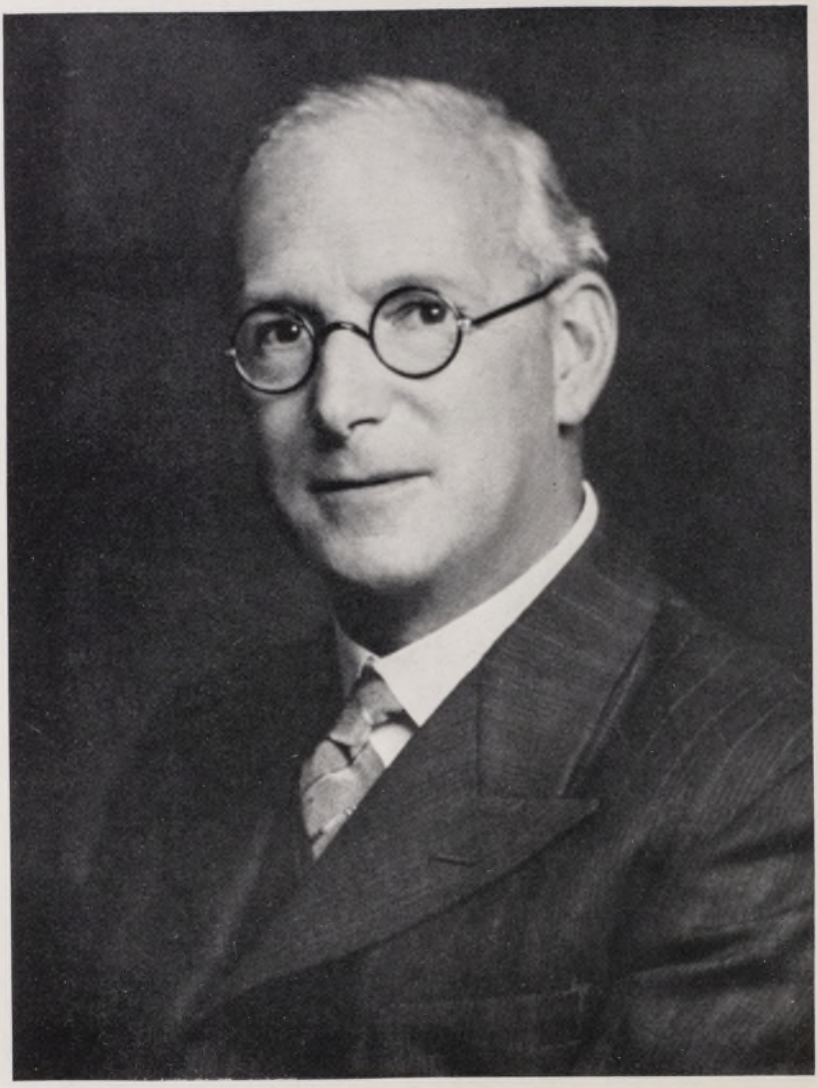

E. J. Mansell

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ERNEST JOHN MASKELL

1895–1958

Ernest John Maskell was born in Cambridge on 1 February 1895. He went to the Cambridge County School (now Cambridgeshire High School for Boys) with a scholarship. His brothers recall that he was very studious, generally preferring a book to games, in which, however, he played his part. His studious inclination, aided by a retentive memory, reaped its reward of prizes. He became a school prefect, in which capacity he showed a quality he retained throughout his life: a marked ability to get on with his juniors, his equals, and his seniors. He had the privilege of being taught by Dr M. Dawson who later became H.M. Inspector of Schools. She encouraged and stimulated his early interest in botany, and Maskell always, and rightly, held her in high regard. When he reached the Sixth Form, or a little later, he, with nine others, formed 'The Honourable Order of the Upper Ten' whose motto was 'Speak truth, live pure, right wrong, follow the Christ the King'. One of their rules was 'That it be incumbent upon every Knight to correspond with every other and with the Rev. C. J. N. Child at least every Christmas'. Many did so maintain contact. Another rule was 'That the Order continue until the death of the last Knight'—Maskell's was the first death. He maintained his connexion with his old school by serving on the Old Boys Society, of which he became President. He was also, for a long time, one of the members of the Governing Body of the school appointed by Cambridge University.

