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Joan Mary Anderson 1932–2015[1]

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Joan Mary (Jan) Anderson pioneered the investigation of the molecular organisation of the plant thylakoid membrane, making seminal discoveries that laid the foundations for the current understanding of photosynthesis. She grew up in Queenstown, New Zealand, obtaining a BSc and MSc at the University of Otago in Dunedin. After completing her PhD at the University of California, she embarked on a glittering career at the Commonwealth Scientific and Industrial Research Organisation (CSIRO) and then Australian National University (ANU) in Canberra. Not only a gifted experimentalist, Jan was a creative thinker, not afraid to put her insightful and prophetic hypotheses into the public domain. Her many notable achievements include establishing the details and the physiological significance of lateral heterogeneity in the distribution of the two photosystems between stacked and unstacked thylakoid membranes and the dynamic changes in the extent of stacking that occur in response to changes in the light environment. Her investigations brought her into collaboration with prominent researchers throughout the world. Recognised with many honours as a leading scientist in Australia, international recognition included Lifetime Achievement Award from the International Society of Photosynthesis Research, and Honorary Fellowships at Universities in the UK and USA.

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Early life: the path to becoming a scientist

> My father taught me to work very hard, to strive for good health, to enjoy life and help as many others as possible.[2]

Joan Mary Anderson, later known as Jan (Fig. 1), was born in Dunedin, New Zealand, the only child of William Arthur and Mary Lee Anderson. Her father was a first-generation immigrant from Essex in England, who was initially a jackeroo on a Taranaki sheep station and then after a serious spinal injury, trained as a doctor. He went on to serve as Mayor of Queenstown and was awarded the OBE in 1954. Queenstown was a small community in an idyllic spot beside Lake Wakatipu, where Jan had a life full of good things—reading, music, poetry as well as swimming, rowing and tobogganing. Jan loved her primary school days. Unfortunately high school meant leaving home to a boarding school, which she hated—a rigid, disciplinarian regime that according to the young Jan was 'designed to banish original thought and teach us lady-like manners' and 'even worse, most of lessons were uninspiring and the science teachers hopeless'. Jan thought she could do much better, and decided to train as a high school teacher rather than as a doctor as her father wished.

Jan won a New Zealand Department of Education scholarship that provided a bursary to help pay for her teacher training at the University of Otago. A condition of such an award was the requirement to undertake an Education Diploma and five years of high school teaching after completion of the BSc degree course. But by now, Jan was revelling in the exposure to science and dreamed of further study—to her delight and surprise she was awarded a postgraduate scholarship to undertake an MSc in organic chemistry, and given a two-year exemption from teacher training obligation.

Figure 1. Jan Anderson, taken in 1996 by Prudence Cuming Associates. © The Royal Society.

Jan greatly enjoyed her organic chemistry project, which involved extracting and chemically characterising several wine-coloured pigments from the fungus, *Daldinia concentrica*. Unfortunately, a

[1] This memoir is also published in *Biographical Memoirs of Fellows of the Royal Society of London*, 2018.
[2] All quotes in this memoir are from an unpublished interview with Jan Anderson conducted in 2013 by the Australian Academy of Science.

similar exemption was not forthcoming when Jan was later awarded a PhD Scholarship, and Jan found herself ready to attend Christchurch Teachers College, with a career as a teacher, not a scientist, beckoning. However, two unexpected events intervened—first, unfinished building renovations delayed the start of her course by five weeks, and second, during this period she was asked to return to the Chemistry Department at Otago as emergency cover for a demonstrator who had been taken ill. During her time back in Otago she had time to pursue some chemistry research, and decided to apply for a one-year Science Research Fellowship in the USA. Following a successful interview Jan visited the Head of Department of Education in Wellington to appeal in person to be allowed another extra year exemption from teacher training. Jan's audacity paid off, and she found herself back in Otago exploring who might be her research host in the USA. Again, fortune intervened: Harold Urey, physical chemist and Nobel prize-winner from Utah, was visiting Otago where he gave a series of lectures about the origin of life, two about photosynthesis. Urey became Jan's first mentor, and recommended his great friend Melvin Calvin, as a host at the University of California at Berkeley. Calvin was carrying out pioneering research, which led to the discovery of the pathway for fixation of CO_2 into carbohydrate by photosynthesis, which later resulted in the award of the Nobel Prize in 1961.

So, on 23 September 1956 Jan arrived in Berkeley, to work in the famous Old Radiation Laboratory where Sam Ruben and Martin Kamen discovered the long-lived carbon-14 radioactive isotope in 1940, that later Calvin, Andrew Benson and James Bassham used to trace the pathway for CO_2 fixation.[3] However, she soon learned that she could not undertake her intended one year's research since the University of California did not recognise her New Zealand post-graduate qualifications. Rather, in order to do research there, she had to enrol as a PhD student—previously Jan had been very happy to have one year in Calvin's laboratory, now perhaps several years might be possible. With permission to extend her leave away from New Zealand for five years, Jan then sought to get Calvin to be her PhD supervisor. This was not straightforward as he had decided not to accept any more PhD students, but with the support of his oldest PhD student, Ning Gin Pon, Jan eventually persuaded Calvin to take her on. Audaciously, Jan declared that she did not wish to work on any of his projects on 'colourless' carbohydrates, but instead wished to study the biosynthesis of the beautiful green chlorophyll pigments. His immediate response was: 'Fine, but if you must propose your own research project, then you must sink or swim alone without my personal supervision', a dictum she obeyed. This was the perfect challenge for Jan: he gave her the confidence to choose and accomplish her own research, and prove to him that she could do it. Ning Gin Pon became her unofficial supervisor and mentor.

With little pressure and the advantage of two years of research experience at Otago and a rather broader education than that of American students, Jan did well. However, each year the new crop of graduate students had to deliver a ten minute lecture in front of the entire chemistry department in a large lecture theatre, before the specially invited speakers. After her talk, an elderly inorganic chemist, Professor Hildebrand asked the first question. 'From where did you get such strange ideas and such a very cute accent?', that drew thunderous applause. This behaviour, that would be totally unacceptable today, destroyed Jan.

> So, frightened, I fled the scene. My Achilles Heel had been exposed. I still am a reluctant speaker.

