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TRIBUTE

Derek Bendall (1930–2014)

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Abstract Derek Bendall carried out pioneering work on photosynthetic electron transport, particularly on protein–protein interactions, cytochromes, and cyclic electron transport, as well as on other topics including the biochemistry of tea. He was a keen musician and a gifted gardener, a devoted family man, and a delightful colleague and friend. The bioenergetics community, especially those working on photosynthesis, will miss him sorely.

Keywords Biochemistry of tea · Biophotovoltaics · Cytochromes · Cyclic electron transport · Robin Hill · Protein–protein interactions

Derek Bendall, who died in December 2014 after a brief illness, made important contributions in many areas of plant bioenergetics, and especially photosynthesis, in a research career spanning 60 years. See Fig. 1 for a recent picture of Derek.

This tribute to Derek Bendall was invited and edited by Govindjee, historical corner editor of Photosynthesis Research.

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Fig. 1 A photograph of Derek Bendall, courtesy of and © Darwin College, Cambridge

Derek was born in Coventry, UK, on July 15, 1930 (Saint Swithin's Day, as he often reminded people if it rained on his birthday). His father was a Master Draper, and his mother a schoolteacher and keen naturalist. He went up to King's College, Cambridge, to read Natural Sciences in 1950 and graduated with First Class Honours in Biochemistry in 1953. He became a research student in the same department under the supervision of Robert (Robin) Hill, continuing the line of bioenergetics research at Cambridge that had begun with David Keilin. In his first publication (Bendall and Hill 1956), he characterized the cytochrome components in *Arum* spadices in an attempt to understand the pathway of cyanide-insensitive respiration that had been described a few years earlier. This paper epitomized much of his future research career, which would involve careful biochemical, and especially spectroscopic, analyses of redox proteins, and build on the earlier advances made by Robin Hill. Derek admired Robin greatly, and a photograph of the roof of Ely Cathedral taken using the elegant and highly effective fish-eye camera developed by Robin (Bendall 1994) hung on Derek's office wall for many years.

After completing his PhD in 1957, Derek spent a year in the lab of Christian de Duve in Louvain, Belgium, working on subcellular fractionation (see e.g., Beaufay et al. 1959). He then spent 2 years studying the biochemistry of tea fermentation, funded by the Nyasaland (now Malawi) Tea Association that had enlisted the help of Robin Hill and Sir Frank Engledow, Professor of Agriculture in Cambridge, to understand why the quality of the tea grown on Mlanje Mountain was poor. Derek was to remain interested in tea (as a consumer, researcher, and scholar) for the rest of his life. He published papers (see e.g., Gregory and Bendall 1966; Forrest and Bendall 1969; Robertson and Bendall 1983) and supervised PhDs (Richard Gregory and Ian Forrest) on the biochemistry of tea, and was working on a more general book on tea at the time of his death.

In 1960, Derek was appointed as a University Demonstrator in Biochemistry at the University of Cambridge, UK. These posts were for a limited tenure of 5 years, and promotion to a Lectureship was rare, as a matter of departmental principle. He, however, was promoted to a Lectureship in 1965 and remained in the Cambridge Biochemistry Department for the rest of his academic career, with sabbaticals at the Johnson Research Foundation (with Walter Bonner) and in Paris (with Pierre Joliot). Although he continued to make important contributions on tea biochemistry, and cyanide-insensitive respiration in plant mitochondria (see e.g., Bendall and Bonner 1971), he focused more on electron transfer processes associated with the light reactions of photosynthesis, which remained the major theme for the rest of his career. He continued to publish in collaboration with Robin Hill (e.g., Hill and Bendall 1968), as well as establishing his own independent program. This included characterization of plastocyanin and photosynthetic cytochromes, and the mechanism of their interactions with other redox carriers (see e.g., Plesnicar and Bendall 1970; Wood and Bendall 1975, 1976). It led to key insights into the roles played by quinones (Rich and Bendall 1980) and energy coupling by the cytochrome *bf* complex (Rich and Bendall 1981). He made a number of further important contributions during the ensuing decades, for example in helping to understand the pathway of cyclic electron transport (technically difficult to study, as a cyclic process) with David Moss (Moss and Bendall 1984) and others. His review on this (Bendall and Manasse 1995) was one of his most cited papers, and 20 years later continues to be cited at a steady rate. With Alison Stewart, Stephen Rolfe, and others, he also advanced our understanding of the polypeptide composition of the electron donor side of Photosystem II in cyanobacteria (see e.g., Rolfe and Bendall 1989).

