

W. Stiles

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WALTER STILES

1886-1966

Elected F.R.S. 1928

Walter Stiles was born on 23 August 1886 at Shepherd's Bush, Hammersmith. He was the eldest child of the family and had one sister born three years later. Both his parents were Londoners. His father, Walter Stiles (1861-1938), was an artist who worked in wood and clay and whose work ornamented many large houses in London and elsewhere. His mother was Elizabeth Sarah Stiles (*née* Dury; 1859-1943). His grandfather, James Stiles, was a corn merchant of Pimlico and the family appears previously to have been long settled in Kent in the neighbourhood of Cobham. James's brother, Walter Stiles, at Cobham, was the grandfather of Walter Stanley Stiles, F.R.S.

On 7 July 1920 Walter Stiles married Edith Ethel May Harwood at St Mary's Church, Stamford Brook, Hammersmith. Her parents came from the West Country, her father from Wiltshire and her mother from Dorset. There were two children; Walter born in 1922 and Ruth Mary born in 1927. The son graduated in physics at the University of Birmingham and now works on irrigation problems as a member of the staff of the Grassland Research Institute, Hurley, Berkshire. The daughter, after graduating at Birmingham in Spanish and Portuguese, went on to the University of Madrid and is now a lecturer in Spanish at Torquay Technical College.

Stiles's education commenced at the public elementary school in Westville Road, Shepherd's Bush (1890-1897). He then, with the assistance of L.C.C. junior and intermediate scholarships, went to Latymer Upper School, Hammersmith, of which he afterwards wrote in enthusiastic terms. Very much, he said, was due to the wisdom of the headmaster, the Reverend C. J. Smith, who, from a modest beginning in 1895, raised the school to a leading position among the grammar schools of London. Personally, he felt that he owed a great deal to the teaching of the Mathematics and Senior Science Master, G. M. Grace, who was a source of inspiration to his pupils. Contemporary with Stiles were Harold Spencer Jones, later F.R.S. and Astronomer Royal; G. K. Livers, afterwards Professor of Mathematics at University College, Cardiff; and D. Orson Wood, for many years an Editor of *Science Progress*.

During his schooldays Stiles spent most of his Saturdays in bicycling with friends in the country to the west, north-west and south-west of London. This

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was at the period when the bicycle was the principal means of enjoying the English countryside, and he records that he developed a love for it which continued through life and which, among other things, later caused him to join the National Trust.

From school he moved in 1905 to Emmanuel College, Cambridge. He was awarded a college exhibition for natural science, a school-leaving exhibition and a major scholarship from London County Council.

In justification of these awards his academic record at Cambridge was distinguished. His subjects for Part I of the Natural Sciences Tripos were physics, chemistry, botany and geology and in 1907 he obtained a first class as he did two years later in Part II. His original intention had been to read physics in Part II, a taste which remained evident in the choice of tools for some of his later researches. When he first arrived at Emmanuel he was placed under A. C. (later Sir Albert) Seward as tutor and, although he was transferred to F. G. (afterwards Sir Gowland) Hopkins when Seward became Professor of Botany in the following year, it is evident that Seward exercised a strong influence over him throughout his period in Cambridge. As a student he found the biological approach so stimulating that he transferred his principal interest to botany and worked under a team of teachers including, besides Seward, F. F. Blackman, F. T. Brooks, C. E. Moss and A. G. (afterwards Sir Arthur) Tansley. The Cambridge Botany School at this time had recently opened its new laboratories and was considered the best equipped botanical department in the country. Stiles found the teaching there lively and stimulating and he also found inspiration in the companionship of his fellow students and postgraduates many of whom subsequently became distinguished in very diverse branches of botany. They included, to mention only three, D. Thoday and H. Hamshaw Thomas, both subsequently Fellows of the Royal Society, and J. Ramsbottom who became Keeper of Botany at the British Museum.