Nevertheless, coming from a remote village and an unknown university at the bottom of the world, the time at Berkeley was astonishing and exhilarating for Jan. A diverse stream of eminent old and young scientists from many different disciplines visited the laboratory. Calvin was a true lateral thinker who loved asking questions, discussing ideas, and even more making hypotheses. This made a huge impression on Jan, who inherited such traits with passion. Berkeley offered not only endless scientific opportunities, but also fascinating cultural and social happenings. For the first time Jan enjoyed ballets, operas, symphony concerts, jazz musicians, drama especially modern theatre, Japanese and French films and an exciting banquet of new tastes: olives, pizza, Mexican and Italian food and doughnuts. Jan's research project developed well, using radioactive carbon-14 to identify the latter steps in chlorophyll biosynthesis in the green alga, *Scenedesmus*, learning how to pursue biochemistry research, and reading widely.

She completed her PhD thesis within three years, publishing two papers with Calvin as co-author.[4] Interestingly they reported the light dependent interconversion of violaxanthin recognized today as a key component in the protection of photosynthetic membranes in strong light. Despite receiving over forty offers to be interviewed for permanent United States academic positions, Jan knew she had to return to New Zealand to fulfil (or relinquish) her education bond. After arriving safely home in Queenstown, a telegram summoned her to Wellington Girls College (the best state girls high school in New Zealand) to be the next senior science mistress. But Jan wanted to be a research scientist, not a high school teacher. She made her decision, and she phoned John Falk, Chief of the CSIRO Division of Plant Industry in Canberra, whom she had met in Berkeley.

> So a week later I came to Canberra and was offered a job; no advertised position, no interview, or even comments from referees were necessarily needed in those halcyon days.

CSIRO Canberra—pioneering studies of the photosynthetic membrane

The focus of Jan's research in Canberra was the photosynthetic membranes of higher plant chloroplasts, that carry out the light reactions of photosynthesis. Jan was inspired by the aesthetic beauty of chloroplast structure. Within thin leaf sections, one can see chloroplasts containing darker green chlorophyll regions that glow intensely red under UV light. As shown in electron micrographs, inside the chloroplasts the continuous photosynthetic membrane is uniquely folded into domains of closely stacked membranes called grana (Fig. 2). These are interlinked by single unstacked membrane domains, whose outer membrane surface is directly in contact with the soluble phase, the chloroplast stroma, where the dark fixation of carbon dioxide takes place. This intricate folding of plant photosynthetic membranes is unique and extremely complicated.

[3] Benson and Calvin (1950).
[4] Blass, Anderson and Calvin (1959).

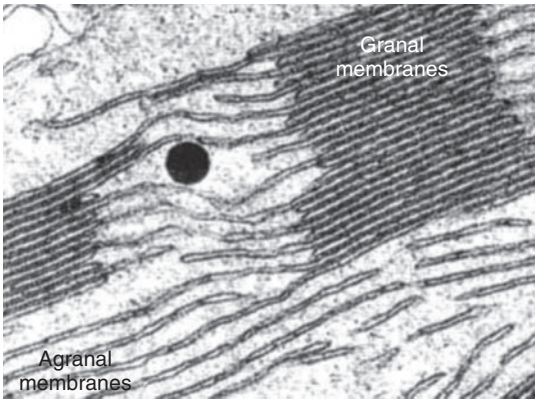

Figure 2. Electron micrograph of chloroplast showing the stacked grana and unstacked agranal membranes (from private collection of Barry Osmond).

Understanding the structure and function of these membranes occupied Jan for her entire research career.

In 1961, Jan began work with Keith Boardman FAA at CSIRO Canberra. It was to be a very fruitful collaboration. That year a new hypothesis had been published in the journal *Nature* by Robert Hill, the Cambridge biochemist, and his student Faye Bendall.[5] This hypothesis suggested that two light reactions, rather than one, were needed to split water and capture solar energy in stable chemical forms in photosynthesis, the so-called Z scheme (Fig. 3). The scientists proposed two photosystems acting in series, with (photo)System II possibly involved in the splitting water to release oxygen, while (photo)System I provided the reducing power for CO_2 fixation. Hill and Bendall further suggested that these two photosystems were linked by two cytochromes, similar to those found in the respiratory electron transfer chain in the better understood mitochondrial membrane.

Boardman and Anderson undertook to test this hypothesis, adopting two strategies to try to separate the putative two photosystems. The first strategy, a biological separation, was to discover if dark-grown etiolated leaves with no chlorophyll pigments would initiate photosynthesis gradually after exposure to light, with one photosystem appearing before the other. This approach failed, partly because it was impossible to isolate active chloroplasts from etiolated bean leaves, although this work did result in Jan's first publication devoted to the study of photosynthesis.[6]

The second strategy was far more successful. Using hydroponically grown spinach, already established in Canberra, and successfully used in photosynthesis laboratories in the USA and UK, active chloroplast membranes were prepared. Then a detergent, digitonin, was used to fragment them into sub-membrane fractions, that were separated using differential centrifugation. Boardman and Anderson speculated that these would be enriched in different components of the photosynthetic electron transfer system. In a paper published in *Nature* in 1964 they showed that the ratio of chlorophyll *a*

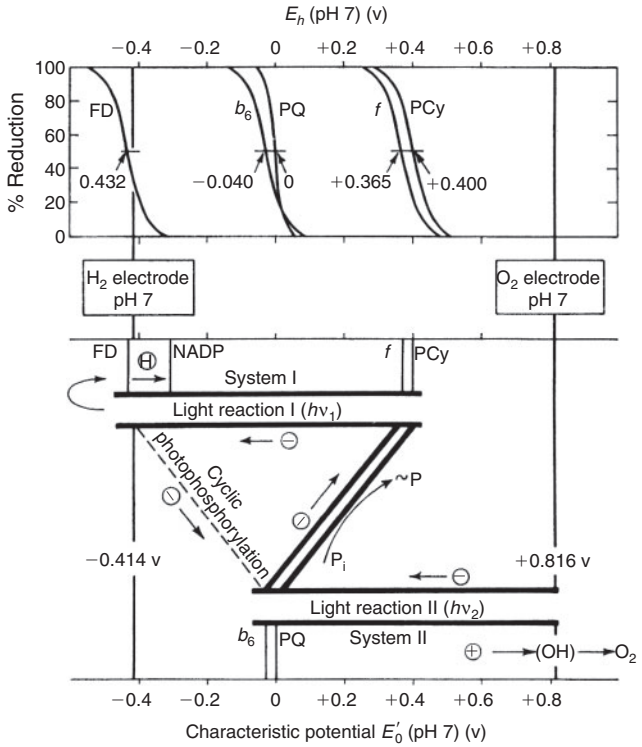

Figure 3. Z scheme for photosynthesis. The depiction of two (photo) systems, one oxidising water and reducing the cytochromes in the electron transport chain, and a second, oxidising those cytochromes and reducing NADP, was the background and inspiration behind Jan's research with Keith Boardman (from Hill (1965)).

to chlorophyll *b* was different in their separated fractions.[7] Later, the landmark discovery was made, published in a paper entitled 'Fractionation of photochemical systems of photosynthesis: I: chlorophyll contents and photochemical activities of particles isolated from spinach chloroplasts'.[8] In this paper they demonstrated the separation by differential centrifugation of a small submembrane fraction with mainly photosystem I (PSI) function from a denser water-splitting photosystem II (PSII) fraction. This partial physical separation demonstrated for the first time that there were indeed two physically distinct photosystems. A thought provoking conclusion was also made that had huge impact on the development of research in photosynthesis: perhaps these two photosystems were located in different parts of the complicated membrane system. They speculated that PSII was concentrated in the stacked grana membrane domains whilst the PSI was more peripheral.

