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Obituary

John Biggins (1936–2004): His ingenuity, tenacity and humor; no-nonsense science with a big heart*

John enjoying the fruits of his research

John Biggins, Emeritus Professor of Biology at Brown University, Providence, Rhode Island, USA, passed away following a heart attack on September 14, 2004. He is survived by his wife Cathy, daughters Susan and Ann, grandchildren Haley, Sarah and Alex and brother Dave.

John was born in Sheffield, UK, on March 30 in 1936. After finishing school, John served in the British Army for 2 years before beginning his undergraduate studies at University College in London. John was already interested in photosynthesis while an undergraduate and, after talking with Vivian Moses at University College, he made the decision to cross the pond and go to the USA for his PhD.

Vivian Moses recalls:

> John was wondering where to do his research degree. Just back from there, I was full of the joys of the Calvin lab, and must have passed that on to him because the next time we met he was indeed a graduate student in Berkeley.

John received his PhD in Plant Physiology in 1965, under the guidance of Rod Park and Melvin Calvin, who was head of the Laboratory of Chemical Biodynamics at the University of California in Berkeley. John's PhD research was very successful and his results were published in *Science* (Park and Biggins 1964). John was also quite busy socially: he met and married Cathy Miller while in graduate school.

Rod Park remembers this time well:

> I first met John in the early 1960s when I had a half time appointment in Professor Melvin Calvin's Laboratory in the old Life Sciences Building on the University of California (UC) Berkeley campus. John was a graduate student in the Plant Physiology Group and had elected to work on photosynthesis. He became particularly interested in structure function relationships and ended up working with me. Actually, he worked largely on his own! John would always ask other researchers for their advice, but usually ended up doing it his own way. This independent spirit was his hallmark, and many others can testify to it. It was still apparent when John and Cathy retired not far from where we

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now have a vineyard in the coast range north of San Francisco. Following completion of his house, John, after asking many of us for advice, planted his own small vineyard. He asked us about rootstocks, varieties and clones of various wine grapes, irrigation systems and the best fencing to keep deer and pigs out of his vineyard. Then he proceeded very successfully, on his own, to do it his way! I am sorry he did not live to enjoy the fruits of these labors.

John worked very hard as a graduate student, but also had time for fellowship and fun, as we would go to La Val's just north of campus for beer on Friday afternoons. He, with several other Brits, rented a house a few blocks north of campus where occasional lively parties were held. I remember his future wife Cathy to be sitting demurely by the pool as chaos surrounded her. Their residence wasn't quite Animal House, but you could see it from there! Cathy gradually domesticated John, and they successfully raised a fine family as he pursued his career.

I am pleased that John, Cathy and some of their friends made a trip to our Rockpile Vineyard a few weeks prior to his passing and will always recall the beautiful day, the wine and food that I shared with my good friend for the last time.

One of John's projects during this time was to build on the 'quantasome concept', first presented by Rod Park and Ning Pon, who was then a PhD student with Calvin. Rod and Ning had published a landmark paper (Park and Pon 1963), showing evidence of the particulate nature of photosynthetic membranes and the incorporation of protein complexes- hence the origin of the word 'quantasome', which some senior scientists in the field may remember. Building on the work of Steinman (1952) the dramatic pictures that Rod and John obtained of paracrystalline arrays of quantasome particles in thylakoid membranes beautifully decorated the cover of Science in 1964 (Park and Biggins 1964). Later, working with Dan Branton at Berkeley, Rod and John applied the freeze-fracture approach to visualizing the particles in thylakoid membranes, in demonstrating their heterogeneity and in determining that their dimensions were compatible with analytical data that defined a minimum unit capable of the photosynthetic light reactions. Although the 'quantasome' turned out not to contain everything that the authors had supposed, it was subsequently demonstrated to be the proteins of the water splitting complex (Seibert et al. 1987), their clear images of a protein filled thylakoid membrane helped bring an end to the prior view that photosynthesis resulted from a collection of pigments and electron transfer cofactors dispersed in a lipid bilayer.