Anatomical and experimental researches

Under the influence of Seward, Stiles's first researches were on gymnosperm anatomy. A paper on *Saxegothaea conspicua*, Lindl. published in 1908 was a general account of the whole tree based on material from two of the very few of any considerable size in the country. The discussion was concerned to relate *Saxegothaea* to the Podocarpeae and the culmination of Stiles's anatomical work was a paper in 1912 on the Podocarpeae themselves running to 71 pages of the *Annals of Botany*. These contributions were in the fashion of their time. The volume of the *New Phytologist* which contained the first of them consisted of 262 pages, 196 of which were devoted to gymnosperm anatomy; mycology, ecology and taxonomy shared the remainder. Although they were so far removed from his eventual fields of interest, these investigations must have afforded wide scope for two of the major characteristics of all his original work: his passionate devotion to the patient and

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accurate determination of facts, and the cautious balancing of probabilities in uncertain fields. Where other authors' papers would be likely to state 'conclusions', Stiles's were apt to have 'concluding remarks'. 'While we must wait for fuller knowledge before making any very definite statement, it would appear . . . ' This, or some equivalent phrase, appeared frequently from 1908 onwards.

At the beginning of 1910 he moved to Leeds to take up an appointment as Assistant Lecturer in the Botany Department of the University and in the following year, J. H. Priestley became Head of the Department. Priestley was a man of impressive and attractive personality with a far-ranging mind. He was interested in plant anatomy, but in its functional and causative aspects. Into this very tricky subject he endeavoured to introduce experimental methods where others had been content to speculate solely from anatomical observation. Stiles has recorded that 'it was largely due to the stimulus of J. H. Priestley' that his interests now moved to plant physiology where they remained for the rest of his life. The preference for experiment over observation must have been a strong link; but in every other respect two more dissimilar minds could hardly be imagined. About the same time Ingvar Jørgensen also arrived in Leeds as a junior assistant to Professor Priestley for some work on the 'electroculture' of crops. Stiles appears to have been associated with this at least to the extent of helping to collect and publish the results some years later. But a much more important collaboration began between the two younger men and lasted for several years. Its subject was the entry of salts into plant tissues.

At this time concepts of the plant cell were dominated by the simpler facts of its water relations and particularly its ability to plasmolyse. It followed that the cytoplasmic lining separating the cell wall from the vacuole, or some layer of the cytoplasm, must be sensibly semipermeable. The problems of uptake were therefore approached as problems of membrane permeability in systems of bombarding ions and molecules. The motive force was due to the diffusion pressure of the particles, and to have attributed any positive action to the cytoplasmic membrane itself would have been regarded as needlessly vitalistic.

It was characteristic that the first two papers published consisted of a review of previous work and a detailed assessment of the possibilities of electrical conductivity measurements as a tool. In 1914 quantitative results were rare and a series of 'Studies in permeability' was undertaken to supply major deficiencies. Points examined were 'antagonism', the effect upon the uptake of ions of the simultaneous presence of others; and the effects on permeability of temperature and various organic substances.

War interrupted these studies and, being in a low medical category, Stiles was seconded from Leeds to London to work for the Royal Society Sectional Chemical Committee on the preparation of local anaesthetics and bacteriological sugars. Later he continued for the Society's Food (War) Committee with work on the digestibility of war bread and in May 1918 transferred to

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the staff of the Food Investigation Board of D.S.I.R. under Sir William Hardy. This brought him again into collaboration with Jørgensen and also with F. S. Adair (later F.R.S.). Many of their experiments were done in the laboratories of Professor W. M. Bayliss, F.R.S. at the Institute of Physiology of University College London; and the writing up was only concluded after Stiles had returned to academic life. In 1922 he produced a lengthy report entitled, 'The preservation of food by freezing with special reference to fish and meat: a study in general physiology' in which theory was as fully honoured as ascertained facts. If this appears somewhat uncharacteristic the following excerpt may seem even more so; it will, however, serve as a good example of his unadorned but serviceable style of writing.

'A single experiment was made by Mr Jørgensen and the writer with a view to determining whether it would be possible to preserve poultry by freezing the birds in brine instead of air. For this purpose a fowl which had been allowed to hang at air temperature for twenty-four hours was immersed in sodium chloride brine at −18 °C for about five hours by which time it was frozen through. It was then thawed in air, and about twenty-four hours after removal from the brine was roasted. The flavour was excellent, and indistinguishable from that of an unfrozen bird similarly treated.' But in 1918 even an experiment so lacking in replication must have had its attractions. Some foods, notably fruit, could not be preserved by actual freezing and the scientific aspects of their cool storage were reviewed by Jørgensen and Stiles in a series of articles in *Science Progress* (1919-1920).