The challenges that researchers in Australia faced at this time should not be overlooked. As Jan recalled:

> The first pioneering years at CSIRO were difficult with primitive apparatus, with all results calculated by slide rules: no calculators, copiers, printers, months to purchase chemicals, equipment or journals from overseas, and so on.

[5] Hill and Bendall (1960).
[6] Boardman and Anderson (1964*a*).
[7] Boardman and Anderson (1964*b*)
[8] Anderson and Boardman (1966).

Figure 4. Researchers from the Department of Plant Biology, Carnegie Institution at Stanford University during Jan's sabbatical in 1966. On the steps are Janet S. Brown (top left), and David C. Fork (top centre) behind and between William M. Hiesey and the Director C. Stacey French. Jan M. Anderson is in the top row, third from the right, adjacent to Jan Amesz and Malcolm A. Nobs (from private collection of Jan Anderson).

Specialist instruments or apparatus were either too expensive or commercially unavailable and had to be built in-house. But CSIRO was extremely fortunate to have John Thorne, a naval radio engineer who built a fluorescence spectrometer with correction for wavelength-dependent instrument response; at that time, it was one of the most advanced in the world. A new Cary spectrophotometer was modified to house a purpose-built cuvette assembly for making measurements on samples cooled to liquid nitrogen temperature. These instruments enabled Jan to investigate the spectroscopic properties of the digitonin fractions, including recording oxidised minus reduced difference spectra of cytochromes b_6 and *f*, that had been discovered by Hill, and placed in a pivotal role connecting PSII and PSI in the Hill & Bendall scheme. While cytochrome b_6 and cytochrome *f* appeared to be located together mainly in the PSI fraction, Jan and Keith Boardman found a third cytochrome, another *b*-type (later called cytochrome b_{559}), that was tightly bound to PSII and clearly an integral component of that photosystem. Later, Jan studied light-induced cytochrome b_{559} oxidation and attempted to gain an understanding of its function in PSII. Fifty years on, researchers are still trying to prove what this enigmatic cytochrome does.

Canberra, both at CSIRO and the ANU, was nevertheless a place of great scientific ferment in the late 1960s. The C4 pathway for photosynthetic CO_2 fixation, discovered in 1966 by Hal Hatch FAA and Roger Slack, was being elaborated and there was growing interest in how this pathway related to the different chloroplast types located in the outer mesophyll layer and the inner bundle sheath layer of the leaves cells. Jan lent her expertise in photosystem characterisation to study these chloroplasts. Together with ANU colleagues including Kam Chau Woo and Barry Osmond FAA, the CSIRO team found that the agranal bundle sheath chloroplasts lack PSII activity, cytochrome b_{559} and the characteristic PSII chlorophyll fluorescence spectrum, that were largely confined to the grana-containing mesophyll cell chloroplasts.[9] This lent strong support for Jan's emerging conviction that PSII and PSI were found in different domains of the chloroplast.

Sabbaticals—to and from Canberra

Like many scientists based in Australia at that time, Jan realised the importance of collaboration with researchers in the rest of the world, particularly the USA and Europe. In 1966, Jan was the first of several Australian plant biologists to be awarded a Carnegie Fellowship at the Department of Plant Biology, the Carnegie Institution of Washington, situated on the Stanford University Campus at Palo Alto (Fig. 4). This centre was at that time directed by biophysicist, Stacey French and was renowned for its array of home-made spectrometers. Jan worked with both French and David Fork. Together they identified and determined many light-induced

[9] Woo, Anderson, Boardman, Downton, Osmond and Thorne (1970).

spectral changes in photosynthetic algal cells, including signals from the reaction centre of PSI. Jan continued her interest in photosynthetic membranes of algae for many years.

The link with the Carnegie proved to be very important in Jan's research career. Later, in 1971, Swedish physiological ecologist, Olle Björkman of the Carnegie, came to Australia to join a collaborative network of ten scientists that gathered together the many aspects of the acclimation and adaptation of the composition, function and structure of chloroplasts in plants growing under contrasting sun and shade light environments. It was shown that grana stacking varied according to the light conditions, with shade and low light chloroplasts having fewer grana but taller stacks compared to sun and high light chloroplasts. Importantly, the composition of photosynthetic components and photosynthetic functions also differed. This was the beginning of a concerted series of investigations by Jan, spanning over thirty years, of how chloroplast structure and function was adapted to different light environments (see below for a discussion of this work).

Jan's second sabbatical was scheduled for 1972. The aim was to learn how to isolate and purify proteins from photosynthetic membranes, because at that time only a few had been isolated. She was awarded a Humboldt Scholarship to visit Berlin and an EMBO scholarship to Copenhagen, but unexpectedly, a travel ban was issued that prevented CSIRO scientists from undertaking international sabbaticals. However, nine months later, in 1973, Jan was awarded another scholarship, this time to visit Paul Levine's group at the Biological Laboratories at Harvard. By then the separation of membrane proteins by the new method of SDS polyacrylamide gel electrophoresis was well established at Harvard, and there Jan used this method to characterise the protein composition of the PSII and PSI digitonin fractions, and various chlorophyll deficient mutant plants that lacked grana stacks. Proteins associated with membrane stacking were identified,[10] and Jan was now at the forefront of the rapid advances in identifying the proteins that make up the thylakoid membrane.

It was Jan's sabbatical to University of Cambridge later in 1973 that would turn out to be the most significant, indeed a pivotal moment in her career. Jan had won a Research Fellowship to reside at Newham College and work in the Biochemistry Department with Derek Bendall on protein isolation and characterisation in photosynthetic membranes during their development. But the coalminers' strike intervened; electricity supply was erratic and soon laboratory research work was possible for only two days a week, and eventually research activity ceased completely for several months.

> This was undoubtedly the most serendipitous opportunity in my scientific career—unlimited time to think, instead of my usual hectic research. Spending my time in the library I soon found a breathtakingly splendid article, I retired immediately to the most perfect ivory tower, my attic room under the roof in the Pightle with cosy heating newly available from North Sea gas.

