BIOGRAPHICAL MEMOIRS

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David Jenkinson was one of the most influential soil scientists of his generation, bringing new insights into the transformations of organic matter and nitrogen in soil. He spent the majority of his career at Rothamsted Research, Harpenden, UK. His studies were influential regarding the role of soil carbon stocks in the context of climate change and the role of nitrogen fertilizer in delivering adequate supplies of food for a growing world population. His research encompassed both fundamental studies on soil processes and immensely practical applications of this knowledge, often utilizing the Rothamsted long-term experiments that have run for over 170 years. He is particularly well known for his development of a method for determining the quantity of organic carbon held in the cells of living micro-organisms in soil, termed the ‘soil microbial biomass’. This breakthrough opened the way for a new wave of soil biological research. David developed one of the earliest computer models for the turnover of organic carbon in soil, known as the Rothamsted Carbon Model, RothC. This model, conceptually very simple, has proved highly successful in simulating and predicting changes in soil organic carbon (SOC) content under different management practices worldwide, being used by over 2600 people in 115 countries. His research using the stable isotope of nitrogen, $^{15}$N, in large-scale field experiments drew attention to the factors leading to inefficiencies in the use of nitrogen fertilizer but also demonstrated that it is possible to achieve high efficiency if good agricultural management practices are followed. It also demonstrated, more clearly than previously, the great importance of soil organic matter as a source of nitrogen for crops and the role of the soil microbial biomass both in immobilizing a proportion of applied fertilizer nitrogen and also in causing confusion in the interpretation of such experiments. By calculating nitrogen budgets for the Rothamsted long-term experiments he quantified

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the deposition of nitrogen compounds from atmosphere to land, laying foundations for later studies concerning the ecological and agricultural impacts of this significant input of nitrogen.

**FAMILY BACKGROUND AND SCHOOL**

David Jenkinson was born in Hollywood Hospital, Beverley Hills, Los Angeles, on 25 February 1928. He was, however, every inch an Irishman and would occasionally mention this unexpected birthplace to new acquaintances in order to tease them. His parents, Hugh and Isabel Jenkinson, had moved to California from Northern Ireland in order to pursue his father’s business interests. David later said that his father had become ‘a very wealthy man and shrewd investor’. He had worked his way to this situation through a series of occupations, mostly involving buying and selling of various products. David remembered the relative wealth of their Californian home because it had a telephone, gas, electricity and running water – very different from the rural Northern Ireland that he would soon experience.

His father’s investments were hit hard by the 1929 Wall Street Crash and in 1932, a year after David’s brother Donald was born, he decided to move the family back to Northern Ireland, where he bought a house with a 40-acre (16-hectare) farm between Armagh and Portadown. However, David described this move as a form of retirement as the farm was too small to be truly economic, although it still involved hard work by family and a few employees. David’s second brother, Jim, was born in 1937, after the family’s move back to Northern Ireland.

David had many childhood memories of tedious farm tasks, including picking fruit in the rain (the fruit being sold to a local jam factory), helping with cattle and sheep, and rounding up hens at night into the henhouse so that they were protected from attack by foxes. He learned about many aspects of farm life during his childhood because several relatives nearby had farms. He became strongly aware of the back-breaking nature of farm labouring and in later years had little time for people who extolled the virtues of ‘traditional’ farming methods but conveniently overlooked the physical effort involved.

During his childhood in this rural setting he became fascinated by natural history. He later recalled the wide range of flowers and birds in the unfertilized meadows and exploring a local quarry with his many cousins. During his years at primary school he became interested in growing vegetables through the influence of the headmaster, who was a Fellow of the Royal Horticultural Society. He taught the children some basic botany and had a garden at the school, which was divided into plots, with each class being responsible for one of them.

David was also encouraged in his gardening efforts by his mother, growing both flowers and vegetables – but vegetables were his main interest. At home, Arthur Mee’s *Children’s Encyclopaedia* was the main source of information on botany, geology and astronomy and greatly enjoyed by the two older boys. This was supplemented by books on birds and wild flowers bought by their mother and aunts. Even when David was still at primary school he was a frequent visitor to the county museum in Armagh, where he learned about the pre-history and archaeology of Ireland, in addition to botany, geology and more recent history. Because he was such a frequent visitor he got to know the curator, Mr. T.G.F. Patterson, who was very encouraging with children and would take items out of the cases to show them. David collected natural history specimens and kept records of the nesting of birds from a young age.

In 1940, during the Second World War, David began his secondary education after winning a scholarship as a ‘day boy’ (as opposed to a boarder) at the Royal School, Armagh. He did not
David Stewart Jenkinson

David did a great deal of reading before going to the Royal School but, during his time there, his outside reading almost ceased because of the time required for homework. But one outside interest did flourish – electronics and radio. He and his brother Donald were encouraged in this by an uncle who had trained as an electrical engineer and provided them with various components. They constructed radios and sometimes became unpopular with their parents because they took batteries from other appliances to run their constructions – batteries were essential at the house because there was no mains electricity and the adults were anxious to listen to their own radios for news of the war. David considered that both he and Donald benefited in their later careers from their early enthusiasm for making electrical equipment: David went on to use mass spectrometers for isotope studies and Donald to use electrical recording instruments in his research in biophysics at University College London.

At about the age of 11 or 12 David suffered a lengthy period of poor health. His medical problems were not understood at the time and, consequently, not properly treated. One of the outcomes of this was that he suffered from chronic asthma for the rest of his life. His childhood ill-health also led to a pronounced curvature of the spine, which he said gave him an inferiority complex, whereas he had previously been a very self-confident child. On the good side, he later commented that it did get him out of playing rugby!

UNIVERSITY DAYS AT TRINITY COLLEGE, DUBLIN

Despite not enjoying his time at the Royal School Armagh, David did well academically. He won a scholarship to study Experimental Science at Trinity College, Dublin; he also won a Louis Purser prize to add to the scholarship – this was worth £20 per year, a huge sum at the time. In 1946 he started the four-year course, which included physics, chemistry and mathematics. He recalled that Trinity College was then in a poor state, being isolated from the mainstream of both British and Irish academia. He considered that science was badly taught but a new man, Wesley Cocker, was appointed Professor and Head of Chemistry soon after David’s arrival. Professor Cocker and other new staff brought the teaching up to date compared with its previous nineteenth-century state, organized great improvements in the laboratories and started research, which had previously been almost absent. David moved towards organic chemistry and in 1950 took both BA and BSc degrees, obtaining first-class honours in Experimental Science.

He greatly enjoyed his student period in Dublin, making many friends and being involved in student societies and in left-wing politics. He joined the Fabian Society and the Promethean Society, which he described in later years as ‘very wicked and left wing’. When asked what they did in the Promethean Society his reply was that they talked a lot, especially about the ills of Ireland and what could be done to eradicate them. Through this society he made friends with many contemporaries who went on to become prominent in various fields, including law, theatre and Irish politics. Some of the talking was done during long walks in the Dublin Hills; walking in the countryside became a source of enjoyment with his family throughout his
life. Some of the people whom David met through the Promethean Society remained lifelong friends. The Society was named after Prometheus, the Titan hero from Greek mythology who stole fire from the gods, making it available for human use and thus helping the development of civilization. This reflects David’s world view that a logical approach to human problems should prevail and bring about progress, without resorting to religion or ideology.

While in Dublin he developed a love of theatre, literature, music and films. He described himself as being ‘on the edge of the theatrical set’. During his undergraduate years he took a keen interest in films and admitted that he spent an inordinate amount of time at the cinema – which led to a period of low marks during the four-year course that jolted him back into more serious study, leading to his first-class degree.

After completing his bachelor’s degree David was invited by Professor Cocker to continue at Trinity to do research in organic chemistry. He published three papers with Wesley Cocker from his PhD, one of which he described as ‘quite good’ and the others as ‘run of the mill’. He was initially assigned to work on the synthesis of a phenyl-substituted reductone (CHOH = COH-CO-C₆H₅) with the hope that this would be more stable than the parent compound. It transpired that it was readily oxidized and, as anaerobic isolation techniques were not available, could not be crystallized. He did isolate a crystalline aniline derivative and establish its structure using ultraviolet spectroscopy (2)* – a technique he would later apply in his initial studies on the chemical structure of soil organic matter. As this line of work could be pursued no further, Professor Cocker asked him to investigate the loss of non-angular groups during aromatization of substituted tetrahydro-naphthalenes. David showed that ethyl or cyclohexyl groups in the 1-position relative to a methoxy or methyl group in the 8-position were eliminated during selenium dehydrogenation (1, 3).