It would seem that some time at least must have been available for permeability studies and in 1919 two papers over the joint names of Walter Stiles and Franklin Kidd were communicated by Bayliss to the *Royal Society Proceedings* B. They were concerned with the rate of absorption of salts by plant tissues and the position of equilibrium attained. To minimize variation, the device pioneered by Stiles & Jørgensen (1915) of taking random samples of uniformly cut disks of storage tissue was again used. The disks were immersed in salt solutions maintained at 20 °C. The establishment of diffusion gradients in the solutions was avoided by shaking and the absorption of ions estimated from the changes of conductivity in the external solutions. It was established that, over a concentration range 0·1N to 0·0002N, the equilibrated absorption ratios, internal concentration (strictly, amount absorbed per unit volume of tissue)/external concentration approximated to an adsorption isotherm. With characteristic caution they commented 'the data presented are regarded as inadequate in themselves to justify the conclusion that the absorption of salts by the cell is an adsorption process and no proposals are put forward as to the mechanism of salt intake by the cell'. They also recorded that, after a brief initial period of rapid withdrawal of salt into the tissue, there follows a long period of slower uptake; but they did not at this time put forward any proposals for multiple mechanisms.

In the autumn of 1919 Stiles took up an appointment as Professor of Botany at University College, Reading. As a result of the work on food

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preservation he had a number of invitations at this time to go to South Africa and to America to advise on fruit transport, and fish and meat preservation. Some of the offers were very tempting; but he returned to botany with great zest and to the other offers he replied always: 'I am a botanist and intend to remain so.'

He continued to work on the salt relations of plant cells both at the bench and in supervising postgraduates. It had been known for a considerable time that plants growing in water cultures containing ammonium salts increased the acidity of the medium, often very considerably. Stiles showed that, underlying this, was the much more general phenomenon of the independent and unequal absorption of the ions of a salt. He and his associate, Miss Gladys M. Redfern (Redfern, *Ann. Bot.* **36**, 167, 1922; Stiles, *Ann. Bot.* **38**, 617, 1924) presented data emphasizing this inequality for a variety of attached roots and disks of storage tissue immersed in single salt solutions. It was further shown that, where the acidity remained more or less unaltered ionic equivalence of the solution was maintained by ions coming out of the tissues. Inequality of uptake was most noticeable in strong solutions, 0·1N, and much less at 0·01N. In the 1924 paper Stiles also confirmed by chemical analysis the earlier conclusion from conductivity measurements that the position of equilibrium in uptake was approximately that for an adsorption both with anions and cations. Similar results were also obtained with a series of acid and basic dyes (Redfern, *Ann. Bot.* **36**, 511, 1922).

At this period relatively little was known of the physics of colloidal systems. Since tissues clearly held numerous gels in their composition the characteristics of the diffusion of electrolytes through gels were likely to affect the uptake of salts, and to require examination accordingly. Between 1920 and 1923 Stiles published a series of papers, one of them in collaboration with G. S. Adair, on the penetration of electrolytes into gels. The addition to the gel of a low concentration of indicator was shown to be a valid method of marking the progress of the electrolyte. Linear diffusion was found, in agreement with other investigators, to follow Fick's law, with diffusion constants lower than those for water and decreasing progressively with the amount of gelatine or agar present in the gel. Differences from diffusion in more homogeneous media were not striking.

