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Fraser John Bergersen 1929–2011¹

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Fraser Bergersen rose from humble beginnings in New Zealand to become a leading microbiologist who specialised in the physiology and biochemistry of legume nitrogen fixation. He and his family emigrated to Australia in 1954. Virtually all of his career was spent in Canberra at CSIRO Plant Industry. In the 1970s, Bergersen and colleagues achieved world-wide prominence when they elucidated the role of leghaemoglobin in facilitating oxygen diffusion to the *Bradyrhizobium* bacteroids in soybean nodules and in the nitrogen fixation process itself. During the rest of his working life, Fraser Bergersen contributed greatly to understanding the role of oxygen, the mode of its delivery, and terminal oxidases in all forms of biological nitrogen fixation.

Introduction

When Fraser John Bergersen died in his eightythird year in Canberra on 3 October 2011, the world lost an eminent plant scientist and Australia lost a distinguished adopted son. For almost all his working life, from the time of his appointment to CSIRO as a Research Officer in 1954 until his retirement from the Australian National University (ANU) as a Visiting Fellow in 2007, Fraser Bergersen worked on manifold aspects of biological nitrogen fixation.

In 1954, we knew a little about nitrogen fixation in legumes. We knew for instance:

- (i) that the fixation took place in nodules formed on the roots of legumes by soil bacteria (species of *Rhizobium*);
- (ii) that the rhizobia gained access to the legume plant by infecting root hairs and developing infection threads therein that acted as pathways to the root proper;
- (iii) the bare basics of nodule structure;
- (iv) that genetically controlled plant characteristics determined the number of nodules that formed on a legume's roots and the ability of those nodules to fix nitrogen;
- (v) that plant nutritional factors were determinants of the magnitude of symbiotic nitrogen fixation;



- (vi) that there existed what appeared to be an orderly system of host/rhizobia specificity (certain rhizobia could infect certain legumes but could not infect others);
- (vii) that, by and large, Australian soils were devoid of rhizobia suitable for agricultural legumes—or, at best, had populations of the root-nodule bacteria that were limited in

¹A similar memoir will appear in *Biographical Memoirs of Fellows of the Royal Society of London*, vol. 59, 2013.

size and nitrogen-fixing ability—and that rhizobial inoculation of seed was mandatory if pasture and crop legumes were to realise their full potential.

By 2007, although many mysteries remained, our knowledge of the symbiotic system had increased by orders of magnitude. We knew:

- (i) that nitrogen fixation took place in bacteroids, that it was catalysed by the enzyme nitrogenase and that leghaemoglobin was essential to the system in order to control the delivery of oxygen (at low partial pressure) for bacteroid respiration;
- (ii) that there were other means besides roothair infection for rhizobia to enter legume roots;
- (iii) the structure of effective and ineffective clover nodules and precise details of their initiation and development;
- (iv) a great deal about the genetic sequences that control nodulation (*nod* genes) and nitrogen fixation (*nif* genes) and about other sequences that regulate their expression;
- (v) far more about the nutritional requirements (often different requirements) of the host plant, the rhizobial bacteria and the symbiosis itself;
- (vi) that root-nodule bacteria are not confined to a single bacterial genus (*Rhizobium*) but are distributed among not less than fifteen genera (both α - and β -proteobacteria) and almost 100 species and sub-species;
- (vii) how to produce the world's finest legume inoculants;
- (viii) and much more besides—for example, the nature of the metabolic exchanges between the rhizobia and the legume during infection and nitrogen fixation; the mensuration of legume nitrogen fixation in various environments.

Fraser Bergersen was in the vanguard of some of these advances and he played a major part in most of the others. Overall, his contributions, both at the bench and as a research leader, to knowledge of the physiology, biochemistry, microbiology, organic and inorganic nutrition, ecology and agronomy of the legume symbiosis and of biological nitrogen fixation were monumental.

Family Background

Fraser John Bergersen was born on 26 May 1929 in Hamilton in New Zealand's North Island, the second son of Victor Emmanuel Bergersen (born in Palmerston North in 1896) and Arabel Huntley Bergersen (née Young, born in Hastings in 1894). Fraser's older brother (Guy Richard, born in Hamilton in 1928) died in infancy, so Fraser was brought up as an only child.

The name Bergersen is Norwegian in origin and in the nineteenth century was a relatively common surname in and around Norway's capital Christiania, now Oslo. Fraser's greatgrandfather, Carl August Bergersen (born circa 1845), his wife Karen and their three young children emigrated from Norway to New Zealand in 1870. They settled in Palmerston North, then known by its Maori name Manawatu, where Carl worked as a blacksmith. The third child of Carl and Karen was Bernard Oscar Bergersen (born in Christiania in 1870 and always known as Oscar) was Fraser's grandfather. He was educated in Palmerston North and became a blacksmith and mechanical engineer in the town. In the early 1890s, Oscar Bergersen married Jessie Guy (born in Nelson in 1873). But for a period in Wellington and a very short time in Sydney, Australia, Oscar and Jessie lived the early part of their married lives in Palmerston North before moving to Hamilton immediately after the First World War. In Hamilton, Oscar conducted a mixed mechanical engineering business until his retirement.

Fraser's father Victor started school in Wellington and completed his primary and secondary education in Palmerston North. He commenced work as a blacksmith and machinist in a Palmerston North foundry. Victor's career as a third-generation blacksmith/engineer was cut short by rheumatic fever. The illness left him with a heart defect that made it impossible for him to continue activity in a strenuous occupation. He spent the rest of his working life first as a salesman and later as a departmental manager in menswear. It was while Victor was working at a Hamilton men's outfitters, J. Varney & Sons, that he met a young woman named Belle (Arabel) Young who worked in the firm's office, and who became Fraser's mother. After a lengthy engagement, Victor and Belle were married in 1923 and made their home in Hamilton. Soon after their arrival in Hamilton, the Bergersens became associated with the Baptist Church. The family attended church services regularly and the Church became of great importance to them. As for Fraser, the Baptist faith was of considerable significance to him throughout his life.

Fraser Bergersen was born in 1929. He was an active, inquisitive child. Both his father Victor and his grandfather Oscar, who lived nearby, maintained comprehensive home workshops. Fraser was a frequent and welcome visitor to the workshops where he liked to 'make things'. His parents had a love of music and Fraser began music lessons as soon as he was big enough to hold a full-size violin. There was little money in the household and Fraser had a newspaper round while at primary school. He had regular vacation employment during secondary school and worked in a butter factory to help pay his way through the University of Otago in Dunedin.

Gladys Irene Heather (born in Bankstown, New South Wales, in 1928) is the daughter of Edmund Faulkner Heather and Heather Irene Heather (née Hanbury). Mr Heather was a minister of religion of the Baptist Church. In 1951 Gladys, who was a stenographer, travelled with a girlfriend to New Zealand on a working (backpacking) holiday. Both girls were of the Baptist faith and, when in Dunedin, they attended a meeting of the Dunedin Baptist Youth Group that met each Saturday evening. There she met another young Baptist, university undergraduate Fraser Bergersen. Gladys soon became a frequent passenger on the pillion of Fraser's 500 cc Indian motor bike. They became engaged (in Sydney) early in 1952 and were married at the Baptist church in Hanover Street, Dunedin, on 5 July 1952. The officiating minister was Gladys' father who, at the time, was the interim minister at the church. They had three children-a daughter, Jennifer Anne (born 1954), and two sons, Philip John (born 1957) and Peter Richard (born 1961).