Derek's meticulous and rigorous approach allowed him and one of us (CJH) to demonstrate the unexpected occurrence of components of the photosynthetic electron transfer chain in nonphotosynthetic membranes of cyanobacteria (Smith et al. 1992). One of his major projects, though, building on his earlier work on plastocyanin, was to understand the nature of protein–protein interactions underlying photosynthetic electron transfer. He focused particularly on the interaction between cytochrome *f* and plastocyanin, and brought a wide range of techniques to bear on the project, including site-directed mutagenesis (in collaboration with John Gray who had held a Fellowship in Derek's lab), Nuclear Magnetic Resonance (NMR), and kinetic analysis. His understanding of the theory underlying protein–protein electron transfer was exceptional for a practical biochemist, and the book '*Protein Electron Transfer*' that he edited (and his own chapter in particular) was typically thorough and remains an important reference work (Bendall 1996). He commented in the preface to that book that '*In the 1990s it seems that research on electron transfer in proteins has entered its exponential phase of growth,*' and this was true for his own work in the area. He published a series of important papers, perhaps most significantly his determination with one of us (MU) of the structure of the complex between plastocyanin and cytochrome *f* using paramagnetic NMR spectroscopy (Ubbink et al. 1998)—an impressive achievement for a complex with a K_D of 0.14 mM (Kannt et al. 1996). Derek stressed that, whereas the majority of protein–protein interactions studied by biochemists were relatively stable, those involved in electron transfer, for example in the photosynthetic electron transfer chain, were much more transient. The biological function of interactions between electron transfer proteins is to form a highly transient complex that is just specific enough to allow a reaction to occur. These complexes are not optimized to have a strong and specific interaction but instead to enable rapid dissociation, allowing for rapid turnover. Derek's realization that weak interactions are fundamentally different from strong ones, posing significant technical difficulties for analysis, was ahead of its time. Only after the turn of the century did this idea become more widespread and new techniques to characterize these transient and often dynamic complexes became available.

The work on protein–protein interactions continued beyond his official retirement in 1997, after which he continued working with one of us (CJH) as an integral member of our group, and jointly advising the work of a number of group members, such as Beatrix Schlarb-Ridley. His decades of experience in photosynthesis biochemistry were invaluable as we initiated the Algal Biotechnology Consortium, aiming to exploit algae for a range of applications, including renewable energy production. He was part of a number of projects in this area, including the use of algal cells for direct electricity production in biophotovoltaic devices (see e.g., Bombelli et al. 2011). However, he had a particular involvement in our joint project on an unusual form of cytochrome c_6, which we and another group had reported as occurring in plant chloroplasts, in contrast to the textbook view (Gupta et al. 2002; Wastl et al. 2002; Bendall 2004). We showed that the protein was not a simple substitute for plastocyanin (Molina-Heredia et al. 2003), and thanks to Derek's encyclopedic knowledge of the literature a potentially confusing situation was avoided by naming the protein 'cytochrome c_{6A}' (Wastl et al. 2004) rather than the 'cytochrome c_x' suggested by others–a name that had already been used for a different cytochrome.

Derek continued to work full time in the group until a few days before his death, and his mind remained as acute as ever. However, he had always balanced commitment to his family and his friends with his commitment to science. In 1958 he married Fay, then a postdoc in Robin Hill's lab [and who described with Hill the famous Z-scheme of photosynthesis (Hill and Bendall 1960)], and they raised three daughters. He was a keen musician, playing the piano, and taking pleasure in building instruments—notably a full string quartet of violins, viola, and cello. He was also a very successful gardener, both at home and in Darwin College, Cambridge, of which he was a Fellow, and memorably arrived at a group fancy dress party as John Tradescant the Younger, identifiable by the plant he was carrying (which also serves as a reminder of how much he valued knowledge of his subject's history).

Derek was always genuinely interested in the work of others, and happy to offer perceptive insights, without forcing them on people. Always modest, he wore his distinction lightly (in 1982 Cambridge University awarded him the Doctor of Science degree which requires '*a substantial body of published work accumulated over a number of years in a distinguished career*'). Two descriptions occurred repeatedly in the tributes that came in after his death—gentleman and scholar—and we miss him greatly. Derek is survived by Fay, their daughters Sarah, Rachel, and Kate, and their families.

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