A paper published in 1927 returned to direct work with storage tissues and examined the escape of salts from them when immersed in distilled water. One of the most interesting results was that salts escaping (possibly, it was supposed, from the surface cells damaged in cutting out the disks of tissues) were absorbed again almost entirely. Reabsorption depended on a certain degree of aeration of the solutions; if aeration was avoided exosmosis continued and the tissue rapidly died. Stiles commented that in attempting to find an explanation for this 'one naturally looks to the respiratory relations of the tissue under the different conditions'. He came to the conclusion that the aeration, which was mainly achieved by shaking, was effective in breaking down diffusion shells of oxygen and carbon dioxide that would otherwise be

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established round the tissue slices. There can be little doubt that the continued exudation of salts from the unaerated tissues was a result of their progressive deterioration and not vice versa. It was therefore a natural, and is still probably a correct, assumption that the failure to absorb salts under these conditions was due to poisoning of the tissues by carbon dioxide or other products of the anaerobic respiration. He was also at pains in this paper to reaffirm that methods of measuring salt uptake that assume final equal concentrations of an ion within and without a tissue, such as the then popular deplasmolysis methods, must lead to fallacious results. Perhaps, more important, he now, for the first time, explicitly spoke of absorption as at least a two-phase process. He wrote: 'We may suppose that the protoplasmic layer (the "membrane") absorbs by adsorption or chemical combination a certain amount of solute, but that also solute diffuses through the protoplasmic layer into the vacuole.'

In pointing out the duality of absorption and a connexion with aerobic respiration, Stiles pioneered two ideas that have played, and are still playing, a major role in studies of salt uptake. By 1938, when he gave his presidential address to Section K of the British Association, several teams of workers had made further notable experimental contributions. He was then prepared to agree that salt exchange equilibria might be equally well, if not better, described in terms of Donnan rather than simple adsorption equilibria. He further agreed that energy needed for salt accumulation might be ultimately provided by respiration; even though, at that time, he considered the available evidence 'does no more than show that this accumulation is a vital process, depending on the normal functioning of the protoplasm'. The further evidence of a more direct connexion was to come later. R. N. Robertson, F.R.S., writes:* 'Thirty years later we are still puzzled by the details of mechanism. It is not surprising that Stiles did not clear up the problem in his day.'

Moreover, it is clear that, as a matter for personal investigation, he was more interested in the permeability aspects of the problem of salt uptake than in the mechanisms of continuous accumulation. Over the period 1930-1935 he carried out and supervised a long series of 'studies on toxic action', which he described as a continuation in a particular direction of his earlier work on permeability. Toxicity, as evidenced by shrinkage or loss of salt by disks of storage tissue, was examined for numerous surface active, acidic and other poisons. A considerable body of data was collected and codified.

The last paper on salt uptake to bear Stiles's name was published in 1946 and, like its immediate predecessors, it re-examined the course of salt uptake by a variety of storage tissues under aerobic conditions; polarographic and chemical analyses of the external solutions were employed. The two phases of absorption noted earlier were a constant feature in varied combinations of salts and tissues. The first phase was now definitely interpreted as the establishment of a Donnan equilibrium between tissue and external solution; the escape of ions from the tissue into distilled water was attributed to the

* Personal communication.

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Photograph of Professor Walter Stiles, from a snapshot in the possession of Mrs. Ethel Stiles.

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same cause, rather than to the cellular damage suggested earlier. The second phase commonly set in before equilibrium was fully established and 'corresponds with the development of increased metabolic activity as indicated by an increase in respiration'. So much was now common ground with the majority of other investigators working in the field.

Most of them were, however, directing their major efforts towards the nature of the link between respiration and 'second-phase' uptake. While Stiles declined to be drawn into this, the realization that salt uptake and respiration were intimately connected commended the latter to him as a subject for research in its own right.

Seeking a method of simultaneous oxygen and carbon dioxide measurement of high sensitivity, he was drawn to the use of the katharometer, which depends on the difference of thermal conductivity between the two gases. He had now moved to Birmingham and, in adapting the method to respiration measurements, he had the co-operation of William Leach (now F.R.S.C. and past Professor of Botany in the University of Manitoba) and Dr G. A. Shakespear, the inventor of the machine. On their own statement 'many difficulties and sources of error were encountered' and, when in 1931 they had been overcome, a detailed account of the technique itself was published in a joint paper by Stiles & Leach. The machine was then put to work on the respiratory quotients of a range of seeds with different reserves, during early stages of their germination. The investigation was described as preparatory to a chemical one; but the latter was never carried out by Stiles and would, indeed, have been entirely foreign to his usual ways.

