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Henry Gerard Thornton, 22 January 1892 - 6 February 1977

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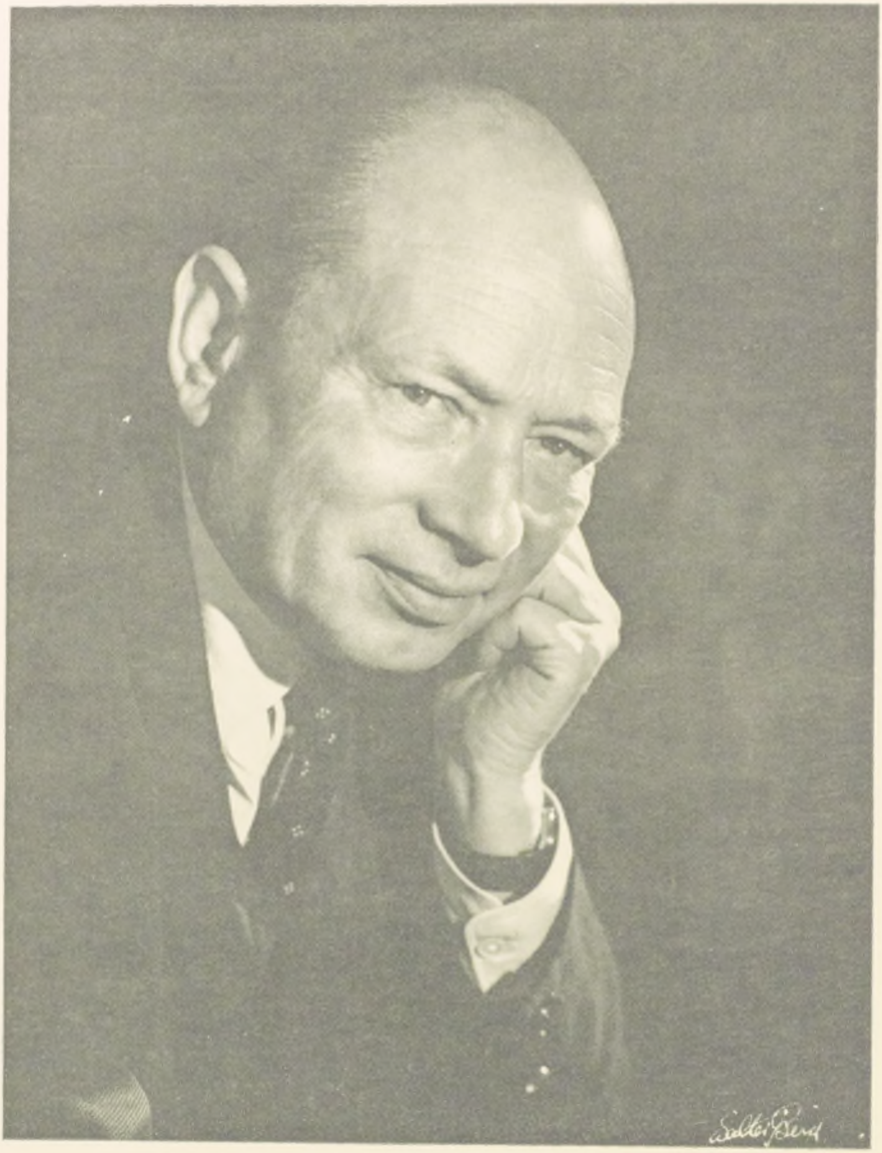

H. G. Thornton.

HENRY GERARD THORNTON

22 January 1892—6 February 1977

Elected F.R.S. 1941

By P. S. Nutman, F.R.S.

Henry Gerard Thornton was born in London in 1892, the elder son of Frank Hugh Thornton, J. P., of Kingsthorpe Hall, Northampton. His father, who was a breeder of shorthorn cattle, exporting prize bulls to Argentina, came from a long line of Northamptonshire landowners which had received an influx of exotic blood in the eighteenth century when an heiress daughter had married a Dutch Huguenot merchant from Smyrna. In more senses than one the father was an enlightened country gentleman, for not only was he instrumental in establishing the first electric light company in the county, but he was also much concerned with rural health and welfare and infant mortality, and introduced hygienic methods for milk production. This interest was no doubt much deepened by the death of his wife Evelyn (*née* Burchell) in childbirth when Henry was 9 years old.

Early Life

Young Thornton's early formative years were spent contentedly in the atmosphere of a well-to-do county family, encouraged in his love of natural history by a kindly father and probably also by his uncle who was a leading amateur breeder of daffodils and certainly by his grandfather, the Reverend Wm Thornton, who was an antiquarian and botanist. Whether this was to the neglect of country pursuits thought more fitting for the youth of the day is not recorded, but he was known not to like horse-riding and among his hobbies were geology, archaeology, heraldry and stamp collecting. He kept meticulous and well illustrated records of all these activities which were later handsomely bound. His father's indulgence went so far as to furnish a room as a laboratory and to equip it with a microscope and other necessary apparatus.

Some of Thornton's early friends at Rothamsted well recall the serene atmosphere of weekend tennis parties at Kingsthorpe Hall to which they were invited some years later, with memories of early experiments in making icecream and of the shocked surprise of sedate aunts on learning that apparently well brought up young ladies and gentlemen worked in a laboratory!

At school, Radley College, Thornton's bents were not especially catered for and compulsory games, which he disliked, took him away from his other pursuits. Gerald Brenan, a fellow schoolboy at Radley, records in his autobiography (1962) the outings of the Natural History Society which he enjoyed with Thornton (whom he disguises as Morton). 'As we trudged or cycled along Morton in his quiet voice would give explanations, and so gradually the scientists' picture of the earth...was unrolled before me.' Brenan also comments on his surprise when invited to Kingsthorpe to find that his studious friend had such a background. While still an unmatriculated schoolboy Thornton attended in 1909-10 the elementary zoology class at New College, Oxford, and in 1911 he entered the advanced class under Professor Bourne, obtaining a first class degree in natural science (zoology) in 1914; Geoffrey Smith was his tutor. The redoubtable Dr Spooner was still Warden and Thornton was able personally to vouch for: 'Mr Jones you are very idle, you have tasted two whole worms.' Among Thornton's contemporaries were Harry Champion, J. B. S. Haldane (with whom he was later again to be associated), J. J. Conybeare, who became consultant physician to Guy's Hospital and specialist in diabetes, and H. J. Laski. Sir Harry recalls their joint formation of an undergraduate society 'The Zoophytes' to bridge the gap between the small and entirely separate schools of Botany and Zoology. At the society's twice termly meetings papers were read jointly by a botanist and zoologist on matters of mutual interest. The inaugural business meeting was held in Geoffrey Smith's rooms on 3 October 1913 and the first papers were given the following month by Thornton and Champion on 'Marine plankton in relation to its food supply'. The titles of papers read at following meetings were: 'The inheritance of sex', 'Symbiosis', 'The inheritance of acquired characters', 'Trophisms', and 'Heterophyletic convergence'—forward-looking topics set out with admirable brevity. Sadly this society seems not to have survived the war.

