BIOGRAPHICAL
MEMOIRS

Frederick Charles Bawden, 1908-1972

N. W. Pirie, F. R. S.

Biogr. Mems Fell. R. Soc. 1973 **19**, 19-63, published 1 December 1973

F. C. Bawden.

FREDERICK CHARLES BAWDEN

1908–1972

Elected F.R.S. 1949

By N. W. Pirie, F.R.S.

Love for the countryside and people of Devon was an extremely important aspect of Fred Bawden's life. As he put it (1952a): 'I come from Devonshire, where we are too modest to claim to grow the best crops of anything; we would be satisfied with the self-evident fact that we produce the best cream and cider, and, of course, the best men.' Not much information is readily available on his ancestry. A member of the family, it is thought, designed and marketed a novel type of plough, but the family seems not otherwise to have been directly connected with farming. Fred's paternal grandfather was a boot-maker, his maternal grandfather a stonemason. Fred's parents, George Bawden and Ellen Balment, lived in North Tawton (Devon) when, on 18 August 1908, he was born; he had an elder brother and sister. George Bawden was Relieving Officer and Registrar of Births and Deaths in North Tawton, but three years later moved to Okehampton to be master of the Poor Law Institution—commonly called the Workhouse. It had a large garden in which George Bawden took a keen interest; he awakened a similar interest in Fred. Potatoes were an important crop in the Institution garden, and their health was an important topic of conversation in the locality. On the principle of 'imprinting', this may in part explain Fred's lifelong attachment to the crop. He records that even as a boy he 'began to appreciate the many problems involved in growing healthy plants'. Fred's mother was matron of the Institution and the children were thus made aware of the problems of human old age, sickness and poverty at an age when most of us are shielded from these things; this probably contributed to his lifelong, unsentimental, concern for the welfare of the 'underdog', and to his critical approach to political institutions. Marjorie Elizabeth Cudmore was a school-fellow in Okehampton and, like Fred, studied botany at Cambridge. They married on 6 September 1934 and had two sons. The notes deposited with the Royal Society in 1949 were withdrawn a few years ago; on these family matters, the notes remaining are uninformative.

The personal enthusiasm of the headmaster, W. Hunter, made botany the dominant science subject in Okehampton Grammar School. In the notes deposited with the Royal Society, Bawden said that it was mainly because of enthusiasm engendered by Hunter that he worked in the plant sciences. Marjorie Bawden is equally appreciative of Hunter's enthusiasm and, helped by R. W. Marsh, she has looked for an explanation. They agree with the suggestion, made by W. C. Moore in his obituary on F. T. Brooks, F.R.S. (*Obituary Notices of Fellows of the Royal Society*, **8**, 341, 1953), that credit for 20 or more scientists educated in the southwest of England achieving distinction in botany and related subjects should go to W. A. Knight, for long the headmaster of Sexey's School (Bruton, Somerset). Brooks was at Sexey's School until 1898 and then went to the Pupil Teachers' Centre in Bristol. Hunter was educated in the north and held various teaching jobs there, but taught science and mathematics at the Pupil Teachers' Centre from 1901 until he went to Okehampton. In later life he spoke of Brooks as a pupil—it would seem that influence did not move in only one direction, and that Brooks passed on to Hunter the enthusiasm he had learned from Knight. There is no record of Hunter having any other connexion with Sexey's School. When Brooks went to Cambridge, he and Hunter still met from time to time. Brooks's lectures on mycology, and on plant pathology in general, influenced Bawden greatly and, because of the connexion through Hunter, lecturer and student established a personal relationship more quickly than they might otherwise have done.

Hunter, though a stimulating field botanist and organizer of botanical excursions on Dartmoor and elsewhere, seems not to have been a notable teacher of the more academic aspects of the subject. Bawden tried for a Devon 'County Major Scholarship' to University College Exeter but failed because, as another unsuccessful school friend put it, 'we could not understand the questions much less attempt to answer them'. Some weakness in formal botany is also shown in the results of the School Certificate examination. He took the examination three times, when 14, 15 and 16 years old, with distinction in mathematics and general science on the last occasion but never more than credit in botany.

When 16 years old he was urged by his father into applying for a job with the local National Provincial Bank: to his relief he did not get the job. A year later he got from the Ministry of Agriculture and Fisheries a scholarship to Cambridge, for 'the sons and daughters of agricultural workers and others'. This could not be taken up until he was 18. The Devon County Education Committee insisted that the intervening year should be spent at a boarding school so that, before going to Cambridge, he could get acclimatized to living away from home. Within three weeks the Committee got a place for him at Crediton Grammar School and supplied a £30 grant. This was before committee-work had been 'speeded up' by the telephone! At Crediton he was pleased at the importance given to chemistry, for he had learnt little at Okehampton, but displeased at compulsory membership of the Officers' Training Corps. This is interesting because a few years earlier he had said to a friend that he sometimes thought of going into the Tank Corps when he left school—but it is in keeping with his general outlook later in life.

Cambridge

At Cambridge, Bawden took botany, chemistry and physiology in part I of the Tripos. The physiology was concerned exclusively with animals; he often commented that he found it much easier to understand the physiology of the animal than the plant. He paid little attention to chemistry because he thought, rightly as the examinations showed, that he had learnt enough at Crediton. He tried to get into Hamilton McCombie's practical chemistry course because it was the only one that fitted the timetable. According to Bawden's account, he was lucky to escape unassaulted, for McCombie regarded his course as a paradise for the chosen few. Within Emmanuel, he was gregarious, cheerful and sport-loving. More pedestrian students marvelled that he could do so well scholastically and also lead such an active social life. One reason was that he had a prodigious memory. At that time, and for many years later, he kept few notes even on the subjects of his research. He kept no card index of papers relevant to his work—he kept the gist of them in his head. It is sometimes said that he read the *Encyclopaedia Britannica* from cover to cover during his year at Crediton. This seems extremely unlikely; his memory was filled with information about the subjects he was working on and not with the *bric-à-brac* with which the enclyclopaedia would have filled it. He probably used the encyclopaedia more consistently than his school fellows and so started the legend.