Considerably later he turned once more to the katharometer for recording respiratory drifts; but also used the manometric methods that had by then become standard. A paper published by J. K. Choudhury (*Proc. Roy. Soc.* B, **127**, 238, 1939) from Stiles's laboratory had described the gas exchange of intact potatoes, artichokes, carrots and red beet; and, with K. W. Dent, Stiles now examined the same tissues in the form of thin slices such as had been used for examination of their salt uptake. The work was carried out in considerable detail, both in air and under nitrogen. Comparison of the results with those of Choudhury for the intact organs and with those from other laboratories for tissue disks showed that the cutting and other manipulations had very complex effects upon respiration rates, and that these might be very difficult to control satisfactorily. It now seems clear that, while cut disks of mature tissue make adequate material for the investigation of the initial 'equilibrating' phase of salt uptake and the accumulation of salts in vacuolated cells, the results obtained with them should not be directly applied to the rapid uptake associated with growth. It is hardly surprising that rapidly respiring and metabolizing cells are here the material of choice.

It may be for this reason, or simply due to the passage of time, that Stiles never attempted to bring his salt uptake results into line with metabolic processes. Although he remained active in retirement for many years after 1947, this was his last paper to describe original experimental researches.

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Books and monographs

Stiles wrote voluminously on many branches of plant physiology. When he became seriously interested in a subject his approach was to read extensively round it and this often led to the publication of an article reviewing methods or results to date before any experimental work was done, or at least made public. Several such articles were published in collaboration with Jørgensen in the *New Phytologist* which, in the 'teens and 'twenties of this century, had a policy of encouraging such public discussion. In 1915 a series was begun on carbon assimilation subtitled, 'A review of recent work on the pigments of the green leaf and the processes connected with them'. It was evidently inspired by the recently published work of Willstätter on the isolation of the chlorophylls, which they recognized as 'undoubtedly one of the most brilliant achievements of organic chemistry' and one which had 'cleared the way for a vast amount of plant physiological work of the greatest importance'. Willstätter's work did not escape all criticism. At a somewhat later time Stiles used to take pleasure in relating how, at a meeting when the practicability of producing crystalline chlorophylls by Willstätter's methods was called in question, he was able to rise in their defence and produce a crystalline sample prepared by himself. The series ran through the pages of the *New Phytologist* for nearly two years, and a somewhat exasperating feature for the reader must have been the fact that all citations (there were more than two hundred of them) were reserved for the last instalment. The whole series was then published separately in book form as *New Phytologist Reprint* No. 10 and the issue was quickly exhausted.

It is a comment on the changes that have since occurred in scientific book publishing that Stiles again chose the same method for his 'Permeability', which ran through the *New Phytologist* from 1921 to 1923 and appeared separately in the following year. It remained the standard monograph of its subject for considerably more than a decade and must probably be regarded as the most important and useful of his surveys.

It was followed in 1925 by *Photosynthesis. The assimilation of carbon by green plants* which was published directly in book form without previous serialization. It aimed, like *Permeability*, at being a complete account of its subject; it was hoped that 'no important work has been overlooked' and, in fact, cited upwards of eight hundred and seventy titles. Nevertheless, it can hardly be said to have had the success of its predecessors. The Jørgensen & Stiles monograph had been content to assess 'recent advances' and had done it admirably at a time when there was much recent work of interest. In attempting a wider coverage, much dead, or at least not very lively, wood was inevitably drawn in. Also, although in 1925, the first of Warburg's investigations of photosynthesis had been published, it was only in succeeding years that the rapid advances made possible by his methods bore their prodigious fruit. Stiles's book accordingly 'dated' very rapidly.

Respiration in plants, written in collaboration with William Leach, was a

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very different undertaking. Limitation to little over a hundred pages of text imposed selection rather than completeness. It no doubt helped that knowledge of the biochemical mechanisms of plant respiration was scanty in 1932 and based largely on surmises that they must be similar to those of yeast and muscle. S. Kostychev's *Pflanzenatmung* (1924) had shown what could be done in the way of direct statement in this field; but both it and its annotated English translation by Charles J. Lyon (1927) were now painfully out of date. Students were grateful for the help that the English authors were able to give them; and have remained so through successive editions to a fourth one, about twice the size of the original, published in 1960.