Thornton served in the 4th Battalion of the Northamptonshire Regiment from 1914 to 1916 when he was seconded to the Royal Flying Corps, no. 17 Squadron, which was posted to Egypt (Suez Canal), Sudan (Darfur) and Salonika. He was a pilot and observer and once flew as observer with Slessor (who later became Marshal of the Royal Air Force) and who remembers him as a 'nice chap'. These were the first airplanes to be seen in Africa. His squadron was attached to the Expeditionary force sent against the Mahdi and to patrol the Suez Canal to prevent mine laying. He contracted dysentery at Salonika and was brought home to serve in the anti-Zeppelin squadron and then attached to the Aeroplane Experimentation Station at Martlesham Heath to develop bomb-sights, etc. Finally, he joined no. 192 Squadron which was being equipped with the new Handley-Pages to bomb Berlin, when armistice was declared. Thornton was appointed as a Lieutenant in the Royal Air Force when it was formed and temporary Captain in 1919.

He was mentioned in dispatches from Salonika but the events he liked best to recall were the informal elements in the operations, the ineffectual dropping of bombs over the side of the cockpit and unrehearsed incidents as when he

was required to demonstrate a new machine-gun to his 'top brass', with nearly disastrous results. This foreshadowed an incident in World War II when Thornton's great friend, R. A. Fisher, in the same Home Guard platoon, had to be disarmed during firing practice because his martial ardour was inadequately matched by very poor eyesight. Ballistic misadventure continued when flying bombs twice blew the roof off Thornton's house near Wheathampstead.

After a whirlwind courtship and short engagement he married in 1924 the 19-year-old Gerda Nørregaard of Copenhagen, whom he met as a translator at a United Kingdom farmers' visit to Denmark. This meeting was also attended by Thornton's father, though the son firmly insisted that his father had no part in the non-scientific activities of the visit. At about this time Thornton was helping R. A. Fisher in his researches on the inheritance of sinistrality in the snail and Lady Thornton recalls that the collecting of the 'horrid creatures' continued even on their honeymoon.

At the end of World War I Thornton's father wrote to Professor Bourne for advice on his son's career, whether to look for openings in the University or in Board of Agriculture establishments.

Thornton's entire scientific career was spent at Rothamsted. He was appointed in 1919 by Sir John Russell to study certain microbiological effects of treating soil with live steam (partial sterilization) which was already known to have large effects on fertility. At this time mycology and bacteriology (mainly medical) were recognized branches of science but microbiology was not yet a discipline in its own right. Thornton had perforce to devise his own tools of trade, though with Geoffrey Smith he had already as an undergraduate published on the nutrition of soil and water protozoa and it is of interest to note that the authors referred in their paper to Russell & Hutchinson's and to Goodey's papers on partial sterilization. The appointment, replacing Hutchinson, was to lead a small Soil Bacteriology Department. This had been built shortly before the war by gift of James Mason, specifically to study beneficial soil microbes, especially those of legume root nodules and was endowed with a liberal annual grant of £50. In 1941 this combined with Cutler's former and larger group working on soil protozoa and to a lesser extent on fermentation, and on the composting of vegetable waste and the biological purification of effluents from sugar beet and milk factories. Hutchinson & Richards (1921) used Thornton's improved methods for counting bacteria in the laboratory work that led to the 'Adco' process for making 'artificial' farm yard manure. Under Thornton's guidance the research interests were increasingly concentrated in the fields of general and legume bacteriology, protozoology and on decomposition studies, in all of which Thornton made his individual contribution. By the end of the 1920s the bacteriology group had outgrown the small James Mason laboratory and were to have moved in 1939 to new accommodation. On the outbreak of war, however, this was taken over by Public Health and it was not until 1941 that a move was made, but with the new laboratory now shared with J. H. Quastel's Soil Enzyme Chemistry Unit, J. B. S. Haldane's group from University College and the Leather Research Association group, all driven from

London by bombing. It would have been natural for Thornton to have felt some annoyance on having suddenly to play host to three research groups in laboratories specially designed for his own work. But the visitors were accepted without protest and Thornton did everything possible to make the newcomers welcome (among whom were H. Kalmus, J. Rendle, Helen Spurway, Ursula Philip, D. Webley and P. G. H. Mann). With so many strong individulists in close juxtaposition occasional friction was inevitable, quietened by their urbane host. I also recall that Haldane's large scale production of *Drosophila* on yeast in milk bottles did not easily mix with some of the bacteriological activities. In this overcrowded but stimulating environment Thornton then survived his final baptism of fire in an incendiary bomb attack. All incendiaries, including one landing on his laboratory roof, were quenched without doing damage.

Before embarking on his microbiological career, Thornton's fossilizing in Northamptonshire led to the finding of major parts of the skeleton of a very large plesiosaur at Kingsthorpe. These were presented to the British Museum and were found to be a new species and named by C. W. Andrews, F.R.S., *Rhomaleosaurus thorntonii* (1932). It is distinguished by the massive solidity of its bone structure, the location of the nasal openings and the morphology of the cervical vertebrae and humerus. A cast of this specimen is exhibited in the Fossil Reptile Gallery of the British Museum (Natural History), South Kensington.

Populations of soil bacteria

Thornton's first four short papers in the early 1920s crystallized and went some way towards solving major problems of counting bacteria in soil. The question of choice of general and reproducible media was re-examined with a wide range of pure chemical substrates, and conditions modified to prevent spreading of colonies; some of the problems of enumeration were solved by applying (with R. A. Fisher) statistical methods and the problem of dispersion was examined in a critique of Whittle's vibration method that anticipated by many years modern ultrasonic techniques. With P. H. H. Gray, Thornton much improved the methods for determining total counts by staining soil films with acid rather than basic dyes, and by making observations on mixed suspensions of soil and of graded indigotin particles he was able to determine the number of contrastedly stained bacteria by simple proportion—the ratio method which needed its own statistical treatment. These methods were later largely superseded by other techniques, some developed in his department—notably the Jones & Mollison (1948) agar film method and those using weak media where the microcolonies were counted under the microscope, and by the adoption of 'most probable number' counting procedures originally developed in milk bacteriology.