In 1953 David met Moira O’Brien, who would later become his wife, through watching plays at the many vibrant theatres in Dublin. They found that they had numerous interests in common, including music, theatre, love of nature and walking in the countryside. During walks in the Dublin and Wicklow hills, Moira came to greatly admire David’s breadth of knowledge and thoughtful approach to life. One thing they did not have in common was their religion: David came from a Protestant family, Moira from a Catholic. However, neither of them was committed to their religious background so, in a way, they also had that in common.

**Brief period in industry**

After completing his PhD in 1954, David left Ireland to take up a temporary job with Hedley’s, a soap manufacturing company in Newcastle upon Tyne, working on the development of new detergents. Although he was offered a permanent position there, he turned it down. In part this was because he did not enjoy the work, it not being sufficiently academically challenging, and in part because he did not enjoy living there, as he missed his wide circle of friends in Dublin. He frequently returned to Dublin for visits and he and Moira continued their friendship.

**Starting in soil science: University of Reading**

In 1955 David was appointed as assistant lecturer in the soil section of the Department of Agricultural Chemistry at the University of Reading. He was appointed by Joseph (Joe)

* Numbers in this form refer to the bibliography at the end of the text.
Tinsley, who later became Professor of Soil Science at the University of Aberdeen. The post was for three years, and was one that David modestly described in later years as a ‘temporary junior assistant lecturership’.

Professor Tinsley’s aim was that David would study the chemical structure of soil organic matter using his experience of organic chemistry from Dublin, including the use of types of spectroscopy that were becoming available. David had experience of ultraviolet spectroscopy from his PhD work and now gained access to an infrared spectrometer through friendship with John Goulden at the nearby National Institute for Research in Dairying. Tinsley had purchased an early electrophoresis apparatus and had high hopes that this would be valuable in determining the structures present in so-called humic acids, materials extracted from soil on the basis of their solubility or insolubility in acid or alkali. Results from electrophoresis were not very informative: David concluded during this period that humic materials in soil were immensely complex and not amenable to characterization by the usual chemical approaches. He considered that this was largely because they are not entirely regular compounds, being produced under genetic control. Later he further developed this line of reasoning, postulating that microbial metabolites released into soil were likely to be subject to random abiotic reactions in addition to further biological transformations. Abiotic reactions might be mediated by free radicals, known to exist in soil, or by surface reactions occurring under the influence of clay minerals or metal oxides. If this is the case, it is impossible to assign specific chemical structures to the so-called humic materials; in fact, no two ‘molecules’ of these materials may be the same. This led David to abandon research on soil organic matter chemistry, concluding that it was intractable with the analytical methods then available.

However, he was pleased with one result obtained using infrared spectroscopy. At the time there was a theory, put forward by Selman Waksman, the distinguished microbiologist and winner of the Nobel Prize for Medicine, that humic substances were ligno-proteins derived from reaction between proteins and lignin, from cell walls. Working with John Goulden, David and Professor Tinsley showed that no recognizable signatures for lignin were present in the infrared spectrum of fractions extracted from soil, in contrast to fractions from compost (4, 5, 7), thus disproving the earlier theory. Using infrared spectroscopy they also identified amide bands in a range of humic substances, the first demonstration that these substances contained peptide bonds.

David paid great tribute to Joe Tinsley, from whom he learned the importance of meticulous care in quantitative analytical chemistry – something that David passed on to all who worked with him throughout his career.

**Rothamsted**

David became aware of Rothamsted Experimental Station (now renamed Rothamsted Research) through annual visits when Reading students were taken to see the long-term ‘classical’ field experiments. He got to know some of the staff, especially J.M. (Jack) Bremner, whom he recognized as an immensely able scientist. When a position became available, Bremner encouraged David to apply and he joined the staff in 1957 (Figure 1). He had expected to collaborate with Bremner but, just as David arrived, Bremner left for a sabbatical at Iowa State University. Although he returned for a year, he then made a permanent move to Iowa as a professor, so the collaboration was short-lived – but David
was influenced by Bremner’s rigorous approach to planning experiments and writing papers. Bremner anecdotes were often told to David’s later collaborators. Bremner went on to be elected to the US National Academy of Sciences and is often called the father of soil nitrogen research.

One of Jack Bremner’s pieces of advice that David passed on to others was ‘catch fish you can fry’. This was used in the context of experimental design. Some scientists in the fields of soils and agriculture tend to design large, complex experiments, with numerous treatments addressing a wide range of questions. With such experiments it often becomes impossible to interpret results unambiguously. The phrase is intended to convey the idea of designing small experiments with clear objectives so that results can be interpreted, after which a separate experiment can be designed to address a different question; what should be avoided is any attempt to include all questions in one experiment. This good advice is as valid today as it was when originally given, and is equally often ignored!

 Decomposition of $^{14}$C-labelled plant material in soil

Very early in his period at Rothamsted, David decided that it would be informative to follow the fate of $^{14}$C-labelled plant material as it was decomposed in soil by the microbial population and as some components were synthesized into relatively stable forms of soil organic matter. He was under no illusions about the difficulty of following decomposition against the large background of existing organic matter in the soil. His first paper on carbon decomposition in soils (9) begins with the following statement: ‘There are formidable difficulties in following the decomposition of plant material in soil under natural or near-natural conditions.’ To use
Figure 2. Diagram of chamber for growing $^{14}$C-labelled plants. Reproduced from David Jenkinson’s 1960 paper describing the apparatus (6). © Martinus Nijhoff 1960, used with permission from Springer.

$^{14}$C labelling required a source of uniformly labelled plant material and led him to design and build a growth chamber to achieve this (6). It was basically a large box made from Perspex that contained ryegrass seedlings in pots (Figure 2). Air was passed through and $^{14}$C-labelled CO$_2$ was prepared and introduced into the stream of air. At suitable times the ryegrass was harvested, dried, ground and then added to soil for decomposition experiments. David was among the first scientists in the world to adopt this approach to soil organic matter research and to utilize radioactive isotopes as tracers. His decision had major implications for much of his later research: some uses of the labelled plant material were as he planned, but some led to totally unexpected lines of enquiry.

In the initial experiments (10) the $^{14}$C-labelled plant material was mixed with soils differing in texture and pH and placed in small lysimeters outdoors under field conditions. The lysimeters comprised short lengths of plastic drainpipe with glass fibre fixed to the base, to retain soil but allow water to drain through. These were set into a bed of sand and exposed to normal weather conditions. Replicates were removed after different periods, a sub-sample of soil taken for analysis, and the remainder returned. This was repeated several times during the first year and then less frequently during the next 10 years.

The most striking result was that decomposition could be regarded as a two-stage process. During the first few months it was rapid, with only about one third of the original labelled carbon still present in soil after six months under the temperate climatic conditions of Rothamsted. After this, decomposition proceeded very slowly during subsequent years (10). Later, David repeated this experiment under humid tropical conditions in Nigeria (45), through collaboration with Dr Abateni (Aba) Ayana and others at the International Institute for Tropical Agriculture (IITA), Ibadan, Nigeria. Decomposition proceeded four times faster but followed the same pattern (Figure 3). David concluded from this result that the same fundamental processes were operating in both environments and that it was reasonable to transfer conclusions on processes from one environment to another.
The soil microbial biomass: development of the concept and a method for measurement

An unplanned outcome from the work on the decomposition of $^{14}$C-labelled plant material in soil was the development of the first method to measure the quantity of carbon held in the cells of living organisms in soil – which David termed the soil microbial biomass. This concept and methodology represent one of his major contributions to soil science research, triggering a paradigm shift in the discipline. The concept of measuring the properties of the entire soil microbial population, such as the total quantity of carbon held in all living cells, was not common in the early 1960s; the main focus of soil microbiology was the identification of organisms responsible for specific processes. David’s experiments on the decomposition of $^{14}$C-labelled plant material in soil clearly demonstrated that, within the total stock of SOC, there existed subsections or fractions that differed greatly in their degree of labelling. He reasoned that the most highly labelled fraction would be soil organisms. This conclusion followed less fruitful experiments using traditional alkaline fractionation approaches, leading to so-called humic materials. Many years later David wrote that he had ‘spent far too much time chemically fractionating soils’.