Education

Fraser had his primary schooling at Whitiora Primary School in Hamilton. He was a good scholar and was Dux of the school in his final year. The prize was a book, *Chemistry Today*, which had a lasting influence on Fraser's life. It stimulated in him an interest in chemistry and in science generally, and it served to complement his childhood experiences in his father's and grandfather's workshops.

Fraser undertook his secondary education at Hamilton High School where he proved to be an excellent all-round student. His special loves, however, were the sciences-physics, chemistry and biology. Two teachers in particular caught Fraser's imagination. Mr Fred Mason taught physics and chemistry. He did so with particular emphasis on the practical aspects of his subjects and on the hands-on involvement of his classes. Mr Horrie Sayers taught biology. His lessons were frequently accompanied by demonstrations, sometimes confronting, of human, zoological and botanical specimens that brought reality to his various biological themes. There was a legacy to Fred Mason's and Horrie Sayers' imaginative teaching styles. In the latter part of Fraser Bergersen's career, he became a committed, inspirational and successful supervisor of candidates for higher degrees.

Fraser commenced tertiary studies at the University of Otago, in Dunedin, in 1948. It was his original intention to study medicine. However, at the time, immediately after the Second World War, places in medical school were almost entirely reserved for returned servicemen. So, in his first year, Fraser studied for a Bachelor of Science, choosing courses that would carry credit should he later transfer to medicine. It never happened. By the time that Fraser entered his second university year, he had become fascinated by microbiology and determined to become a professional microbiologist. He completed his BSc studies in 1951 and immediately joined the diagnostic laboratory of the University's Department of Bacteriology as a Research Associate where he worked towards his MSc (awarded in 1954). In 1962, the University of New Zealand conferred upon Fraser a DSc in recognition of his work on legume nitrogen fixation.

A Career Condensed

From his first introduction to biological nitrogen fixation in 1954 until his 'final' retirement 53 years later, Fraser Bergersen's career was a continuum. Certainly from the middle years, he had administrative responsibilities but they were never so demanding as to interfere with his research. Fraser did his very best work in the laboratory where his patience, his manipulative skills and his ability to design special equipment complemented a compulsion to investigate the unknown and to measure the unmeasurable. The outcome was a systematic, gradual unravelling of the intricacies of a highly complex biological system. But Fraser never lost sight of the fact that the end-point of biological nitrogen fixation was the enormous contribution that it had to make to agricultural productivity, the health of the environment and the welfare of mankind. So, on a regular basis, he broke away from the confines of his laboratory to get his hands dirty. Although he was probably less at home in the field than he was at the bench, he was always an effective field worker. This was manifest first in the resolution of a problem of subterranean clover inoculation in the winter bleakness of the New England Tablelands grazing country in northern New South Wales, later in using novel techniques to make field measurements of soybean nitrogen fixation under the searing summer sun of western New South Wales, and finally in identifying the role of the poly- β -hydroxybutyrate content of nodules in maintaining nitrogen fixation into the late reproductive stage of irrigated soybeans grown in the soporific humidity of the Murrumbidgee Irrigation Area. There were many other forays into the field between times. Fraser travelled a good deal and spent periods of study leave at the Universities of Wisconsin and Sussex. Nevertheless, his own science practised in his own environment was easily his primary concern. He loved his Canberra laboratory.

It is no doubt an over-simplification but it is a convenience to divide the career of Fraser Bergersen into three phases: learning the trade (1951–1959), the working scientist (1959–1994) and scientist emeritus (1994–2007).

Learning the Trade

The University of Otago's Department of Bacteriology in Dunedin, where Fraser Bergersen took up his first professional appointment as a Research Associate in 1951, was an apt training ground for a microbiologist since it was the main diagnostic laboratory for the province of Otago and had a close working relationship with the University's Department of Pathology. Before his appointment there, while still an undergraduate, Fraser undertook a project dealing with antibiotic resistance in bacterial pathogens. The outcome was one of the first reports of multiple antibiotic resistance in *Staphylococcus aureus*—some strains were jointly resistant to penicillin and aureomycin. The findings were published in *Nature* in 1951 (1). Thus, Fraser had the distinction that his first scientific publication appeared as a letter to *Nature* before the award of his first degree. In Dunedin, he also did cytological work with *Escherichia coli* (then known as *Bacterium coli*) and *Bacillus megaterium* (4, 5).

In 1951, Otto (later Sir Otto) Frankel was appointed the second Chief of the CSIRO Division of Plant Industry in Canberra. Frankel's mandate was to strengthen the Division's fundamental research 'by building up a range of strong disciplinary groups' (Evans 1999). One of those disciplines was microbiology, including symbiotic nitrogen fixation. In 1953, Frankel arranged for the secondment of Phillip Nutman from Rothamsted Experimental Station in England. At Rothamsted, Nutman was studying the physiology and genetics of legume nodulation. His role in Canberra 'was to develop an integrated programme of research about the biology of nitrogen fixation by nodulated legumes' (181). Substantial legume research was already in progress in the Division of Plant Industry when he arrived, but only a tiny proportion of it related to nitrogen fixation. During his three-year tenure, Nutman recruited two young scientists, Fraser Bergersen and Alan Gibson. Fraser and Alan became close colleagues and collaborators and remained so throughout their forty-year careers with CSIRO. Fraser commenced duty as a Research Officer on 16 March 1954 (at 2.30 pm!). His salary was £980 per annum. The appointment was subject to a two-year probationary period but that was waived within twelve months because, in the words of Otto Frankel, 'he is a person whom we wish permanently to attach to this Division'.

The circumstances of Fraser's appointment to CSIRO sparked an administrative incident. Otto Frankel arranged for him to fly from Dunedin to Canberra for interview. This apparently breached CSIRO regulations regarding international travel, even though the cost was borne by the Plant Industry budget. As a consequence, Frankel was reprimanded by CSIRO's Secretary, Finance and Supplies. Frankel did not take kindly to reprimands, especially from people whom he regarded as mere bureaucrats. His fiery retort wasted no words in rejecting the reprimand.

Although some fourteen years Phillip Nutman's junior, Fraser had much in common with him. While each of them was temperamentally drawn to basic research, they both understood the potential of efficient legume nitrogen fixation for plant vigour and soil fertility in particular and for agricultural productivity in general. They made it their business to know plant breeders, agronomists and farmers, they fostered applied investigations as well as more academic studies, and they brokered a lasting, productive relationship between fundamental and applied research.

The Bergersens arrived in Canberra in 1954. Although it was Australia's capital city, it was then merely a country town with a population of 27,000. It was growing quickly, however, and had a housing problem. For the first few weeks, Fraser, Gladys and baby Jennifer were accommodated in a hostel until they found a house to rent. It was not until 1956 that they moved into their first real home, in the suburb of O'Connor, barely 2 km from CSIRO's Black Mountain laboratories.

