David Alan Walker (1928–2012)

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Abstract David Alan Walker, Emeritus Professor of Biology, University of Sheffield, UK and Fellow of the Royal Society, died on February 13, 2012. David had a marvelous 60 year career as a scientist, during which he was a researcher, mentor, valued colleague, and a prolific writer in the field of photosynthesis. His career was marked by creative breakthroughs in isolation and analysis of chloroplast metabolism in vitro and simple but valuable technical advances for measurement of photosynthesis in vivo that remain relevant on a global scale to production of crops and biofuels, as well as plant responses to climate change. We include here personal remembrances by the authors (GEE and UH), and by (in alphabetical order): Zoran Cerovic (France), Bob Furbank (Australia), Geoffrey Hind (USA), John Humby (UK), Agu Laik (Estonia), Peter Lea (UK), Ross Lilley (Australia), Barry Osmond (Australia), Simon Robinson (Australia) and Charles Stirling (UK).

Keywords Intact chloroplasts · CAM · Robin Hill · Charles Whittingham · C₃–C₄ photosynthesis · Oxygen electrode · International society of photosynthesis research (ISPR) · Meirion Thomas

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David, the son of Cyril and Dorothy Walker, was born in Hull, England. He attended the South Shields Boys High School (now Harton Technology College) from 1939 to 1946. Following his national service in the Fleet Air Arm of the Royal Navy of UK, David entered Kings College, Newcastle, then part of the University of Durham, where he received his Bachelor of Science, and, subsequently his PhD under Meirion Thomas in 1958. Later, in 1968 he was awarded the Doctor of Science at the University of Newcastle in recognition of his exceptional contributions of published work in his field. The author of over 230 publications, including several books, David was made a Fellow of the Royal Society in 1976. In 1991, he received a Humboldt Research Prize, and in 2004, he received the inaugural Communications Award from the International Society of Photosynthesis Research (ISPR). For his accomplishments and a list of some of the publications, which illustrate his outstanding contributions to our understanding of the mechanisms involved in photosynthesis see: http://en.wikipedia.org/wiki/David_Alan_Walker; and online information in Orr and Govindjee (2010, pp. 188, 189, 197, 198), and at http://www.hansatech-instruments.com/david_walker.htm. See Fig. 1 for two photographs of David Walker taken at two different times.

For a colorful, informative and detailed description of David's career, including how he came to study plant biology and chloroplast function, see his memoir, "*Tell me where all past years are*" (Walker 1997, see also Walker 2003a). Besides his many contributions to our understanding of the photosynthetic process, David spent equal time over many years in technical developments. These include methods for the isolation of intact, fully functional chloroplasts, and oxygen electrode systems for studying photosynthesis, which were combined with chlorophyll fluorescence analysis to simultaneously measure O₂

Fig. 1 Two photographs of David Walker taken at different times

David Alan Walker (1928–2012)

evolution and photochemistry, and the fate of energy absorbed by Photosystem II.

As a science writer, David was unique; he was both eloquent and literate. According to David, *“By the time that I was four, long before infants’ school, my mother (Dorothy) and my ‘mad’ aunt had taught me to read, thereby giving me the finest gift that any child could receive. I learned to read fast and to read widely.”* (Walker 1997). David’s ongoing goal in life was to make science accessible to, and appreciated by, the general public. His approach incorporated science, history, art, poetry, humor, nature and the environment. In addition, he agonized over science and politics, which was captured in his writing. Along with his outstanding style of writing, he also incorporated illustrations by his son Richard, making the science very accessible to the public. In August, 2004, David received “The Communications Award” from the International Society of Photosynthesis Research for his outstanding efforts to communicate photosynthesis to the general public. This was in recognition of contributions beyond his more than 200 publications in science journals. David said he appreciated the encouragement engendered by this award, his colleagues in research and friends, and that he was pleased to be a part of the international community.

The following sections summarize the path of his scientific career, innovations in design of equipment, and major written works for scientists and the public, and conclude with personal remembrances by some friends and colleagues.

The path and highlights of David’s scientific career

David’s career in science began in 1948, when he was released from the Royal Navy, and enrolled in

undergraduate studies at King’s College, Newcastle (then part of University of Durham). After receiving his BSc in 1952, David spent a year in 1953 at Purdue University (Indiana) with support from the Fulbright foundation. While there, he worked with Harry Beevers on castor bean mitochondria. On his return to the UK, David went back to Newcastle to work with Meirion Thomas on a PhD, where he made a significant contribution to Crassulacean Acid Metabolism (CAM). David noted, “Having devised a way of getting to grips with succulent leaves full of acid and short on protein, it led me to conclude that dark acidification in CAM was attributable to the combined efforts of phosphoenolpyruvate carboxylase and malic dehydrogenase and light deacidification to malic enzyme” (Walker 1956, 1960, 1962, 1997).