Figure 3. Decomposition of uniformly labelled ryegrass in England (Rothamsted) and Nigeria (International Institute of Tropical Agriculture). Redrawn from (45). Note that timescale, in years, is four times greater in England (upper $x$-axis) than in Nigeria (lower $x$-axis).
Table 1. Labelled and unlabelled CO₂-C evolved by soil exposed to partial or complete sterilization treatments, inoculated with fresh soil and incubated for 10 days at 25°C. The soil had previously been incubated with labelled plant material for one year under field conditions and its organic carbon contained 1.8% ¹⁴C. (Adapted from (11).)

<table>
<thead>
<tr>
<th>Treatment</th>
<th>¹⁴C-labelled (µg C g⁻¹ soil)</th>
<th>Unlabelled (µg C g⁻¹ soil)</th>
<th>Labelled C in evolved CO₂-C (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>None</td>
<td>14.7</td>
<td>146</td>
<td>9.2</td>
</tr>
<tr>
<td>Air-drying</td>
<td>23.2</td>
<td>195</td>
<td>10.6</td>
</tr>
<tr>
<td>Irradiation (0.25 Mrad)</td>
<td>33.8</td>
<td>238</td>
<td>12.4</td>
</tr>
<tr>
<td>CH₃Br vapour</td>
<td>47.5</td>
<td>239</td>
<td>16.6</td>
</tr>
<tr>
<td>CHCl₃ vapour</td>
<td>49.4</td>
<td>259</td>
<td>16.0</td>
</tr>
<tr>
<td>Oven-dried (80°C)</td>
<td>54.6</td>
<td>347</td>
<td>13.6</td>
</tr>
<tr>
<td>Oven-dried (100°C)</td>
<td>56.0</td>
<td>493</td>
<td>10.2</td>
</tr>
<tr>
<td>Autoclaving (120°C)</td>
<td>58.6</td>
<td>524</td>
<td>10.1</td>
</tr>
</tbody>
</table>

David’s realization that soil organisms represented a highly labelled fraction in his ¹⁴C experiments, and the implications of this for the concept of the soil microbial biomass, occurred at a time of active research by others in a totally different field and this coincidence of timing appears to have been significant in the development of his thinking. Plant pathologists at Rothamsted and worldwide were experimenting with soil fumigants, which were broad-spectrum biocides, to control soil-borne plant fungal diseases and parasitic nematodes. It was frequently observed that, even in soils with no apparent pest or disease problem, plant growth was stimulated. In many cases this was attributed to additional mineralization of nitrogen compared to unfumigated soil, though other factors were also thought to be involved, as discussed by David (11) and, later, by Powlson (1975). The source of this additional nitrogen was a matter of interest. As a key aspect of fumigation was the killing of organisms, decomposition of the killed soil microbial cells was considered a likely source, with recolonizing micro-organisms utilizing cells of killed organisms as food, and excess nitrogen from them being mineralized and released as inorganic nitrogen. This would also account for the period of enhanced soil respiration observed following soil fumigation, measured as enhanced evolution of CO₂ and uptake of oxygen. This line of reasoning appears to have been the breakthrough in David’s thinking that led to the idea of using fumigation as a means to measure the quantity of carbon held in organisms before being killed by the fumigant. His thinking was also influenced by the work of H.F. Birch, who had shown that drying and rewetting of soil also led to a flush of CO₂ evolution and mineralization of nitrogen; this study was drawn to David’s attention by N.J. Barrow, an Australian visiting scientist who worked with him on biological fixation of nitrogen in anaerobic soils (8) – another example of cross-fertilization of ideas between different areas of study.

Table 1, taken from David’s classic 1966 paper (11), shows the key results that led to his proposal of using chloroform (CHCl₃) fumigation followed by incubation as a means of estimating the quantity of carbon held in the cells of living soil organisms. He used one of the soils from his ¹⁴C-labelling experiments and measured the amount of CO₂ evolved, and its degree of ¹⁴C labelling, when incubated in the laboratory under standard conditions (25°C for 10 days) after various treatments. ¹⁴C enrichment of the total organic carbon in the soil was only 1.8%, yet the CO₂-C evolved from untreated soil when incubated was more than
five times as enriched (Table 1). This indicated that carbon involved in biological processes leading to CO₂ evolution was far more heavily labelled than the SOC as a whole. All of the treatments tested increased total CO₂ evolution but, importantly, several of them greatly increased the percentage of labelled carbon in the CO₂ evolved. Fumigation with chloroform or methyl bromide (CH₃Br) almost doubled this proportion compared with the CO₂ from untreated soil to around 16% (Table 1). David reasoned that the carbon in cells of microorganisms (the soil microbial biomass) was likely to be the most heavily labelled organic carbon fraction, so a treatment giving the greatest increase in ¹⁴C labelling of evolved CO₂ must be selectively acting on it. Because CHCl₃ was easier to use than CH₃Br, and was thought to be less toxic to humans, he used CHCl₃ fumigation for further work. Although oven-drying and autoclaving increased evolution of labelled CO₂ by a similar amount to fumigation, they also increased evolution of unlabelled CO₂ by considerably more. He interpreted this to mean that these treatments, in addition to killing organisms, rendered additional non-biomass (and more lightly labelled) forms of organic carbon decomposable and thus were less selective.

An important conclusion from the results with labelled soil was that CHCl₃ had very little effect on the rate of decomposition of non-biomass organic carbon in soil. Following this conclusion, and several other simplifying assumptions, David set out the following expression for estimating the quantity of carbon in soil microbial biomass ($BC$) as follows (11):

$$BC = FC/k_C$$

where:

- $FC$ is the flush of decomposition following chloroform fumigation defined as (CO₂-C evolved by fumigated soil during a 10-day incubation at 25°C) – (CO₂-C evolved by untreated soil during the same period)
- $k_C$ is the fraction of the biomass carbon decomposed and evolved as CO₂ during the incubation.

A preliminary value for $k_C$ was derived by growing a ¹⁴C-labelled culture of a single species of soil bacteria, *Nitrosomonas europaea*, adding this to soil and measuring the amount of ¹⁴CO₂ evolved after CHCl₃ fumigation and incubation under the standard conditions. It was found that 28% of the bacterial carbon was evolved (11), giving a $k_C$ value of 0.28 but, to avoid an appearance of spurious precision, this was rounded to 0.3. The value was later revised to 0.45 on the basis of experiments with a wider range of organisms (21).

The 1966 paper (11) also contains descriptions of several experiments designed to test other hypotheses that had been put forward to explain the flush of CO₂ evolution and nitrogen mineralization observed after so-called partial sterilization treatments. The results led to other explanations being rejected. This paper is elegantly written and warrants re-reading today as an example of a clear but closely argued account of complex experiments. Ten years later, David revisited the issues with David Powlson. They examined in detail the impacts of CHCl₃ fumigation on soil metabolism (14) and measured the fluxes of decomposition caused by fumigation, gamma irradiation, air-drying or autoclaving when applied to a range of soils differing in organic matter content, soil type, pH and management (14, 15). These experiments confirmed the earlier conclusions that chloroform fumigation killed soil organisms, rendering them decomposable and giving rise to the flush of decomposition, but had little effect on the decomposability of non-biomass SOC. They also confirmed the conclusions from ten years earlier that effects of treatments involving heating or drying were not specific to organisms...
but also increased the decomposability of non-biomass organic carbon. The flush of nitrogen mineralization following CHCl₃ fumigation was also taken as strong indication of an impact on soil organisms because of the narrow carbon:nitrogen ratio of organisms compared to topsoil organic matter as a whole. The potential for using the nitrogen flush as a measure of the quantity of nitrogen held in the biomass was noted at this time (13, 14), though it was another nine years before a specific method for measuring biomass nitrogen content was established (28) through David’s long-lasting collaboration with Phil Brookes.

The biomass carbon method described above later became known as the chloroform fumigation–incubation (FI) method, so called to distinguish it from the method developed later based on fumigation followed by extraction and termed the fumigation–extraction (FE) method. In a completely independent test of the FI method, a comparison was made of microbial biomass carbon as estimated by CHCl₃ fumigation and as derived from direct microscopy in a set of eight soils (17). A modification of the Jones and Mollison (1948) direct counting method was used. Instead of simply counting total numbers, micro-organisms were classified as spherical (bacteria) or cylindrical (hyphae) and allocated to predetermined size classes. A total biovolume for each soil was derived and a biomass carbon value calculated by making assumptions about dry matter content and carbon concentration of organisms. From this tedious work it was found that, for seven of the eight soils studied, there was a close relationship between biovolume and biomass carbon as measured by FI, and this was taken as strong independent evidence for the validity of the FI method. The conclusion was later strengthened when direct microscopy was applied to a wider range of soils (38).