Upon his arrival in Canberra, Fraser hit the ground running. In his earliest work, he drew on his cytological experience from Dunedin to study the structure of effective and ineffective clover nodules and their rhizobial contents, at first with the light microscope (6, 10) and soon afterwards using electron microscopy (16). At the same time, he had his first involvement with field studies-in the New England region of New South Wales. There was a problem of inoculation failure of newly sown subterranean clover. Fraser found that a soil microbial factor interfered with seedling nodulation (13). The significance of the finding was, however, soon overtaken by improvements in Australian legume inoculants and in methods of applying them to legume seed. Fraser played a part in these developments as well; he filed a patent to protect a novel form of legume seed inoculation (15).

Fraser's early cytological studies soon bore fruit (16, 41). Photomicrographs² of the central tissue of nodule cells revealed the existence of clumps of bacteroids (the symbiotic form of the rhizobia within the nodule) enclosed in membrane envelopes. Fraser speculated that these structures represented the primary site of nitrogen fixation, and he planned to test the hypothesis in a biochemical study using the stable nitrogen isotope ¹⁵N as a tracer. At first he was hamstrung in this endeavour because clover nodules were so tiny. He therefore selected a more tractable model system based on soybean nodules. For the next forty years, Fraser's glasshouse was continually occupied by pots of nodulated soybeans in various stages of development. It was necessary, however, first to prepare extracts of nodule contents in a way that did not jeopardise the nitrogen-fixing system. It was here that Fraser's inventiveness, first manifest as a child in his father's and grandfather's workshops, came to the fore. He designed a press that could prepare nodule breis (the fluids obtained from crushed nodules strained free of intact host-cell components) and cell-free extracts under anaerobic conditions. The device was constructed in the divisional machine shop. Like the soybeans in the glasshouse, this elegantly engineered nodule press remained part of Fraser's laboratory equipment for most of his career.

To some extent Fraser was working in an intellectual vacuum. Other laboratories around the world were engaged in unravelling the secrets of nitrogen fixation in free-living diazotrophs, but only one group, at the University of Wisconsin in Madison, was working with the legume system. In 1958-9, Fraser was able to arrange a twelve-month period of study leave in Wisconsin, to work with Perry Wilson and to exchange ideas with the doyen of nitrogen fixation research Bob Burris. His time there was a watershed in his career. At once, it provided a benchmark for all his subsequent work on the complexities of the physiology and biochemistry of legume nitrogen fixation and it entrenched him as a significant, if youthful, authority in the field.

In Wisconsin, Fraser pursued his hypothesis that the primary site of nitrogen fixation in legume nodules was somewhere in the membrane envelope and its content of bacteroids. At first, his isotopic work seemed to suggest that ¹⁵N was incorporated in the membrane envelope itself (23). But it soon became apparent that this was an artefact and that the location of nitrogen fixation was elsewhere within the envelope.

² Some of these photomicrographs are reproduced in the book *Root Nodules of Legumes: Structure and Functions* (102).

(It subsequently emerged that the envelope had a role in the regulation of oxygen supply without having any direct role in the nitrogen-fixing process.)

Fraser had other activities. In the late 1950s and early 1960s, there was debate in Australia about the origins of the legume symbiosis, about alkali production by slow-growing rhizobia in contrast to acid production by fast-growers, and about the symbionts' requirements for calcium. The main protagonists in the debate were Don Norris from the CSIRO in Brisbane (Norris 1956, 1958), and Lex Parker from the University of Western Australia (Parker 1957). Although peripheral to the central debate, Fraser exercised some moderating influence on what had become a rather bitter dispute with a scholarly paper on rhizobial nutrition which, *inter alia*, defined the organisms' requirements for calcium (25).

The Working Scientist

How do Legume Nodules Fix Nitrogen?—The Physiology

In 1959, Fraser returned to Canberra inspired from his twelve-month sojourn in Wisconsin. While there, he had come to a realisation of how little was known about biophysical and biochemical aspects of symbiotic nitrogen fixation. Whereabouts in the nodule did the fixation take place? What catalysed the process and what were the initial products? Did the process require oxygen to function and, if so, how much and how was it delivered? What was the role of the membrane envelopes that enclosed the bacteroids within the nodule? Fraser was determined to tackle these questions and his experience in Wisconsin had armed him with inklings of how to go about it. Two significant events approximately coincided with Fraser's return to Canberra. First, the Division of Plant Industry acquired an isotoperatio mass spectrometer thanks to funding from the Rockefeller Foundation. Not long afterwards, Graham Turner joined Fraser's group to take charge of the mass spectrometry unit. He was to become Fraser's most frequent collaborator; together, they co-authored more than fifty papers. Second, Fraser commenced an ongoing association with Cyril Appleby, a Plant Industry scientist who was becoming a leading authority on the chemistry and biochemistry of haemoproteins.

A propos the first significant event, the acquisition of the mass spectrometer allowed Fraser to extend the use of techniques with the stable nitrogen isotope ¹⁵N that he had learnt in Wisconsin. It was a key development that, for very many years, remained the most reliable means of tracing products that eventuated when ¹⁵N-amended nitrogen gas was incorporated into plants, nodules, bacteroid cells isolated from nodules, and cell-free contents of bacteroids. Until 1965, the majority of Fraser's work was centred on intact nodules, and he was the first to show that ammonia was the initial soluble product of the fixation process in soybean nodules (35, 42).³ Then he demonstrated nitrogen fixation in disrupted nodules (38, 39, 42, 44), thus opening the way to the study of nitrogen-fixing enzymes in cell-free preparations from bacteroids. This work of Fraser's (1966-8) sparked a flurry of activity in laboratories in the United States, the United Kingdom, France and the USSR. Workers at the Du Pont laboratories in Delaware had already succeeded in producing a nitrogen-fixing extract from the free-living diazotroph, Clostridium pasteurianum (Carnahan et al. 1960).⁴ This Du Pont discovery, in turn, led to the identification of the enzyme nitrogenase that is the catalyst for the fixation of nitrogen. Fraser applied himself to elucidation of how nitrogenase might work in a much more complex symbiotic system, specifically the nodules of soybeans. He succeeded in making soybean nodule extracts that contained active bacteria and he was able to demonstrate that these bacteria were a source of nitrogenase.

³ More than three decades later, these findings were challenged (Waters et al. 1998). Bergersen remained convinced that his original work was sound and the results valid. Nevertheless, he and co-workers undertook an exhaustive set of new experiments using ¹⁵N and soybean bacteroids prepared with a variety of procedures. The work was done in David Day's laboratory at the Australian National University. The original findings were unambiguously confirmed: NH₃/NH₄⁺ was the principal nitrogenous product from soybean bacteroid nitrogen fixation (180, 183)-see also below. ⁴ In the widest sense, the exciting outcome of the Du Pont study (Carnahan et al. 1960) has clear priority in the field. Bergersen's equally exciting paper describing nitrogen fixation in washed soybean bacteroids appeared seven years later (42).

Otherwise, progress was quite slow. Then the Princes of Serendip entered the equation. It was already known that nitrogenase was inactivated by oxygen, so Fraser's ¹⁵N experiments on nodule extracts in pyrex cuvettes were conducted under strictly anaerobic conditions. For many months, nitrogen-fixing activity did not occur. Then one morning, while monitoring the gas phase within the cuvettes, one out of ten was found to have activity. Close examination of that cuvette revealed a tiny crack in the pyrex that admitted a little air. It suddenly became clear that, while the nodule bacteroid preparation itself had to be done anaerobically, a small partial pressure of oxygen was required to drive the process of nitrogen fixation.