David received his PhD in 1958. Robert (Robin) Hill of the University of Cambridge had been David’s external PhD examiner. David and Shirley, newly married, moved to Cambridge when he was offered an Imperial Chemical Industries postdoctoral fellowship to work with Robin. The result was an association, which lasted for more than 40 years. David had great admiration for Robin, whom he described as a modest man with a remarkable intellect who essentially gave us the Z-scheme (see reviews, Walker 2002a, b, and http://www.hansatech-instruments.com/forum/uploads/david_walker/zScheme.htm for an animated version of the Z-scheme inspired by an original illustration by Richard Walker, David’s son).

After Cambridge, David accepted a lectureship from Charles Whittingham at Queen Mary College in the University of London. There, he also met Tom Delieu, who later became his closest friend and a valued colleague in the subsequent design and development of oxygen electrode systems for measurements of photosynthesis.

Geoffrey Hind writes:

“When Charles Whittingham took up the Professorship at Queen Mary College, U. of London (1958), he sought to push all the current hot topics in photosynthesis research: 1) O₂ evolution/photorespiration, 2) carbon pathways, and 3) photophosphorylation. He took care of #1 personally and #2 was assigned to David. I was hired as a graduate student and assigned #3 (Whittingham knew me as one of his plant physiology undergrads at Cambridge). David’s carbon team included Douglas Graham, Roger Hiller and Graham Pritchard; but, Whittingham also asked David to be my second supervisor since, through his interaction with Robin Hill, David had discovered the remarkable ability of pyocyanine to catalyze photophosphorylation.”

In 1962, David, Shirley and their two young children, Richard and Marney, stayed 6 months at the Connecticut Agricultural Experiment Station, New Haven, where David was supported by a Charles F. Kettering Fellowship to work with Israel (Zuni) Zelitch. The family returned to England where David accepted a position from Charles Whittingham to work on isolating fully functional chloroplasts. David noted this changed his life forever. At that time, isolated chloroplasts removed from their *in vivo* environment showed little capacity for CO₂ assimilation (only 1 %, or less, compared to that in leaves). The research, utilizing radioactive bicarbonate, led to his first publication showing significant rates of CO₂ assimilation by isolated chloroplasts (Walker 1964). Following this, a very exciting moment for David was his discovery of CO₂ dependent O₂ evolution using a Clark electrode, with the associated lag period which occurred before attaining high rates, and his demonstration that addition of 3-phosphoglycerate could abolish the lag period (Walker and Hill 1967; see Walker 1997). This was followed by experiments with the addition of various metabolites, which indirectly indicated whether they were capable of entering the chloroplasts. An important finding was that CO₂ dependent O₂ evolution required inorganic phosphate (Pi) with a ratio of O₂ evolved per Pi added of 3 to 1. The discovery of a requirement for Pi contributed greatly towards understanding the *in vivo* mechanism of photosynthesis. The results led to the conclusion that, if sugar phosphates are exported, there must be a corresponding import of Pi, and to the hypothesis that specific permeases which exchange Pi with sugar-P could account for the inhibition of photosynthesis by above optimum levels of Pi and its reversal by sugar-P (Walker and Crofts 1970). This provided information which led to the identification by Hans Heldt and colleagues of a Pi/triose-P antiporter which is a central player in carbon assimilation, controlling export of photosynthate from the chloroplasts in exchange for Pi.

Further, David and colleagues later demonstrated CO₂ dependent O₂ evolution in a reconstituted chloroplast system (in chloroplasts having lost their envelopes with release of the stromal enzymes of the C₃ cycle) (see Walker and Slabas 1976).

In 1970, David became Professor of Biology at the University of Sheffield, where he continued his life-long, and exceptionally productive, career. In 1979, he was given funds to develop a “Research Group for Photosynthesis” which later became The Robert Hill Institute, named after his mentor, Robin Hill. What follows are additional illustrations of his work, and comments by some colleagues.