Another book aimed at student readers was *An introduction to the principles of plant physiology*, first published in 1936, with a second edition in 1950. This was a general textbook of plant physiology and as such was in more or less direct competition with others. Probably only Stiles could at this date have written so evenly over the whole field of plant physiology at an 'advanced student' level. The title and the heavy format given to it by the publishers were perhaps a little forbidding; but the book was popular, at least with pass-level students, on account of its completeness and its clarity at the level chosen. Concerning the title, Stiles once said that the simpler one he would have preferred had already been appropriated. He was engaged at the time of his death on a third edition which is being completed.

In the early 1940s, Stiles occupied himself with the 'trace elements' in nutrition and much time was spent in working at methods for their estimation in materials of plant origin. He published a monograph in 1946, *Trace elements in plants and animals*, with a second edition in 1951. A third edition in 1961 was issued with the more restricted title, *Trace elements in plants*.

Besides these longer works Stiles kept up, through his working life, a long series of review articles for such journals as *Science Progress* and *Scientia*; but of all his numerous publications only two were in any degree polemical. Both of these were written in collaboration with another author, and one of them was gently chiding his lifelong friend, David Thoday, whom, 46 years later, he appreciated in these *Biographical Memoirs* (**11**, 177). The article (with Ingvar Jørgensen) began: 'In the March-April (1918) number of this journal, D. Thoday fired the maroon, as it were, for a warning of the bomb he intended to drop on us in the May-June number.' After this opening salvo the paper quickly turned to the presentation of new experimental data.

Teaching

Except during the First World War, Stiles was teaching in University Departments from 1910 to 1951 and for 32 of these years as Professor and Departmental Head. With a temperament reserved to the point of shyness he did not make a quick impact on freshmen students; but those who were with him for any length of time came to appreciate his real interest in them personally as well as in their work. One who has since specialized in other

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fields writes of him as a tutor: 'Whenever I had to go to him on academic or other matters he was invariably kind and helpful in spite of his obvious preoccupation with permeability and other aspects of plant physiology. As a very young student I was greatly in awe of him.' But, as usual, the awe ripened into appreciation. Many of his pupils have in after years expressed gratitude for his wise counsel. 'The impression he gave to his students was of a scholar and a gentleman, detached from the everyday life of the undergraduate, but when necessary a kindly guide in their studies and in their occasional conflicts with authority.'

By some quirk of university regulations it once fell to his lot to reprove a young lady, not so very greatly his junior, for returning to college at what was considered in the 1920s an unseemly hour. This was perhaps not quite his line of country. On learning that it was 'not much after midnight' he said: 'Oh, I don't call that very late,' and passed quickly to another matter.

His meticulous idea of the conduct becoming a university lecturer is illustrated by Professor Lilian Hawker; the occasion was his election into the Royal Society. 'We greeted him with an assortment of musical instruments as he entered the lecture room, and when the noise died down he calmly said: "Thank you, now last week we were considering the enzyme lipase . . . ".'

The Botany Department at Reading when Stiles came to it in 1919 was not a large one or lavishly equipped; but it was lively with post (First) war optimism. Stiles undertook the teaching of all branches of plant physiology himself; morphology, anatomy and their concomitants were taken by Dr Theodora Prankherd to whom Stiles later (1940) paid tribute; and juniors were assigned to systematics where, he cryptically remarked, they could do least harm.

His own lectures were as widely based and as carefully prepared as his monographs and, indeed, their preparation must often have gone hand in hand. They had no purple patches and were a total contrast to those of Miss Prankherd who could, and did, make fireworks of fossil anatomy. The stimulus of those alternating doses of muted and overt enthusiasm remains an abiding memory after all but half a century.