At the age of eighteen he went to Emmanuel College as an Entrance Scholar. In 1915 he was placed in the First Class of Part I of the Natural Sciences Tripos and was awarded the Frank Smart Prize in Botany. At this stage his academic studies were interrupted by his joining the Friends' Ambulance Unit. In this service he formed a close friendship with a Fellow of his college, Mr L. H. G. Greenwood, who writes: 'I first came to know him when he was an undergraduate here before 1914, but I remember little about that time. We became close friends during the war at the military hospital in York, mainly staffed by the Friends' Ambulance Unit, of which we were both members. In the often trying conditions of service there, his unselfish and co-operative friendliness, together with his complete efficiency, did much to make things go smoothly and happily. Later, for a shorter time, we were together at the hospital in Courtrai also run by the Unit, and the same remarks apply to his service there.'

When the war was over he returned to Cambridge to resume his academic studies. In 1920 he was placed in the First Class in Part II of the Natural Sciences Tripos (Botany) and was awarded the University Frank Smart

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Studentship. He was one of those students who had the fortunate experience of listening to the lectures on plant physiology given by F. F. Blackman. It would have been strange if Maskell had not responded. He became a research student under Blackman's supervision. With wise guidance and his own ability Maskell laid a secure foundation for a successful career of research and later of teaching. Before he had finished his work for the Ph.D. degree he joined the Horticulture Unit, housed in the School of Agriculture at Cambridge, as a plant physiologist, but before he had really started a research problem he moved to the Rothamsted Experimental Station. Here he had the advantage of contact with R. A. Fisher, from whom he rapidly acquired a sound basis of statistical knowledge at a time when few biologists appeared to realize its importance. He later made good use of this acquisition. After a short stay at Rothamsted he joined T. G. Mason in 1926 at the Cotton Research Station newly established in Trinidad. Judged by the publication of important papers on translocation this was a most fruitful collaboration. Unfortunately Mason died soon after Maskell and had no opportunity to give in writing his personal impression of Maskell's contribution. This short spell produced most of Maskell's work that has been published. Dr E. Phillis, who succeeded to Maskell's post when he left for Cambridge in 1931, and who overlapped with Maskell for about three months and saw him again in Trinidad when Maskell spent a sabbatical leave there, writes: 'Maskell's contribution was the introduction of precision into the more general views of Mason. Maskell was responsible for the statistical side of the work, plus the methods of routine analysis. He was also responsible, I believe, for the training of the local staff, who formed an extremely competent group. He gave them an understanding of the problem they were working on, and was remembered with great affection by many people of all grades in St. Augustine and district for many years after he left'.

Meanwhile Blackman was anxious to build up a nucleus of plant physiologists in Cambridge and he secured Maskell's return to the Botany School, where he became a Lecturer in 1931. Here he spent the next twenty years of his life. If it was not productive of published papers it was in many other ways. At first he gave special post-graduate lectures on a variety of topics in plant physiology. Later he took over Blackman's elementary lecture course on the physiology of the cell, and when Blackman retired from his Readership in Botany in 1936 he became responsible for the biochemical portion of Blackman's lectures in the advanced course. For a time he conducted an elementary course in practical plant physiology. Throughout he supervised the training in research of a succession of research students. He played a full part in helping in the successful running of a scientific department, not the least of which was the Physiology Club for research students, now called the Blackman Club. This, and his lectures, involved wide reading, and those who had the privilege of being members of the Club and of attending his lectures will remember to what good use a wide reading, filtered through an able mind, was put. At his lectures the blackboards were filled before the

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lecture with a mass of factual detail, neatly arranged in tabular and graphical form. The result was that the keener students, who could find the time, would come before the lecture to copy the data. He rightly valued his teaching experience, not only for the help which he was able to give to others but for the ideas it gave him for further research work.

His activities were not limited to his service to his department; he led a full life inside and outside the University. His ability and kindliness fitted him well for this. During the Second World War he found time to serve his college as acting steward and the college gave him further opportunities by electing him to a Fellowship. He served on that hard-worked body the General Board of the University on which he played a full part, serving on many of its special committees.

His distinction as a plant physiologist was recognized by his being made a Reader and later when the Headship of the Sub-Department of Plant Physiology became vacant he was appointed to this. He was elected a Fellow of the Royal Society in 1939.