Innovations in developing equipment

David spent years developing and perfecting equipment to analyze photosynthesis *in vitro* by polarographic measurement of O₂ evolution (e.g. in isolated chloroplasts, protoplasts, photosynthetic cells) and *in vivo* (leaf discs). Following David’s design, his colleague Tom Delieu, a master craftsman, built the first prototype. With his typical sense of humor, David wrote at the end of his paper with Tom: “In advocating the virtues of the oxygen electrode we would not wish to convey the impression they are yet entirely foolproof. They are like the legendary little girl in that when they are good they are very, very good; but, when they are bad they are horrid.” (Delieu and Walker 1972). David linked up with John Humby, the result of which was a long and fruitful collaboration in marketing apparatus through Hansatech Instruments. In the early 1980s, David had Tom construct an instrument that would measure oxygen in the gas phase, which became the leaf disc electrode (where light response of photosynthesis and maximum quantum yields can be readily analyzed). Polarographic equipment was also further developed to simultaneously analyze O₂ evolution and the fate of energy absorbed by PSII by chlorophyll fluorescence. These instruments stimulated a great deal of new research around the world and led to the establishment of the “gold standard” for the quantum yield of C₃ photosynthesis *in vivo* (Björkman and Demmig 1987).

Two important scientific meetings flowed from these developments. Peter Horton, in reflecting on the truly immense contributions David made to photosynthesis research at Sheffield, recalls an exciting event from the early days of the Hill Laboratory when he convened a symposium with the title, “*What Limits Photosynthesis?*”, a question which is still largely unanswered in many respects and very pertinent to all the renewed interest in “improving photosynthesis”. David later organized a Royal Society discussion meeting in London on “New Vistas in Measurement of

Photosynthesis” that brought together these and other technical advances for measurement of photosynthesis in vivo (Walker 1989; Walker and Osmond 1989). (See <http://www.hansatech-instruments.com/nostalgia.htm>; Delieu and Walker 1981, 1983; Walker 1987, 1992a, b, 1997, 2003a.)

Major books and making science accessible to the public

David made major, lasting contributions in his writings about photosynthesis and its relevance to mankind, not only for scientists, but in forms that were readily accessible and appealing to people of all ages and at all levels of scientific sophistication (Fig. 2).

In recognition of this, David was conferred with an Honorary Doctorate of Letters by the University of Sheffield in 2006.

His books relating to origins and mechanisms of photosynthesis and techniques include: Edwards and Walker (1983); and Walker (1987, 1992b, 2002c, 2003b). The

former, “ C_3 – C_4 ...” was a major undertaking. It was a long process from beginning (1977) to completion. David took on the tedious logistics and time consuming process of getting the book published (1983). He had known the publisher Michael Packard since the late 1960s, and enlisted him as publisher and promoter of the book’s distribution. Michael noted theirs was a lasting friendship.

In their preface to a recent book on C_4 photosynthesis, Raghavendra and Sage (2011) wrote:

“The second notable treatise was C_3 – C_4 : *Mechanisms, and Cellular and Environmental Regulation, of Photosynthesis* by Gerry Edwards and David Walker (Blackwell Scientific, 1983). This book was notable in that it provided the first in depth, textbook style-summary of the C_3 , C_4 and CAM pathways as understood at that time. For the second generation of C_4 plant biologists who came of age in the late-1970s and 1980s, this book was the C_4 bible, the text to memorize, and later, when they were academics, the book to assign to their students. For nearly 20 years, one could not be a C_4 biologist without having

Fig. 2 Illustrations of types of books and the Pub understanding of science by David Walker. Visit: http://www.hansatech-instruments.com/david_walker.htm for free download including (i). Books on photosynthesis: ‘Global Climate Change’, ‘Energy, Plants and Man; Like Clockwork’; ‘ C_3 , C_4 ’. (ii). ‘A Leaf in Time’; Spanish translation

of ‘A Leaf in Time’; ‘A New Leaf in Time’. (iii). Technical Manual: ‘The use of the Oxygen Electrode and Fluorescence Probes in simple measurements of Photosynthesis’. (iv). PowerPoint Presentations: ‘Starch Pictures’; ‘The Z-scheme’. (v.) Quizzes: ‘The Pub Understanding of Science’

intimate familiarity of “ C_3 – C_4 ,” “for its breadth of scope addressed everything from the detailed biochemistry to ecological performance of C_3 , C_4 and CAM species. Even today, nearly 30 years later, “ C_3 – C_4 ” remains one of the most straight-forward and understandable introduction to C_4 plant biology for students as they move beyond the simple treatments in plant physiology textbooks.”