These methods were applied to studying changes in bacterial numbers in the differently manured plots on the farm and in steamed soils where a major interest was the short-term fluctuations in bacterial numbers. There is now

doubt as to the agricultural importance of these changes; they remain a largely unexplained microbiological curiosity. In all these studies Thornton was impressed by the great variety of soil bacteria and by their variability which he discussed in 1938 with characteristic caution preferring the descriptive terms 'dissociation' and 'saltation'. He considered 'mutation' to be inadvisable because it implied a knowledge of genetic mechanisms that were not yet identified. When they were, Thornton enthusiastically accepted the new immensely broadened horizons.

Among the soil bacteria that received early attention were those that tolerated the disinfectants used in glasshouse practice and for the preservation of materials and structures in contact with soils. Thornton & P. H. H. Gray isolated many bacteria able to break down phenols, cresols and napthalenes; these were mostly species of *Pseudomonas*, *Flavobacterium*, *Mycobacterium and Clostridium*. Thornton & Gray also showed that addition of nitro groups increased the toxicity of the disinfectant and additions of the chlorine atom increased its resistance to microbial attack, information later to prove an important lead in the discovery of selective hormone herbicides. Although Thornton did not himself publish on the subject he encouraged and influenced the work of B. N. Singh (e.g. 1948) on bacteria as food for protozoa and other less well known groups of the larger microorganisms. This very fruitful field of fundamental research sprang from the intensive studies on fluctuations in microbial numbers, and led to much valuable work on protozoan taxonomy, ecology and physiology. Later the interests of his department widened to include work on the actinomycetes, soil fungi and mycorrhiza.

The legume root-nodule symbiosis: early inoculation studies

In the meantime Thornton was becoming increasingly interested in the root nodule bacteria, for the study of which the James Mason laboratory was founded, and it is in this field that he made his most important contributions to soil microbiology.

Interest at Rothamsted in nitrogen fixation began, however, in the mid-years of the previous century at the time of Boussingault's early experiments and of the Lawes–Liebig controversy on the source of nitrogen for plants. It was also strongly stimulated by Hellreigel's (1886) discovery that only nodulated legumes fixed atmospheric nitrogen. This was reported at a Berlin meeting of the Agricultural Chemical section of the Naturforscher Versammlung presided over by Lawes's collaborator Sir Henry Gilbert, F.R.S. These results were confirmed the following year at Rothamsted, and in 1888 Beijerinck first isolated the nodule bacteria.

In Germany these advances were soon applied in agriculture—by the production of 'seed inoculants' of nodule bacteria for legumes ('Nitragin'). Early experiments in the United Kingdom were disappointing, and Thornton's first work in this area was to devise media which helped the 'inoculated' bacteria to migrate from the seed into the root zone. This, combined with careful

selection and control of the strain of bacteria, led to positive responses of lucerne to inoculation. In 1923 a grant from the Royal Agricultural Society of England enabled Thornton to supervise field trials initially at 30 centres and later at 50 more. These demonstrated striking benefits especially in areas where lucerne had not been grown before and gave rise to a demand by growers for cultures. At first cultures were issued to farmers from Rothamsted. Nine hundred cultures were supplied in 1925 and more than 1000 in 1928. Because of the amount of work involved arrangements were made in 1930 for a commercial supply. Of the two firms approached the Royal Agricultural Society of England chose the 'trustworthy and efficient' firm of Allen & Hanbury Limited to produce inoculants under their licence, and with samples routinely tested by Thornton. The cost to the farmer was 3/- per acre. Skim milk was used as a carrier for the agar-grown bacteria. A tablet of soluble calcium phosphate was added to the milk to help the bacteria to become established in the soil. The seed was moistened with the 'inoculum', dried at ordinary temperatures and sown immediately using a normal drill. The arrangement between Rothamsted and Allen & Hanbury's continued until 1963 when production was discontinued for commercial reasons following the take-over of this firm by Glaxo Limited.

The beneficial effects of phosphate which Thornton demonstrated gives an interesting sidelight on the influence of current opinion on data interpretation. Phosphate appeared to increase the proportion of motile cells, it was thought through an effect on the life cycle of the organism in soil. Life cycles in bacteria were much in favour and the rod, cocci and bacteroid forms of rhizobia in culture and in the nodule readily lent themselves to such arrangements; the 'banded rods' were wrongly thought to break up into swarmers, a confusion that still persists.

Thornton and colleagues examined the effect of inoculum size on nodulation and the keeping properties of inocula, in pot and field trials with lucerne and beans. These showed that more nodules were formed by large inocula of freshly prepared bacteria than by inocula containing as little as one-tenth the standard inoculum or by inocula stored at room temperature for up to four weeks. Yield, however, was quite unaffected by these treatments. Cultures of lucerne were also sent in 1927 by ship around the world and to Buenos Aires and back, and were found to nodulate satisfactorily on their return. Nevertheless Thornton preferred to rely on a wide margin of safety; in retrospect a wise decision that helped the practice of inoculation to become firmly established. The question of preinoculation of seed by the seed merchant although considered by Thornton as early as 1930 was not followed up because he considered the risk of producing poorly inoculated seed was greater than the advantages of more convenient use by the farmer. Much later a simpler process involving peat as a carrier was developed in Australia; this lends itself better to preinoculation although Thornton's argument still carries weight.

Bacterial strain variation and stability are of crucial importance in the choice of inoculant material. American work had already demonstrated some variability

in the symbiotic properties of lucerne bacteria, but generally to a small degree, and also that most strains were stable. These fortunate circumstances allowed inoculation procedures to be developed for lucerne without the complications that held up practical application elsewhere for other groups of legumes.

The strain selected by Thornton for commercial lucerne inoculation was obtained at some time before 1928 from the Planteavls Laboratorium, Copenhagen, Denmark. It has proved remarkably stable in its symbiotic properties and is still in use in many laboratories. Thornton wrote and spoke widely on the value of lucerne inoculation and it soon became standard farming practice. His experiments also demonstrated the need for inoculation of exotic legumes such as soyabean but not other agricultural legumes, except in certain circumstances.

Thornton's pioneering and successful work on inoculants was based upon numerous properly designed and conducted field trials, mostly done on private farms, and presumably relying on local help and labour. This represented a considerable achievement in organization and persuasion, especially when the whole series was completed in three seasons. Today this would require a small army of helpers and generate a mountain of paper work.