The direct microscopy work threw up an unexpected observation that intrigued David for many years, and still remains unexplained. If spherical (non-hyphal) organisms were placed in volume classes on a logarithmic basis (e.g., 0.1–1, 1–10 and 10–100 µm³, each class was found to contain an equal biovolume. We still do not know whether this reflects some underlying ecological principle, but it holds for all the soils examined by David and his colleagues (17, 47).

Although the 1966 paper (11) is now regarded as seminal, when looking back some 40 years later, David was amused that it made rather little impact at the time it was published. By contrast, the series of five papers with David Powlson and others (12, 14–17) published 10 years later had considerable impact and led to widespread use of the FI method. The final paper in the 1976 series, giving practical details of the method (16), was classified as a citation classic by the ISI in 1987 and David was invited to write an essay on the work leading to the FI method (34); in early 2017, the 1976 paper had had more than 1600 citations.

Controversies surrounding the chloroform fumigation–incubation method

The FI method immediately attracted controversy, often from the group led by Professor Eldor Paul, initially in Canada and later in the USA. Shields et al. (1974) claimed that the value obtained for biomass carbon was erroneously large and that CHCl₃ was rendering some non-biomass organic carbon decomposable. This led David Jenkinson and David Powlson to conduct additional experiments to test these claims and the results demonstrated them to be unfounded (14, 15).

A remarkable feature of the FI method is that, after fumigation and the dissipation of the initial flush of CO₂ due to the mineralization of the fumigation-killed biomass, the rates of evolution of CO₂ in the fumigated and non-fumigated soils are approximately equal for periods of weeks or even months (e.g. (14), Kemmitt et al. (2008)). This implies that the
small recolonizing population in the fumigated soil, which is also far less diverse than in unfumigated soil (Reber 1967; Dominguez-Mendoza et al. 2014; Chen et al. 2015), can mineralize the large pool of humified and recalcitrant soil organic matter to the same extent as the undamaged population. David and his colleagues David Powlson and Phil Brookes were well aware of this paradox, but it was not until 1984 that it was brought into sharp focus through stinging criticism, again from the group of Professor Eldor Paul. Voroney and Paul (1984) argued that it was inconceivable that the recovery population in fumigated soil could be mineralizing ‘background’ non-biomass organic carbon to the same extent as in unfumigated soil. The CO₂ evolved after CHCl₃ fumigation should be regarded as solely derived from killed biomass and, consequently, it was incorrect to subtract the CO₂ evolved from the unfumigated control soil when calculating biomass carbon.

As is often the case in science, disagreement led to new research aimed at resolving the issue. This culminated in a paper published in 1996 (55), in which the evidence in favour of using the control is clearly set out, finally putting the controversy to rest.

_{Adenosine 5'-triphosphate (ATP) in soil and the adenylate energy charge of the soil population_}

In 1976 David was invited to spend nine months as a Hannaford Research Fellow at the Waite Institute in Australia, to work with Dr Malcolm Oades, who later became Director of the Institute. This was followed by three months working with Dr Jeff Ladd at the CSIRO Division of Soils. With Malcolm Oades, David developed a method for measuring the ATP content of soil (20). ATP is regarded as the ‘energy currency’ of cells and around this time there was growing interest in the energetic state of microbial cells in soil. The method they developed derived from a meticulous study of the numerous factors that can interfere with ATP measurements in soil and even totally invalidate them. A key factor is the necessity to deactivate ATPase enzymes; otherwise ATP released from cells is rapidly degraded, thus giving an erroneously low value. They selected trichloracetic acid as the basis for the extractant because of its effectiveness in deactivating enzymes. Two years earlier Paul and Johnston (1977) had published an alternative method that consistently gave smaller values for soil ATP concentration. David was convinced that this was because of the failure to stop ATPase activity in their extractant, a difference of opinion leading to another long-running dispute. David’s interpretation was later vindicated by work he did with Phil Brookes and Kevin Tate from New Zealand, who spent a sabbatical at Rothamsted (24, 35).

Where correct methodology was used, David and others in many subsequent studies found a remarkably close relationship between soil ATP content and microbial biomass carbon as measured by FI or related methods ((19,40), Contin et al. 2001). This was taken as yet another independent test of the idea that soil microbial biomass carbon could be reliably measured by chloroform fumigation, first by the FI method and later by the FE method described below. In addition, ATP has been used as an alternative way of estimating biomass carbon based on the observed constancy of the ATP concentration in biomass (Figure 4).

The high value observed for ATP concentration in the soil microbial biomass was a complete surprise, being typical of a population undergoing active growth, yet the energy input to soil is generally small compared to the size of the population, so a low-energy state would be expected. David pursued this line of work with Phil Brookes and Kevin Tate, developing a method for measuring the adenylate energy charge (AEC) of the soil microbial population. AEC is defined as a linear measure of the metabolic energy stored in the adenylate energy
Figure 4. Close relationship between microbial biomass carbon content of aerobic soils as measured by the chloroform FI method and soil ATP content using acid extraction methods. Redrawn from (40).

pool (Atkinson 1977): $\text{AEC} = \frac{[\text{ATP}] + 0.5(\text{ADP})}{[\text{ATP}] + (\text{ADP}) + (\text{AMP})}$. In actively growing cells it is stabilized between about 0.8 and 0.95, but it can theoretically range from 0 (all AMP) to 1.0 (all ATP). Lower values indicate a population that is stressed, senescent or incapable of cellular biosynthesis (Atkinson 1977; Karl 1980).

David and his colleagues found soil AEC to be surprisingly high, in the range 0.8–0.9. The combination of a large soil microbial biomass content, which must be in a largely resting state yet maintaining a high concentration of ATP, and a high AEC value, raises many questions regarding the survival strategies and ecology of soil microbes that are still unresolved. David’s work was instrumental in drawing attention to these. In 2005 he wrote the following:

Treating the soil biomass as an undifferentiated whole is of course a gross over-simplification: any proper understanding cannot ignore the role played by the different components of the system – the bacteria, actinomycetes, fungi, algae, the protozoa and the larger soil animals, or their interactions with each other and with plant roots. Nevertheless I believe it is a useful simplification, if only to bring into focus the energy limits within which the whole system must work. (Personal communication)

Later developments with microbial biomass measurements: extraction methods for carbon, nitrogen and phosphorus

For all its benefits, the FI method had several significant drawbacks. Major ones were its unsuitability for use in acid soils, as shown in the 1976 series of papers (15), and the fact that it cannot be used in soils following recent additions of substrate such as fresh plant material. In 1985 an American PhD student, Eric Vance, joined David’s group as a Fullbright scholar. His aim was to investigate, with Phil Brookes, the use of the FI method in acidic forest soils. Eric showed that the reason for the failure of FI in acidic soils was that mineralization of
non-biomass soil organic matter was largely inhibited in fumigated acidic soils (37, 38); so it transpired that, in the special case of strongly acidic soils, the contention of Voroney and Paul (1984) regarding the invalidity of the control was correct. Eric also showed that the extra carbon made soluble by CHCl₃, and extractable by 0.5 M K₂SO₄, was closely related to soil ATP content and so could be used as an estimate of biomass carbon (38). This gave rise to the FE method for biomass carbon, and the paper describing the method (36) remains the most widely cited paper in the journal *Soil Biology & Biochemistry*, currently at over 4500 citations.

Using similar reasoning to that leading to the FE method, David was active in stimulating research to develop methods for measuring phosphorus (22, 25) and nitrogen (26–28) in the soil microbial biomass.

### Modelling the turnover of organic carbon in soil: the RothC model

In the mid-1970s David embarked on modelling the dynamics of SOC through collaboration with James Rayner, a talented mathematician working in the same department at Rothamsted. David was convinced that developments in computing made modelling a productive way forward in soil carbon and nitrogen research. They produced the first model to be developed in this period, which became known as the Rothamsted Carbon Model (RothC; 18), which subsequently went through various versions as understanding developed; Figure 5 shows the structure of the current version (54, 57, 60). David was well aware that soil organic carbon and nitrogen must exist in a continuum of forms ranging from highly dynamic to very stable. However, in the 1970s, he and most others embarking on such work considered that treating soil organic matter as several discrete fractions or pools, each having a defined turnover rate,
was a reasonable simplification and made mathematical description of the processes, and ultimately modelling, more tractable.