Regarding David’s electronic book, *Like Clockwork*, John Allen wrote in a review (Allen 2002) “*Like Clockwork* is thought provoking. It is also fun. And, in spite of David Walker’s major and lasting contributions in photosynthesis research, there are still open questions, and a humility that leaves for the reader to form his own opinions.” Also, a Review in *New Scientist* (13th January 2001 No. 2273) stated, “*Like Clockwork* does for photosynthesis what *A Brief History of Time* does for theoretical physics: it takes a baffling but fundamental process and makes it easy to understand. David Alan Walker uses the electronic book format to explain the transfer of energy from sunlight with lots of clear, colorful diagrams and relevant links.”

David also wrote two books which were said to be aimed at readers between ages 9 and 109, with the aim of providing an entertaining and light-hearted overview of the mechanisms and origins of photosynthesis, whilst remaining factually sound and concise (Walker 2002c, *A Leaf in Time*; Walker 2006, *A New Leaf in Time*).

On receiving the ISPR Communications Award in 2004, in recognition of his contributions beyond his more than 200 publications in science journals, David said he enjoyed writing, but....

“The problem lies not in the writing, but in the peripherals that can sometimes be tedious in the extreme. If authors manage to write something, there are still hazards to be negotiated like proof-readers (e.g. for the C_3 – C_4 book deciding photon should be changed to proton), copy-editors, type-setters (as were), publishers who trash books, distributors, book sellers, editors who have problems, libraries and political correctness. So it is very nice, when enthusiasm starts to flag, that authors are sometimes offered kind encouragement. Now I feel refreshed, my enthusiasm rekindled and immensely grateful to my colleagues in photosynthesis for honoring me in this way.”

With this mindset, David devoted time to making his major works available in digital form; in conjunction with the ISPR they are hosted by Hansatech Instruments (see http://www.hansatech-instruments.com/david_walker.htm). Early on, he believed there was a role for digital books in facilitating retrieval of information from “a library which never closes.” He recognized that texts which depend heavily on cited

references, “books” in Portable Document Format (PDF) which contain embedded hyperlinks, can guide and facilitate rapid retrieval of reliable information from the Internet.

David’s books were also greatly enhanced by colorful illustrations drawn by his son, Richard (e.g. Fig. 3; also see Web resources at <http://www.photosynthesisresearch.org>).

A favorite activity of David’s around Christmas time was to go to pubs for singing of traditional Yorkshire Christmas carols, which he thoroughly enjoyed. Thus, maybe it’s not surprising that another outreach effort to promote science to the general public was his development of a series of multiple choice questions which were placed on designed beer mats (coasters) for pubs. In 2000, he got a Millennium award to distribute 90,000 of them! (Fig. 2, also see http://www.hansatech-instruments.com/pub_understanding.htm). David also took pleasure in creating high-resolution pictures within leaves based on the distribution of starch: see starch prints at the above web site.

David wrote extensively about sources of energy, photosynthesis, biofuels, plants and man, the greenhouse effect, and global climate change in his books “*Energy, Plants and Man*,” (Walker 1992a) and “*Global Climate Change*” (Walker 2002d). In his last paper, “Biofuels—for better or worse?” (Walker 2010), David was concerned about some of the unrealistic benefits, or claims, being made about biofuels and their potential to contribute to road and air transport without full scientific vetting. He discussed the limitations considering the efficiency of conversion of solar energy into chemical energy by photosynthesis, the land area required to produce enough biomass to run an automobile for a year, fossil fuel inputs versus biofuel output, and land use for production of crops versus biofuel. In January, 2009, he wrote in *The Guardian*: “Greenpeace is right to express reservations about the prospect of biofuels (of whatever nature) making a significant contribution to air transport (Report, 31 December). The land area that would be needed would be immense. Despite claims to the contrary, biofuels consume about as much energy to produce as they yield when they are burned. It is therefore also disingenuous to suppose that non-food crops are without impact on world food supplies.”

In summary, David carried with him fond memories during his career. This includes his earliest research on chloroplasts, which led to demonstrating how, in the absence of their cellular environment, they could match their performance in vivo, his satisfaction in constructing apparatus to analyze rates of photosynthesis, the recognition he received for disseminating scientific information to the public in a form which continues to be available, and the many colleagues who shared in his journey. David retired from the University in 1993, though as already shown, his scientific career was far from over. He and Shirley were at last able to spend most of the time at their beloved holiday

Fig. 3 **A** Richard Walker, David's son. Richard was an illustrator and collaborator for some of David's published works. Three illustrations are shown; **B** See web resources at: <http://www.photosynthesisresearch.org>; **C** from Walker (1992a); **D** from Walker (1987)

home in Biddlestone, which over the years had become, "... a refuge, a hiding place from the more unpleasant aspects of academic life ..."