The influence of fresh straw on the growth of soyabeans and field beans was also studied and the beneficial effects (provided that more phosphate was also added) were thought, probably erroneously, to be caused by stimulation of the numbers of bacteria in the root zone. Other agriculturally important questions were the effects of nitrogenous fertilizer and the extent to which the N-fixing system was influenced by management, or benefited the grass grown with the legume. Increasing doses of nitrate fertilizer were shown to depress progressively nodule number and size and the volume of the active N-fixing tissue, without markedly affecting yield, but in seed mixtures nitrate stimulated the grass at the expense of the legume. These questions were being more extensively researched elsewhere, but Thornton's important contribution was to demonstrate the responsiveness of the nodulated legume to external factors.

Alongside these practical matters Thornton undertook important research programmes on more fundamental aspects of nodulation, namely the physiology of the infection process, the nature of the root-hair curling reaction, the structure and development of normal and of genetically or physiologically aberrant nodules, the ecology of rhizobia in United Kingdom soils and competition between strains, and, in collaboration with J. & A. Kleczkowski, the bacteriophages and serology of nodule bacteria.

It had long been known that most legumes are infected through their root hairs which become deformed or curled prior to infection. Within such hairs a tubular infection thread is formed that contains the bacteria and which grows into the root. From this structure the bacteria later escape into the cells of the developing nodule and after transformation into the enlarged 'bacteroid' can then fix atmospheric nitrogen.

So far as the infection process was concerned Thornton was specially interested in the nature of the root hair curling reaction and the physiological conditions that predispose a plant to infection. With H. Nicol he demonstrated curling with bacteria-free culture filtrates. This activity did not reside in the gummy portion of the secretion and was heat stable at neutral pH. Their suggestion that the active principle contained a plant auxin was confirmed by Chen (1938) using the biological assay procedures then available. This was followed by tests with a wide range of known plant growth-promoting substances and led *inter alia* to work on selective hormone herbicides described in a later section, and to the demonstration that root secretions themselves stimulated the production of the curling factor.

Thornton also showed that auxin production was inhibited by nitrate (counteracted by dextrose), the mechanism of which was not to become known for a decade. More recently it has been shown that auxin is not the only factor concerned with curling and infection and Thornton, as did other workers in the field, appreciated its possible morphogenetic effects, and noted that although root hair curling occurred on the very young seedling, the infection of the hair and formation of the nodule took place some days later, coinciding in lucerne with the opening of the first leaf. Neither removal of the emergent first leaf nor stem apex materially affected initial infection and nodulation, but both were advanced either by growing the test seedling intermingled with older plants or by adding root medium in which older plants had been grown. Susceptibility to infection was thus dependent upon a physiological change in the host marked by first leaf opening and by the exudation of some material into the root medium. The exuded material stimulated rhizobial growth on the root surroundings but Thornton concluded this factor was not responsible for initiating infection, because rhizobia from clover and peas unable to infect lucerne were similarly stimulated.

Nodule structure

At this time little was known of the details of further nodule development, a gap that Thornton proceeded to fill in a series of careful anatomical studies on lucerne, beans and clover. The unrivalled microphotography was done with the help of Victor Stansfield, then a member of Thornton's department and later to lead the station's photographic section. Victor was a kindly but somewhat temperamental and blunt Yorkshireman, the only member of Rothamsted's staff that loudly addressed his boss as Jerry. The work was done with an elderly Leitz binocular microscope, with fine optics, even if of pre-plano design. The Leitz microtome used in these studies was bought by Thornton, who had a keen eye for well-made instruments even if a trifle old-fashioned. Some years later he purchased locally a fine 1775 Dolland microscope, complete in every particular, which he presented to the department.

Thornton was the first to observe that more than one infection thread can penetrate a developing nodule. Particular attention was given to the stimulation

of host cell division that is pronounced in the early stages, and to the rapid differentiation of the young nodule into its different parts and especially the formation of the uninfected meristem. He described minutely the escape of bacteria from the infection threads into the host cells, and their accelerated multiplication and transformation into swollen bacteroids. Also recorded was the development of the nodule's vascular traces and the system of endodermi separately enclosing them and the bacteroid zone. At this time it was not known that the bacteroids were no longer viable. However, Thornton noted their lysis in old nodules which were then colonized by rod-forms arising from infection threads and intercellular spaces.

He supposed that the infection thread sheath was cellulosic, later confirmed by a visiting worker to the department. Although his nodule illustrations show mitotic figures, surprisingly he did not discover that the interior tissues of the nodule were polyploid.

Abnormal and ineffective nodules

Thornton investigated two kinds of abnormality: those related to altered environmental or to nutritional factors, and those caused by intrinsic defects in the bacteria that prevent, or much reduce, nitrogen fixation. Even under optimum conditions nodules eventually decay, possibly, it was thought, through a reduced supply of carbohydrate. This hypothesis was examined by placing nodulated plants in the dark and following the changes that subsequently took place in the nodule. He showed that the bacteroid tissue quickly degenerated in darkened plants with the coccoid bacteria of the infection threads invading the cell wall and intercellular spaces causing the nodule tissues to disintegrate. Inadequate aeration on the other hand, though it impaired nodule function, was not seen to lead to active parasitism. On other experiments, in collaboration with W. E. Brenchley, he showed that boron deficiency, which is known to interfere with the normal processes of differentiation of vascular tissue and likely therefore to inhibit translocation, also leads to a parasitic condition in the nodule of *Vicia faba*. These results were thought to support the notion that the balance between symbiotic and parasitic phases was chiefly a matter of carbohydrate supply. This explanation, however, could not so easily be invoked to explain the effects of nitrate on nodule development. Although the end result of supplying nitrate was the same as that of boron deficiency, the way in which it came about was different, viz. by the thickening of cell walls, shrinking of cell contents and nuclei and excessive suberization of the endodermis.

Nor could carbon/nitrogen balances within the plant account for inherent ineffectiveness accompanied by rapid breakdown of the nodular tissues, because it is often characteristic of such nodules that they accummulate carbohydrate as starch. Thornton and Chen showed that ineffectiveness in clover, pea and soyabean, the nodules of which differ structurally in important respects, was essentially a developmental defect—a failure to form the N-fixing bacteroid

tissue, or if it were formed to cause its very short persistence. By making careful measurements on their sectioned material they convincingly demonstrated that the different amounts of nitrogen fixed in each host by each strain of bacteria were wholly and exactly accounted for by the product of aggregate bacteroid volume, its duration and a constant rate of fixation, a finding of great value for further work, confirmed in many later studies. At this time other workers attributed ineffectiveness simply to a failure to form leghaemoglobin, known to be essential for N-fixation, an argument that Thornton demolished by showing that haemoglobin accumulation was dependent upon bacteroid formation.