One of us (KS) arrived in the Calvin Lab as a postdoc in 1960. As a physical chemist with no prior experience in photosynthesis and not much in biology, I found John to be a wonderful source of knowledge, experimental approaches and British directness and humor. John introduced me to the Warburg apparatus for measuring photosynthesis. My background was in gas-phase photochemistry, and I found it difficult to accept the cumbersome process and time-consuming techniques involved in staring for hours at manometers attached to reaction vessels moving rapidly back and forth in illuminated shaker baths to collect too few data and which were then subject to elaborate corrections and formulaic calculations. We were interested in determining the quantum requirements of the photosynthetic light reactions and their wavelength dependence. This was at early times in the two-light reaction hypothesis, and controversy still raged between labs all over the world – this was exemplified locally for us by the differing views coming from the Calvin lab and the Daniel Arnon lab at Berkeley. John and I decided to try a new spectroscopic approach, which took advantage of the remarkable craftsmanship available in the mechanical shops associated with the Calvin group in the Lawrence Radiation Lab. To determine the excitation spectrum of Photosystem II (PS II), we designed a multi-compartment reaction vessel, which allowed illumination through a transparent bottom of 12 identical 2 ml aliquots of a reaction mixture containing chloroplasts along with the Hill-reaction acceptor ferricyanide or ferricyanide-DCIP. The extent of reaction was determined spectrophotometrically by monitoring the reduction of the ferricyanide. To determine the wavelength dependence, we placed an interference wedge between the light source and the bottom of the multi-compartment reaction chambers, which had been elegantly machined by the Lawrence Berkeley Lab technicians in a side-by-side

arrangement in a block of black lucite to which the transparent bottom was attached. Thus, the compartments were illuminated simultaneously, each by a different wavelength between 592 and 716 nm. The red-drop in quantum efficiency was readily apparent (Biggins and Sauer 1964) and the results helped to resolve a controversy over the point of interaction of DCIP in the electron transport.

In our next study we determined the wavelength dependence and quantum efficiencies of the $DCIPH_2$ (+DCMU) to NADP (a PS I reaction) and the H_2O to NADP reaction (requiring both PS I and PS II). We found that the quantum yield for the PS I reaction increased about two-fold at long (far-red) wavelengths, whereas that of the complete H_2O to NADP reaction decreased dramatically at long wavelengths. The results were consistent with the view that PS I and PS II absorb approximately equally at short wavelengths, but PS I absorption is dominant in the far-red region. Furthermore, the quantum yields indicated that each light reaction was operating at near maximum efficiency in the wavelength region(s) where the corresponding antenna pigments absorbed (Sauer and Biggins 1965) There was wonderful synergy in the interaction between John, the plant physiologist, and his physical chemistry side-kick in all of these studies. It is through collaborations like ours that the delights of science can truly be appreciated.

After finishing his PhD, John landed a tenure-track job at the University of Pennsylvania in 1965 and he and Cathy moved to Philadelphia where their daughter Susan was born. Their stay in Philadelphia was relatively short, and Ann was born in Berkeley when John returned to California as a visiting professor, just prior to the family's ultimate move to Rhode Island. John took a position at Brown University in Providence, Rhode Island in 1970, where he was to stay until his early retirement in 1998.

One of John's early research interests at Brown was in measuring linear and cyclic electron transport (Biggins 1973, 1974; Maxwell and Biggins 1976) and this work translated into the development of fast scanning and kinetic spectrometers in collaboration with Bill Shipp (Shipp et al. 1976). His skill in developing spectroscopic techniques combined with his interest in structure-function of the photosynthetic apparatus led to his use of linear dichroism to study pigment organization in the thylakoid membrane (Biggins and Svejkovsky 1981; Biggins 1982).

One of us (DB) has fond memories of John from this time. I met John in 1984 when I started a 2-year postdoctoral fellowship under his supervision at Brown University. John and Cathy more or less adopted me into their family during my stay in Rhode Island and we have stayed close ever since. It was an exciting and productive time for me. John's interest had turned to the regulation of light harvesting in phycobilisome-containing organisms, the light-state transition (Biggins 1983). It turned out to be a very good time to join his lab and we ended up publishing a series of papers together on the mechanisms of the light state transition in red algae and cyanobacteria (Biggins et al. 1984, 1985; Biggins and Bruce 1985; Bruce and Biggins 1985). There was a wonderful energy in the laboratory; we worked side by side at the bench and shared a lot of enthusiasm for the project. Among other things, John taught me a lot about science, grant writing, politics, organizing conferences and cycling. He also took me under his wing and introduced me to the photosynthesis community. At my first Gordon conference, John sat me down at a table with George Cheniae, Jack Myers and a bottle of Jack Daniels whiskey, so I might gain some 'historical perspective'. Needless to say I found it difficult to follow the next morning's sessions! It was fun working with John. He was at the bench much more often than in his office and was relentless in his pursuit of science. For that matter he was relentless in his pursuit of any project; he was incredibly efficient, and always got things done. John was constantly pushing himself to master new techniques, do new things and think outside the box. He never stayed too long in one research area, and was always looking for new challenges. For all of his intensity, John also had a wonderful sense of humor, which sometimes caught those who didn't know him well by surprise. His 'roast' of Bob Blankenship at the 1993 Eastern Regional Photosynthesis Conference was typical of John and unforgettable; he had the audience in tears of laughter.