From David's friends and colleagues

Ulrich Heber (University of Würzburg, Germany), coauthor of this Tribute, recalls:

"Friendship has many faces. Predominant among them are mutual sympathy, common interests and gratitude resulting from fruitful and trusting interaction. In the mid-1960s, I had gotten myself into serious trouble by publishing what appeared to be unacceptable, if not untrue. I had dared touching on problems of intracellular interactions and transport in leaves by asserting that phosphorylated intermediates of both photosynthesis and respiration cross intracellular membrane barriers such as the chloroplast envelope, thereby linking metabolic pathways which differ in direction. This claim was criticized at a

meeting of the German Botanical Society at Munich. Subsequent defensive publications made little impact until David Walker, a Brit, saved my German reputation. David elegantly demonstrated that chloroplasts not only release phosphorylated products of photosynthesis but also respond to such products when they are added from outside. Apparently the chloroplast envelope did not act as an impenetrable barrier to charged intermediates. What a relief, but who was the savior? Until then, I had not known David. I invited him to come to Duesseldorf; he came. We decided to try joining forces. Groups from Sheffield, Göttingen and Düsseldorf met for discussions and exchange of ideas.

We also met at international conferences. In Moscow, David refused to use the famous transport system of the Metro, remembering his early days of travelling in the London Tube. In the French Alps, David enjoyed the hospitality of Roland Douce and Richards Bligny but preferred the gentle hills of Northumberland. A fellowship from the Royal Society

permitted me to escape to Sheffield for experimental work whenever administrative pressures prevented me from pursuing my scientific interests at my own university. The Royal Society had promoted David to the position of Fellow. In London he showed me the signature of Sir Isaac Newton in the Book of Fellows. Retirement came to David a little earlier than to me. Although he was a Yorkshire man, through study, and Shirley, he was attached to Northumberland. They had purchased a cottage in Biddlestone, a hamlet several hundred km north of Sheffield. Needing asylum and peace for work and mind no less than I did, he added a greenhouse and a shack to it which housed a computer and equipment necessary for measuring photosynthesis and chlorophyll fluorescence. After retirement, he spent as much time there as Shirley would allow. Alone, or with my wife Svetlana, I joined him repeatedly.

David was not only a top scientist, but also a master of language. Once I asked a respected Japanese colleague what the difference is between science and art. Takahama-san responded immediately: no difference at all; they are the same! David was an artist. It seems to me that he could be compared to an able silversmith both in his experimental work and in his writing. His work is filigrane art. Details permit full understanding of whatever he touches. His work is in contrast to the woodcutting done by many scientists: the work is correct, but detailed understanding is not provided and cannot be gained from reading. I admired David. He has gone; I miss him."

Gerry Edwards (Washington State University, Pullman, Washington, USA), coauthor of this Tribute, remembers:

"In 1977 I took my sabbatical leave with David because I was interested in chloroplast functions in C_4 plants, and I was aware of his excellent work on C_3 chloroplasts. On arriving in Sheffield, I learned David already had a vision for a book on photosynthesis, and was well into writing the first part (energy, laws and light, and photochemistry). As you can imagine, being the junior scientist, I was surprised and honored by the confidence David showed in inviting me to join him in this effort. Besides time working on the book, we were able to do some interesting research showing the utility of protoplasts for isolation of functional chloroplasts from plants, resulting in two papers (Edwards et al. 1978a, b, also see Appendix A in Edwards and Walker 1983). I also found myself with a wonderful group of colleagues including Simon Robinson of Australia, Alice Herold, and Richard Leegood. Lasting friendships were formed.

The whole family also spent the summers of 1983 and 1989 in Sheffield, where David and I continued our research collaboration (Edwards and Walker 1984; Walker and Edwards 2004) and discussed means to address the interest in a revised edition of the " C_3 – C_4 " book. By 1983, The Robert Hill Institute was fully established. Away from the University of Sheffield, in an area of impressive Victorian homes, the complex consisted of a large building, greenhouses and garden plots. It was a great work environment.

David and Shirley were always great hosts. Besides wonderful gatherings at their home near the Institute, they also included me and my family in other activities, such as pub visits (see pub singing, above), and walks in the beautiful moor country around Sheffield. It's worth noting that David knew the location of many pubs, and most of his favorites seemed to be in lonely spots on those same moors.