It was the structure of the chloroplast thylakoid membranes that occupied Jan's thoughts. The accepted dogma at that time was that membrane structure followed a proposal made by Gorter and Grende in 1925 that envisaged the proteins on either side of the membrane with all the lipids shielded inside—the 'sandwich membrane model'. But in 1972, a very different model for biological membranes was put forward—the fluid protein-lipid mosaic model in which the membrane was proposed to consist of a lipid bilayer into which membrane spanning proteins were inserted and to which extrinsic proteins were attached.[11] Jan was the first to discuss plant photosynthetic membranes in terms of the fluid mosaic model. Her review, a 'tour de force' in photosynthesis research, written during her Cambridge sabbatical, covered virtually every aspect of chloroplast membrane structure and function, with nearly 300 references.[12] It was replete with hypotheses depicting how chlorophyll might be associated with proteins (Fig. 5), and how the various protein components, PSII, PSI and the cytochromes she had helped discover were organised and how they may span the membrane, and be arranged asymmetrically so that functions might be concentrated in particular domains. Jan argued convincingly that the PSII was separated from PSI and linked her previous work on protein identification to the large particles observed in freeze-fracture electron microscopy. Moreover, she envisaged that the photosynthetic proteins might move within a dynamic photosynthetic membrane, suggesting that the elucidation of the dynamics of the molecular organization of photosynthetic membranes would be important to understand their complex composition, structure and function. Her vision was extraordinary. Anticipating research that continues to the present day in the concluding paragraph, she asked

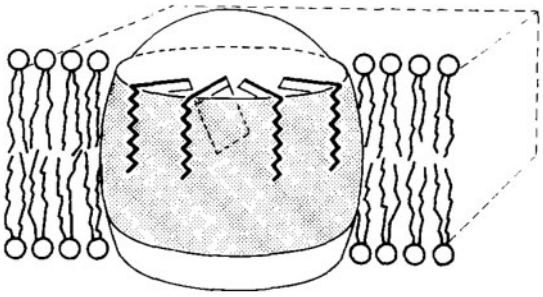

Figure 5. Chlorophyll proteins. Depiction of how chlorophyll might be associated with protein in a fluid mosaic model of the thylakoid membrane (from Anderson (1975) with permission from Elsevier).

> Is the prime difference between grana and stroma thylakoids due to the localization of chlorophyll-protein complex 2 mainly in grana? Is chlorophyll-protein complex 2 involved in thylakoid membrane stacking?

Complex 2 later became known as LHCII, and building also upon the work of Charles Arntzen, Andrew Staehelin, Achim Trebst, Phillip Thornber and many others, Jan's ideas ushered in a new era of photosynthesis research, setting the research agenda for many years to come.

Continuing the protein biochemistry she had started with Levine, Jan wanted to resolve an important piece in completing the membrane puzzle; where was all the chlorophyll? In the sandwich model, chlorophyll was pictured as being dissolved in the protected inner lipid phase, whereas as Jan now imagined it all

[10] Anderson and Levine (1974).
[11] Singer and Nicolson (1972).
[12] Anderson (1975).

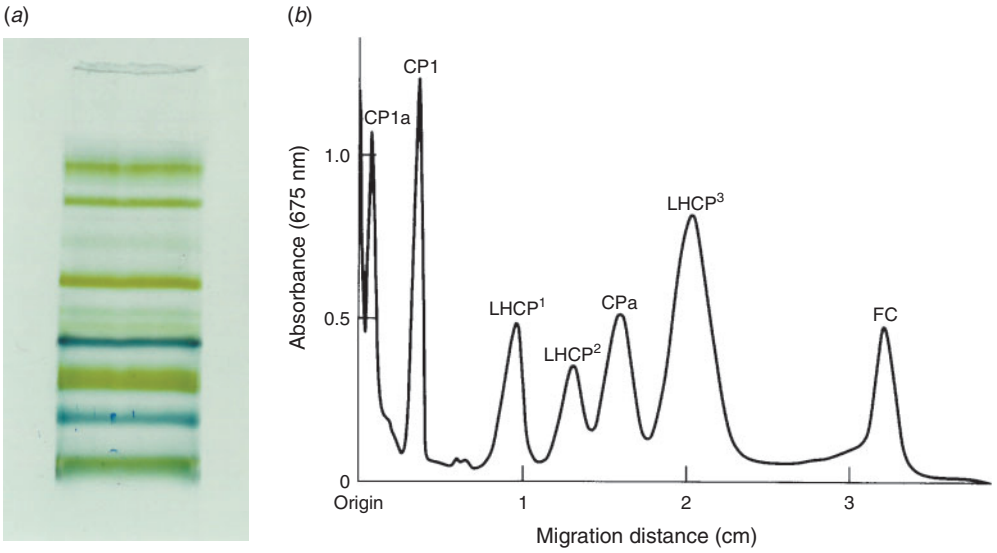

Figure 6. Separation and identification of chlorophyll protein complexes of plant thylakoid membranes. (*a*) Photograph of a non-denaturing 'green' polyacrylamide gels of thylakoid membranes. (*b*) Densitometric scan at 675 nm of a green gel scan showing the six chlorophyll protein complexes, with free pigment comprising only ~10% of the total (adapted from Anderson, Waldron and Thorne (1978)).

being bound to the proteins she had identified in her digitonin fractions. The idea of the chlorophyll-protein complex was re-stated, in line with the much earlier, and largely ignored, work of Phillip Thornber who first introduced the idea chlorophyll-proteins.[13] In order to investigate this problem, Jan perfected a modification of the SDS polyacrylamide gel procedure to produce 'green gels' (called this because the chlorophylls separated with the proteins giving green bands on the gels—Fig. 6*a*), a new method that separated proteins in a non-denatured state. With this method, and after many trials in which the detergent treatments were optimised, Jan finally demonstrated that over 90% of both chlorophylls and carotenoids were indeed associated with protein (Fig. 6*b*). Her green gels revealed six different chlorophyll-proteins.[14] In this paper it was suggested that the main light harvesting complex, LHCII existed mainly as a trimer in the native membranes. Later, 2-dimensional electrophoresis revealed the polypeptide composition of the chlorophyll proteins, Jan being the first to definitively identify those that formed the reaction centre of PSI. It cannot be overstated how major this advance was—the notion of chlorophyll proteins opened up a new era of photosynthesis research in which all kinds of approaches, in chemistry and physics, sought to understand the factors determining the efficiency of light absorption, energy transfer, and photochemistry at the molecular level, fundamentally how binding to protein tuned the properties of chlorophyll molecules to carry out their specific functions.