His happy and fruitful spell at Cambridge came to an end in 1951 when he succeeded to the Mason Professorship of Botany at Birmingham University on the retirement of Professor W. Stiles. Unfortunately his early death in 1959 resulted in his tenure being short. Nevertheless his unceasing activity enabled him to contribute much. He co-ordinated the efforts of his colleagues in the planning of the new Biology Building and displayed his wide botanical interests and love of plants in the management of the University Botanical Garden.

His parents were Baptists but he joined the Society of Friends when an undergraduate. Despite all his other activities he devoted much time to service to the Society. For many years he was a much-appreciated Elder of the group at Cambridge whose Meeting House is in Jesus Lane. Friends record that his 'vocal ministry', which was most helpful and simple, has left vivid memories. In it he made great use of quotations from poetry—poetry and pictures were a great source of inspiration for him. He served on the Governing body of the Friends School at Saffron Walden and Mr Howard Diamond, who was the Chairman of the Governors, writes: 'Maskell served as a Governor of the School for eighteen years from 1933 to 1951. His work on the Governing Body was appreciated because he formed a link between the School and the University, and was able to advise senior boys and girls regarding their preparations for university entrance. Needless to say, the staff also turned to him, not only for help and advice on his own subject of botany, but to draw on his wisdom and knowledge on all educational matters. Maskell's interest in the life and work of the school stemmed from the fact that it set out to help all its scholars, whether members of the Society of Friends (whence the foundation arose) or Essex County scholars, to secure the best available grammar school education without reference to the means of their parents; and to this end he gave generously. No doubt reference will be made elsewhere in the memoir to Maskell's deep appreciation of

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poetry, especially modern poetry. This gift he sometimes extended to the school community at Saffron Walden, where he would talk to the school, and especially to the older scholars, in a way which fired their imaginations and lifted their thinking into a new range.'

He had close contact with the late Professor Sir Arthur S. Eddington, F.R.S., and was active in the establishment of the Arthur Stanley Eddington Memorial Lecture.

Outside the University and the Society of Friends he gave generously of his time and wide experience in service on committees—Agricultural Research Council (1952-1957), the executive committee of East Malling Research Station, the governing body of the Grassland Research Station, the Scientific Advisory Committee of the Empire Cotton Growing Corporation, the Advisory Panel of the Indian Tea Research Association, the governing bodies of Studley Horticultural College and King Edward's School, Birmingham. To these he brought not only knowledge but wisdom. It is not surprising that with all these activities he sometimes seemed a tired man, but he derived refreshment from his home life and his religion. The end of a holiday always saw him full of vigour again.

In 1922 he married Elisabeth Rose McCormick, who shared many of his interests outside science, particularly his love of gardening. They made their home and garden a place where he and their many friends could find refreshment.

Their only son unfortunately suffered from physical handicap. The anxiety this caused and the sad blow of his death soon after his entry to the Leys School were borne with great fortitude.

They were hoping to enjoy his retirement by returning to Cambridge, but his tenure of the Chair at Birmingham was dogged by illness. He was seriously ill with pneumonia in the spring of 1958 and, though he returned with characteristic determination to carry on, he probably went back too soon. He died a few months later on 20 December 1958.

Translocation in plants

Maskell's main published contribution to plant physiology is that on translocation in plants. When Maskell joined T. G. Mason at the Cotton Research Station, Trinidad, they began the series of researches on translocation of carbohydrates, nitrogen and minerals in cotton for which they are chiefly remembered. Mason, while in Dublin, had already worked on the problem of translocation, confirming in yams the very rapid transfer of dry weight that Dixon had found in potatoes, and which had led Dixon to question the long-accepted belief that organic nutrients were transported in the bark. The measured transfers of dry weight, 3 to 5 grams per square centimetre of phloem per hour, implied a flow of solution of, say, 10 per cent sugar at velocities around 100 cm/h through the sieve-tubes and fine sieve pores, a possibility that Dixon denied. He proposed instead that tissues other

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than the bark, probably the wood (xylem), must be contributing largely to the transport, thus beginning a controversy that was finally resolved by Maskell and Mason in favour of the phloem.