Though we weren't able to see David and Shirley often in later years, we kept in touch via an occasional email and Christmas cards. Shirley is an artist, and most of the cards are from her paintings of scenes in and around Biddlestone. Needless to say, we treasure them. We last met David and Shirley in 2007 in Cambridge, at the C_4 -CAM satellite meeting to the Photosynthesis Congress (Figs. 4 and 5). It would be hard to overestimate the impact that David's friendship had on my career. He was a true mentor to me and will be sadly missed."

Ross Lilley (University of Technology, Sydney, Australia) recalls:

Fig. 4 A photograph taken at the C_4 -CAM satellite meeting to the International Photosynthesis Congress in Cambridge, 2007. *Left to right:* Barry Osmond, Sandy Edwards, Cornelia Osmond, Shirley Walker, David Walker and Gerry Edwards

Fig. 5 Special Dinner at the C₄-CAM satellite meeting to the International Photosynthesis Congress in Cambridge, 2007. *Left to right: David Walker, Shirley Walker and the waitress*

“In 1974 I left sunny Adelaide with my wife, and duly arrived in Sheffield by train on a dull, damp October evening for what was to be a three-year stay. But the Sheffield weather did nothing to dampen the warm welcome as David met us on the platform and whisked us in his new Range Rover (he owned one long before these vehicles became trendy) to his home where we met Shirley and their children, Richard and Marney.

David had recently moved to Sheffield from Queen Mary College, London, and when the talk turned to science, I learned that spinach grown in the Yorkshire climate produced thin sickly leaves, from which it was impossible to prepare intact chloroplasts, a key expertise of David and the starting point for much of his research. This problem persisted through the long Sheffield winter, so I initially used thylakoids to study photophosphorylation.

At that time, David and I made a habit of meeting first thing in the morning, at the (then) Tapton Gardens, where the University had a plot of land and a rudimentary glasshouse in which the gardeners were struggling to grow spinach capable of yielding intact chloroplasts. After agonizing over the miserable state of the spinach, we would walk down Western Bank to the University, discussing the research plans for the day. Occasionally, the conversation would turn to the desirability of having a research laboratory in the peaceful environment of those gardens, next to the plant growth facilities. Years after I moved on, David fulfilled that pipe-dream.

David was a most serious and dedicated researcher, but had an element of panache that made working in his lab a delight. Early in my stay, I noticed a bottle of gin tucked into the bottom corner of a deep freezer. As warmer weather arrived in the following spring, the spinach grew better and we were able to isolate intact chloroplasts, leading soon to progress in understanding how inorganic phosphate influenced their photosynthetic performance. Whenever especially good experimental results emerged, David would, in the late afternoon, find that bottle of gin and other ingredients so we could all share a round of dry martinis in the lab.

The unpredictable Sheffield climate had summers that, to an Australian, seemed more like a slightly warmer winter. But on rare occasions there would be a clear and hot day that lifted everyone’s spirits, and on such a day David was likely to announce, mid-morning, that we should cancel our experiments for the day and immediately come to his house. There we would enjoy a barbecue with David and Shirley’s legendary hospitality. On other occasions, we would travel to Northumberland where, in the village of Biddlestone with its ancient stone houses, a cross-section of David’s friends, ranging from technicians to professors, would assemble for a weekend of walking and enjoying the ambience of the local pub.

Progressively, David developed a hydroponic glass-house facility for growing spinach that delivered an almost continuous supply of freshly isolated chloroplasts. From these we prepared pure stromal extracts and reconstituted chloroplasts to make advances in the understanding of intact chloroplast function, and of the effect of light intensity on the metabolism of 3-P glycerate through its dependence on a high ATP/ADP quotient. The latter led me to develop a quantitative spectrophotometric assay for Rubisco, and we demonstrated the full activity of Rubisco in chloroplast extracts.

David’s ability to describe complex scientific topics concisely and eloquently made his writing well-known and remains a prime example of effective communication of science to a wide audience. At scientific meetings, when divergent views of competing research groups sometimes generated heated discussions, David would disarm a vociferous opponent with a polite and humorous comment. When in the lab, his passion for tinkering with equipment sometimes resulted in significant improvements, especially with the oxygen electrode and the use of leaf discs.

David Walker was the quintessential English gentleman, who showed that it is possible to be successful in the competitive world of science while also being polite, friendly and considerate of others. He was a wonderful friend and mentor.”

