also was in attendance. It was evident to all, however, that Bessel had attained the status of an independent and innovative scientist.

The sectors of Bessel's flashing light apparatus must never have cooled down for very long. Within a year after the measurement of oxygen flash yields, the apparatus was redesigned. Now the reaction vessel was a cuvette that was cross-illuminated by a weak measuring beam from a monochromator. Any small changes in the transmission of an algal or chloroplast suspension could be observed by a photocell. Were there absorption changes that might reveal photochemical intermediates formed during a short flash and removed during the following dark period? There were. Actually there were several absorption changes observable across the spectrum. Bessel zeroed in on one of these, a reversible absorption change at 700 nm that he speculated might be the "eventual final photoreceptor of photosynthesis." At this point the tribute of Lou Duysens is appropriate: "The long working hours and inexhaustible inventivity and drive necessary to get such an apparatus working successfully in a relatively short time, and to carry out and analyze a large number of experiments, were amply rewarded. . . .Bessel discovered the far-red absorption changes associated with the reaction center P700 of system 1."[1]

By 1957 Bessel's accomplishments had become highly visible. He had outgrown his position at Wageningen, and no appropriate position in The Netherlands was open. Like many Dutch scientists before him, Bessel had become available for export. A position as director of a new institute in West Germany was offered; Bessel and Nell visited and together concluded that they should reject the offer. One major consideration was that the rigidity and formal protocol of the establishment was incompatible with their own life-style. Among other inquiries was one from the Research Institute for Advanced Studies (RIAS) in Baltimore. By 1958 the Kok family—now with three children—had found a new home in northwest Baltimore, not far from the converted mansion that housed the RIAS laboratories.

RIAS was then about two years old and not well known even in the United States. It was a subsidiary of the Martin Company, a corporate investment as an institute for basic science. In the course of a European trip, its director, Welcome Bender, had stopped to see Bessel in Wageningen, and his recruitment was that simple. Bessel elected to accept a position as a "staff scientist" in an unproven, industrially supported institute. There were no trappings to the position—

[1] L. N. M. Duysens, "In Memory of Bessel Kok," in *Proceedings, Fifth International Congress on Photosynthesis*, ed. G. Akoyunoglou (Philadelphia: Balaban International Science Services, 1981), pp. xix–xx.

not even the conventional one of academic rank—but only the promise of logistic support and freedom of choice in research.

Bessel had joined a small group labelled "Bioscience" and with a common bond of interest in photosynthesis. Within the year he had become the de facto leader of the group. No one worked harder, sprouted ideas faster, or drank more martinis at Friday afternoon parties. Welcome Bender managed the whole institute with the light touch of one who understood the needs of basic research. I was one of many visitors who joined in the excitement of the place. In later years other corporate managers were less supportive, but by that time Bessel and his group had achieved a position of strength.

In a former wine cellar Bessel assembled an improved version of his machine, which now could be called a split-beam phosphoroscope. A new sector program allowed measurements just before and just after the flash and was especially useful in studying the absorbance changes near 700 nm. Now the characteristics of the "700 pigment" were revealed: it was repeatedly bleached, even by rather weak flashes of far-red light, and its absorption regained in each subsequent dark period. Of course the measuring light (as at 700 nm) was itself a "far-red." If the measuring beam was made brighter, there was nothing left for far-red flashes to bleach. But now a new behavior appeared: if the flashes were red (instead of far-red), then each flash restored absorption of the "700 pigment." Here were reciprocal effects of red and far-red light like those described by Robert Emerson for the quantum yield of oxygen evolution.

At this stage Bessel acquired a young collaborator: George Hoch, a biochemist. The collaboration doubled the number of techniques of measurement but far more than doubled the imaginative interaction of two minds bouncing ideas back and forth. The first fruit of their effort came in a joint paper in a 1960 symposium entitled "Light and Life." In that paper they opened the modern era of thinking about photosynthesis by the first explicit statement that there must be two photochemical reactions "the first sensitized by chlorophyll a and a direct photochemical bleaching of P700; the second sensitized by accessory pigment, acting indirectly via mediation of dark steps, and restoring P700." The hypothesis was rephrased in other ways, presented as a diagram, and considered in terms of other related phenomena. Bessel and George had come with the ultimate excitement of science: they had discovered and understood an important truth that no one else had yet seen. But the reception of their paper was a disappointment. From the record of discussion one would judge that they had dropped an egg instead of a bomb. They had made the tactical error of presenting too many data, too many kinds of experiments. Most of the questions centered on experimental details that now appear trivial.

Unfortunately, publication of the symposium proceedings was delayed for over a year. By that time important publications from the laboratories of Lou Duysens and Robin Hill had derived independently the two-light-reaction hypothesis from other data. And the Hill-Bendall model became the convenient Z-scheme.

By 1960 the "black box" of photosynthesis had been opened up, and its bits and pieces were strewn about. The following decade was a time of fitting the pieces together. Now Bessel's work moved into high gear. It was remarkable in terms of the number of papers published and the variety of subjects addressed. It was even more remarkable in the number and diversity of collaborators: some came as senior scientists, some as postdoctoral students, and some as technicians; some even came from the ranks of high school students employed by the lab each summer. In the midst of this rather frantic pace, two particular events should be recorded. In 1963 Bessel and Andre Jagendorf served as coorganizers for a photosynthesis conference held at Airlie House in Virginia. In spite of the burden of new information let loose by the two-light-reaction hypothesis, that meeting is remembered as a very light-hearted conference.[2] And in 1964 Nell and Bessel became citizens of the United States.