How do Legume Nodules Fix Nitrogen?—The Biochemistry

The second significant event following Fraser's return from Wisconsin, his collaborations with Cyril Appleby, was ground-breaking. Cyril Appleby and Fraser Bergersen were temperamentally quite different people. Cyril was (and remains today) an extrovert, overtly enthusiastic about his field. In contrast, Fraser had gravitas, was somewhat reserved, and was a little cautious in forming his hypotheses and in interpreting his findings. Despite their working in different Plant Industry sections located in different buildings, Fraser and Cyril saw a great deal of each other, they argued, they challenged one another's hypotheses, and they teased each other's intellect. But they shared an ability to do elegant, expressive experiments. Together, this disparate partnership was responsible for spectacular advances in the understanding of the biochemistry of symbiotic nitrogen fixation. The real starting point of their collaborative success was three-pronged:

- (i) Fraser's finding that symbiotic nitrogen fixation was a micro-aerobic process, not an anaerobic one at all;
- (ii) Cyril's expertise as a haemoprotein biochemist;
- (iii) their interaction with animal haemoglobin physiologists Jonathan and Bea Wittenberg of the Albert Einstein College of Medicine, NewYork.

Leghaemoglobin is a monomeric, oxygenbinding haemoprotein that has a unique presence in nitrogen-fixing legume (and non-legume) nodules where it is manifest as a red pigment. (It has similiarities to myoglobin and to other haemoglobins but has much higher oxygen affinity.) At first, leghaemoglobin's role in legume nitrogen fixation was not understood. Experiments showed that nitrogenase activity in intact nodule tissue was suppressed by carbon monoxide whereas carbon monoxide was without effect on bacteroids washed free of leghaemoglobin. However, nitrogenase activity was enhanced when oxygenated leghaemoglobin was added to the bacteroid suspensions but this enhancement was abolished by addition of low levels of carbon monoxide. Since carbon monoxide competes with oxygen for binding by leghaemoglobin, these experiments suggested that leghaemoglobin functioned in nodules by virtue of its oxygen-binding properties and that this supported nitrogen fixation. (Some prudence was necessary in interpreting these results because carbon monoxide can also combine with bacteroid oxidases, although at lower affinity.)

Cyril Appleby was skilled in the preparation of purified proteins. Bergersen/Appleby experiments in which pure leghaemoglobin was added to shaken suspensions of soybean bacteroids led to increased nitrogenase activity. While this result was gratifying, it did not resolve 'whether leghaemoglobin was acting in facilitated diffusion with final delivery of molecular oxygen near the bacteroid, or whether there was a specific, direct interaction between oxyleghaemoglobin and an efficient oxidase located on the bacteroid surface'. Jonathan Wittenberg came to Canberra for about three months in 1973, bringing with him several oxygen-carrier proteins. Others were obtained locally including earthworm leghaemoglobin that Cyril purified from Lumbricus terrestris dug from the compost heap in the backyard of Fraser's home. Were any of these materials able to substitute for leghaemoglobin in stimulating bacteroid nitrogenase activity, it would effectively eliminate the hypothesis of 'specific direct interaction with an oxidase on the bacteroid surface'. There followed a series of complex experiments using the various carrier proteins. The aim was to investigate and establish the nature of facilitated oxygen diffusion to *Bradyrhizobium* bacteroids (69). The experimental protocol was a compromise of Bergersen, Appleby and Wittenberg methods.

An over-simplified summary of the outcomes is that leghaemoglobin functions in co-operative fashion with a specifically-adapted, efficient oxidase system in bacteroids, thereby producing ATP very efficiently at low concentrations of free oxygen. Such activity is maintained as leghaemoglobin becomes substantially deoxygenated. As the Wittenbergs precisely put it, 'leghaemoglobin facilitates the diffusive flux and delivery of free oxygen at very low partial pressures'; or, as Cyril Appleby enthusiastically put it, 'leghaemoglobin is a magnificent oxygen buffer at these same low pressures'.

This period was the most exciting time in Fraser Bergersen's career. The excitement reached its height during 1973 when Jonathan Wittenberg was in Canberra. That was a time of intense intellectual and experimental activity and it had a most satisfying culmination. Fraser revelled in it and, in later years, took pleasure from recollections of its highlights.⁵

Following their pivotal discoveries, Cyril Appleby and Fraser Bergersen tended to follow separate paths. Cyril retained a lifelong and intense interest in haemoglobins, their origins and their wider functions in the plant kingdom, while never losing sight of their roles in bacteroid respiration, nitrogenase function and nitrogen fixation. Fraser moved into the physiological definition of terminal oxidases and aspects of the production and utilization of ATP in bacteroids. These latter studies had bearing on the energetic efficiency of biological nitrogen fixation and implications for the effective use of nodulated legumes in world agriculture. Fraser's capacity to design items of novel equipment, and to have them engineered in the splendid Plant Industry workshops, stood this work in good stead. For instance, a continuous-flow chamber had application wider than in work on legume nitrogen fixation; it facilitated the study of the expression of certain nif genes in continuous culture of the free-living diazotroph, Klebsiella *pneumoniae* (103, 112). Despite these diverse interests, Fraser remained fascinated for the rest of his working life by the roles of oxygen, the mode of its delivery, and terminal oxidases in all forms of biological nitrogen fixation. This fascination is attested to by a series of 23 papers published between 1976 and 2001, many of them co-authored with international visitors to his laboratory.

The Role of Poly- β -hydroxybutyrate in *Extending the Period of Nitrogen Fixation*

There is a long-held perception in many quarters that nitrogen fixation in annual legumes peaks at flowering and then declines. There is an alternative view that the majority of nitrogen fixed by crop legumes accumulates after flowering. The conflict, which remains to be properly resolved, may be an artefact of methods used for measurement of nitrogen fixation (D. F. Herridge, personal communication). In the early 1990s, while making field measurements of nitrogen fixation in the Murrumbidgee Irrigation Area of New South Wales, Fraser Bergersen and colleagues noted that substantial fixation persisted into the late reproductive, pod-filling stage in a crop of irrigated soybeans (160). They were intrigued. Some little time earlier, Fraser had published on various aspects of the occurrence in nodules of the energy-yielding substrate polymer, poly-βhydoxybutyrate (PHB) (152, 153, 156, 159). It was already known that PHB could comprise up to 50% of the dry weight of soybean bacteroids. Fraser therefore turned his attention to the accumulation and means of utilization of PHB. First, he demonstrated that the extent of PHB accumulation was under rhizobial strain control. (Strains that were hup⁺ accumulated PHB in the soybean nodule; others that were hup^- did not.⁶) Then it was found that the maintenance of nitrogen fixation into late pod-fill depended on how accumulated PHB was utilized during the plant's

⁵ In writing of these momentous events, we have relied greatly on Cyril Appleby's entertaining paper 'The Wittenbergs: A personal appreciation' (Appleby 2008). Bea Wittenberg did not accompany Jonathan when he visited Canberra in 1973 because of the demands of their young family. Nevertheless, Bea played a major role in the design of the experiments that were so productive.