Agu Laisk (Tartu University, Tartu, Estonia) writes:

“David Walker was an important sign post at a crossroad of my life pathway, where I turned to the right—thanks to David. He introduced me to the world of the very first intimate processes of photosynthesis. Largely thanks to David I came to understand the whole complexity of photosynthesis. And most important to a scientist—I understood what is yet to be understood there. Our minds well resonated on quantitative mathematical approaches, encouraging me to continue.

In this world we all are shaped and polished by the hands of our teachers and friends. David was a teacher for me. In his mild way, accompanied by a soft smile (and sometimes by a malt), he made me believe in the power of logical thinking.”

Peter Lea (Lancaster University, Lancaster, UK) remembers:

“David was always keen to share his knowledge and enthusiasm with as many people as possible, particularly with young overseas students. He taught in a number of three-week courses funded by the UNEP (United Nations Environment Program), entitled “Bioproductivity and Photosynthesis in a Changing Environment”, organized by David Hall. These courses took place in Barbados, Brazil, China, India (twice), Kenya, Mexico, Thailand (twice) and Yugoslavia. They involved a considerable amount of logistical organization in order to get the necessary equipment through customs and to grow plants that were able to provide high yields of active chloroplasts. Several editions of a training manual were published; the last included two chapters by David (Walker 1993; Leegood and Walker 1993). Despite all his hard work in the lab and the often intense heat and humidity, David could always be found in the bar at sundown recounting stories of the day’s experiments.”

John Humby (Hansatech Instruments) recalls:

“In 1972, a mutual Cambridge friend, Derek Bendall, introduced me to David, who, with Tom Delieu, was seeking a manufacturer for the instrument they had developed. To our fledgling company, with instrument production capabilities, it proved a fortunate match.

David’s help and encouragement were always available to us and it is true to say that we would not be where we are today without him. It is a privilege to have worked with him professionally, and at the same time to have had the pleasure of his warm friendship for so many years.”

Zoran G. Cerovic (Université Paris-Sud, France) writes:

“I worked in David Walker’s lab at Tapton Hill twice (1983–1986) during what are now called ‘The Thatcher years.’ These were, for sure, difficult years for the British scientific community, but for me coming from an Eastern-block country, it was heaven. David created an atmosphere of camaraderie in the lab and in the pubs that transformed the Robin Hill Institute into a melting pot of sciences and cultures. In 6 month’s time a very young student, as I was, could learn and defend his views to the whole of the photosynthesis community passing through the lab, whether for shorter or longer periods. I admired how David, wearing his legendary smile, guided his postdocs with kindness and generosity. They were all to become today’s leaders in many branches of plant science. David’s legacy is much more than a very impressive opus of scientific publications: it is a free spirit transmitted by generations of plant scientists.”

Simon Robinson (CSIRO Plant Industry, Australia) remembers:

“We have very fond memories of our time in Sheffield (1977–1979). This was my first postdoctoral position and chosen because it seemed from afar to be one of the best labs working on photosynthesis in the world. It was, and I learnt an enormous amount from David, not only about science, but also about people, life, the universe and everything else. Once most people had left for the day, David would sometimes bring out a bottle of malt whiskey, which we drank out of beakers in the lab while discussing everything from photosynthesis to politics. David was one of the sharpest intellects and most lucid communicators I have ever met, but he was also a wonderfully warm, decent and caring person who understood the importance of people and maintaining balance in life. While science was an important part of his life, so too were his family and friends, visits to the pub and walks in the beautiful countryside around Sheffield. David and Shirley were wonderful hosts who adopted us during our time in Sheffield and we grew to become firm friends. David was a great mentor and friend, truly ‘a scholar and a gentleman’, who will be sadly missed by all who knew him.”

Bob Furbank (CSIRO Plant Industry, Australia) writes:

“I just wanted to say something about David’s ability to inject some humor and literary value into his science, particularly the former via Richard’s cartoons. My memory of him will always be a cartoon from his O₂ electrode manual (see Fig. 3d). I think he would like this image of him to be remembered. David told me that being able to “look” at data was the most important skill to learn in science; but, what I think he really meant was to be able to “feel” the data; something he excelled at. After 5:00 PM when David and I shared a whisky in his office, it was often the discussion about those few “juicy grapes” in the day’s experiments that taught me the most.

