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HISTORY AND BIOGRAPHY

Tribute to Prof Keith Boardman, AO, FRS, FATSE, FAA on his 100th birthday (August 16th 2026)

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Abstract

Keith Boardman carried out brilliant research when he led a group as Chief Research Scientist in the Commonwealth Scientific and Industrial Research Organisation (CSIRO), Division of Plant Industry (Canberra) from 1960 to 1977. This research was highly successful. Working with Dr. Jan Anderson (a Fellow of the Royal Society (FRS) and a Fellow of the Australian Academy of Science and Technology (FAA), Boardman was able to isolate the first convincing separation of Photosystem I and Photosystem II particles (Boardman and Anderson 1964). In a short period of less than twenty years, Keith Boardman, with the aid of Jan Anderson, brought photosynthesis into the modern era. Keith then had a productive career as an administrator with the CSIRO (becoming Chairman and Chief Executive) and advisor on science to several government bodies. Keith Boardman was honoured by election as a Fellow of the Australian Academy of Science and Technology (FAA, 1972), a Fellow of the Royal Society (FRS, 1978), a Fellow of the Australian Academy and Engineering (FATSE, 1986) and an Officer of the Order of Australia (AO, 1993).

Keywords Photosynthesis · Photosystem I · Photosystem II · Photosystem separation · Photochemical activity · Digitonin · Differential centrifugation · Chlorophyll fluorescence · Photosynthetic electron transport chain

Research career

Keith Boardman graduated his B.Sc. (1946). Having studied chemistry, physics and applied mathematics, majoring in chemistry in Year 3, he completed his M.Sc. in 1948 in organic and physical chemistry at the University of Melbourne. After a period with the Wool Research Organization which later became part of the Commonwealth Scientific and Industrial Research Organisation (CSIRO), he obtained a scholarship to carry out a Ph. D. degree at the University of Cambridge, as a member of St John's College. His research involved the use of paper and ion-exchange chromatography in the separation of sugars and proteins. This was an exciting period in Cambridge with research leading to several Nobel Prizes including James Watson and Francis Crick, Alan Hodgkin and Andrew Huxley, Max Perutz and Fred Sanger. At the Molteno Research Institute, David Keilin was making pivotal discoveries on cytochromes. Keith Boardman, also at the Molteno, decided to study cytochrome *c* and isolated it at a higher purity than ever before, and this earned Keith Boardman a post-doctoral fellowship (1953–1955) to study haemoglobin and other proteins, resulting in several highly influential research papers.

In loving memory of Dr. Boardman, who passed away on Monday 26th October 2026.

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Fig. 1 Keith boardman with Jan Anderson. Photo taken outside the Biological Laboratories of Harvard in 1973, whilst Jan was on sabbatical with Paul Levine and Keith was visiting Lawrence Bogorad at Harvard. Source: Photo provided by Fred Chow.

Research at the division of plant industry, CSIRO, Canberra

At the end of 1955, Keith Boardman decided to return to Australia to take up a position as Research Scientist in the Biochemistry Section of the Division of Plant Industry. (CSIRO). At that time John Falk was the head of the section with a strong research interest in porphyrins. Keith Boardman decided to use his previous skill in protein separation to try to isolate chlorophyll-proteins from intact chloroplasts. Up to this time the isolation of chlorophylls in polar solvents resulted in chemical changes which denatured the chlorophyll, and which shifted the peak absorption by about 15 nm to the red. He decided to try to use an approach using water-soluble detergents. Following on a period of research on the separation of protochlorophyllide, he turned his attention to the separation of chlorophylls from spinach leaves.