⁶ Some strains of *Bradyrhizobium* (*hup*⁺ strains) possess an uptake-hydrogenase enzyme that allows the hydrogen that is emitted as a normal part of the nitrogen fixation reaction to be recycled within the plant (e.g. Arp 1992). Other *Bradyrhizobium* strains (*hup*⁻) do not possess the enzyme and free hydrogen gas is emitted from their symbiotic systems into the environment where it is almost instantaneously taken up by soil microflora (e.g. Osborne 2010).

reproductive stage. For plant/rhizobial associations with prolonged nitrogen fixation, Fraser postulated a strategic mechanism for preserving the oxygen demand of nodules during seed development so that the concentration of free, dissolved oxygen was kept within those limits that allowed nitrogen fixation to proceed (169). The work opened up distinct practical possibilities for increasing total nitrogen fixation in certain food legumes. Notwithstanding Fraser's findings, some curiosities regarding the occurrence and role of PHB in legume nodules remain unresolved. (Sprent [2009] has briefly reviewed the literature dealing with the subject.) Two aspects are particularly troubling: (i) PHB is a polymer that is widely produced by bacteria under oxygen-deficient conditions; (ii) PHB accumulation also involves uncontrolled uptake of solutes under conditions where they cannot be fully metabolised. Accordingly, it could be argued that PHB accumulation in legume bacteroids is a sign of inefficiency.

Measuring Legume Nitrogen Fixation

In the early 1980s, Fraser became conscious of a pressing need to define with some precision the input of legume nitrogen into phase-farming systems. He was aware that, without meaningful measurements of legume nitrogen fixation and its input of fixed nitrogen into farming systems, it would never be possible to assess with assurance the real value of legumes to overall agricultural productivity. Existing measurement of nitrogen fixation was based on the nitrogen difference method or on the ¹⁵N soil enrichment technique (Peoples et al. 1989). Nitrogen difference yielded results that were merely qualitative, and with 15N soil enrichment there was a high risk of contamination. While it might be an exaggeration to say that Fraser's objective was to measure the unmeasurable, he aimed to have a means of making reliable quantitative measurements. With David Herridge from the New South Wales Department of Agriculture, and Mark Peoples from Plant Industry, he set about developing improved methods (i) based on the natural abundance in soil of $\delta^{15}N$ and (ii) based on the nitrogen content of translocates from nodulated roots to plant shoots. Initially, the ¹⁵N technology involved laboratory and glasshouse studies to define better analytical techniques and isotope discrimination phenomena. With the translocate technology (already initiated by David Herridge in glasshouse experimentation), it was found that many legumes translocated the products of their fixation as ureides. This work led to the refinement of the 'ureide assay' as a field-based technique. Subsequently, the collaborators went to the field in order to demonstrate the utility of their methods. They were able to show, in large-scale field experiments and in farmers' paddocks, that both techniques provided realistic estimates of legume nitrogen fixation and the input of legume nitrogen to various ecosystems. These aspects of Fraser's work had application in research in Australia and South-East Asia that was funded by the Australian Centre for International Agricultural Research (ACIAR)-see later.

Influential Leader

Scientific Leadership

When Phillip Nutman left Canberra to return to Rothamsted in 1957, work on biological nitrogen fixation within Plant Industry was consolidated into an informal 'Rhizobium Group' within the Microbiology Section. (Actually, the word 'Rhizobium' implied too narrow an interpretation of the group's activities; in reality it was a 'Nitrogen Fixation' group.) Fraser Bergersen was the natural leader of the group. This leadership was formalised by Otto Frankel in 1961. (Subsequently Fraser was also appointed Chairman of the Microbiology Section.) The Rhizobium Group established a worldwide reputation as a centre of excellence for nitrogen fixation research. Much later Jim Peacock, then Chief of Plant Industry, was to write that Fraser's 'leadership of the Rhizobium group was absolutely seminal in developing and maintaining the tremendously high standards and reputation that the group enjoyed'. Fraser himself gave credit for the Rhizobium Group's reputation to successive Plant Industry Chiefs, Otto Frankel, John Falk, Lloyd Evans and Jim Peacock, each of whom embraced 'the maxim attributed to Sir David Rivett, the first chief executive of the Council for Scientific and Industrial Research (later CSIRO), to the effect that a research leader should recruit the best scientists, work to give them the resources they need, and give them

freedom and encouragement to get on with their work'.

The Microbiology of Stubble Conservation in Cropping Systems

Fraser was responsible for initiating a programme of work on the utilization of crop residues as an energy source for free-living diazotrophs in cereal cropping systems. This research was led by Margaret Roper. It played a part in the acceptance of stubble-conservation farming as a viable farming practice that enhanced the nitrogen status of soils used for cereal cropping.

Cost Benefit Analysis of Australian Legume Nitrogen Fixation Research

Appraisal of the monetary value of scientific research is fraught with imponderables. With projects of an academic nature, however creative, it is a virtual impossibility. Just how, for instance, does one put a value on Fraser Bergersen's discoveries relating to the intricate physiology and biochemistry of nodule bacteroid function? They are immensely valuable findings that cannot be valued monetarily. With applied research that has a direct impact on practical agriculture, the task is a little easier. Indeed, the Australian Bureau of Agricultural Research Economics (ABARE) made one such study relating to legume nitrogen fixation. In the 1950s, Fraser Bergersen and colleagues John Brockwell and Jack Thompson were pioneers in work on seed coating and inoculation as an aid to the inoculation, nodulation and nitrogen fixation of pasture legumes (15, 17; Brockwell 1962; Brockwell and Whalley 1970). This work was continued by John Brockwell in Plant Industry for more than a decade. In 1999, ABARE calculated that the development of seed coating and inoculation for the pasture plant subterranean clover had, through the addition of fixed nitrogen to the soil, led to increases in the productivity and profitability of wool, meat and cereal enterprises worth more than AU\$1 billion to the Australian economy.

Recognition

Following Fraser Bergersen's death, Janet Sprent spoke for many of us when she dwelt upon one aspect of the legacy that he left to those who follow in his footsteps. She wrote 'It is a pity that Fraser did not live to see the plethora of bacteria now known to nodulate legumes, or the wider range of nodule structure and metabolism now known to exist. We have come a long way from the days of rhizobia being fast- or slow-growing, nodules being only determinate or indeterminate, and infected only via root hairs. Many of these recent studies are based on and are a tribute to the meticulous and insightful work of Fraser and his colleagues. Who else would have had the patience to dissect electron microscope photographs in order to assess the volumes of the various components of a soybean nodule (102). I hope that younger readers of this biographical memoir will look carefully at Fraser Bergersen's publications and realise that there is much to be learnt from them.'

CSIRO recognised Fraser's continuing achievements as a scientist by an unprecedented rate of promotional advancement. Within 28 years of his appointment as a Research Officer in 1954 he had attained Chief Research Scientist (2M), the highest recognition that CSIRO confers on scientists. Recognition was not confined to CSIRO. He was elected a Fellow of the Royal Society of London in 1981 and of the Australian Academy of Science in 1985, and in 2000 he was elected a Member in the General Division of the Order of Australia (AM) for services to science.