Another Anders(s)on—toward a new model for thylakoid organisation

Jan's career as a researcher benefitted hugely from her great personal qualities that inspired long and trusting relationships with a small number of close collaborators, some of whom have been mentioned already. But, no more so does this apply than to her collaboration with Bertil Andersson (Fig. 7).

Figure 7. Bertil Andersson and Jan at a conference on 'Why Grana?' at Arnsberg, Germany, 1998 (from private collection of Jan Anderson).

> After the International Congress of Photosynthesis in Reading, once again serendipity intervened. Departing at the Reading railway station, a young Swede, Bertil Andersson bounded along the platform, and declared that he was coming to Australia to work with me when he had finished his PhD, because my 1975 review had been his inspiration in Lund.

Bertil gained an EMBO Fellowship to visit Canberra, bringing with him expertise in the aqueous two-phase polymer partition

[13] Thornber (1975).
[14] Anderson, Waldron and Thorne (1978).

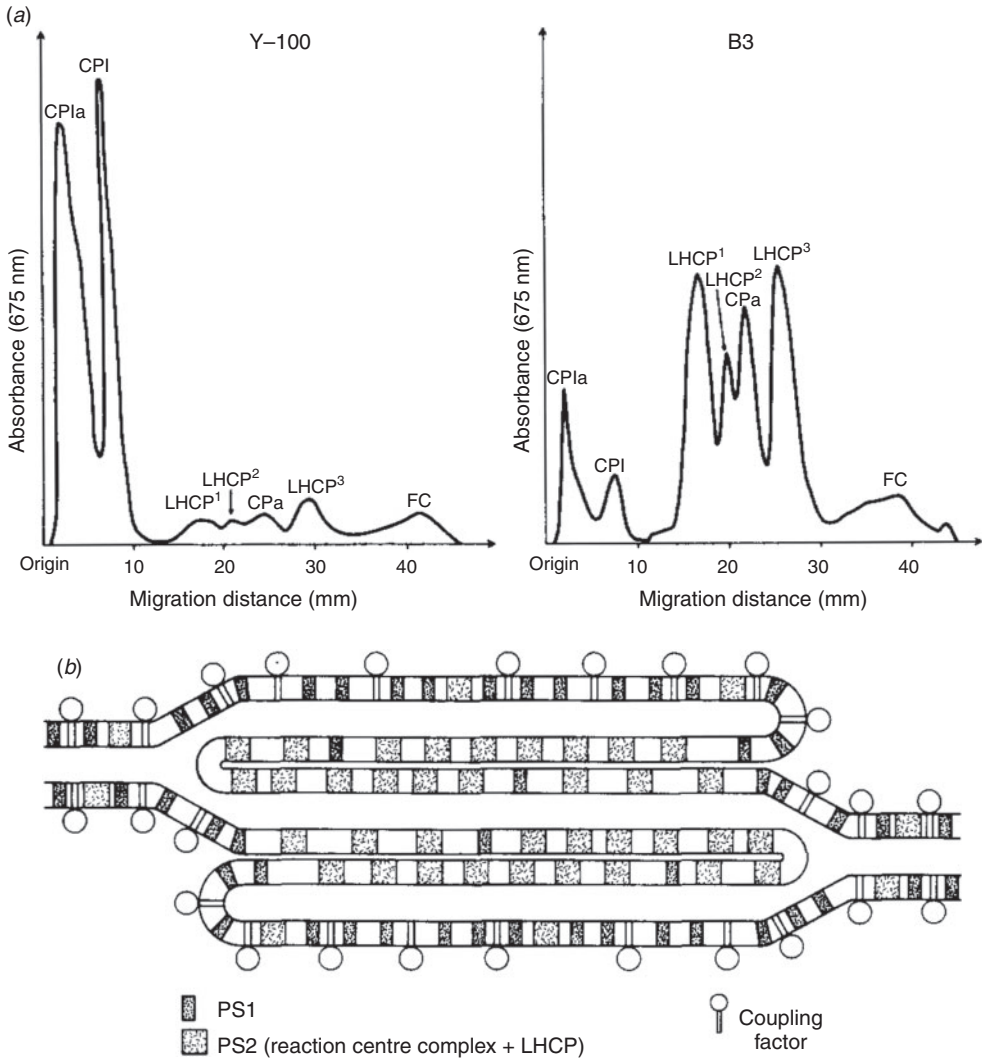

Figure 8. Lateral segregation of chlorophyll protein complexes in thylakoid membranes. (*a*) densitometric scan of green gels of Yeda press fractions, Y-100 enriched in PSI complexes and B3 enriched in PSII. (*b*) model for the distribution of PSII and PSI complexes in stacked and unstacked membranes. (Adapted from Andersson and Anderson (1980) with permission from Elsevier).

method of Albertsson developed during his PhD. This technique enabled Bertil to separate intact membrane vesicles derived from non-appressed and appressed membranes. Most importantly this technique did not involve the use of detergent to disrupt the membranes. The aim of the Andersson and Anderson collaboration was to compare the content of the main chlorophyll-protein complexes of the photosynthetic apparatus resolved by Jan's improved 'green gel' method using this new membrane fractionation method. Following Yeda-press fragmentation of thylakoids, stroma thylakoids (Y-100) were separated from granal stacks (Y-40) by differential centrifugation, and enriched inside-out vesicles (B3) were isolated by aqueous polymer two-phase partition of the granal fraction (Y-40 fraction).[15] Stroma thylakoid fractions were highly enriched in PSI complex together with some 10–20% of PSII and the light harvesting complex known as LHCII (Fig. 8*a*). By contrast, the grana appressed vesicles were substantially depleted in PSI complex and enriched in PSII and LHCII. Allowing for the contamination of some right-side-out vesicles in the appressed inside-out vesicles, they proposed that PSI is exclusively restricted to non-appressed domains, comprising the grana end membranes, grana margins and stroma thylakoids (Fig. 8*b*). Thus, the ground-breaking idea that there was a lateral heterogeneity of distribution of the photosystems was supported, with PSI exclusively in stroma-exposed thylakoid domains and PSII and LHCII mainly, but not exclusively located in appressed membranes. Later, they showed that the cytochrome b_6f complexes existed in both stacked and unstacked regions, indicating that plastocyanin rather than plastoquinone (as previously thought)

[15] Andersson and Anderson (1980).

Figure 9. Jan's research group at CSIRO, with (from left to right) Fred Chow, John Evans, Stephanie McCaffery, David Goodchild, Hugo Scheer and Robert Porra (from private collection of Jan Anderson).

was carrying out the long-range transport of electrons between PSII and PSI.