Jan Anderson had joined Boardman's laboratory in 1964, after completing her Ph.D. degree in California with Melvin Calvin (Fig. 1). Together Boardman and Anderson used digitonin, a non-ionic detergent, at 0.5%, to solubilise the pigment proteins of the chloroplasts. Differential centrifugation of the dissolved fractions was found to produce particles with differing ratios of Chl *a/b* and differing photochemical activities. Boardman and Anderson (1964) had obtained a crude physical separation of the two photochemical processes. This followed on from the work of several scientists in the 1960s showing the presence of two photosystems of photosynthesis in higher plants and the proposal of Hill and Bendall (1960) of the "Z" Scheme, with two photosystems, Photosystem II and Photosystem I, connected by a cytochrome complex. The physical separation of the two photosystems was a pivotal achievement, which has galvanised research across the world ever since. While the isolation of PSII particles was fairly crude and lacked oxygen evolution, the work was quickly followed up around the world, leading to oxygen-evolving particles and refined spectral observations. Keith Boardman attended the 6th International Congress of Biochemistry in New York in July 1964 and his and Jan Anderson's discoveries caused great excitement. Thus, this breakthrough stimulated much further research, especially on electron transport in chloroplasts (see Fig. 2 and Govindjee et al., 2017 for more details on the "Z" Scheme of photosynthetic electron transport).

At this time, John Thorne was recruited into the laboratory and with the recording spectrophotometer/

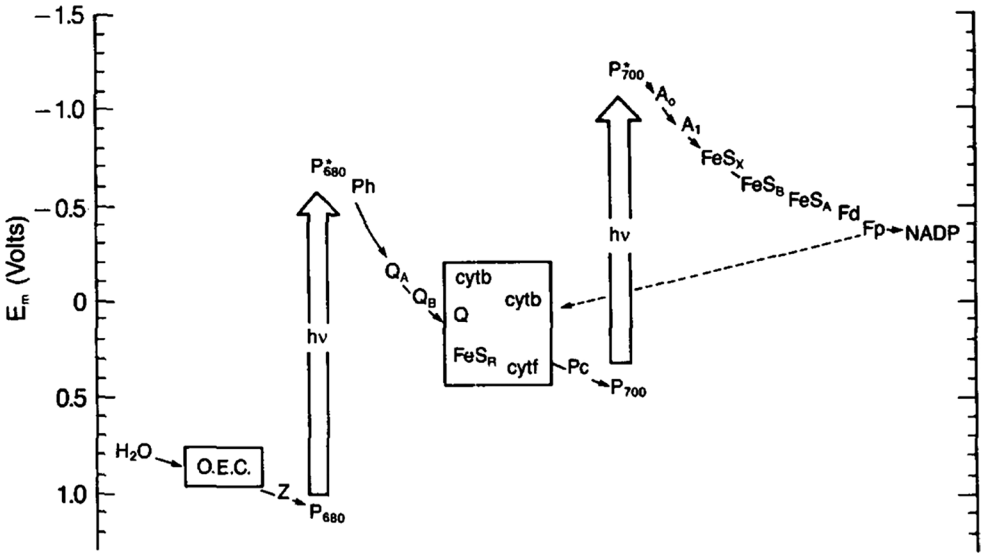


Fig. 2 A contemporary Z Scheme of Photosynthesis from Blankenship and Prince (1985). The scheme of 1982 contains much more information about the components of PSI and PSII and the intermediate cytochrome b_6f complex. The dotted arrow from Fd/FP to the cytochrome b_6f complex indicates the potential for cyclic electron transport, for which evidence accumulated at that time. With permission

spectrofluorometer that John built they were able to record the spectral characteristics of the two fractions and the presence of cytochrome b_6 and cytochrome f in both fractions. Roger Hiller had also joined the lab in 1968 and helped to publish five papers on the cytochromes of bean leaves and spinach chloroplasts (Boardman 1968; Boardman and Anderson 1967; Hiller and Boardman 1971, 1972; Boardman et al. 1971; Hiller et al. 1971). Further purification showed that the PSII fraction emitted fluorescence predominantly at 683 and 693 nm, while the PSI fraction emitted fluorescence at 735 nm (Boardman et al. 1966a; Anderson and Boardman 1966; Boardman 1968).

These were momentous discoveries backed up by the work of others in Britain, Europe, Japan and the United States (e.g. Wessels 1962, Duysens and Amesz 1962; Cederstrand and Govindjee 1966). The work in Canberra, attracted many researchers to the laboratory and involved diversification into ecology, bioenergetics, biosynthesis and structural studies of chloroplasts and photosynthesis (Boardman et al. 1966a, b, 1971, 1972; Boardman 1980, 2023; Woo et al. 1970).