Incoming plant material or manure was regarded as being composed of two compartments, termed ‘decomposable plant material’ (DPM) and ‘resistant plant material’ (RPM), the ratio of DPM to RPM being adjusted to represent different types of material. Jenkinson and Rayner found that, for simulating short-term changes in soil organic matter content, it was sufficient to have two compartments to represent the organic carbon in soil, one with a slower turnover rate than the other. But in order to match longer-term data a third compartment was needed that turned over extremely slowly. A further reason for requiring a very stable pool was the observed great age of at least part of the carbon in soils found by David using radiocarbon dating applied to soils from the Rothamsted long-term experiments (48). In the original versions of the model (18), microbial biomass (BIO) was used as the soil carbon compartment turning over most rapidly, with a turnover time of 2.4 years. The other two soil carbon compartments were termed ‘chemically protected organic matter’ (COM) and ‘physically protected organic matter’ (POM); these names represented thinking at the time about the mechanisms leading to stability of organic matter in soil. The turnover times of POM and COM were 71 and 2857 years, respectively. David later abandoned the COM and POM compartments on the grounds that there was no experimental means of determining them separately. In later model versions (39, 44, 54, 57, 60) COM and POM were replaced by ‘humus’ (HUM) and ‘inert organic matter’ (IOM), as in the current version shown in Figure 5.

IOM, a somewhat controversial concept, and often accounting for about 10% of total soil carbon, was introduced to represent two types of carbon. One was carbonized material such as charcoal, which occurs in many soils in small quantities; the other, more importantly, consisted of some forms of organic carbon that, while perhaps not 100% stable, had such a long turnover time that assigning the pool an infinite value was a reasonable approximation.

In 1996 a soil carbon model evaluation exercise was held at Rothamsted, organized by Pete Smith, in which a range of SOC models were tested for their ability to simulate trends in soil carbon content in 12 long-term experiments from contrasting situations worldwide. RothC was one of a set of five models that were equally successful in matching measured data on total SOC content (56) but David pointed out that RothC was unique because simulated values for biomass carbon could be compared with measured data and used as a second test of its validity. He was unhappy with a tendency for modelling to be divorced from experimental science and argued for the approaches to be strongly interactive. He once encapsulated his approach in the following memorable statement in a lecture: ‘Experimenters should do their experiments with models in mind and modellers should do their modelling with experiments in mind.’

RothC can be used in two different ways. It can be used in ‘forward mode’ to predict how known changes in management, such as the amount of plant debris entering the soil annually, will alter the stock of carbon held in that soil; this is the most obvious and common way of using such models. But it can also be used in ‘inverse mode’ to calculate the quantity of organic inputs that must be entering the soil annually to maintain a particular measured stock of organic carbon. By using it in inverse mode it is possible to estimate net primary production (NPP) of the vegetation growing on the soil (48, 51, 53, 59, 61) after taking account of plant removals, such as in harvested plant materials. In either mode an output from the model is the amount of CO₂ evolved from the soil, of obvious interest in studies concerning greenhouse gas emissions and climate change.
For many years, all versions of RothC applied to a single surface layer of soil, normally
the plough layer in an arable agricultural soil, or its equivalent. Later, working with Kevin
Coleman, David developed a version that simulated soil carbon changes in consecutive soil
layers (69) using data from the Rothamsted long-term experiments (65, 68), obtained through
experimental work by Paul Poulton, Phil Brookes and others.

The RothC model continues to be widely used, in both research and teaching: in early 2017
the total number of registered users was over 2600, drawn from 115 different countries, and
including 379 new users in the previous year. David was pleased with the impact made by the
model; he once wrote that ‘RothC has been widely used and even more widely plagiarized’.
He was keen to keep models simple, once summarizing his approach by saying that he aimed
for a model that is ‘as simple as one can get away with whilst still giving results that are
somewhere near the truth’.

**Soil carbon, the global carbon cycle and climate change**

David was among the first in the soil science research community to recognize the significance
of the world’s soil carbon stocks in the context of climate change – either accelerating
global warming through additional release of CO₂, or slowing it by locking up additional
carbon through increased plant growth, leading to additional carbon entering the soil via
roots or residues. His paper in *Nature* in 1991 (46) was the first quantitative assessment of
the reinforcement, or positive feedback, to climate change through increased decomposition
of soil organic carbon in a warmer world. It was achieved by innovative use of the RothC
model and indicated that the additional CO₂ released from soil was likely to be significant,
but not sufficient to cause a runaway reinforcement effect. It was estimated that, in the next
60 years, increased temperature was likely to cause an additional evolution of CO₂ from
SOC decomposition equivalent to about 19% of projected fossil fuel emissions over the same
period.

Some 13 years later, David and his colleagues were approached by scientists from the
Hadley Centre for Climate Research and this led to a collaboration in which RothC was
linked with the Hadley Centre’s Global Circulation model. The study also showed a positive
feedback to climate change through increased SOC decomposition (66) and demonstrated the
importance of appropriate modelling of soil carbon stocks; earlier studies by global climate
scientists had treated soil carbon as a single unit instead of a more complex multi-compartment
entity. This study was one of the earliest attempts to treat soil carbon dynamics seriously in
the context of climate change.

In 2010 David published a comprehensive account of the factors influencing climate
change, both natural and anthropogenic (70). It was written for people who were technically
or scientifically literate and had some interest in the subject, but not specialists in climate
science. He recognized the need for this when one of his sons was given responsibility for
environmental matters within a multinational engineering company and needed information
on climate change: but he had not expected it to grow into a 100-page document! The title of
the article is typical of his practical approach to a complex subject that has major ramifications
for many people: ‘Climate Change: a brief introduction for scientists and engineers – or
anyone else who has to do something about it.’

Since the 1990s there have been many claims that climate change can be significantly
slowed through sequestration of carbon in agricultural soils through reduced tillage, land-use
changes such as afforestation, or greater returns of plant residues or manures to soil. David
was sceptical, considering that some of the claims were greatly exaggerated. Using RothC in inverse mode is a means of estimating the quantity of organic inputs required to increase SOC by a given amount, and thus assess whether a claimed rate of increase is feasible. Following a conference held in his honour in 2009 entitled ‘Soil Organic Matters’, three of David’s colleagues wrote a review paper to reassess the issue of carbon sequestration in soil (Powlson et al. 2011), partly inspired by his views. The paper, entitled ‘Soil carbon sequestration to mitigate climate change: a critical re-examination to identify the true and the false’ was published in a special issue of the European Journal of Soil Science, but was unfortunately published just after his death in 2011.

Nitrogen transformations in agricultural ecosystems and the efficiency of use of nitrogen fertilizer

Although his early work at Rothamsted concentrated on relatively short-term studies that were often laboratory-based, David was always aware of the Rothamsted long-term experiments, of which the Broadbalk Wheat Experiment was the earliest, having started in 1843. He quickly appreciated their value and later began collaborations with A.E. (Johnny) Johnston, one of the main experts on the experiments (Figure 6). David was fascinated by the fact that soil carbon and nitrogen content in several plots in the Broadbalk Experiment was at ‘steady state’, being constant over many years, so that inputs were in balance with outputs. This enabled significant simplification to mathematical treatment and modelling. There was a particular fascination in the case of nitrogen because the ‘nil’ plot, receiving no fertilizer or manure since 1843, still gave a small yield of wheat which removed about 15–20 kg N ha⁻¹ yr⁻¹; yet the soil organic nitrogen content did not decline. This meant that there must be an input of nitrogen from external sources at least equal to the removal.