Hormone herbicides

The selective hormone weedkillers (chlorophenoxy acids) were independently discovered in the early years of the war by Templeman's group at Jealotts Hill (I.C.I.) and by Thornton and his colleagues at Rothamsted. The Rothamsted work owed much to collaboration with J. H. Quastel, Director of the A.R.C. Unit of Soil Enzyme Chemistry located in Thornton's department (an effective symbiosis), and to the then current studies on the nature of the clover root hair curling factor involved in the infection by nodule bacteria, and also to work on the microbial breakdown of aromatic compounds in soil referred to above.

Using the pea hypocotyl assay Chen had recently shown that the root hair curling factor produced by *Rhizobium* in culture resembled indol-3-acetic acid (IAA) and experiments were next done to examine the curling activities of pure samples of this and related compounds at concentrations down to 0.1 part per million with the use of sterile-grown red clover plants. Beside showing effects on root hair growth these substances were found to be highly toxic to the whole plant, causing striking morphogenetic effects and to offer possibilities for controlling plant growth. In experiments to examine this aspect, however, it was found that they lost much of their toxicity when applied to plants grown in unsterile soils, presumably owing to rapid inactivation by microbial breakdown. A compound of comparable toxicity was then sought that might be less liable to attack. Among those chosen were various chlorinated aromatics including 2,4-dichlorophenoxyacetic acid (2,4-D) and related compounds and their methyl esters, the auxin-like properties of which had only recently been reported by Zimmerman & Hitchock (1939) at the Boyce Thompson Institute. Quastel, who thought that chlorinated derivatives of phenoxyacetic acid might be fairly resistant to bacterial attack in the soil, obtained samples of these substances privately. When these were tested at Rothamsted in the autumn of 1942 it was found not only that 2,4-D retained its high toxicity to clover and beet at concentrations of less than 1 part per million in unsterile Rothamsted allotment soil (high organic clay loam) and in Woburn soil (low organic sandy loam) but also that 2,4-D was without effect on wheat. Further experiments showed that this chemical was not readily leached from soil but, nevertheless,

did not persist for more than a few weeks possibly because of slow microbial attack. Thornton later obtained enrichment cultures able to break down 2,4-D and pointed out that the effectiveness of these compounds as herbicides was wholly dependent upon their limited persistence in soil.

The results were communicated to Dr W. W. C. Topley, Secretary of the Agricultural Research Council, on 17 November 1942 when it was learnt that Templeman's group had become equally interested in the chlorinated phenoxy-acetic acids in their search for new herbicides. Further work was done jointly by the Rothamsted and Jealotts Hill groups in fruitful and friendly cooperation over a period of two years and larger scale field trials were set out in the Norfolk battle training areas. In the early stages of the joint work the very sensitive and rapid biological assay by inhibition of clover seedling root growth was specially useful and the writer recalls the preparation at Rothamsted on Christmas Eve, 1942, by Thornton, Templeman and himself of thousands of agar tubes containing dilutions of various compounds which were then taken by car to the Jealotts Hill greenhouses away from prying eyes. Because of their possible offensive use, later sadly proved in Vietnam, an embargo was placed on publication until after the war.

Some of the security precautions of the kind beloved by non-scientists were often puerile, as in the allocation of code names and strict monitoring of the correspondence and reports, while leaving the actual experimental work and accumulation of data wholly unsupervised.

The first preliminary report on 2,4-D as a weedkiller was made in America in 1944 by Hamner & Tukey (1944) in ignorance of the earlier work in the United Kingdom and of the Churchill–Roosevelt 1943 agreement that arranged for the confidential exchange of classified information but prohibiting its publication during the war—a dispensation which, in retrospect, seems to have served no useful purpose.

The A.R.C. was additionally sponsoring work on weed control by Blackman's group at Oxford which in 1943 involved the field testing of these new compounds. All the United Kingdom work was published together in *Nature* in 1945.

Thornton was concerned that Rothamsted's part in this epoch-making discovery should be recognized. After the war he took no further part in the practical aspects of this discovery but N. Walker in his department was engaged in fundamental bacteriological and biochemical studies on the breakdown of this and other herbicides and pesticides. Using the Quastel–Lees soil perfusion method, Audus (1951) was the first to obtain an organism (*Bacterium globiforme*) that decomposed chlorophenoxy acids, and in 1953 Walker isolated a strain of *Flavobacterium* able to utilize 2,4-D in pure culture.

Ecology, serology and the viruses of *Rhizobium*

When first described, symbiotic ineffectiveness was considered more an interesting curiosity of passing academic interest rather than a matter of practical

importance. This was evidently not the opinion of Thornton who undertook a survey of the effectiveness of hundreds of strains of clover nodule bacteria isolated from all parts of England and Wales and a few from Scotland. He had already established that ineffectiveness was rare in medic bacteria and somewhat commoner in clover bacteria.

To facilitate comparison between material tested at different times an efficiency index was calculated for each strain. This related strain performance to that of standard strains and to plants with and without nitrate and allowed statistically valid comparisons to be made. These surveys, summarized in various reports but never published in full, showed that ineffective strains were abundant and often dominant in the hill pastures of the west and north and infrequent in the lowland areas of the south and east. It also showed that strain effectiveness was a continuously variable property, ranging from those forming nodules that fixed no nitrogen, and were indeed parasitic in reducing yield below that of unnodulated plants, to strains able to provide the host with all the nitrogen it needs for growth. The occurrence of ineffective strains was highly correlated with altitude but not with any kind or combination of soil type or characteristic, suggesting possibly an effect of temperature. Later studies by others have confirmed this distribution but without providing a general explanation, if indeed such exists, applicable to all areas. This distribution of ineffective strains in upland pastures is agriculturally important because without a nitrogen input from an effectively nodulated legume the productivity of these areas will remain low. Their soils are often shallow, acid and poor, subjected to heavy leaching by rainfall, and because of their short growing season cannot give sufficient return from cultivating and fertilizing.