The most important things I (DB) learned from John were about living, lessons taught by his own example. John was dedicated to his family and he had created a successful balance between work and

home. He worked hard all day, but at 5:15 P.M. it was time to 'put out the fire and head west' so he could spend time with Cathy, Susan and Ann. If an experiment were running late, John would improvise. On one occasion he stained an acrylamide protein gel with Coomassie blue in the backseat of his car while driving home for dinner and de-stained it overnight in his kitchen before bringing it back to the lab for drying the next morning! John always found a way to do what had to be done. I'll always remember my time with John at Brown University with great affection. John was an amazing mentor and a wonderful friend whom I miss dearly.

John was a strong proponent of photosynthesis research; he was one of the initiators of the Eastern Regional Photosynthesis Conference and he organized the International Congress on Photosynthesis held in Providence in 1986. The 1986 Congress is a fond memory for many photosynthesis researchers. Gernot Renger put it particularly well in a note he sent to one of us (KS):

> 'We also admired John's enormous success in organizing the Providence Congress. We agreed that this was the last 'family party' of the photosynthesis people; afterwards the meetings became much more 'professional' and business like.'

Beverley Green expressed similar sentiments:

> 'I never got to know John very well, but I certainly did have the impression of a warm and generous nature, and the sense of humor. He was particularly generous in dedicating more than a year of his life to make the 1986 Congress a big success. It was the best and most fun of all the congresses.'

John took a well-deserved sabbatical at Saclay in France after the 1986 Congress. True to character, he used this time to completely change his research focus and embarked on a study of the role of vitamin K_1 as the secondary electron acceptor (A_1) in PS I (Biggins and Mathis 1988; Biggins 1990).

John is very fondly remembered at Saclay as evidenced by the following comments to one of us (KS) from William Rutherford:

> We at Saclay were shocked by the news about John. He was a very popular character here: part of our mythology in fact. His year here was fun for everyone and we have fond memories. I was looking forward to getting the chance to see him do his wine talk after what you told me when you visited. I am sad that now I won't get the chance.

John continued his work on PS I, expanding from vitamin K_1 to the Fe sulfur centers, which he continued into the 1990s. In typical John fashion, he pushed himself into new techniques and ultimately was using site-directed mutagenesis and protein engineering to investigate the Fe cluster domains of PS I (Rodday et al. 1993, 1995; Scott and Biggins 1997).

John retired at age 62, and he and Cathy finally moved back to California, something they had long dreamed of doing. John was a handyman and had done many renovations on their home in Rhode Island. He scaled this up somewhat and was intimately involved in the construction of their new home in the Sonoma Valley. Never able to sit still, he added a vineyard and started working towards wine production. John became very popular with the local wine making community who valued his enthusiasm and expertise in biochemistry and microbiology. He had also found himself another research niche! John was not content with the status quo in wine making and was applying his considerable research expertise to improving wine.

John had been an athlete all of his life, and this continued after retirement. A number of his friends and colleagues have memories of trying to keep up with John on a bicycle on any number of Gordon conference cycling adventures. He was still riding regularly in the Sonoma Valley, and was in better shape than ever due to the amount of hill climbing he had to do. This is one of the reasons John's heart attack caught us all by surprise. He was so strong and energetic. For many of us John was invincible which has made his death difficult to comprehend.

We miss John, his insight, wit, humor and energy. He was a positive force in the photosynthetic community and a major influence in many of our lives. Although we wish he could have enjoyed his retirement for many more years it is

comforting to know how content John was in California. He and Cathy had recently celebrated forty years of marriage, and they were now living much closer to daughters Susan and Ann and their families. He was full of plans for the future and in the middle of exciting new projects. He was happy.

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