Mason probably initiated the study and it is not difficult to read between the lines of the opening sentences of their first paper a decision to devote the practical resources at their disposal to this important theoretical end: 'Such problems as the shedding of flower-buds and young bolls, the condensation of sugar to form cellulose in the lint hair, and the variations in habit and development as a result of climatic and other causes could not be profitably attacked until a great deal more information was available relating to the machinery responsible for the transport of sugars and the factors determining the rate and direction of movement within the plant-body.' And their plan of campaign is clearly stated: 'An adequate theory of translocation involves a solution of at least four problems: (1) The channel of transport; (2) the factors determining the direction of movement within that channel; (3) those determining the rate of movement within the channel; (4) those determining interchange between the channel and other tissues.' They solved the first of their four problems at the broad histological level; the remaining three are still unsolved after 34 years.

Earlier ringing experiments, in which either wood or bark was removed and the effect on the growth of plant parts beyond the ring determined, had not unequivocally decided which was the channel of transport. Although removal of a ring of bark caused growth to cease, adherents to the wood-theory objected that the ringing might also have damaged the wood, particularly the outer region. Mason and Maskell measured the variations in amounts of total carbohydrate and of sugar in the leaves, bark and wood, expecting that the transporting tissue would exhibit fluctuations in sugar content closely following those in the leaves. They found that it was the bark not the wood that showed daily fluctuations in sugar content parallel with, and closely following, those in the leaves. This still left the possibility that sugar might move in the wood and be transferred into the bark, but this was eliminated by experiments showing that the transport still went on into flaps of bark separated from the wood, but attached at their upper end.

To this careful, clear and decisive work, Maskell's contribution most probably included the comprehensive statistical design and the application of Student's *t* test to establish the significance of the differences measured. The results laid the foundation of all subsequent work on translocation until the advent of radio-isotopes made possible approaches of a different kind.

Their next series of experiments was directed towards the solution of the second and third of their stated problems; the factors determining the rate and direction of movement of sugars. From their earlier work they had drawn an analogy between the translocation process and simple diffusion in that the sugars moved down concentration gradients, but enormously faster than by diffusion. They set out to determine just what this acceleration amounted to, and how far the analogy could be pressed. They found that movement of

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sugar was always down a concentration gradient of sugar, and that reverse movement in the stem and reversal of the concentration gradient could be induced by changing the positions of source and sink. They could not, however, demonstrate movement of sugars into darkened mature leaves. Their analyses and correlations showed further that the mobile substance was sucrose and that it was probably moving in the sieve-tubes. The rate of the movement was found to be $2-4\times10^4$ times what would be expected from diffusion in aqueous solution.

The mechanism by which this high rate is brought about was and remains obscure. In the polemics of the period there were four schools of thought: that of Münch believing in the mass flow of sugar solution under pressure through the sieve-tubes; that of Curtis believing in the circulation of the protoplasm in the sieve-tubes; that of van den Honert believing in the spreading of molecules by surface tension over interfaces; and that position to which Maskell and Mason found themselves driven by their adherence to the diffusion analogy, and which received the name 'activated diffusion' hypothesis. This was the most vague of the four since no tangible mechanism was envisaged and no testing experiments could be done. Consequently it has not suffered the discredit that has overtaken the other three.

Maskell and Mason then turned their attention to the transport of nitrogenous substances in the cotton plant. The very many samples already collected for the carbohydrate work were still available, and by analyzing these for nitrogen they economically built up a picture of the daily nitrogen balance of leaves, bark and wood. The analyses suggested that organic nitrogenous compounds were formed in the leaves from nitrates imported via the wood, and the organic nitrogen exported from the leaves through the bark. The rate of movement (calculated as grams of asparagine per square centimetre of phloem per hour) was about one-tenth of that of the carbohydrates.

Having established these similarities of nitrogen movement to carbohydrate movement, they set out to investigate the relation of movement to concentration gradients, and the 'acceleration of diffusion'. The problem was a formidable one: 'It will be seen that the solution of this problem involves the solution of a number of subsidiary problems, viz. (1) the channel of transport, whether the sieve-tubes or some other tissue, (2) the nature of the mobile compound or group of compounds, (3) some estimate of the concentration of the mobile form in the channel of transport. With the technique available hardly one of these questions could be settled independently of the others. The problem resembles that of the solution of a set of simultaneous equations.' From a mass of analyses of six nitrogen fractions vertically in leaf, bark and wood, and transversely through the bark, they could find no support for their gradient hypothesis. Any gradient they could detect was negative in the direction of transport, so they were led to postulate a positive gradient of mobile compound(s) in the sieve-tubes masked by negative gradients of storage nitrogen in other tissues of the bark. They further investigated the