Internationalist

International Scientist

The name Fraser Bergersen first came to the closer attention of the international nitrogen fixation community in the early 1960s (e.g. 28, 29, 30), but he was not known personally until he accepted an invitation to present a paper at the 9th International Microbiology Congress in Moscow in 1967. Fraser made an immediate impression in Moscow with a thought-provoking presentation, a lucid exposition of the interpretation of his results, and a willingness to discuss his hypotheses. Invitations to international conferences and workshops quickly followed. In the next twenty years he visited the United Kingdom, the United States, the USSR, Czechoslovakia, Ethiopia,⁷ France,

⁷ In 1967, Fraser Bergersen represented Australia at the Second International Conference on the Global Impacts of Applied Microbiology in Addis Ababa. At the time, it was rather unusual for Ethiopia to host

the Netherlands, Mexico, Brazil, Nigeria, Kenya, the Philippines, Malaysia, Thailand, Japan and China; regular international visits continued for the rest of his career. Fraser took a special interest in the development of biological nitrogen fixation research in Brazil because he saw in Brazil in the 1970s what he had seen when he arrived in Australia in the 1950s. He made several visits to the EMBRAPA Agrobiologia laboratories at Seropédica (Km 47, Rio de Janeiro) where he formed a strong working relationship with Dr Johanna Döbereiner, a pioneer in the identification of associative nitrogen fixation by gramineaceous species and free-living diazotrophs. Reciprocally, Fraser's laboratory in Canberra was a much-sought-after destination for visiting scientists. From the late 1960s until the mid-1990s, there was a succession of some fifty visitors from all six continents. All but two of them contributed to published papers.

In 1978, when China was emerging from the traumas of the Great Leap Forward and the Cultural Revolution, a delegation of Chinese nitrogen fixation scientists visited Australia, the visit being sponsored jointly by the Australian Academy of Science and Academica Sinica. To general astonishment and delight, the leader of the delegation was Professor H. K. Chen. Mr Chen (as he was then) had done cytological work on ineffective clover nodules with Dr Henry Thornton (Chen and Thornton 1940) as a visitor to Rothamsted Experimental Station in the late 1930s, but his whereabouts and activities following his return to China in the very early days of the Second World War had not been known outside China.8 In 1983, there was a reciprocal visit to China by a party of Australan nitrogen fixation scientists. Fraser Bergersen led that party. When visiting the headquarters of Academica Sinica in Beijing, Fraser presented the President, Dr Lu Xia Xi, with his books *Methods for Evaluating Biological Nitrogen Fixation* (89) and *Root Nodules of Legumes: Structure and Functions* (102) as a token of appreciation of the friendship and hospitality bestowed on the Australian visitors by their Chinese hosts. Subsequently, the former book was reprinted in the Chinese language and became as widely used in China as it was elsewhere in the world.

The Royal Society of London

It is generally accepted that the true nature of the symbiotic relationship between legumes and root-nodule bacteria was 'discovered' by Hellriegel and Wilfarth (1886). It was a discovery in the sense that their epic paper finally convinced the majority of the scientific community of the phenomenon of legume nitrogen fixation. The Royal Society of London celebrated the centenary of the discovery with an interdisciplinary symposium. This was organized and its proceedings edited jointly by Fraser Bergersen and John Postgate (130). The contributors were all distinguished in their respective fields and their contributions attested to the advances made in biological nitrogen fixation research in the century 1886–1986.

The Australian Academy of Science

Fraser Bergersen was Foreign Secretary of the Australian Academy of Science from 1989 to 1993. As such he attended meetings of the International Council of Scientific Unions (ICSU now the International Council for Science). He was active in fostering bilateral relationships, particularly the exchange of scientific personnel, between Australia and the United Kingdom, China, Japan, France, Chinese Taipei and Finland. He did much to promote the inauguration

international scientific conferences. In recognition of the significance of this meeting, its inaugural session at Africa Hall, Addis Ababa, was opened by His Imperial Majesty, Haile Sellassie I, Emperor of Ethiopia. Later, delegates were invited to attend a dinner at the Emperor's Jubilee Palace. Emperor Haile Sellassie, himself a committed internationalist, hosted the dinner. In later years, Fraser took pleasure in recounting the events of the occasion, the intense formality of the surroundings, and the charisma of Haile Sellassie and his willingness to chat informally with the delegates to the conference.

⁸ Chen's visit to the Canberra laboratories unearthed a series of coincidences: (i) Chen's mentor at Rothamsted was Henry Thornton who had subsequently mentored Phillip Nutman who in turn mentored Fraser

⁸ Bergersen; (ii) some of Chen's studies at Rothamsted involved cytological work on ineffective clover nodules (Chen and Thornton 1940) as did Fraser's early work in Canberra (6, 9, 10); (iii) while at Rothamsted Chen identified the production of an auxin-like compound by clover root-nodule bacteria (Chen 1938) as did one us (JB; Kefford *et al.* 1960).

of the Bede Morris Fellowship scheme, an initiative to commemorate Morris's long-standing association with French scientific institutions.⁹

Fraser's period as the Academy's Foreign Secretary coincided with the intense political and social activity in Eastern Europe that followed the break-up of the former USSR. Although it was beyond Australia's capacity to make any substantial contribution, Fraser Bergersen was concerned for the welfare of emerging scientific initiatives in Eastern Europe and he made sure that his sentiments were aired. Closer to home, he wrote in the concluding sentence of his report at the end of his term as Foreign Secretary that 'it is clearly the case that there are many unfulfilled opportunities for the Australian Academy of Science to develop scientific linkages with our near neighbours'.

The Australian Centre for International Agricultural Research

The Australian Centre for International Agricultural Research (ACIAR) was established following enabling legislation by the Australian Parliament in June 1982. Sir John Crawford was appointed as Chairman of the Board of Management and Professor Jim McWilliam was appointed as the first Director. (Some years earlier McWilliam and Fraser Bergersen had been Plant Industry colleagues.) ACIAR's mission is 'to improve the well-being of people in developing countries and Australia through international collaboration in research and related activities that develop sustainable agricultural systems and appropriate strategies for natural resource management'. Fraser led one of ACIAR's very first projects (no. 8305), 'Development and evaluation of methods to measure biological nitrogen fixation', involving the Rubber Research

Institute of Malaysia and later the Chiang Mai University, Thailand, alongside Australian partners CSIRO Plant Industry and the New South Wales Department of Agriculture. Various legumes are an integral part of the rubber cultivation cycle in Malaysia and of inter-cropping systems throughout South-East Asia, but little was known of their contributions of fixed nitrogen to those ecosystems. The project co-ordinator for Project 8305 was Mark Peoples and David Herridge was a major collaborator. The project lasted four years. It led to the acceptance of the 'ureide assay' as a reliable means of estimating the proportions of plant nitrogen arising from nitrogen fixation in the field. (This assay was to become a standard technique for the determination of nitrogen fixation in legumes-mainly tropicals and sub-tropicals-that translocated the products of their fixation as ureides.) It confirmed the value of inter-cropping legumes with nonlegumes. It trained Malaysian and Thai scientists in practical nitrogen fixation research. A methodological handbook was produced in Thai and in English (Peoples et al. 1989) and more than thirty papers were published. Most significantly, Project 8305 went some way to establishing the credentials of ACIAR as a first-class research organization. It was the forerunner of a number of other ACIAR-funded, Bergersen-led projects in Indonesia, Malaysia and Thailand (and in Australia) and of linkages with the International Rice Research Institute (IRRI) in the Philippines that confirmed Bergersen's reputation as a scientist who could apply his science profitably to fields at home and abroad.