Another event that became memorable was the extended visit of Anne and Pierre Joliot in 1967. This was something more than collaboration; rather, it was a convergence of the conceptual and instrumental developments of two laboratories. The Joliots had developed the art and technology of the polarographic measurement of oxygen at a platinum electrode. They brought this tool with them and sharpened it still further to measure reduction of a low-potential viologen dye by the reducing side of the photosynthetic mechanism. Together with techniques already available, there were now multiple windows through which to view interaction between the two photoreactions. The resulting joint papers were magnificent in the simplicity and clarity they brought to a complex subject.

On his return to France, Pierre Joliot engaged the activation phenomenon for oxygen evolution that he had discovered years before. After several minutes of darkness there was a delay in oxygen evolution during the first seconds of light. Now he observed the oxygen yields from short electronic flashes given in sequence after a dark period. Flash yields (Y) showed an interesting oscillation with a period of four: Y_1 was zero, Y_2 was small, and Y_3 was maximum and almost twice the steady-state yield to which the system damped out after several cycles. The pattern of oscillation

[2] A. Jagendorf, "In Memory of Bessel Kok," in *Proceedings, Fifth International Congress on Photosynthesis*, ed. G. Akoyunoglou (Philadelphia: Balaban International Science Services, 1981), pp. xxi–xxiii.

obviously contained information about the cryptic events of oxygen evolution. Pierre was led to a double two-step model that released two oxygen atoms in sequence. Bessel, now working independently, repeated the measurements and observed the oscillations, though with some small differences: Y_2 was very small and Y_3 was often much more than twice the steady-state yield. Though small, the differences were real, and they were incompatible with Pierre's model. They led Bessel to a flurry of effort that taxed the stamina of his younger colleagues. He assembled their elegant experiments to create a simple linear model that accumulated 1-2-3-4 charges to produce a molecule of oxygen. With a characteristic touch, Bessel called his model the "oxygen clock." In retrospect it appears that rather small technical improvements led Bessel to a model that was simpler and apparently more nearly correct than that which Pierre had derived. The history of research on photosynthesis records some acrimonious debates and personal animosities that arose under less stressful conditions. It is a tribute to both men that, in spite of the clash of their scientific results, they continued to be close personal friends, communicated their current findings to each other, and became joint authors of a review paper.

Following the oxygen clock there were obvious problems of proton release that—like oxygen—could be digitized by flash illumination. And quietly pursued in the background was continuing development of mass spectrometric measurements applied first to the interactions between photosynthesis and respiration and later to an extraterrestrial life detection system. It would take a rather detailed catalog—which in fact is provided by the bibliography—to do justice to the work of Bessel and his many collaborators.

Bessel Kok died in Baltimore on April 27, 1979, after a prolonged battle against lymphoma. He is survived by his wife, Cornelia Hendrika—Nell—a quietly resourceful lady who once hid him from labor camp conscription, later helped him reach out for his ambitions, and shared his love of family. She lives in the home into which the Koks first moved in 1958. Also surviving is a daughter, now Cornelie Angeline Forbush; two sons, Johannes Allart Bessel and Allart Alexander Bessel; and three grandchildren.

Among Bessel's scientific family of colleagues and friends there are many memories. From that legacy, at least a few recollections that provide special insight should be set down in writing:

- He appreciated a good hypothesis deeply and had the strength of character not to let an ugly fact stand in the way.
- He had a knack for discerning the "nuggets" of a problem.
- He was extraordinarily open-minded to any new concept or experiment, even if it came from a younger or unknown scientist and even if it was a contradiction to his own ideas.
- He could make you a better scientist just by asking questions.
- He had a basic belief that if he could measure anything with ten times greater sensitivity than had been achieved before, he was bound to discover something new.
- He had learned to smile while criticizing.
- He was always searching, either for a simpler hypothesis or for a better joke.

An appropriate conclusion to this memoir is taken from one of the several tributes[3] to Bessel that have been written.

[3] G. Cheniae and J. Myers, "Bessel Kok (1918–1979): A Tribute," in *Photosynthesis I: Energy Conversion in Plants and Bacteria*, ed. Govindjee (New York: Academic Press, 1982), pp. xxi–xxiii. Reprinted by permission. See footnotes 1 and 2 for two other tributes. A fourth is L. N. M. Duysens and C. J. P. Spruit, "In Memoriam Bessel Kok (1918–1979)," Vakbl. Biol., 59 (1979):210.

Bessel's scientific accomplishments reveal too little of a unique character that had many facets. Some may have seen only the outer veneer as a brusque and, at times, even boorish personality. Some may have felt his patience and his sensitivity to all people, whatever their walk in life. Some may have seen his intolerance of the trappings or of the pomp and ceremony of science. Some have enjoyed him as a witty and boisterous drinking companion.

Bessel was an uncommonly dedicated man, dedicated to his family, to his science, and to the joys of life. He pursued each endeavor with unrelenting fervor and passion and with enormous mental and physical stamina. He wore only a thin cloak of inhibitions, happily shared warmth and encouragement, but also gave sharp and sometimes brutal criticisms. His standards for his own work were uncompromisingly high, and he expected as much from others. Many of us earned his criticisms, some experienced his praise and encouragement, but all of us learned from Bessel.

On behalf of . . . many we salute and toast you, Bessel, for your scientific accomplishments, for your free spirit, and for all the fond personal remembrances you gave us.

I AM INDEBTED to Nell Kok who shared with me the story of her life with Bessel. I am indebted to Richard Radmer who assembled the bibliography and provided data from files of the Martin Marietta Laboratory. And I am grateful to many others of the Kok circle who shared their thoughts and recollections, notably, Welcome Bender, Leonard Bongers, George Cheniae, Lou Duysens, George Hoch, Andre Jagendorf, Anne and Pierre Joliot, Olga Owens, and Pete Zill.

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