Like all new ideas, the concept of the lateral segregation of PSII and PSI was not readily accepted. Following the Fifth International Photosynthesis Congress at Halkadiki in 1980, Jan remarked:

> A discussion session chairman referred to it as a 'crazy idea, fit only for the waste paper basket, which would not be discussed'.

Prior to the 1980s it was thought that LHCII was a common light-harvesting antenna that was shared between PSII and PSI, a tripartite unit, so that the two photosystems had to be close to each other. Thus, part of the difficulty of accepting the notion of lateral separation of the photosystems was that no antenna protein specific for PSI had been found. Andersson and Anderson noted that the LHCII/PSII ratios were similar in all the subchloroplast fragments they analysed, suggesting to them a close structural linkage only between LHCII and PSII, rather than it being shared between the photosystems. Then John Mullet and Charles Arntzen discovered that PSI had its own previously unknown antenna chlorophyll-proteins,[16] thereby adding support to the Andersson and Anderson model. Further, Jim Barber recognised that a lateral separation of at least some PSI from PSII in the grana would better explain his observations on the changes in spillover from PSII to PSI upon membrane stacking and unstacking *in vitro*.[17] Similarly, the discovery of LHCII phosphorylation[18] gave a functional context to the lateral separation model: upon phosphorylation its association with PSII in the grana is decreased, so destabilising thylakoid stacking and regulating photosynthetic light harvesting and electron transfer.[19] These functional studies and more refined structural analyses over the next decade added more and more evidence in support, so that a decade later it became widely accepted, and Jan's place in the history of photosynthesis research was cemented. The ideas of Anderson and Andersson were beautifully expressed in an article in *Trends in Biochemical Science*.[20]

Photoacclimation: long-term adjustment of thylakoid membrane structure and function

Jan's quest then became not only to describe in more detail the protein composition of the variety of different membrane domains that emerge from her model, but also to understand more clearly the functional significance of this organisation of the membranes: answering the question 'Why Grana?' became her mission. At the same time, Jan realised the connection to an earlier fascination—how were the grana formed during plant development and how and why did the content of grana differ between plants grown in different light environments.

Jan had assembled a team of postdoctoral researchers at CSIRO to answer these questions. Ta-Yan Leong joined from the Carnegie Institution in 1981, followed by one of the authors (Wah Soon (Fred) Chow) coming from the Glasshouse Crops Research Institute, England, with John Evans returning from Cambridge, both in 1985 (Fig. 9). WSC became Jan's long-term colleague, collaborator and friend—together they published a total of 67 papers. The group

[16] Mullet, Burke and Arntzen (1980).
[17] Barber (1982).
[18] Bennett (1977).
[19] Horton (1983).
[20] Anderson and Andersson (1982).

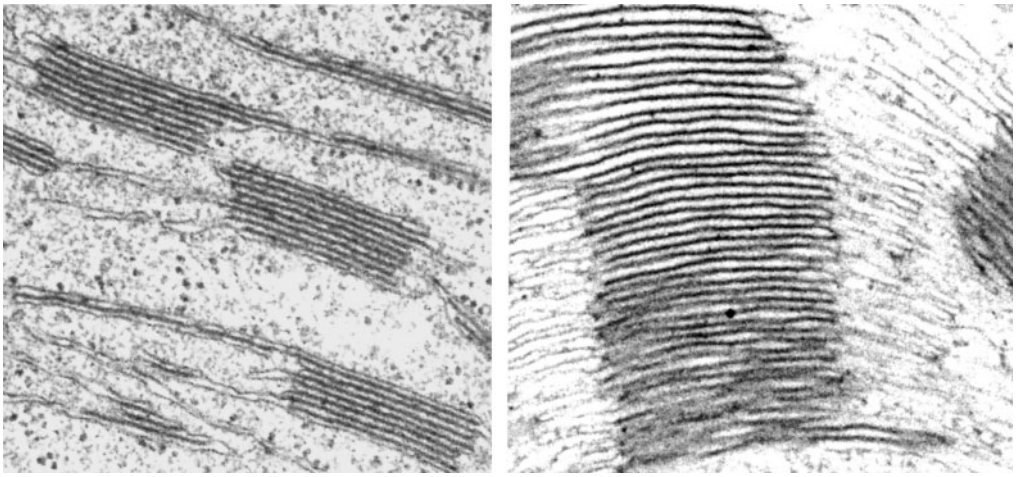

Figure 10. Electron micrograph showing the giant grana stacks found in shade grown *Alocasia* (right), compared to a 'normal' chloroplast from spinach (left) (from private collection of W. S. Chow).

was superbly supported by Stephanie McCaffery, a research assistant from 1983 until 1995. It is also important to mention here the important contribution of David Goodchild, a skilled CSIRO electron microscopist, who contributed enormously to Jan's work on the structure and function of grana.

This was another period of prolific research output as Jan and her colleagues led the world in the field, which became known as photosynthetic acclimation—the ability of plants to adapt photosynthetic capability to light, both light quantity and quality, over the entire irradiance range, a crucial factor in allowing them to succeed in habitats ranging from deeply shaded forest floors to sunlit deserts. The descriptions of the acclimation of the thylakoid membrane to light intensity and spectral quality carried out during this period were meticulous and remain a highly cited and definitive study.[21] It was shown how in low irradiance, the content of PSII decreases but its antenna size increases, and this is associated with an increase in amount of appressed thylakoid membranes. At the same time the content of electron transport chain components such as the cytochrome b_6f complex decreased, as did the ATP synthase and the enzymes of CO_2 fixation. Jan eloquently explained these changes in terms of the 'the coordinated allocation of resources to achieve and maintain optimal rates of photosynthesis' and this ensures all plants have constant, high quantum yields at limiting light. In contrast, in high irradiance, the converse was found—the antenna size decreases and the amount of grana stacking is reduced, whilst the capacity for electron transport and CO_2 fixation increases.

One notable controversy that emerged during this research on photoacclimation was the exact stoichiometry of the two photosystems, and whether this is fixed or variable: this question was almost as controversial as the lateral segregation issue, with Jan again going against the tide of current opinion. The accepted dogma was that it must be fixed at 1:1 (after all that is how the photosynthetic electron transport system appeared in our text books), but Jan reasoned that there was no reason to expect this since they are located in different membrane domains. Indeed the Anderson group found that the ratio of PS II to PS I is considerably greater than 1.0 and moreover it varied according to the light environment. These results were confirmed in collaboration with Anastasios Melis from the University of California Berkeley, who had developed new methods to measure photosystem stoichiometry. Together, they demonstrated that the change in stoichiometry was a response to alteration in the spectral quality of the light environment—growth in light that was preferentially absorbed by one photosystem over the other tended to induce an increase in the content of the reaction centres of the other photosystem.[22]

Several landmark reviews were published, one with the magnificent title 'The grand design of photosynthesis: acclimation of the photosynthetic apparatus to environmental cues'.[23] In this review, Jan focussed also on how the acclimation was regulated—how might the light environment be detected by plant leaves, and what signals are elicited to bring about the responses that she had discovered. The answers to these questions are still subjects of great debate in plant science research.