The significance of the work of Fraser and his close colleagues in the development of practical methods for measuring the amount of nitrogen fixed by legumes in the field cannot be over-estimated. Recent reviews of nitrogen fixation world-wide by crop and pasture legumes (Peoples et al. 2009, 2012) list many hundreds of measurements. The majority of them were made using techniques that had been pioneered by Fraser Bergersen, David Herridge and Mark Peoples. (Many similar measurements have been made for leguminous trees and shrubs, e.g. Peoples et al. [1996]). These studies have gone a long way towards our greater understanding of the extent to which legumes contribute to the health and productity of diverse ecosystems.

⁹ Bede Morris was a distinguished Australian medical scientist who specialized, amongst numerous other activities, in the role of lymphocytes in the development of the immune system. Following his tragic death in 1988 in a road accident while on sabbatical leave in France, a group of friends and colleagues in Canberra raised a sum of money to establish an award to encourage visits of young scientists between France and Australia. These funds, later augmented by a grant from Le Fondation de France, are administered by the Australian Academy of Science.

Scientist Emeritus

Fraser Bergersen's official retirement from CSIRO after forty years'service coincided with the occasion of his 65th birthday on 26 May 1994. But it was a retirement in word only it was not in Fraser's nature to abandon his beloved science. Immediately he took up two fellowships—Visiting Fellow in the School of Biochemistry and Molecular Biology at ANU (1994–2007) and Honorary Research Fellow at CSIRO Plant Industry (1994–7).

Fraser rounded off his CSIRO career in appropriate fashion with the preparation of his monograph, 'Research on Biological Nitrogen Fixation in CSIRO Plant Industry, 1952–1998'. He wrote the text in 1999 during a four-week residency at the Rockefeller Foundation's Study and Conference Center in Bellagio, Italy. Assembling the appendices, mainly a citation of the 718 publications that resulted from the research, took a little longer. The monograph was published in *Historical Records of Australian Science* in 2001 (181).

It is a privilege that comes to few scientists to do some of their better work in the twilight of their careers. It should come as no surprise that Fraser Bergersen managed to do so. His period as Visiting Fellow at the ANU was productive. Between 1994 and 2000, he maintained an office in the School of Biochemistry and Molecular Biology, working in the laboratory of David Day on bacteroid and plant respiration and on nitrogen fixation. Fraser had established a strong link with this group a little earlier via his cosupervision of Harvey Millar (now Professor of Plant Biology at the University of Western Australia) as an Honours student. He continued as Harvey's co-supervisor during his PhD, adapting some of his unique methodology to the study of mitochondria from soybean nodules, especially the use of leghaemoglobin in a continuous flow chamber to provide accurate measurements of the multiple oxidases of plant mitochondria (168). Fraser also collaborated closely with an international visitor, Laura Green, on work that led to the discovery of a novel pathway of carbon metabolism in Bradyrhizobium japonicum (178). In addition, he supervised Youzhong Li's project on the products of nitrogen fixation released by soybean bacteroids (180, 183). This latter work was an important confirmation of ammonia as the major product, refuting recent claims to the contrary (Waters *et al.* 1998)—see above. Fraser was a mentor of several other PhD candidates and postdoctoral fellows in ANU's School of Biochemistry and Molecular Biology and provided crucial data for some of their publications. His vast knowledge of symbiotic nitrogen fixation was of great value to students writing their theses and papers; he was highly respected, indeed revered, by those whom he mentored.

Personal Reflections on a Career in Science

Fraser Bergersen took two opportunities for public in-depth reflection on his career. The first was in 2001 as a conclusion to his contribution to *Historical Records of Australian Science* (181). The second was in 2004 when he was interviewed by David Salt (Fenner School of Environment and Society, ANU) for the Australian Academy of Science (2012) in its series, 'Interviews with Australian Scientists'.

Fraser reflected in both 2004 and 2001 on the extent to which the funding and administration of science had changed since he was appointed to CSIRO in 1954, and how this had affected the way scientists went about their work. Prior to about the mid-1970s, CSIRO was funded almost entirely by appropriations from the Australian Federal Treasury, and external funding was miniscule. So, for the first half of his career, Fraser and others like him were able to pursue topics the development of which occupied a substantial time-frame, and were able to take a research field from infancy towards maturity. In more recent times, as CSIRO research has become almost entirely dependent on external funds, such an approach has become increasingly difficult. Few funding agencies wish to support projects that will make continuing demands on their resources. This has had consequences for the flexibility with which science is conducted.

Fraser believed that not all scientists have coped well with these changes. He implied that Australian scientists were fortunate in that change to the funding structure of science had come to Australia later than it had to some other countries. He recalled that his visit to Wisconsin in 1958–9 had been supported by a continuing National Science Foundation grant made to Professor Perry Wilson. He observed that every branch of science agrees that long-term public-interest academic research is essential as a support base for the more applied studies so beloved of many funding agencies. Finally, he asserted that scientists must learn to use today's funding structures in ways that are good for science as a whole.

In the conclusion to his contribution to Historical Records of Australian Science (181), Fraser reflected on the administration of science and some of its modern frailties. He expressed his admiration for the administrative tenets of Professor Max Perutz, founder of the Laboratory for Molecular Biology at the University of Cambridge: '(i) choose outstanding people and give them intellectual freedom, (ii) show genuine interest in everybody's work and give younger colleagues credit, (iii) facilitate interchange of ideas no secrecy, (iv) enlist skilled support staff who can design and build apparatus and instruments'. It was precisely these principles, espoused by four successive Chiefs of CSIRO Plant Industry-Otto Frankel, John Falk, Lloyd Evans and Jim Peacock, that gave Fraser Bergersen the freedom he needed to pursue his studies of biological nitrogen fixation in his own way. Without it, he could not have achieved what he did.

Honours and Politics

Fraser Bergersen was elected a Fellow of the Royal Society of London (FRS) in 1981 and of the Australian Academy of Science (FAA) in 1985. This was a juxtaposition of the usual sequence and it was a rare and significant event. Fraser was proud of it.

At one time, not so much earlier, someone who had been elected FRS and who had moved to Australia was virtually guaranteed immediate election as FAA. As some sort of corollary, for people working in Australia, FAA tended to be seen as 'a mere staging post on the way to election' as FRS. The existence of this nexus was first publicly questioned by the then President of the Australian Academy, Sir Macfarlane Burnet, at a Royal Society meeting in 1967. Burnet argued that the arrangement was not in the better interests of the independence and prestige of the Australian body. One of his propositions to rectify the arrangement was quite radical. He suggested that 'the Royal Society be asked to accept no further Australian nominations for

election as Fellow', but that suggestion got little support. In time, however the nexus began to 'break down of its own accord'. By 1991, as Rod Home (1991) colourfully put it, 'the painter [between the Australian Academy of Science and the Royal Society] has, if only recently, been cut'. Testimony to Home's viewpoint is the fact that Fraser Bergersen had to wait four years from the time of his election as FRS in 1981 before he became a Fellow of the Australian Academy of Science in 1985.¹⁰

Fraser Bergersen—His Religion and His Science

Fraser Bergersen came from a religious background and he married into a religious family. He was a believer in God. He was one of the very few scientists of our acquaintance who was comfortable with the perceived contradictions of science and religion. We were puzzled. Upon enquiry, we came to the realisation that Fraser's religion and his science were both equally real for him. At the time of his death, he had been a committed member of the Canberra Baptist Church for very many years. The Baptist faith is essentially a lay movement without hierarchy and, indeed, it is a very democratic movement. This was a philosophy that Fraser found most appealing. As a respected senior member of the Church, Fraser was, from time to time, approached by other parishioners for advice or guidance which he gave gladly and with sincerity.