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changes in gradient accompanying changes in movement: 'If we stop transport or reverse its direction we should affect only, or mainly, the dynamic gradient of translocatory material. While, therefore, the net gradient may be negative, the *change* in the net gradient, when the rate or direction of transport is altered, should be positively correlated with that change in movement, and should be a measure of the change in the dynamic gradient.' Elaborate analyses and reasoning produced some support for the idea of a masked positive gradient of mobile nitrogen, for reversing the direction of transport resulted in a steepening of the original negative gradient. This, they argued, was due to the reversal of the masked positive gradient which was now added to the masking negative gradient, not subtracted from it. In so far as quantitative estimates were possible the acceleration of nitrogen diffusion appeared similar to that of carbohydrates. 'This suggests that the acceleration mechanism in the sieve-tubes acts impartially on sugars and nitrogen compounds.' Of the nitrogen fractions analyzed, they could not identify any one as wholly static or wholly mobile. Further attempts to identify the mobile compound(s) by observing changes in nitrogen fractions where the bark was interrupted by a ring led to a similar conclusion, viz. that all nitrogen fractions including the labile protein contribute to the longitudinal movement in the sieve-tubes. This conclusion was perhaps inevitable because of the fact that the different fractions proved very labile, easily converted from one form to another within the bark more rapidly than they moved.

Maskell and Mason next turned their attention to transport of mineral nutrients. Having shown that nitrogen from the roots was transported to the leaves by the wood as nitrate, elaborated, and exported as organic nitrogen to other parts of the plant, they were anxious to find whether phosphorus and metallic ions followed similar paths. By the well-tried techniques of analyses above and below rings and reversals of source and sink, they showed that this pattern of distribution held for phosphorus and potassium, and that *en route*, there were extensive exchanges of the transported nutrients between the mobile and various immobile phases. Redistribution of calcium from the leaves was very slow. The gradients of mineral concentration were not always the same as the direction of movement, and the masking-static-gradients were again invoked.

By now the controversy between the several protagonists of the mechanisms already mentioned was reaching a head. Maskell and Mason had so far remained uncommitted to any definite mechanism for the acceleration of diffusion, but in the literature of the day much space is devoted to 'the critical experiment' which would decide between the mass-flow hypothesis and its opponents. One such was to demonstrate transport of two substances in opposite directions simultaneously; and Maskell's last contribution to the joint work was his part in an experiment of this kind. They failed again to make mature leaves import carbohydrate, so could not show that nitrogen was coming out while carbohydrate was going in; but in the stem they were able to demonstrate upward movement of stored organic nitrogen at the same

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time as carbohydrate was moving in the opposite direction. The argument was not settled, however; the adherents of the mass-flow theory shifted their ground and suggested that different sieve-tubes were specialized for transport in different directions.

Not the least important contribution to plant physiology were the ideas he developed in his lectures; ideas partly derived from, and forming the basis for, much of the research done by students under his supervision. Unfortunately his development of these ideas is unpublished.

Carbohydrate metabolism

Carbohydrate metabolism had long been a field of special interest to plant physiologists in the Botany School at Cambridge, and it was thus natural that Maskell should begin in 1933 a general investigation of the metabolism of carbohydrates in plant tissues. His first student, A. G. H. el Gawadi used carrot slices held either in water or in sugar solutions and this work led to the recognition that the sucrose of the medium was inverted either in the external solution or in some readily accessible part of the cell. A careful analysis of the changes in the amounts of sucrose and of the hexose sugars in the tissue led Maskell to recognize a balance between these sugars. Earlier workers had noted that the proportion of sucrose to the hexose sugars might vary widely either in the same plant tissue at different times or as between different plant tissues. It was, however, Maskell who first recognized the form of the balanced relation commonly shown between sucrose and the hexose sugars in plant tissues. This balance has the graphical form of a Michaelis rectangular hyperbola when hexose content is plotted against sucrose; in low concentrations of hexose, sucrose may increase nearly proportionally with increase of hexose, in higher concentrations of hexose, however, sucrose increases greatly for a small increase of hexose. Maskell observed this form of relation in carrot slices, both when the slices were held in water under starvation conditions and also when the slices were fed with either sucrose, glucose, or fructose in the surrounding medium; the balance was also maintained under anaerobic conditions. A similar form of curve was shown in leaves attached to the plant during a 24-hour period during which the sugars first increased because of photosynthesis and later decreased because of translocation.