David encouraged his soil microbiologist colleagues Peter Dart, John Day and John Whitty to assess whether biological nitrogen fixation was a feasible source of nitrogen. Although they found evidence of some nitrogen fixation activity by cyanobacteria in Broadbalk soils (Whitty et al. 1977), it seemed unlikely to be sufficient to account for the necessary input. This led to the proposal that nitrogen was entering the soil/crop system from a combination of inorganic nitrogen dissolved in rain and so-called ‘dry deposition’ of nitrogen from gases or particulates. Nitrogen inputs in rain were well understood and had been measured at Rothamsted over many years (Brimblecombe & Pitman 1980; Goulding et al. 1986; Goulding & Poulton 1985). However, in the 1960s little attention had been given to deposition of nitrogen from the atmosphere in gaseous or particulate forms: this mechanism is now well known and its environmental impacts a matter of considerable concern (RoTAP 2012). Subsequent measurements at Rothamsted by Keith Goulding and colleagues confirmed that substantial inputs were occurring in this way (Goulding 1990; Goulding et al. 1998). At their peak in the 1990s, total atmospheric deposition was up to 45 kg N ha⁻¹ yr⁻¹ to arable crops and perhaps 100 kg N ha⁻¹ yr⁻¹ or more to woodland (Goulding et al. 1998), with potentially significant effects on carbon sinks (62, 63). Deposition has now decreased to no more than 25 kg N ha⁻¹ yr⁻¹ due to reductions in emissions of nitrogen oxides from industry and vehicles and of ammonia from agriculture.

During the 1960s and 1970s the rates of nitrogen fertilizer applied to crops by farmers in the UK and Europe increased greatly and nitrogen came to represent a major part of their input costs. This trend in agriculture inevitably led to interest in measuring the efficiency of use of applied nitrogen and ways of increasing this, and thus saving costs. In addition, there was a
growing recognition of the environmental implications of nitrogen escaping from agricultural land to the wider environment. Initially the focus was on nitrate reaching drinking water or contributing to eutrophication of surface waters but increasingly the focus moved to the gaseous emissions of nitrous oxide and ammonia. During the late 1970s David, in discussion with ‘Johnny’ Johnston and David Powlson, started planning a major new programme on nitrogen use in agriculture. He identified the opportunity for using $^{15}$N-labelled fertilizers as this allowed nitrogen from fertilizer to be distinguished from the large background of nitrogen present in soil organic matter.

David was clear that, for any new research using $^{15}$N-labelled fertilizer to be meaningful, it must be based on crops growing in open field plots under realistic agronomic conditions, and not in pots or small enclosed containers in the field, as in most previous work. In addition to these practical drivers for research on nitrogen fertilizers and the academic interest in nitrogen cycling in agro-ecosystems, David recognized that technical developments in isotope-ratio mass spectrometry now made a large-scale programme feasible. Furthermore, the cost of purchasing $^{15}$N-labelled compounds, while still high, had decreased to a level that made field studies possible within a realistic budget. He persuaded the head of department and took delivery of a new mass spectrometer in 1979 to facilitate a programme that was funded largely
by grants from the then UK Ministry of Agriculture, Fisheries and Food (MAFF) over more than ten years (Figure 7).

At the outset David and his colleagues developed the necessary methodology. One requirement was a method of sample preparation for converting the nitrogen in crop and soil samples into nitrogen gas for analysis in a mass spectrometer; as well as delivering the required accuracy, the method had to be suitable for analysing the large numbers of samples expected from the field experiments. The method developed ((30); Figure 8) was used for many thousands of samples over the coming years, though it was later superseded by developments permitting linkage of an elemental analyser directly to an isotope-ratio mass spectrometer. The other practical requirement was a method for applying $^{15}$N-labelled fertilizer to experimental plots in the field. It was decided that, despite the cost of $^{15}$N, labelled plots had to be large and set within normal agronomic experiments. It was finally concluded that $^{15}$N-labelled plots measuring 2 m $\times$ 2 m were appropriate and these would be set within normal agronomic plots and be subject to as near normal agricultural operations as possible. It was essential that a predetermined quantity of $^{15}$N-labelled fertilizer was applied to the soil surface extremely uniformly. Using solution rather than solid made it easier to achieve an even spread but the standard methods of application tested were found to be either too slow
Figure 8. The $^{15}$N-fertilizer applicator described in (23) designed and built at Rothamsted, being used by Dr Andy Macdonald in a field experiment. Photograph taken by David Powlson. (Online version in colour.)

or to give uneven application. Eventually David and colleagues worked with engineers in the Institute’s workshops, Adrian Hobbs and Terry Woodcock, to design and build an applicator based on a peristaltic pump that gave reproducible and accurate delivery and was sufficiently rapid for applying solutions to a large number of field plots (23). The machine (Figure 8) was hand-operated and delivered solution to a $2\,\text{m} \times 1\,\text{m}$ area; larger plots were built up from this. The machine was quite heavy and had the general appearance of an old-fashioned iron bedstead. In the paper describing the spreader it is stated that ‘it weighs 62 kg when complete and can be carried by two people’ – an important point as it sometimes had to be carried several hundred metres across fields to reach experimental sites, then lifted numerous times between plots. There was some amusement among the team after gaining experience of carrying it on many occasions: in an earlier draft of the paper, David had said ‘it could be easily carried by two people’.

Another factor vital to the success of the programme was the decision on the soil sampling method used. In order to obtain soil representative of the $^{15}$N-labelled plot, it was clear that a large volume had to be sampled. David and his colleagues designed a method in which two holes, each of 30 cm diameter, were drilled to a depth of 23 cm (plough depth) using a suitably modified commercial post-hole borer of the type used by farmers to make holes for inserting fence posts. The volume of the holes had to be precisely predetermined and the soil carefully weighed to ensure that results were quantitative. This procedure was very laborious and challenging for the team, especially when the drill hit a large stone. The sampling method led to some 50 kg of soil being obtained from each replicate $^{15}$N plot. This was sieved to a mesh size of 6.25 mm (1/4 inch), a small sub-sample taken, and the majority of the soil returned to the hole. Somewhat narrower diameter holes were drilled for sampling deeper soil layers. The procedure, involving returning most of the soil to the hole after expending so much effort to remove it, caused some amusement when explained to members of the public passing the experimental sites!

After David’s retirement in 1988, leadership of the nitrogen programme was taken by David Powlson. Both he and David Jenkinson were clear that the success of this work –
which was probably the largest field-based study using $^{15}$N-labelled fertilizer in the world – owed a great deal to the skills and dedication of talented colleagues. In the early days the meticulous analytical skills of Gordon Pruden were vital; the group was shocked by his untimely death in 1984. Subsequently, Paul Poulton and Andy Macdonald brought vital skills in both field experimentation and analytical chemistry, as well as scientific insights. Numerous technical staff, students and visiting scientists also made valuable contributions, with Phil Hart, a PhD student from New Zealand, making particularly crucial inputs in the early days.

The first $^{15}$N field experiments were set within some of the Rothamsted long-term sites; winter wheat in the Broadbalk Experiment followed by pasture on Park Grass and spring barley on Hoosfield. The Broadbalk experiments showed that nitrogen applied in spring to winter wheat was frequently used fairly efficiently; above-ground crop recoveries at the time of harvest were frequently 60–70% of the $^{15}$N applied. In addition, about 20% was retained in soil in organic forms comprising nitrogen in the microbial biomass, crop roots and other forms of organic matter (33). In excess of 80% of the applied nitrogen was therefore often accounted for. This is illustrated for nitrogen applied in spring to winter wheat on a different site in Figure 9. Even today, it is still common for some agricultural scientists to overlook the immobilization of a significant quantity of applied fertilizer nitrogen into soil organic matter and to assume that all nitrogen not taken up by the crop is lost; this is clearly a major misunderstanding of the situation, leading to grossly inflated estimates of loss.

It was found in this work, and in later experiments with other crops on different soil types, that the loss of spring-applied $^{15}$N (i.e. that not accounted for in crop or soil at the time of harvest) was greatly influenced by the quantity of rainfall shortly after nitrogen application. There was a surprisingly close relationship between nitrogen loss during the crop growing season and rainfall in the three-week period following nitrogen application as measured by $^{15}$N recovery in crop plus soil (49). Losses ranged from as little as 1% to 35%, being greater when rainfall was higher during this short period when much nitrate from applied nitrogen fertilizer still remained in the soil. A similar, but less close, relationship was observed for other arable crops (58). By using the nitrate leaching model developed at Rothamsted by Tom Addiscott,
it was shown that, under normal conditions for the south-east UK, and with some exceptions, losses of spring-applied nitrogen fertilizer are predominantly caused by denitrification rather than leaching (Addiscott and Powlson 1992).

An important finding was that nitrogen fertilizer applied to wheat in the autumn, around the time of sowing, was used very inefficiently owing to nitrate leaching during winter and was generally of no benefit to final crop yield (31). In the 1980s it was still common practice for farmers to give autumn-sown crops a ‘starter’ dose of nitrogen. This finding was part of the evidence leading to the phasing out of such practice; later, when nitrate vulnerable zones were introduced, autumn nitrogen applications were banned in these areas.