The supervision of postgraduates he performed on a daily basis and was always available for discussion as problems arose. He was a stimulating supervisor because he was himself so patently committed to the advancement of physiological knowledge. He was exceedingly generous in questions of authorship and many researches suggested, daily supervised and revised in the writing by him were published without his name on the title page. It is now even sometimes difficult to trace the extent of his influence and participation. His tenacious memory enabled him to keep track of his associates long after they had left him and well-meaning introducers were sometimes floored by: 'But I know him, he was one of my students.' Among his pupils were G. F. Asprey; C. T. Hickman and E. S. Twyman; now Professors of Botany in Cardiff, London, Ontario, and Grahamstown, South Africa, respectively; the late R. H. Dastur, Professor of Botany in Bombay;

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Lilian E. Hawker, Professor of Mycology in the University of Bristol; Gladys M. Redfern, who, as Mrs G. M. James, continued research and teaching in the Botany Department at Oxford, and also the writer of this memoir.

Societies and awards

While at Cambridge, Stiles was awarded the Walsingham Medal for 1911, for an original essay on a biological subject. He obtained the Cambridge Sc.D. degree in 1922 and was made an Honorary D.Sc. of Nottingham University in 1953. When he retired from the Mason Professorship of Botany at Birmingham he was made Professor Emeritus (1952) and a Life Governor of the University in 1954.

He was a great supporter of scientific societies and was honoured by them in various ways. He was a member of the Central Committee for the Study and Survey of British Vegetation and a founder member of the British Ecological Society which grew out of it in 1913. Even longer was his connexion with the British Association which he joined in 1910 and on whose Council he served from 1951 to 1954. He was honoured by being made President of Section K for the Cambridge Meeting of 1938, and continued to serve the Association until failing health made it impossible. Other societies he joined included the Linnean, the Biochemical and the Society for Experimental Biology. He was appointed a Corresponding Member of the American Society of Plant Physiologists. He was elected into the Royal Society in 1928 and on several occasions served on the Botany Sectional Committee. He was, on occasion, Chairman of the Government Grants Committee F, and served on Council from 1935 to 1937.

Concluding remarks

When he retired from the Chair of Botany at Birmingham in 1951, having reached the age limit, Stiles returned to Reading to begin an active retirement that was to last for over fourteen years. He was elected an honorary member of the University's Senior Common Room and joined the Friends of the University of Reading and the Berkshire Archaeological Society, becoming a member of its Council in 1961. In 1958, at the invitation of the Czechoslovak Academy of Sciences, he visited universities and biological institutes in Prague, Bratislava and Brno, including the famous garden in which Mendel had worked, and the archaeological institute at Nitra in Slovakia.

Stiles was an easy and tireless traveller and, during his later career, was frequently on the continent for congresses or for pleasure. During his retirement he and his wife spent a winter in Jamaica and an early summer in Spain, both at times when their daughter was working in the country. They found the visits particularly worthwhile because they were entertained freely

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in Jamaican and Spanish homes in the manner of the country. He fitted so well into the Spanish scene as to elicit the comment that he might well be a Spaniard.

Relieved of the day-to-day responsibilities of departmental administration, he resumed writing and contributed numerous articles on aspects of respiration and nutrition to the monumental *Encyclopaedia of plant physiology*, to *Science Progress* and other publications. He also published in *Nature* an account of his observations on the state of plant physiology in Czechoslovakia.

One of his main hobbies for many years had been gardening, particularly fruit-growing. The names of many of the older apple varieties he found attractive, and this led to a hobby of collecting varieties in danger of extinction and keeping them in cultivation, and even to prolonged hunts for surviving material, with which his Head Gardener at Birmingham did many successful grafts. He took a large selection of these with him back to Reading and kept them going until recently. Characteristically, he did not claim for any of these half-lost varieties that they excelled modern ones in food value or flavour. Another interest that lasted as long as he could walk about was in photography. His taste was rather on the austere side, usually involving architectural subjects, and reflected the knowledge that had grown up with him owing to his father's profession.

Although he was a frequent attender at scientific gatherings, Stiles remained, throughout his long career, a slightly withdrawn figure more apt to answer a question than to push forward an assertion. His most important original contributions to plant physiology were made round the twenties and thirties. Whatever place these eventually take in the history of the subject, it may already be said that he had two important influences: one was in originating good quantitative methods of work on his chosen topic and in improving them over many years; and the other was in his clear, dispassionate presentation of the work of others.

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W. O. James

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From 1918 to 1963 articles on recent advances in plant physiology were regularly contributed to *Science Progress*.

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