Thornton's surveys showed the extent of the problem and confirmed his earlier studies on the clover bacteria of hill pastures near Aberystwyth, where in collaboration with local advisers he attempted to introduce effective strains but with little success; the sown clover stimulated the local poor strains rather than those introduced on the seed. However, introduced strains differed amongst themselves in their capacity to establish themselves even temporarily in hill soils, and this led to a series of studies, the first of their kind, on the nature of the competition between strains outside the root, and on their ability to nodulate the host. To avoid any complicating influence of the soil these experiments (with clover, peas and soyabeans) were done in sand culture using mixed inocula of strains, some of which could be fairly well identified on reisolation from nodules by their growth characteristics, but for others this had to be inferred from the types of nodules formed. Despite these limitations, the conclusions reached, applicable to each host, were that the number of nodules formed by a strain depended upon its ability to compete saprophytically with other strains outside the root and on its intrinsic 'virulence' or capacity to form many rather than few nodules. Thornton was able to interpret the different patterns found with each host to their contrasted growth habits, the perennial clover continuing to nodulate, and the soyabean with a determinate habit forming nearly all its nodules during its shorter vegetative phase. He was then able to select an

effective clover strain that competed well in mixtures containing the ineffective Welsh strain 'Coryn', in the laboratory and in field trials, but only to a limited extent.

With Fred & Nina Kleczkowski serology was next applied to the problem of identifying strains using agglutination and precipitation, the only convenient tests then available. They showed that clover strains, even from the same site, could differ serologically though they generally contained common antigens and, moreover, that the clover and pea bacteria were serologically related. This restricted the use of the method in competition studies, a problem resolved only in the last decade or so by gel-diffusion, electrophoretic and fluorescent antibody methods and by genetic marking. Thornton's work also showed no relationship between serology and symbiotic properties such as virulence or effectiveness.

Also with Nina Kleczkowska he explored the possibility of using phage resistance for strain marking, but again found limitations because of the complex nature of phage susceptibility and also because phage-resistant mutants tended to be avirulent or ineffective in fixing nitrogen. Thornton had earlier collaborated with H. H. Mann in experiments (never published) to find the cause of clover and lucerne sickness in fields where no pathogen seemed to be involved. Nutritional deficiency or excess, toxic accumulation of growth substances, *Rhizobium* strain ineffectiveness and presence of bacteriophage were in turn invoked, but none provided an explanation.

Since Thornton's retirement in 1957 there have been striking discoveries in the fields he pioneered or advanced, in all of which he continued to take the keenest interest until early 1977.

Contributions to science

To attempt to extract the essence of Thornton's direct and indirect contribution to science is difficult, and requires a measure of detachment not easily assumed. Nor can early influences upon him in his research career be traced with certainty. E. J. Russell (whose memoir he wrote) and R. A. Fisher were no doubt important in guiding and stimulating his interests but very soon his programmes became self-sustaining. He was essentially a simple man with a single-minded purpose consistent with his outlook and way of working. There was no flitting from one fascinating topic to the next but an orderly progress with each new departure based upon earlier work. Thornton was neither a strikingly original experimenter nor a brilliant theoretician. He was a Boswell rather than a Johnson, or a Julian Huxley rather than a Sergeius Winogradsky (both of whom he knew well), and being genuinely modest he was always ready to consider the opinions of others. In 1953 Thornton wrote for the Royal Society the obituary notice of S. N. Winogradsky.

His reputation was first established by his inoculation studies—a model of how laboratory work can be applied to an agricultural problem when collaboration is effectively organized and circumstances favour extension and development. He became recognized more widely through his fundamental

studies on nodule physiology and structure and counting methods for bacteria and from his review articles and those written with Lettice Crump, Jane Meiklejohn and F. A. Skinner. He influenced, and was influenced especially by the American and Australian schools of nodule studies, chiefly through Perry Wilson, Elizabeth McCoy and the Allens in Wisconsin and J. M. Vincent and H. Jensen in Sydney. Among visiting workers to his department Americans, Canadians, Australians and Indians were prominent. Shortly before the war H. K. Chen from Peking was a particularly successful collaborator. Thornton appreciated his fine experimental techniques, and also the delicate way in which material was labelled in elegant Chinese characters.

Once his department was firmly established, Thornton helped in the running and administration of Rothamsted, and the planning of his new laboratories, completed in 1939, and also those for post-war expansion to extend the department's work on antibiotics, which never came to fruition. He was a foundation member of the Institute of Biology and when its president from 1962 to 1963 he took a prominent part in establishing the Fellowship and was keenly interested in science education and the setting up of the Biological Education Committee, and in university matters. He was elected a Fellow of the Linnean Society in 1948, Sir Gavin de Beer being his principal sponsor, and was a member of the Society of General Microbiology since its inception, the Society for Experimental Biology, Genetical Society, Association for Applied Biology, Prehistoric Society and the Baconian Society; in 1961 Thornton helped to organize the celebrations of the quatercentenary of the birth of Francis Bacon, who was also a citizen of St Albans. He was a governor of St Albans School.

In 1941 Thornton was elected a Fellow of the Royal Society, interestingly at the same time as C. D. Darlington, H. W. Florey and Winston Churchill. He was a Member of the Council from 1948 to 1950, and Foreign Secretary from 1955 to 1960. The last year of this office coincided with the Society's Tercentenary Celebrations and no doubt this was in mind when he was appointed. The very arduous preparations for this important occasion exercised to the full his considerable diplomatic skills and organizational talents (which he tended to hide from public view) and no doubt his fluent French—then still an indispensable vehicle of international communication—and some knowledge of German were valuable assets. His article on the international bond of science which appeared on 19 July 1960 in *The Times* Special Number on the Royal Society Tercentenary gives an historical account of the part played by the Society and its Fellows in the international field of science from the seventeenth century.

He believed strongly that East–West relations, then at a low ebb, could best be improved by encouraging personal contacts among scientists; a view strengthened by the visit he made to Russia in 1956 with a delegation led by Lord Adrian, and the exchange visits he helped to promote. He signed on behalf of the Royal Society the first formal agreement with the Academy of Sciences of the U.S.S.R.

He gave the Leeuwenhoek Lecture in 1955 and organized important symposia at the Royal Society and elsewhere. From 1943 until about 1966 he served on

many Royal Society Committees, sometimes as chairman, on Government Grant Boards, on numerous National Committees and the Unesco Committee and its panels concerned with arid zone research, Earth sciences and natural resources. He was a Vice-President of the Royal Society and was knighted in 1960, and for some years continued to take part in the Society's work and activities, regularly attending its meetings and those of the Royal Society Dining Club, and only gradually relinquished his responsibilities as his health, never robust, increasingly made travel difficult.

In running his department he used a light rein, encouraging rather than directing the work and allowing the maximum of freedom, much appreciated by his staff, especially in retrospect. Reserved but kindly and invariably courteous even when sorely tried, his fine manner protected him against the gauche encounter. He was somewhat shocked, and even incredulous, when told of modern trends in the organization of science and methods of publicity.