A finding with significant impact on policy concerned the quantity of nitrate in soils after crop harvest in autumn; this nitrate is the starting point for that leached to watercourses during winter, causing the perceived problem of nitrate pollution that had become highly political. The experiments with $^{15}$N-labelled fertilizers showed that, with some specific exceptions and assuming that nitrogen was applied at the recommended rates and correct time, less than 2% of the fertilizer nitrogen applied in spring was present in the soil as nitrate at the time of harvest in autumn (42). This showed that the vast majority of nitrate leached during winter was derived from the ongoing decomposition of soil organic matter. Consequently, nitrate leaching could
not be decreased by merely cutting fertilizer applications as was commonly assumed at the time. Fortunately, this message was taken on board by policy makers in the UK and EU and later regulations to limit nitrate pollution of waters were better informed and less simplistic than had been feared.

Having embarked on experiments using $^{15}$N-labelled fertilizers, David addressed an issue concerning the interpretation of such experiments that had generally been ignored by others. It had often been observed that, where $^{15}$N-labelled fertilizer was applied, the amount of unlabelled nitrogen (i.e. nitrogen derived from soil) taken up by plants was increased compared to a control not given nitrogen. This is often termed a priming effect, with various explanations proposed to explain it, including increased mineralization of organic matter caused by the added nitrogen or increased root growth leading to greater exploration of the soil volume. But David was not convinced by these explanations and considered that the observation often resulted from the concurrent mineralization and immobilization of nitrogen by soil organisms. He introduced the term Added Nitrogen Interaction (ANI) and the concept that these could be *real* or *apparent*. An ANI would be *real* if one of the above mechanisms truly occurred. However, in the context of concurrent mineralization and immobilization, it was likely that part of the added labelled nitrogen could stand proxy for unlabelled nitrogen that would otherwise have been immobilized. In this situation, the observed ANI would be *apparent* as the added nitrogen would not be altering the actual rates of the processes and the observed result would be an artefact. In addition to immobilization, an apparent ANI can be caused by any process removing inorganic nitrogen from the mixed pool of labelled and unlabelled nitrogen; these processes could be denitrification or, in certain circumstances, plant uptake. A practical impact of an ANI is that the recovery of fertilizer nitrogen by a plant, as measured using $^{15}$N, is artificially depressed and so gives a false view of the efficiency when nitrogen fertilizer is used. With various colleagues David wrote two papers on this subject (29, 32) that were important contributions.

A central aspect of the field $^{15}$N experiments was that the fate of labelled nitrogen that remained in soil at the end of the first year was tracked over several subsequent years. It was found that the retained nitrogen was rapidly immobilized into soil organic matter and re-mineralized only slowly. Typically, about 20% of the applied nitrogen was retained in soil in organic forms after harvest in the year of application. In one large set of experiments an average of 6% of this residue was taken up by a crop in the following year (64), representing only 1–2% of the nitrogen originally applied. In a second residual year crop uptake averaged about 2% of the residue. *Figure 11* shows results from the Park Grass experiment at Rothamsted, where $^{15}$N residues were followed for 18 years (67), probably one of the longest such experiments ever conducted worldwide. In this soil under grass, 36% of the applied nitrogen was retained in soil at the end of the first year – more than in arable soils. After 18 years about half of this residue was still present in the soil. Of the original $^{15}$N residue that had been mineralized over the subsequent 18 years, and was thus no longer in soil, about half had been taken up by herbage and half lost. Data of this nature is invaluable in building models of soil nitrogen dynamics and in throwing light on the underlying processes.

*Modelling nitrogen dynamics in soil, fertilizer advice and the SUNDIAL model*

David’s first model of the nitrogen cycle (43) concerned fundamental nitrogen cycle processes and was based on meticulous measurements of the flux of nitrogen through the soil microbial biomass using soils from the Broadbalk $^{15}$N experiments made by an early Chinese visiting
scientist, Prof. Shen Shan Min (41). It showed a surprisingly large annual flux of nitrogen through the biomass of about 125 kg N ha\(^{-1}\) yr\(^{-1}\). In the late 1980s David started work on nitrogen modelling with the practical aim of building a system for use by farmers and their advisers to determine the quantity of nitrogen fertilizer to apply to a specific crop in a specific field. This grew out of data and understanding from the field experiments using \(^{15}\)N-labelled fertilizers. Initially he worked on this with Nicola Bradbury, Andy Whitmore and others (50, 52) and then with Jo Smith, who further developed the model and tested it on data from a wide range of farms. The model became known as SUNDIAL, derived from *Simulation of Nitrogen Dynamics in Arable Land* (Smith et al. 1996).

**OTHER SELECTED SCIENTIFIC ACTIVITIES**

David was a member of the Royal Society group that produced an influential report ‘The Nitrogen Cycle in the United Kingdom’ in 1983. In 1995, he was an organizer of a Royal Society Discussion Meeting on ‘The Exchange of Trace Gases between Land and Atmosphere’. For many years he was on the editorial boards of the journals *Soil Biology & Biochemistry* and the *Australian Journal of Soil Research*, and he served on the Council of the British Society of Soil Science and the Agriculture and Environment Committee of the Society of Chemical Industry.

In the early 1980s he organized, with David Powlson, a meeting at Rothamsted called the Nitrogen Workshop. At this time a large number of projects related to nitrogen had started in the UK through funding from the then Ministry of Agriculture and others, driven by political concern about increasing concentrations of nitrate in drinking water. In the pre-internet era there was a need for the different groups to know what the others were doing. This meeting was
intended to promote scientific interchange and collaboration. But it also had an ulterior motive.

David was concerned that, before long, administrators would perceive that the numerous
projects represented duplication of effort and would impose a bureaucratic form of top-down
coordination. The Nitrogen Workshop, to which key administrators from funding bodies were
invited in addition to scientists, was intended to demonstrate that scientists could organize
effective coordination themselves. The meeting was considered a great success and afterwards
different groups offered to host subsequent meetings every one to two years; they later became
European events. Within a short while the meetings attracted over 300 participants compared
to the 30 at the first meeting. The nineteenth Nitrogen Workshop was held in Sweden in 2016.

On 26 June 2008 a new building, named after David Jenkinson, was opened at Rothamsted
Research (Figure 12). The building comprises facilities for processing crop and soil
samples from field experiments, soil physics laboratories, and growth rooms with high-grade
containment for research on plant diseases. The building was officially opened by Professor Sir
David Read FRS, at the time Chairman of the Board of Rothamsted Research, in the presence
of David Jenkinson and his family. At Rothamsted it is customary to name buildings after
former directors; this was the only building to be named in honour of a distinguished scientist
who had not been Director of the Institute.*

* A video of the opening ceremony is available at https://www.youtube.com/watch?v=PYz51ln2hLo.
David Jenkinson: the man, his values and his family

David was a gentle and kind man with a strong sense of justice and fairness. He was impressed by Darwin, and he espoused the philosophy that life is there for us to make the very most of it, for others as well as ourselves. He had a very diverse range of interests, from literature and the arts to Irish folk music and nature. He was widely read and knowledgeable about an enormous range of subjects, including areas of science far outside his own expertise, as well as history, politics and the arts. As a light-hearted test of his knowledge, James Rayner, a colleague and friend at Rothamsted, would sometimes casually mention a random obscure topic in coffee-time discussions, saying how he felt ignorant about the subject. David never failed to respond by saying that he had read a book on the subject and proceeding to provide information. Without questioning David’s wide knowledge, colleagues did wonder if there was occasionally an element of bluff in his responses to James’s teasing!

About the time that David moved to the University of Reading, Moira moved to work at the Niels Bohr Institute in Denmark, during which time they kept in contact by letter. Later Moira moved to a position in the Physics Department at University College London. By this time David was working in Rothamsted, in Harpenden, only 30 miles from London, and they met most weekends. They married at St Albans Registry Office on 16 March 1958 and set up home in Harpenden, where they raised four children: twins Hugh and Philip, born 14 August 1959; Maeve, born 3 March 1964; and Robert, born 17 December 1967. Philip became a design engineer and emigrated to Australia, Hugh a civil engineer, Maeve a professional violinist, and Robert a mechanical engineer. Between them the children produced a clutch of grandchildren whom David doted on with an affection which was deeply reciprocated.