After this period of 22 years of ground-breaking research, Keith Boardman left research and joined the Executive branch of the CSIRO organisation in 1977, eventually becoming Chairman and Chief Executive of CSIRO in 1987, retiring in 2000.

However, Keith Boarman's research influence carried on for a long time. There was a great interest in the role of thylakoid stacking. And Keith Boardman continued to publish papers for some time (Boardman and Thorne 1971, 1977; Robertson and Boardman 1975; Boardman 1980; Heber et al. 1979). In 1977, Fred Chow joined the laboratory leading to many discoveries of plastid structure and function including the role of cytochromes (e.g. Chow et al. 1978, 1980, 1982).

In 1978, Bertil Andersson joined the laboratory to work with Jan Anderson, having been attracted by the fame of the Boardman and Anderson discoveries. With his knowledge of aqueous polymer two-phase separation of membranes and the interest in the Boardman/Anderson laboratory in thylakoid architecture, they were able to isolate enriched grana (appressed lamellae) separate from intergranal (non-appressed) lamellae. The granal stacks were characterised as containing largely PSII, whereas the stromal lamellae contained largely PSI. This led to one of the first proposals for a membrane model of electron transport in higher plant thylakoids (Fig. 3) and to the proposal of lateral heterogeneity in green chloroplasts (Fig. 4, Andersson and Anderson 1980; Anderson and Andersson 1982). This proposal for stacked grana connected to unstacked intergranal membranes containing largely PSI has been a rich source for approaches to the sub-fractionation of thylakoids from green plants (Anderson 2002, 2012). It was a pivotal turning point in our understanding of the architecture of thylakoids, and owed much to the continuing research by Keith Boardman and his colleagues (e.g. Goodchild D.J. and Park, R.B. 1971, Boardman 1972).

The 100th Birthday Party for Keith Boardman took place on Saturday, 5–8 pm 15th August, at the Commonwealth Club, 25 Forster Cres, Yarralumla, Australian Capital Territory (see Fig. 5).