He travelled fairly widely in Europe, Russia and the near East, but never to India or Australasia. He did, however, very briefly visit America to see the World Fair in 1939, taking one of the earliest regular air passages, only to have to return hurriedly and retrieve his son, who was staying in Denmark, because of the imminent outbreak of war. Holidays were often taken in Scandinavia or in France, botanizing with his friend John Rammel in the foothills of the Alps or Pyrenees. He was an exceptionally good field botanist and regretted the shrinking flora of Hertfordshire. In about 1925 he searched unavailingly for the Grass of Parnassus (*Parnassea palustris L.*) which had been last recorded in the neighbourhood in 1909 by Winifred Brenchley. Outside science his interests were in paintings, books and especially old pottery, china and glass. He was a very good cook and the meals he prepared for his guests were elegant and continental rather than English in style. He was a member of the Savile and Athenaeum Clubs.

Like his friend Fisher, who saw no reason to depart from the faith of his forbears, he was a staunch and lifelong member of the Established Church. Since 1954 his home was a restored medieval cottage, formerly thought to be a charnel-house, immediately adjoining the Abbey, and he became well known by the clergy and workers in the Abbey. Some years ago St Albans Abbey was the location of a comedy TV serial that became very popular in America. On one occasion a visiting American devotee of this programme knocked at his door, mistakenly thinking it was the verger's and asked to be shown around. Thornton (now Sir Gerard) of course obliged. At the end a generous tip (a ten shilling note) was proffered, and graciously accepted.

He died at his home on 6 February 1977 and is survived by his wife, his son—who is Keeper of Furniture and Woodwork at the Victoria and Albert Museum—and by two grandchildren. Thornton will be remembered with affection and respect

The writer of this Memoir is grateful to Sir Gerard's family, to past and older members of Rothamsted staff, to members of the past and present administrative

staff of the Royal Society and to many others for interesting facts and personal recollections.

The photograph is by W. Bird.

References

Andrews, C. W. 1922 Note on the skeleton of a large plesiosaur (*Rhomaleosaurus thorntonii*, sp. n.) from the upper Lias of Northamptonshire. *Ann. & Mag. of Natural History* (9) **10**, 407–413.

Audus, L. J. 1950 Biological detoxication of 2,4-dichlorophenoxyacetic acids in soils: isolation of an effective organism. *Nature* (*Lond.*) **166**, 356.

Blackmann, G. E. 1945 A comparison of certain plant-growth substances with other selective herbicides. *Nature, Lond.* **155**, 500–501.

Brenan, G. 1962 *A life of my own: childhood and growth*. London: Hamish Hamilton.

Chen, H. K. 1938 Production of growth substances by clover nodule bacteria. *Nature Lond.* **142**, 753.

Hamner, C. L. & Tukey, H. B. 1944 The herbicidal action of 2,4-dichlorophenoxyacetic and 2,4,5-trichlorophenoxyacetic acid on bindweed. *Science* **100**, 154–155.

Hellriegel, H. 1886 Welche Stickstoffquellen stehen der Pflanze zu Gebote? Tageblatt der 59 Versammlung Deutscher Naturforscher und Aerzte in Berlin, 18–24 September 1886, p. 290.

Hutchinson, H. B. & Richards, E. H. 1921 The utilisation of straw and the production of artificial farmyard manure. *J. Min. Agric.* **28**, 398–411.

Jones, P. C. T. & Mollison, J. E. 1948 A technique for the quantitative estimation of soil microorganisms. *J. gen. Microbiol.* **2**, 54–69.

Singh, B. N. 1948 Studies on giant amoeboid organisms. 1. The distribution of *Leptomyxa reticulata* Goodey in soils of Great Britain and the effect of bacterial food on growth and cyst formation. *J. gen. Microbiol.* **2**, 8–14.

Slade, R. E., Templeman, W. G. & Sexton, W. A. 1945 Differential effect of plant growth substances on plant species. *Nature, Lond.* **155**, 497–498.

Walker, N. 1953 The decomposition of chlorinated aromatic compounds by soil bacteria. *Rothamsted Report for 1953*, pp. 65–66.

Zimmerman, P. W. & Hitchock, A. E. 1939 Experiments with vapours and solutions of growth substances. *Contrib. Boyce Thompson Institute* **10**, 481–508.

Bibliography

1914 (With G. Smith) On the nutritive condition determining the growth of certain fresh-water and soil Protista. *Proc. R. Soc. Lond.* B **88**, 151–165

1922 On the development of a standardised agar medium for counting soil bacteria, with special regard to the repression of spreading colonies. *Annals Appl. Biol.* **9** 241–274.

(With R. A. Fisher & W. A. Mackenzie) The accuracy of the plating method of estimating the density of bacterial population. *Annals Appl. Biol.* **9**, 325–359.

1923 On the vibration method of obtaining a suspension of bacteria in a soil sample developed by C. L. Whittles. *J. Agric. Sci.* 13, 352–353.

1924 (With N. N. Gangulee) Seed inoculation of lucerne (*Medicago sativa*) and its relation to mobility of the nodule organisms in soil. *Nature Lond.* **114**, 932.

1925 (With W. E. Brenchley) The relation between the development, structure and functioning of the nodules of *Vicia faba* as influenced by presence or absence of boron in the nutrient medium. *Proc. R. Soc. Lond.* B. **98**, 373–399.

1926 Bacteria in soil. *Encyclopaedia Britannica* (13th ed.) **29**, 298–299.

(With N. N. Gangulee) The life cycle of the nodule organism *Bacillus radicicola* (Beij), in soil, and its relation to the infection of the host plant. *Proc. R. Soc. Lond.* B **99**, 427–51.

1927 (With R. A. Fisher, On the existence of daily changes in bacterial numbers in American soil. *Soil Sci.* **23**, 253–259.

1928 (With P. H. H. Gray) The estimation of bacterial numbers in soil by direct counts from stained films. *Nature, Lond.* **122**, 140–141.

1929 The effect of fresh straw on the growth of certain legumes. *J. Agric. Sci.* 19, 563–572.

Soil bacteria. In *System of bacteriology*, **3**, 88–109. London: Medical Research Council.

The 'inoculation' of lucerne (*Medicago sativa*) in Great Britain. *J. Agric. Sci.* **19**, 48–70.

The role of the young lucerne plant in determining the infection of the root by the nodule-forming bacteria. *Proc. R. Soc. Lond.* B **104**, 481–492.