Moira and David and their children led a happy and sometimes boisterous family life. The family recall holidays on the west coast of Ireland, the long journey from Hertfordshire being undertaken in a Volkswagen camper van fully packed with canoes, fishing rods, violins, geology hammers and children. If there was a mountain nearby, it would certainly be climbed; a flower to be picked and pressed undoubtedly would be (unless endangered); and a fish to be caught – caught it would be (well – sometimes).

David was generous in the time and consideration he gave to scientific colleagues, both long-term collaborators and the many visiting scientists and students from around the world. Numerous scientists sought his advice on planning experiments or interpreting results. He had a skill for extracting the salient points from a mass of data, often starting by drawing up a table or plotting a graph using pencil and paper. Many scientists worldwide benefitted from his advice in this way and it was common for enquirers to leave after such sessions having a totally different interpretation of their results than they had held at the start of the discussion.

David always went to considerable trouble to ensure that visiting scientists from abroad were well looked after. On one occasion he found that the rented house he had arranged for a visitor had been left in a very dirty state by the previous tenant and there was no time for the normal cleaners to correct this. Without hesitation, he obtained buckets and mops and led a group of volunteers from his scientific group to do the necessary.

David Jenkinson was an exceptional man who made an important and lasting contribution to his field of science and to wider scientific advancement. He inspired the love and admiration of his family, friends and scientific colleagues worldwide. Moira and David lived together in Harpenden until his death in 2011.
Honours, degrees and awards

1950 BA and BSc with first-class honours in Experimental Science, Trinity College, Dublin
1954 PhD in Organic Chemistry, Trinity College, Dublin
1976 Hannaford Research Fellow, Waite Institute, Adelaide, Australia
1979, 1984 Individual Merit Promotion
1988 Visiting Research Fellow, then Visiting Professor, Soil Science Department, University of Reading
1991 Fellow of the Royal Society
1993 Massey Ferguson National Agricultural Award
1995 Honorary Member of the Soil Science Society of America
2003 ISI Highly Cited Researcher
2008 Official opening of new building at Rothamsted Research named in his honour
2009 International conference entitled 'Soil Organic Matters' held to mark David Jenkinson's achievements and review current progress in subject areas for which he laid foundations

Acknowledgements

We thank members of David's family for background information, in particular Moira Jenkinson, Robert Jenkinson and David's brother Donald Jenkinson, who also kindly assisted with updating references to publications.

Sources of information. In addition to their personal knowledge of David Jenkinson, information from his family and reference to his published work, the authors have referred to the National Life Stories produced by the British Library. David was interviewed for this project in 2010. The full recordings are available online at: http://sounds.bl.uk/Oral-history/Science/021M-C1379X0006XX-0001V0; edited extracts at http://www.bl.uk/voices-of-science/search?q=david+jenkinson; full transcript at http://sounds.bl.uk/related-content/TRANSCRIPTS/021T-C1379X0006XX-0000A0.pdf. The portrait of David Jenkinson is © The Royal Society 1991.

Author profiles

David Powlson

After receiving his honours BSc in Chemical Sciences at the University of East Anglia in 1968, David Powlson came to Rothamsted Experimental Station (now Rothamsted Research) to work under the supervision of the late David Jenkinson FRS. His PhD (1972, as an external student, University of Reading) was awarded for his work on developing the chloroform fumigation-incubation method for measuring the quantity of organic carbon held in the cells of living organisms in soil (the soil microbial biomass). He then spent two years with the Malaysian Agricultural Research and Development Institute working on the management of acid sulphate soils. He returned to Rothamsted and collaborated with David Jenkinson on various aspects of soil carbon and nitrogen dynamics, often using the Rothamsted Long Term Experiments. This research included collaboration with Phil Brookes to develop a method for measuring phosphorus in the soil microbial biomass. He also worked on applications of $^{13}$C- and $^{31}$P-NMR spectroscopy for elucidating the chemical structures present in soil.
organ売 matter though collaboration with Professor Edward Randall, Queen Mary University of London. In 1980, with Jenkinson and A.E. ‘Johnny’ Johnston, he began a large programme of research on the efficiency of use of nitrogen fertilizer by crops, pioneering new approaches for using $^{15}$N-labelled fertilizers in unconfined field plots. This stimulated later international work on nitrogen fertilizer use efficiency using $^{15}$N supported by the joint Division of the UN Food and Agricultural Organization and the International Atomic Energy Agency. With Professor Pete Smith FRS he initiated a major evaluation of soil organic carbon models using data from long-term experiments globally and established the Soil Organic Matter Network (SOMNET), under the auspices of the Global Change and Terrestrial Ecosystems (GCTE) project of IGBP. He has collaborated with numerous international scientists on the impacts of soil management and land use change on soil carbon stocks and he has critically examined the extent to which sequestration of carbon in soil can mitigate climate change. He was Head of the Soil Science Department (later Agriculture and Environment Division) at Rothamsted Research between 1990 and 2003. On retiring in 2006 he was appointed Lawes Trust Senior Fellow at Rothamsted and since then has been active in leading projects in China on the improved management of nitrogen fertilizers. He has also worked with scientists at CIMMYT on the impacts of conservation agriculture on soil carbon. He spent a period as President of the British Society of Soil Science (1998–2000) during which he initiated the ongoing series of Eurosorb conferences with other Soil Science Societies in Europe. He was elected an Honorary Member of the British Society of Soil Science in 2006 and currently holds Visiting Chairs in Soil Science at the University of Reading, UK, and Nanjing Agricultural University, China. He has published more than 140 papers in international peer-reviewed journals.

**Phil Brookes**

Professor Philip Brookes graduated from Lanchester Polytechnic (now Coventry University) in 1972 with a First Class Honours Degree in Applied Zoology and Chemistry. He received his PhD for research into the mineral nutrition of the two indigenous British oak species, from the same university, in 1976. He was appointed as a Scientific Officer in the (then) Chemistry Department of Rothamsted Experimental Station (now Rothamsted Research) in 1976 where he initially worked with the late Dr Geoffrey Mattingly and A.E. ‘Johnny’ Johnston. He later transferred to the laboratory of the late Professor Jenkinson FRS and began work with David Jenkinson and David Powlson to develop a method to measure soil microbial biomass phosphorus. This introduced him to the concept of the soil microbes being measured as a discreet pool of soil organic matter as initially proposed by Jenkinson and Powlson. Phil found David Jenkinson to be a very inspirational group leader and many joint scientific research papers followed. These included a method for measuring nitrogen in the soil microbial biomass and measurements of ATP and adenylate energy charge in soil that raised intriguing questions about the survival strategies of micro-organisms in soil.

The group attracted a great number of talented graduate students and post-doctoral workers. One of them, Eric Vance from the University of Missouri, USA, was awarded a Fulbright Scholarship to work with him in David Jenkinson’s group in the 1980s. This collaboration resulted in the publication of a paper showing that soil microbial biomass carbon could be measured by a simple chemical procedure, termed fumigation-extraction (FE), which offered several advantages over the previous fumigation-incubation (FI) method developed by Jenkinson and Powlson. The FE method is now the most highly cited scientific paper in the journal *Soil Biology & Biochemistry*. Phil later showed, with Goswin Heckrath, that the
leaching of phosphate from soil to water is very much larger than previously recognized. This opened up a considerable amount of international research on the mechanisms leading to phosphate pollution of surface waters. He retired from Rothamsted in 2011. Since then he has enjoyed a new career at the Institute of Soil & Water Resources and Environmental Sciences, Zhejiang University, Hangzhou, China, heading a research group in microbial ecology. He holds Honorary Professorships at Coventry University, UK, Zhejiang University, and four other Chinese scientific institutes. He has published more than 300 scientific papers, about half in refereed scientific journals. In 2016 he was awarded the prestigious Westlake Friendship Award from the Zhejiang Provincial Government, for his scientific contributions to the province. When not in China, he spends most of his spare time fishing (usually unsuccessfully) for wild Irish brown trout in the beautiful lakes of Ireland, with his Irish friends. He also enjoys riding through the Irish countryside on his electronic bicycle.

REFERENCES TO OTHER AUTHORS


Biographical Memoirs


BIBLIOGRAPHY

The following publications are those referred to directly in the text. A full bibliography is available as electronic supplementary material via http://dx.doi.org/10.1098/rsbm.2017.0007 or via https://doi.org/10.6084/m9.figshare.c.3841240.


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