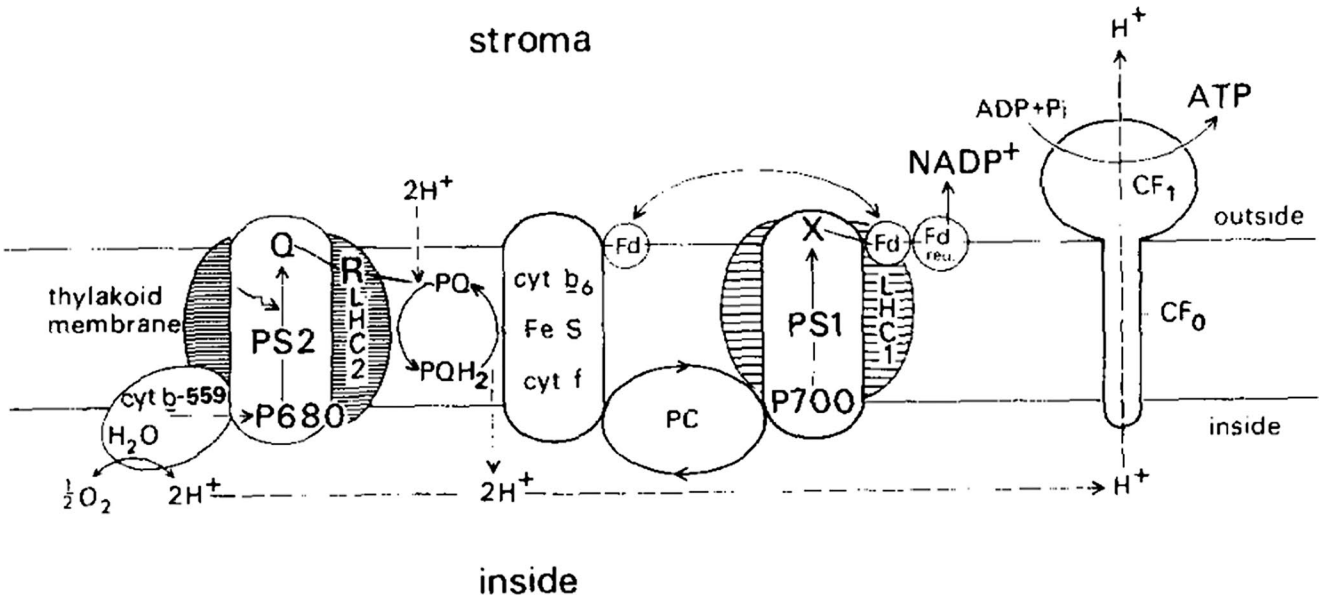


Fig. 3 One of the first diagrams to show the membrane model for the two photosystems, the cytochrome b/f complex, the ATPase and the accumulation of protons on the stroma side of the thylakoid membrane. From Anderson and Andersson 1982; with permission

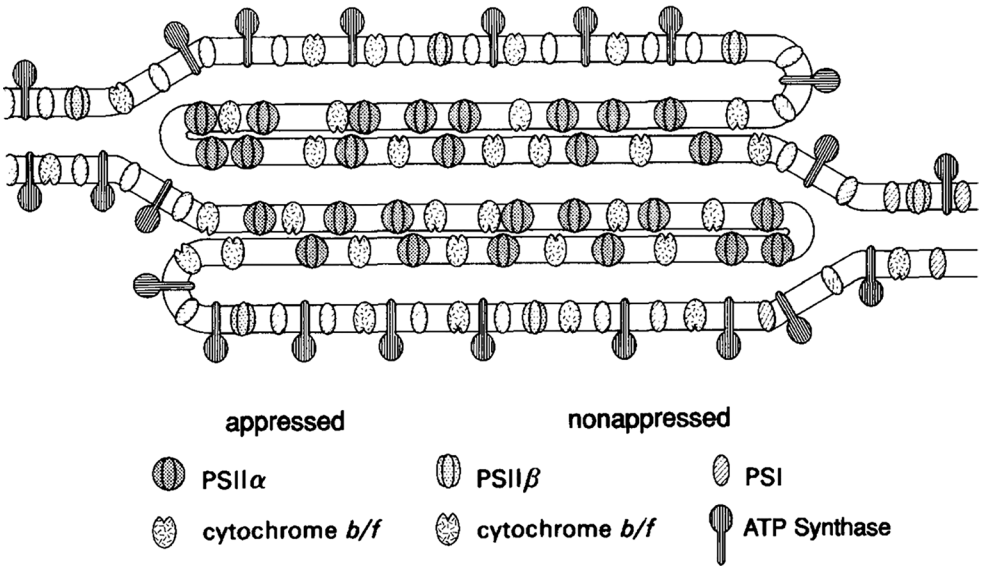


Fig. 4 The schematic model of the lateral heterogeneity in the distribution of PS II and PS I between appressed and non-appressed thylakoid membranes of higher plant chloroplasts, which contain grana (modified by Anderson and Andersson 1982 from Andersson and Anderson 1980). The unusual pattern of membrane folding was chosen as it seemed to explain how thylakoid membranes could be easily unstacked. The major advance on the first scheme of lateral heterogeneity was the identification of the cytochrome b_6f complex in granal (appressed) stacks and in stroma (non-appressed) lamellae. Anderson and Andersson 1982; with permission



Fig. 5 Photo of Keith Boardman at his 100th Birthday Party, which took place 5–8 pm on Saturday, 15th August, at the Commonwealth Club, 25 Forster Cres, Yarralumla, Australian Capital Territory. Photo provided by Keith Boardman

Personal appreciations of Prof. Keith Boardman, AM, FRS, FATSE, FAA, at 100 on 16th August 2026

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My hearty congratulations to Dr Keith Boardman on reaching age of 100, joining a very small group of centenarian photosynthesis researchers. I am forever grateful to him for having been my thesis examiner, postdoctoral supervisor and mentor.

I first met Keith in Canberra when I was Alex Hope's PhD student in Adelaide. I stopped in Canberra on my way to Brisbane, visiting Keith's lab to learn their method of growing spinach in water culture to produce tender leaves conducive to the isolation of intact chloroplasts with high photosynthetic activities. Keith was later to become one of the two examiners of my thesis, along with Jim Barber at Imperial College London.