From all the data obtained with carrot, Maskell obtained a curve of best fit, which was closely similar in form to that of a Michaelis rectangular hyperbola, the curve being nearly parallel to the sucrose axis in high sugar content. Maskell recognized that this balance represented a special case of the dynamic state common to all chemical reactions occurring in living matter. The following formulation, though set out for the sucrose/hexose system, may thus be of wide general application. Maskell formulated this observed relation as being due to two opposed series of reactions, as shown below:

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$$\text{sucrose} \underset{\text{condensation}}{\overset{\text{hydrolysis}}{\rightleftharpoons}} \text{glucose} + \text{fructose}$$

He then treated each series of reactions as being enzymic; taking Hy as the concentration of the products of hydrolysis and C as the concentration of the condensed product sucrose, V_c and V_{hy} as the maximum rates of condensation and hydrolysis, K_c and K_{hy} as the Michaelis constants for the condensing and hydrolyzing reactions, he obtained the following equations:

$$C = V_c K_c \frac{Hy}{V_{hy} K_{hy} + (V_{hy} - V_c)\ Hy}$$

$$\text{or } (C/K_c) = \frac{(V_c/V_{hy})\ (Hy/K_{hy})}{1 + (1 - V_c/V_{hy})\ (Hy/K_{hy})}.$$

Thus if V_c is greater than V_{hy}, C increases to infinity as the concentration of the hydrolytic product approaches asymptotically a maximum value

$$Hy_{\text{max.}} = \frac{K_{hy}}{(V_c/V_{hy} - 1)}.$$

At that time the biochemistry of the synthesis of sucrose was not understood, but Maskell realized that energy would be needed for the synthesis and he therefore developed a further formulation in which the rate of synthesis was linked with the rate of respiration. Moreover, since the rate of respiration is often correlated with the concentration of sugar, a second formulation was given where the rate of synthesis is linked with the rate of respiration, the latter being correlated with the concentration of sugar.

Maskell's other great interest was in the control of the rate of respiration. At a surprisingly early date he realized that the Pasteur effect could be due to the controlling influence of (a) the concentration of inorganic phosphate and (b) the adenosine triphosphate/adenosine diphosphate ratio on the rates of glycolysis and of the tricarboxylic acid cycle. He therefore suggested that K. S. Rowan should determine the changes of *ATP* content when green peas were transferred from air to nitrogen. Peas were a good choice of material since they contain a large amount of *ATP* and Rowan was able to show that the *ATP* content decreased in nitrogen. The Pasteur effect in peas was thus associated with a decrease of *ATP* in nitrogen and this compound may well retard glycolysis in air by a back-reaction. Another controlling factor must, however, be the concentration of fructose-1,6-diphosphate and the content of this compound was shown to increase in air. While, then, the complete elucidation of this complex mechanism must await further study, Maskell undoubtedly made a considerable contribution to its understanding.

A special aspect of the control of respiration rate in plants is the so-called climacteric stage in various ripening fruits where the onset of ripening is

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associated with a large increase in the rate of respiration. Maskell suggested that the phosphate mechanism might also control the onset of the climacteric and this idea stimulated the work on this subject since carried out both by C.S.I.R.O. at Sydney and by Biale's group in California.

Maskell's lectures to second year and Part II students were based little on text books, but depended largely on his own work. His great interest was in the dynamic state of metabolism and this subject was clearly discussed in his lectures.

Information about Maskell's boyhood was kindly supplied by his brothers, Mr H. Maskell and Mr A. Maskell, that about 'The Honourable Order of the Upper Ten' by Mr L. V. Slater, one of the original members, and that about his membership of the Society of Friends by Mr A. K. Dewey.

The account of Maskell and Mason's work on translocation is by Dr M. J. P. Canny, and that on carbohydrate metabolism by Dr J. Barker.

G. E. Briggs
M. J. P. Canny
J. Barker

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