1930 (With P. H. H. Gray) The fluctuations of bacterial numbers and nitrate content of field soils. *Proc. R. Soc.* B **106**, 399–417.

The early development of the root nodule of lucerne (*Medicago sativa L.*). *Ann. Bot.* **44**, 385–392.

The influence of the host plant in inducing parasitism in lucerne and clover nodules. *Proc. R. Soc. Lond.* B **106**, 110–122.

1931 Lucerne inoculation and the factors affecting its success. *Imperial Bureau of Soil Science Technical Communication* no. 20. 39 pages.

The cultivation and inoculation of lucerne. *J. Farmers Club* 19–34.

1932 (With H. Nicol) Suggestions to prospective growers of lucerne. *J. Min. Agric.* **39**, 46–52.

Lucerne in England and Wales. *J. Min. Agric.* 39, 420–428.

(With H. Nicol,) The culture of lucerne in Great Britain. *J. Roy. Agric. Soc. Eng.* 93, 1–20.

1934 (With H. Nicol) The derivation of the nitrogen of crop plants, with special reference to associated growth. *Biol. Rev.* **9**, 383–410.

(With H. Nicol) Some effects of clipping the tops upon root development in lucerne. *J. Agric. Sci.* **24**, 532–539.

(With H. Nicol) The effect of sodium nitrate on the growth and nitrogen content of a lucerne and grass mixtures. *J. Agric. Sci.* **24**, 269–282.

(With H. Nicol) Further evidence upon the nitrogen uptake of grass grown with lucerne. *J. Agric. Sci.* **24**, 540–543.

Review of the work of the Bacteriology Department. *Rothamsted Experimental Station Report* 1–9.

(With P. H. H. Gray) The numbers of bacterial cells in field soils as estimated by the ratio method. With Appendix by R. A. Fisher, F.R.S. *Proc. R. Soc. Lond.* B **115**, 522–543.

1935 (With C. B. Taylor) Short period fluctuations in bacterial numbers in soil. *Trans. 3rd Int. Congr. Soil Sci.* **1**, 175–179.

The symbiotic relationship between soil bacteria and higher plant as exemplified by the *Leguminosae*. *Trans. 3rd Int. Congr. Soil Sci.* **2**, 81–94.

1936 (With J. E. Rudorf) The abnormal structure induced in nodules on lucerne, (*Medicago sativa L.*) by the supply of sodium nitrate to the host plant, *Proc. R. Soc.* B **120**, 240–252.

(With H. Nicol) Reduction of nodule numbers and growth produced by the addition of sodium nitrate to lucerne in sand culture. *J. Agric. Sci.* **26**, 173–188.

The action of sodium nitrate upon the infection of lucerne root hairs by nodule bacteria. *Proc. R. Soc. Lond.* B **119**, 474–492.

1936 (With H. Nicol) Stimulation of root-hair growth in legumes by sterile secretions of nodule bacteria. *Nature, Lond.* **137**, 494.

The present state of our ignorance concerning the nodules of leguminous plants. *Sci. Prog.* **31**, 236–249.

1938 Bacterial strains, and variation. In *Evolution: essays presented to E. S. Goodrich* (ed. G. R. De Beer) pp. 221–229. Oxford: Clarendon Press.

1939 A suggested explanation of the 'inefficiency' of certain strains of rhizobia. *Trans. 3rd Comm. Int. Soc. Soil Sci.* New Brunswick, A, 20–23.

1940 (With H. K. Chen & H. Nicol) The growth of nodule bacteria in the expressed juices from legume roots bearing effective and ineffective nodules. *Proc. R. Soc. Lond.* B **129**, 475–491.

(With H. K. Chen) The structure of 'ineffective' nodules and its influence in nitrogen fixation. *Proc. R. Soc. Lond.* B **129**, 208–229.

1941 (With H. Nicol) Competition between related strains of nodule bacteria and its influence on infection of the legume host. *Proc. R. Soc. Lond.* B **130**, 32–59.

1944 (With A. Kleczkowski) A serological study of root nodule bacteria from pea and clover cross inoculated groups. *J. Bacteriol.* **48**, 661–672.

1945 Effective and ineffective strains of legume nodule bacteria. *Nature, Lond.* **156**, 654.

(With P. S. Nutman & J. H. Quastel) Inhibition of plant growth by 2:dichlorophenoxyacetic acid and other plant growth substances. *Nature, Lond.* **155**, 497.

1947 The biological interactions of *Rhizobium* to its host legume. *Antonie van Leeuwenhoek* **12**, 85–96.

The biology of ineffective strains of *Rhizobium*. *Proc. 4th Int. Congr. Microbiol.* Copenhagen, 471–472.

1949 Problems presented by nodule bacteria and the legume host. *Agric. Progr.* **24**, 1–6.

1950 (With J. Kleczkowska) Use of antisera to identify nodules produced by inoculation of legumes in field. *Nature, Lond.* **116**, 1118.

1952 A discussion on symbiosis involving micro-organisms. Introduction. The symbiosis between *Rhizobium* and leguminous plants and influence on this of the bacterial strain. *Proc. R. Soc. Lond,* B **139**, 171–175.

(With L. M. Crump) Micropredators in soil. *Rothamsted Experimental Station Report* 164–172.

1953 (With F. A. Skinner) The interactions of actinomycetes with other micro-organisms in soil. *6th Int. Congr. Microbiol. Symposium on Actinomycetales* 174.

Sergei Nicholaevitch Winogradsky. *Obit. Not. Fellows R. Soc. Lond.* **8**, 635–644.

Some problems presented by the microbiology of arid soils. *Desert Research,* Special Publication no. 2, 295–301.

1954 The nodule bacteria and their host legumes: some problems that they still present. *Sci. Progr.* 166, 185.

1956 Soil organisms and root relationship. *Scient. Hort.* **12**, 32–37.

The ecology of micro-organisms in soil (Leeuwenhoek Lecture). *Proc. R. Soc. Lond.* B **145**, 364–374.

The development and present problems of soil microbiology. *J. Sci. Food Agric.* **2**, 93–101.

1957 A note on the visit to Russia of the Royal Society Delegation in 1956. *Notes Rec. R. Soc. Lond.* **12**, 230–236.

(With J. Meiklejohn) Soil microbiology. *Ann. Rev. Microbiol.* **11**, 125–148.

1960 The 'invisible college' that became the Royal Society of London. Special article. *R. Netherland Acad. Sci. Amsterdam* 9–16. Reprinted from *Verslag van de Gewone Vergadering der Afdeling Natuurkanda, Deel* **59**, 2, 29.