David and I both liked a pun, but occasionally it backfired. He put up a poster at one of our little conferences in Göttingen when he was shedding doubt on Warburg’s 4 quanta per CO₂ fixed. The caption read “4 quanta Otto? 9 danke!” Of course 9 is neun in German, leading to some confusion and the pun was lost! Perhaps it also loses something in translation but it made us laugh! To lose a mentor and a friend is doubly sad.”

Charles J. Stirling (University of Sheffield, UK) writes:

“When you visited your local pub in Millennium Year, you would have been confronted by a question such as ‘What percentage of the cells in your body are human?’ The question was on the beer mat under your glass. When you returned a week later the answer would be on the mat, which would also have next week’s question on it. This pub quiz with a difference was one of the zany bright ideas of the man whose life we celebrate today. David Alan was not only a scholar of the first rank but, sadly, one of a much rarer species of scientist wanting to share the wonders and excitement of science with intelligent and receptive non-experts of any age.”

Barry Osmond (University of Wollongong and Australian National University) recalls:

“A friend and mentor of great warmth and encouragement, David Walker brought Robin Hill across from the Biochemistry Department in Tennis Court Road to the Botany School off Downing Street one drizzly afternoon in Cambridge to discuss “ β -carboxylation” photosynthesis with a young plant physiologist. David was to write later that “A plant physiologist, by the way, is one who pretends to be a biochemist when he is talking to botanists and a botanist when he is talking biochemists, whereas, in reality, he is neither one thing nor the other” (Walker

1988). In the haze of memorable moments past one wonders whether David’s insight might have been strengthened during that first meeting!

In November–December of 1970, David contributed to a workshop on photosynthesis and photorespiration in Canberra, and subsequently built strong links with many colleagues in the former Research School of Biological Sciences in the original Institute of Advanced Studies in the Australian National University. During a visit in 1981, he creatively deployed a Plant Productivity METER SF-10 (an early chlorophyll fluorescence device) to interrogate the S-M-T transients during induction of photosynthesis in spinach leaves (Walker 1981). This may have been the beginning of his long association with oscillations in “secondary fluorescence kinetics” that led to development of novel instrumentation, and remarkable progress in understanding regulation of photosynthetic metabolism in vivo.

Like many others, I was drawn to Sheffield for several brief but remarkably stimulating encounters in the Hill Laboratory. One of the more memorable emerged from David’s vexation with the carefully nurtured, but recalcitrant, AR-grade spinach grown in the Tapton Hall greenhouses that refused to produce oscillations in chlorophyll fluorescence and O₂ evolution from leaf discs. Any old barley leaf would oblige but not spinach, then the ‘gold standard’ in photosynthesis research. His antipodean colleague was impressed by the remarkably thick and lush leaves from the spinach canopies, many of which when appropriately dressed (Walker 1988), found their way into the salads for which David and Shirley were renowned. I guessed that chloroplasts in the strongly lit upper palisade mesophyll were probably sun adapted and that those on the underside were probably shade adapted. By simply turning the spinach leaf disc over, the weak LED actinic light then available in the Hansatech O₂-electrode/chlorophyll fluorescence system (<http://www.hansatech-instruments.com>) was strong enough to extract admirable oscillations in both parameters from spongy mesophyll cells, in conformity with then current concepts of photosynthetic regulation.”

The team assembled in Sheffield at the time endorsed the event (Fig. 6), then proceeded for a celebratory excursion to an adjacent watering hole. The “subsequent ramifications” were explored during David’s next visit downunder (Walker and Osmond 1986). It is difficult to overstate the creative stimulus that gushed from such encounters or the camaraderie and support David lavished on his colleagues wherever and whenever they met.

Fig. 6 “At last, photosynthetic oscillations in spinach leaves”. Endorsement and celebration of the observance of oscillations in photosynthesis in 1982. Signatures: Peter Horton, Ulrich Heber, Geoffrey Hind, Richard Leegood and David Walker

David’s last crusade on biofuels, like all others was imbued with careful assessment and presented in compelling prose. “Retro-agriculture (the use of biomass for transport fuels) may, despite its intrinsic drawbacks still be judged to have a role in energy security and conservation. As such, its purpose will not, however, be well served by exaggeration of the yields...or failure to recognize the constraints imposed by the laws of physics.” (Walker 2009). We have lost a giant and will long rest on the shoulders of David Alan Walker.”

David is survived by his wife Shirley, at their homes in Sheffield, Yorkshire, and Biddlestone, Northumberland, and by his daughter Marney, son Richard, and granddaughter, Billie.

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