Further, Jan's group were the first to properly document the amazing biological diversity of thylakoid membrane composition across species. Spurred on by the earlier collaboration with Olle Björkman, and the ecophysiological studies of Barry Osmond FAA at ANU, Jan defined the characteristics of species such as *Alocasia*, which inhabits the highly shaded forest floor, and *Trandescantia*. Remarkably, *Alocasia* behaved in the expected way—all the features found in the earlier studies (mainly using pea plants) were observed in terms of photosystem composition, light harvesting antenna, grana stacking and so on. But the changes were more exaggerated—huge grana stacks were observed in *Alocasia* plants adapted to low light (Fig. 10), but *Trandescantia* behaved very differently.[24] There was little difference in the ratio of appressed to

[21] Reviewed in Anderson, Chow and Goodchild (1988).
[22] Chow, Melis and Anderson (1990).
[23] Anderson, Chow and Park (1995).
[24] Chow, Adamson and Anderson (1991).

unappressed membranes, photosystem content or antenna size between sun and shade grown plants, thylakoid structure appearing locked into the shade mode. Acclimation was of a different kind—the amount of thylakoid membrane per chloroplast was less in high light, so that the content of ATP synthase and ribulose bisphosphate carboxylase were higher on a chlorophyll basis. Increase in photosynthetic capacity in moderate light compared to very low light was observed and plant biomass was much higher in high light than low light, although the explanation for this was thought to lie in the other beneficial plant traits. Chloroplast movement was implicated as a part of the strategy of these plants to deal with light stress, and it was only in response to light quality that adjustments in thylakoid composition were observed.

Photoinhibition

Research into photoacclimation led to another avenue for Jan and her colleagues. During the 1980s observations made in several laboratories had shown that in high irradiance PSII can be inhibited, a phenomenon termed photoinhibition. Some of this work was done in Canberra, but also with a molecular and biochemical approach in the laboratories of Itzak Ohad, Charles Arnzten and Bertil Andersson. It was shown that this loss of function arises from photodamage of the reaction centre pigment protein complex, in particular the D1 protein. It was demonstrated that there was a continuous process of damage and replacement of the D1 protein. Jan realized the complexity this must involve, given that the D1 protein is part of a large PSII macrocomplex buried in the grana membranes, whereas newly synthesized proteins were introduced into the unappressed stromal membranes. Thus continuous protein trafficking between stacked and unstacked membrane regions must be occurring.

In 1994, Young-Il Park, an Australia/South Korea Exchange Post-doctoral Fellow joined Jan's laboratory to work on this problem. This was another period of prolific publication with new insights into the dynamics of photoinhibition. Most previous work in this field had been done on isolated thylakoid membranes exposed to non-physiological light intensities and under conditions when natural protective mechanisms were either inactive or overwhelmed. Jan realized that to get at what really happens in nature, whole leaves need to be studied at natural light levels. Using this approach, Park demonstrated that photoinhibition was a light dosage effect, in contrast to the prevailing view the rate of light absorption was the determining factor.[25] They calculated the probability of photodamage and estimated that during a sunny day, the entire population of D1 protein in PSII complexes has to be replaced at least once by this Dl protein repair cycle in the unstacked membranes.

The visit of three Scandinavian scientists, Cecilia Sundby and Gunnar Öquist from Sweden and Eva-Mari Aro from Finland greatly contributed to Jan's quest to discover the detailed molecular mechanisms of the Dl protein repair cycle. With Sundby, Jan found that during photoinhibition the damaged reaction centres are only repaired when light stress was alleviated.[26] Following this, Anderson and Aro found that damaged centres remained in the grana stacks during high light.[27] They speculated that this might have a function—could the damaged centres, known to dissipate absorbed radiation, have a function in protecting the pigments and proteins from further damage?

Gunnar Öquist focused on how plants grown under different light environments responded to high light intensity. In a highly cited paper, highly cited paper, Öquist, along with WSC and Jan, demonstrated that when a 60% of PSII were closed, irrespective of the actual light intensity, photoinhibition resulted.[28] This observation cemented into the accepted body of knowledge the notion of excess irradiation: photoinhibition occurs whenever the rate of irradiation exceeds the capacity of photosynthesis (and photoprotection) to dissipate excitation pressure in PSII.

Thus again, Jan made fundamental and original insights into an area of photosynthesis research not previously thought to be influenced by the structure and function of the thylakoid membranes. Once again, the lateral heterogeneity and the formation of grana stacks was found to have a crucial role, this time in photoinhibition.

Transfer to Australian National University

In 1994, CSIRO decided to phase out photosynthesis research by mid-1997, when Jan was due to retire and when MD (Hal) Hatch would have retired a year earlier. Thus, Jan moved to Barry Osmond's 'Photobioenergetics Group' in the ANU in May 1996. As adjunct professor at the ANU, Jan continued her research until her death in 2015. Inevitably less prolific than in earlier decades, Jan continued to apply herself to her mission to understand grana, particularly the question 'Why grana?' Indeed, Barry Osmond, with the help of his wife Cornelia, organized a conference with the title 'Why Grana?' to honour Jan at Arnsberg, Germany, in 1998 following the 11th International Congress on Photosynthesis in Budapest, the proceedings being published in a special volume of the *Australian Journal of Plant Physiology*.[29]

A collaboration between Jan and Wah Soon Chow who now had his own research group, also at ANU, aimed at deciphering the thermodynamics of grana formation. Thus the question became 'How Grana?' A study carried out by Jan, WSC and his PhD student (Eun-Ha Kim) and author Peter Horton (PH) led to the conclusion that the main attractive force that overcomes the electrostatic repulsion between thylakoid membranes is probably not van der Waals attraction (as previously thought) but has its origin in the maximization of the entropy of the system.[30]

Jan saw how the new methods of genetic manipulation might give a new approach to understanding the structure and function of the thylakoid membranes, greatly extending the knowledge gained years before from the study of mutants lacking chlorophyll *b* (which hence meant the absence of LHCII and other light harvesting proteins). Thus in collaboration with Stefan Jannson at Umea, Jan investigated plants in which specific light harvesting proteins had

[25] Anderson, Park and Chow (1998).
[26] Sundby, McCaffery and Anderson (1993).
[27] Anderson and Aro (1994).
[28] Öquist, Chow and Anderson (1992).
[29] Anderson (1999).
[30] Kim, Chow, Horton and Anderson (2005).