Although he spoke little about his religion in his research environment and little about his science in his church environment, Fraser Bergersen did not live two lives. He found no intellectual conflict between his religion and his science. He was able to integrate the two in a way that made him spiritually comfortable. That was a fortunate circumstance.

The respect with which Fraser was held as both Christian and scientist was manifest in 2002 when he was appointed to a committee that was charged with reporting to the Archbishop of Canberra and Goulburn on the implications

¹⁰ In writing this paragraph we have drawn heavily on Rod Home's intriguing paper 'A world-wide scientific network and patronage system: Australian and other "colonial" Fellows of the Royal Society of London' (Home 1991). Indeed, passages between quotation marks are direct quotes from the paper.

of stem-cell research. The result was a paper that formulated a response to the issue that was balanced both ethically and theologically.

Family Man

As befitting one with a demanding occupation, Fraser Bergersen's relaxations were simple ones. He came from a background that was musical, was a violinist himself and had a pleasant singing voice; Gladys was a pianist and played the organ at church services. Music played an important part in the Bergersen household and Fraser and Gladys were avid concert-goers. Fraser's musical taste was classical and background music was a theme in the home-played at higher volume when Gladys was out than when she was at home. Fraser's and Gladys' love of music rubbed off on to their family. Their children were encouraged in their playing of instruments and there was great pride in the musical accomplishments of their grandchildren. At Fraser's Thanksgiving Service, his elder son Philip remarked on the extent to which he and his two siblings, Jennifer and Peter, had absorbed so many of life's skills from their father.

Fraser's garden was informal yet immaculate. He grew summer and winter vegetables as well as ornamentals that were a thoughtful balance between annual and perennial. Sometimes his science intruded into his garden. Earthworms from the compost heap were a source of haemoglobin; nodules from legume roots were used to isolate strains of rhizobia.

Fraser and Gladys had a wide circle of friends from a wide net of acquaintances. Prominent among them were friends that they made through science. Janet Spent was typical. She remarks that 'I was fortunate to spend two periods of several weeks at CSIRO Plant Industry during the time when Fraser was at his most active. Although not working directly with him, I followed his seminal work with great interest. I had the pleasure of Fraser's and Gladys' hospitality at their home. Subsequently, Peter (my husband) and I enjoyed having Fraser stay at our house in Wormit (Scotland) during one of his European trips. Although he was usually considered not to be particularly gregarious, we found his company most entertaining'.

But the Bergersens' oldest and closest friends were drawn from their church community. Both Fraser and Gladys loved being part of the Church, they were active in church life and they valued the fellowship and the mutual support. Fraser's friends rightly regarded him as a great scientist, as a good church man and, above all, as a gentleman.

Honours, Awards and Appointments

During his illustrious career, Fraser Bergersen was the recipient of many distinctions and significant appointments. They include:

1951	Research Associate, Bacteriology
	Department, University of Otago
1952	BSc (NZ)
1952	Lecturer, Bacteriology Department,
	University of Otago
1954	MSc (NZ) 1st Class Hons
1954	Appointed to the CSIRO Division
	of Plant Industry as Research
	Officer
1958–1959	National Science Foundation
	Fellow, University of Wisconsin
1960	Promotion to Senior Research
1700	Officer, CSIRO
1962	DSc (NZ)
1963	Promotion to Principal Research
1705	Officer, CSIRO
1967	Promotion to Senior Principal
1707	Research Scientist, CSIRO
1968	David Rivett Memorial Medal
1969	Australian Convenor, Nitrogen
1707	Fixation Sub-Committee,
	International Biological
	Programme
1969–1994	0
1)0)-1))+	Biology & Biochemistry
1970	Member, Australian Inoculants
1970	Advisory Committee
1971	Symposium Convenor Pacific
	Science Congress Various times
	Consultant (nitrogen fixation) to
	FAO, UNESCO, UNEP, IITA,
	the Rockefeller Foundation
1972	Committee Member, Review of
	the New South Wales Department
	of Agriculture
1972	Promotion to Chief Research
=	Scientist I, CSIRO
1973	Nuffield/Underwood Travelling
	Fellow, University of Sussex
	, - · · · · · · · · · · · · · · · · · ·

1974–1979	Member, International Advisory
	Committee, Programa Fixãçao
	Biológica de Nitrogénio,
	EMBRAPA, Brazil
1976	Member, New South Wales
	Advisory Committee on Research
	in Agriculture
1979–1985	Program Leader, Nitrogen in
	Agriculture (CSIRO Plant
	Industry)
1981	Elected FRS (Fellow of the Royal
	Society of London)
1982	Promotion to Chief Research
	Scientist II, CSIRO
1985	Elected FAA (Fellow of the
	Australian Academy of Science)
1985	Chairman, CSIRO/ANU Research
	Grants Committee
1987–1993	Member of Council, Australian
	Academy of Science
1989–1993	Foreign Secretary, Australian
	Academy of Science
1994–1997	Honorary Research Fellow,
	CSIRO
1994–2007	Visiting Fellow, Australian
	National University
1997	Resident, Bellagio Study and
	Conference Center of the
	Rockefeller Foundation
2000	Appointed AM (Member in the
	General Division of the
	Order of Australia)

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We are particularly grateful to members of the Bergersen family who helped us fill gaps in this memoir. In 1997 while at Bellagio, Fraser compiled a personal memoir entitled 'Roots in New Zealand, branches in Australia'. Thanks to Fraser's wife Gladys, we were given access to this document; it proved a comprehensive source of information about Fraser's antecedents. Thanks to Fraser's son Philip, we were able to read the transcript of the eulogy that he gave at the Thanksgiving Service for his father; we have used extracts from this tribute, sometimes verbatim, in writing about Fraser Bergersen, the family man. It is a special pleasure to acknowledge Rev. Dr Thorwald Lorenzen, Professor of Theology at Charles Sturt University and Pastor of the Canberra Baptist Church, who willingly

gave us guidance about Fraser Bergersen's religion in particular and about the Baptist Church in general. In 2004, Fraser gave an interview for the Australian Academy of Science as part of the Academy's 'Interviews with Australian scientists' series. We are indebted to the Academy for its electronic publication of the interview; it was a valuable source of Fraser's recollectons and reflections about his own career and about contemporary changes in the conduct of science. Helen Kaminski and Rosanne Walker, respectively, lent us archival material from CSIRO Plant Industry and the Australian Academy of Science. Cyril Appleby was especially informative about that seminal part of Fraser's research that helped elucidate the role of leghaemoglobin in legume nitrogen fixation. Cyril Appleby, David Herridge, Elainne Leach, Jim Peacock and Mark Peoples read a penultimate draft of the manuscript for us and each of them made contributions to its content and accuracy; we thank them sincerely. The photogragh of Fraser Bergersen was taken by the Godfrey Argent Studio, London.

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