In September 1976, as the draft of my thesis was being completed, Keith offered me two months of work in his laboratory in the CSIRO (Commonwealth Scientific and Industrial Research Organisation – an organisation that also turns 100 this year) Division of Plant Industry, supplemented by a further one month offered by Rutherford (Bob) Robertson, Director of the Research School of Biological Sciences at the Australian National University (ANU). Keith picked me up at Canberra Airport one Sunday evening, and we went straight to his lab, continuing the discussion on the "bobbing up and down" hypothesis on how protons might be accumulated in the thylakoid lumen; this hypothesis had just been proposed by Robertson and Boardman (1975).

After submitting my thesis from Canberra in December 1976, I went back to Adelaide to work under Alex Hope. In May 1977, however, I was called back to Canberra to work in Keith Boardman's lab on an 18-month appointment at the CSIRO Division of Plant Industry. Since the mid-1970s, Keith had begun to serve more in a science administrative role at the CSIRO headquarters. In 1978, he joined a five-person Executive of CSIRO, later succeed Dr Paul Wild as Chairman and Chief Executive of CSIRO in 1987.

As Keith's time was mostly spent away from his laboratory, he wanted me to continue some of the research work, chiefly working with his colleague, Dr (John) S W Thorne (1921–1983), a British radio engineer during World War II

who had later joined CSIRO Plant Industry to work in photosynthesis. John had designed a spectrofluorometer; this instrument, made in the CSIRO Plant Industry workshop, was rather advanced at the time, complete with correction for the wavelength-dependent sensitivity that is peculiar to each instrument.

In mid-1978, Jim Barber offered me a postdoctoral position at Imperial College London. I knew the kind of research that he was focusing on at that time. Since my own work at the lab in Canberra had not been productive, I decided to change to research that was more related to what I would be doing in London – the electrostatic properties of thylakoids that control thylakoid stacking and the maximum chlorophyll fluorescence yield of Photosystem II as affected by cations. In Keith's lab, I used a technique that Keith Boardman and Jan Anderson (1964) had employed 15 years before to make their highly significant discovery – the physical isolation of the two photosystems as separate entities, with quite different properties, that had been postulated by others to function in series in electron transport. To study the mechanism of thylakoid stacking, I needed a quick method of determining the extent of thylakoid stacking in a large population of isolated envelope-free chloroplasts, without resorting to the slow technique of electron microscopy that examines a few chloroplasts at a time. I used the gentle, non-ionic detergent, digitonin, to break the stacks away from the stromal lamellae that inter-connected them, terminating the detergent action by dilution into a cold suspension medium; digitonin had been used by Boardman and Anderson (1964) to separate the two photosystems. The detergent-disrupted stacks could be collected by centrifugation to determine the chlorophyll content; the greater the extent of stacking, the more chlorophyll (enriched in chlorophyll *b*) was collected in the pellet. This method turned out to be very convenient and could be readily applied, even with reasonable time resolution in the processes of unstacking and restacking. Collaboration with Keith Boardman, John Thorne and two PhD students from the Department of Applied Mathematics in the Research School of Physical Sciences at ANU was fruitful during my remaining five months at CSIRO Plant Industry, resulting in three peer-reviewed publications dealing with the influence of electrostatic properties on the stacking of photosynthetic membranes (Sculley et al. 1980; Chow et al. 1980, 1982).

In subsequent years, I continued contact with Keith by email. Occasionally, I stopped by at his home after leaving the University early, just to chat or to bring a paper or two on photosynthesis that I thought he might be interested in reading.

May Keith continue to enjoy keeping in touch with certain developments in photosynthesis research, as he has been doing. I extend my Best Wishes to Keith on his 100th birthday.

Roger Hiller

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After completing my Ph. D. at Queen Mary College, University of London, with Charles Whittingham, I carried out a post-doctoral fellowship from 1965, with Professor J.A. Bassham at the Lawrence Berkeley Laboratory, where Bassham worked on the discovery of Calvin, Bassham, Benson (CBB) cycle of CO_2 fixation, for which Melvin Calvin was awarded the Nobel Prize in Chemistry in 1961. In 1968 I was in London attending a conference where I met Keith Boardman. Keith invited me to join his group in the Division of Plant Industry, CSIRO, Canberra to study cytochromes in leaves and chloroplasts, which I readily accepted.