(*a*) (*b*)

Figure 11. Jan at the Royal Society meeting convened in her honour in 2012 by Professors Jim Barber and Peter Horton at Chicheley, UK. (*a*) with Peter Horton; (*b*) with Barry Osmond and his wife, Cornelia, together with Jan's long-term, assistant Stephanie McCaffery (from private collection of W. S. Chow).

been removed by modern genetic methods. Then, with ANU colleagues she investigated plants in which the content of cytochrome b_6f complex had been reduced.

Conclusions—thylakoid dynamics

In more recent years, Jan's attention turned from the relatively static view of the structural organization of plant thylakoid membranes during long-term acclimation to the dynamic changes following rapid transitions in irradiance. Several significant contributions to the literature were made, with her hallmark of imagination and creativity. She rightly identified the importance of the membrane domains that connected the grana to the stromal membranes, the margins and the end grana membranes. More recent work has confirmed her thinking as these have been shown to be areas of membrane where interactions between different protein complexes take place.

In 2012, Jim Barber and PH organized a meeting on 'The plant thylakoid membrane: structure, organization, assembly and dynamic response to the environment'. Held at the Royal Society of London's Chicheley Hall, this meeting honoured Jan and her research achievements, and celebrated her 80th birthday (Fig. 11). In a special volume of *Philosophical Transactions* are Jan's last two publications: 'Lateral heterogeneity of plant thylakoid protein complexes: early reminiscences',[31] and 'Towards elucidation of dynamic structural changes of plant thylakoid architecture'[32] The later article sets out the relationships between (a) the long-term alterations in thylakoid organisation that she had documented so meticulously and (b) ideas emerging from other laboratories about the remarkable extent of the short-term flexibility in these structures. This excited Jan, and her last publication in many respects was a fulfilment of her predictions, made nearly forty years previously, also in the English countryside. It was a fitting finale to a remarkable contribution to photosynthesis research, and one that WSC and PH are very proud to have been a part of.

Jan continued to contribute, of course, for example, by visiting London for a conference in honour of Jim Barber and visiting Cambridge again in 2015. She died on 28 August 2017, three weeks after the last of a series of falls. A memorial service was held in Canberra, attended by her many friends and colleagues from around the world. Messages recalling memories and expressing respect and admiration for her great achievements in life and in science were assembled in a special article in *Photosynthesis Research*, 'Remembering Jan Anderson'.[33]

In 2017, the International Society of Photosynthesis Research instituted the 'Jan Anderson Award' to celebrate her achievements in the broad area of structural aspects of photosynthesis. In recognition of Jan's support for young scientists and her appreciation of the importance of personal contact and collaborative research, this biennial Award is a travelling fellowship that will allow mid-career researchers to present their findings at venues in both Northern and Southern Hemispheres. The 'Jan Anderson Award' joins the two other premier awards of the Society that recognise high achievements in photosynthesis research: named for Andrew Benson and Melvin Calvin, and named for Robin Hill, and fittingly both Calvin and Hill had influenced Jan's career in different ways.

Jan, more than a scientist

Jan's qualities as a caring and compassionate human being were not only appreciated by her colleagues and friends in science, and it is fitting to end this memoir with mention of her long relationship with Jack Barrett. Jan and Jack first met whilst Jan was on sabbatical at Stanford, and their relationship continued after Jack moved to

[31] Anderson (2012).
[32] Anderson, Horton, Kim and Chow (2012).
[33] Chow, Horton, Barrett and Osmond (2016).

Canberra in 1977. They published several papers together on the analysis of the unusual chlorophyll proteins found in the photosynthetic membranes of diverse algal species.

They provided very complementary qualities in their work together. Certainly, Jan valued Jack's editorial guidance and organising capacities when it came time for her to assemble investigations for publication. Jan had a very creative and impulsive line of reasoning, which allowed her to make great leaps in resolving deep scientific conundrums. Jack was different. While Jan took on and slayed the paradigmatic dragon, Jack provided a protective parachute for her intellectual high-flying.

Collaboration in professional life was followed on by partnership in private life. Jack and Jan's personal relationship was never a particularly easy one, even in the decade before Jack's deteriorating health began to impinge on social events and professional studies. But there was enduring mutual attraction and respect, and the course of their relationship was enormously important in shaping Jan's later life. Inevitably, the challenges thrown up by Jack's various illnesses from about1984 brought changes, but she was able to hold on to her affection for Jack, and indeed to maintain it long after his death in 1997.

Jan did not have children of her own; instead she took on Jack's children, demonstrating an immense curiosity about and pride in their development and that of their partners, and (once another generation arrived) their offspring. She could be extremely interested in even small details of their progress, a generous patron of various talents and a tower of strength in times of need. Chris Barrett, an author of this memoir and one of Jack's children said, 'Jan tended to treat Jack's children—most of us well on the way to adulthood by the time she got to know us—as if we were her own. She could make a wonderful companion—of that there is no doubt. Where Jan's qualities as a caring and loving person tended to come out best was with her adopted grandchildren. She really can claim the role of grandparent. She showered them with affection; she nurtured their growth; she sponsored their learning; her interest in them burned bright; she provided an inspiration. Jan's intellectual curiosity has passed on to her adopted family. Whether by osmosis or contagion, her willingness to challenge the intellectual status quo and to rediscover the world for herself is a quality to which others are attracted and which they emulate. Jan may be gone, but her spirit roams free.'

Epilogue

> I feel extraordinarily lucky that much of my work was in an earlier idyllic era when research was judged by its excellent quality, and above all creativity was encouraged. Younger scientists were trusted to create their own research goals. More recently, it seems that the joy of discovery from creative research and the advancement of hypotheses to be tested that I enjoyed so much is often stifled. Most scientists today find themselves constrained by an ever-expanding bureaucracy responding to often-changing corporate and national goals which distracts them from pursuit of longer-term goals. The uncertainties of the competitive granting systems with its ever-changing rules is also definitely baffling, time-consuming, and certainly inimical to creative research. But above all, it is one's colleagues that are so very important. I feel so privileged to have had so many opportunities for sabbatical visits to some of the best photosynthesis laboratories in the world, and also for many scientists to visit me in Canberra. I am forever grateful to all my wonderful colleagues here and around the world. Without them, nothing could have been achieved.

Conflicts of interest

The authors declare no conflicts of interest.

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