My work in Keith's lab came soon after Keith Boardman and Jan Anderson had discovered the method of separating enriched Photosystem I and Photosystem II particles after digesting spinach chloroplasts with digitonin followed by differential centrifugation (see first part of this article). This pivotal discovery had made world-wide news and was the reason I was attracted to move to Australia in 1967. I worked with Keith Boardman on the cytochromes of plant leaves and spinach chloroplasts (Boardman et al. 1971; Hiller and Boardman, 1971, 1972 and Hiller et al. 1971). This work established the role of cytochromes b_6 and *f* as components between PSII and PSI, confirming the scheme of Hill and Bendall (1960) – see Fig. 2. The work on cytochrome *b-559* in the early 1980s led to equivocal conclusions about its presence in PSI or PSII or between PSII and PSI and it was not until later that it was definitely ascribed to cyclic electron flow in PSII. Remarkably this discovery was made in Keith Boradman's laboratory by Ulrich Heber (Heber et al. 1979), although, as pointed out in that paper, there had been hints at such a cycle before this.

I left Keith's group for a Senior Lectureship at Macquarie University in 1972.

Keith was always very kind to me, and I wish him a wonderful time as he reaches 100.

Govindjee Govindjee

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I have the greatest regard for the personal life and the extensive work of Keith Boardman who turned 100 on August 16, 2026. My Heartfelt Congratulations to him on this Great Day. Below, I will mention just one "story" from the past.

Although Wessels (1962) was the first to attempt to physically separate Photosystem (PS) I and PSII from the thylakoid membranes, it was Boardman and Anderson (1964) who were the first to provide complete quantitative information on all the components and their functions. Cederstrand

and Govindjee (1966; submitted on October 11, 1965) examined both the PS I and PS II systems - extending the measurements to the degree of polarization of chlorophyll *a* fluorescence and to 77 K emission spectra fully supporting the conclusions of Boardman and Anderson - through independent measurements. Further, it was exciting for Govindjee to read the Boardman et al. (1966) paper on the fluorescence of PSI and PSII (communicated on May 31, 1966); unfortunately for me, Boardman and Anderson were not aware of Cederstrand and Govindjee (1966) paper although they had cited Krey and Govindjee (1964) on the fluorescence of the red alga *Porphyridium*.

For the overall wonderful journey of Keith Boardman, see Boardman (2023), and for an overview on the history of the Two-Light and Two-Pigment Systems, in oxygenic photosynthesis, see Govindjee (2023).

My heartfelt best wishes to Keith Boardman on his 100th birthday.

Tony Larkum

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I first met Keith Boardman in early 1970 when I arrived in Australia from a postdoctoral fellowship with Prof Walter Bonner at the Johnson Foundation in Philadelphia, USA. We immediately struck up a strong relationship, which continues to the present time. Keith was very kind to me and welcomed me into his family, while at the same time developing my ideas on chloroplast research and introducing me to Prof R.N. (Bob) Robertson, who was the Master of University House, Australian National University and an avid researcher into mitochondrial and chloroplast physiology.

I came to Australia with a strong background in Bioenergetics. At the Agriculture Department, University Oxford University, I completed a D.Phil. in the Bioenergetics of phosphate uptake in plant roots. A major interest at the time was in the chemiosmotic theory of Peter Mitchell, who (later in 1978) won a Nobel Prize for this work and while still at Oxford we travelled across to Cambridge University to consult with Dr. Brian Chappell and his Ph. D. student, Anthony (Tony) Crofts, both studying mitochondrial bioenergetics. My interest was stimulated and when I won an Agricultural Research Council Fellowship to join Christ's College, Cambridge and work with Dr. Enid MacRobbie in the Botany School, I decided to work on the osmotic relations of chloroplasts. This resulted in a paper in *Nature* (Larkum 1968). Also working with MacRobbie was Dr. Fay Bendall, whom I knew as the co-author of the famous paper on the "Z" scheme of chloroplasts by Robert (Robin) Hill and Fay Bendall (1960), postulating an electron transport chain of two photochemical photosystems joined by a cytochrome complex. It was not long before Fay introduced me to Derek Bendall, her husband, a reader in the Biochemistry Department and then to Robin Hill, a memorable occasion.

Next, I took up a Research Fellowship at the Johnson Foundation, which allowed me to study the cytochromes and 518 nm electrochromic shift of isolated chloroplasts, and resulted in five scientific papers.

Thus, on arriving in Australia, and setting up a laboratory in the Botany School, University of Sydney, I was able to grasp the significance of the physical isolation of Photosystem I and Photosystem II. Keith Boardman invited me to work with him and several co-workers in the Division of Plant Industry, CSIRO. My major interest at the time was the reactions and CO_2 uptake of whole chloroplasts (Larkum and Boardman 1974), but also, I was able to contribute to the purification techniques for Photosystem I and Photosystem II and the identification with John Thorne of the fluorescence characteristics and cytochrome content of the fractions, which were obtained by sucrose-gradient centrifugation, instead of differential centrifugation. In this work Roger Hiller from Macquarie University also contributed valuable work on the cytochromes *f*, b_6 and *b-559* (Boardman et al. 1971; Hiller Anderson and Boardman, 1971; Hiller and Boardman 1971, 1972). As a result of my own research into cytochromes at the Johnson Foundation, Roger and I became good friends.

Sadly, for us researchers, Keith was already being sought after by the administration of CSIRO, as his leadership qualities were recognised. He was appointed to the Executive of the CSIRO in 1977 and became the Director in 1987.

Notwithstanding that, his great breakthrough in separating the two photosystems was recognised worldwide and attracted many workers in photosynthesis from around the world and from which the lab benefitted greatly at that time and for long after. Amongst these visitors were Robin Hill, G. Govindjee, Sam Wildman, Rod Park, Eva-Mari Aro and many others.

One further thing which benefitted me was the offer to Keith to contribute to a book on Solar Energy organised by Prof. Harry Messel, the larger-than-life physicist at the University of Sydney. I had the personal benefit of writing a part of a chapter and also delivering a lecture to the University of Sydney Summer School (Boardman and Larkum 1974). This opportunity opened my mind to the future possibilities of curbing global warming, which at that stage was a far-too distant possibility. I made then a fairly shocking assertion that to survive and to avoid global warming the human race needed to become vegetarian! Later Keith was able to expand on these observations on the efficiency of natural photosynthesis in the field (Boardman 1980).

For myself the legacy to the Boardman/Anderson lab meant that I continued researching with Jan Anderson, who took over the research responsibilities of the lab

concentrating on chloroplast architecture, which was the next concept arising from the physical separation of the two photosystems. The outcome of this work is described in the first section of this Tribute.

While many of Keith's contemporaries have sadly passed away, I am glad to be here on this joyous occasion to recognise Keith's wonderful friendship and collegiality, not the least for his pivotal discoveries in photosynthesis in the 1960s and the 1970s.

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Keith - you may not have registered our first encounter in the mid 1960s when as President of Australian Biochemists you addressed an audience of about twenty seated on chairs assembled in the Institute of Anatomy, Canberra.

(now the heritage listed national film and sound archive).

This PhD student from Armidale via Adelaide was attending his first research conference and still recollects his surprise on learning that Keith and his team had used a natural detergent to separate the two photosystems in the photosynthetic apparatus.

Today the global community of plant biologists is celebrating this discovery and Keith's Century. The emails of Australian plant biologists are running hot in response to Govindjee's requests for notes and anecdotes for inclusion in retrospective publications highlighting Boardman's many achievements.

For example, in his remarkably comprehensive interview with Ralph Slatyer for the Australian Academy of Science, I discovered that my then wife and I had unknowingly followed the Boardman family to UCLA and to Cambridge (Labs of George Laties and Tom ap Rees) on a CSIRO post doc fellowship.

I hope Keith Boardman will allow a further personal comment drawn from this interview; starting with his cricketing days when making 100 runs he had probably achieved a 'ton or two'.

Author contributions All authors contributed to the main part of this article. The personal reminiscences were written separately by each author.

Data availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare no competing interests.

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