According to the rules governing the Ministry scholarship, he had to take the Cambridge Diploma in Agricultural Science. For two years, during which he held a Senior Scholarship from Emmanuel, he worked with Brooks on cereal rusts. His Diploma Thesis (1930), 'The distribution and perennation of cereal rusts', starts with an impressive survey of the literature on black, yellow, brown, crown and dwarf rusts, their dependence on non-cereal hosts for over-wintering, and the effects on them of temperature and the nutritional state of the plant. The experimental part of the thesis contains some farm observations on the incidence of rust infections in 1928 and 1929 and experiments on the incubation periods and resistance to cold of four species of *Puccinia*, three attacking wheat and one attacking barley. Some plant pathologists, knowing nothing of this early work on rusts, and having come to think of Bawden as primarily a virus worker, were surprised at his extensive knowledge of mycology. This knowledge and interest is well illustrated by his book *Plant diseases* (1948e, 1950i). In that book, and in general articles written later, he devotes half or more of the space to fungus infections.

R. N. Salaman, F.R.S., persuaded the Ministry of Agriculture and Fisheries to establish the Potato Virus Research Station in Cambridge in 1927. In 1929 he was looking for another colleague and was clearly intent on making a good appointment. There were several applicants for the post, but it was not filled immediately. Helped by an enthusiastic letter from Brooks, Bawden got the job in spite of the phrase '. . .Mr Bawden has no special knowledge of plant viruses . . .' in the letter of recommendation. He started work in the summer of 1930. Salaman was well aware that the capacity to do research is a matter of temperament rather than training.

The 'Research Station' was a draughty, inadequate, unheated shed alongside some more adequate greenhouses. As Bawden put it (1970) '. . . the most sophisticated piece of apparatus [was] a recalcitrant Primus stove'. But he had access to space for laboratory work in the School of Agriculture, the Molteno Institute and, latterly, the Department of Pathology. His attitude towards Salaman can best be described as critically affectionate. He enjoyed the frequent invitations to Salaman's luxurious home, where he was treated as a member of the family, and he recognized the breadth of Salaman's culture and the importance of his contribution to knowledge of potato varieties and viruses, but he resented Salaman's somewhat feudal outlook. The job, like most jobs at that time, was underpaid: Salaman called what Bawden got a salary; the larger amount that he himself got, he called an honorarium. Bawden tried for a research fellowship at Emmanuel with a thesis consisting mainly of the work he had published alone and with Salaman (1932a, b); he was unsuccessful but got a £15 Sudbury-Hardyman Dissertation Prize.

The move in 1936 from Cambridge to the post of Virus Physiologist at Rothamsted was a logical development from work on potato viruses. It therefore differed from the earlier nodes in Bawden's educational and scientific development. Until 1936 he had seldom been a wholly free agent. He was certainly lucky in avoiding the bank, he was probably lucky in getting to Cambridge rather than Exeter and in establishing such good rapport with Brooks and Salaman. But if he had not worked with them he would probably have taken up plant breeding with Sir Rowland Biffen, F.R.S., and would have been as successful in that subject as in the one into which luck thrust him. Some people decide early what they want to do and, with varying degrees of success, do it; Bawden had to be more adaptable.

Bawden came to chemistry late in his school-days; he absorbed it then as a concentrated dose and did little more than refresh his memory while at university. Perhaps for that reason he approached the subject sceptically and, unlike most other pathologists, he was wholly unbemused by it. He did not have to struggle through a morass of chemical indoctrination, and quickly accepted the idea that the sharp distinctions that others were trying to make between molecules and viruses were as unreal as the evidence they presented purporting to demonstrate the purity and homogeneity of virus preparations. At the same time, and again unlike most pathologists, he had learnt enough chemistry to understand the detailed chemistry of viruses and was familiar with the changing pattern of argument and assumption about their physical structures.

Rothamsted

At Rothamsted Bawden had more scope than he had had in Cambridge. Conditions for making virus preparations were still primitive: the only centrifuge he had access to was a curious contraption with a rope drive and a starting switch reminiscent of the gear on a rather old-fashioned tramcar. But he no longer had to cycle two miles to get material from his greenhouses to the lab and his serological equipment. At that time he was rapidly gaining scientific recognition. Through Salaman he met, at the International Botanical Congress in Cambridge in 1930, most of those working on plant viruses; he renewed acquaintance with them at the Congress in Holland in 1935, and on their visits to Cambridge and Rothamsted. Henderson Smith, the head of the Department of Plant Pathology at Rothamsted, was no longer an active research worker, but he had been instrumental in bringing Empire Marketing Board money to Rothamsted to establish the Department, he had a circle of friends among virus workers as wide as Salaman's, and he understood more clearly than most biologists the implications of the observations we were making on the properties of virus preparations. Furthermore, these observations attracted some publicity and made Bawden's name known to a still larger group of plant pathologists.

The move to Rothamsted came at a time when we were just beginning to collaborate closely. We met two or three times a month but mostly we exchanged preparations and results by post. This separation was probably beneficial. It is lamentably easy to think that one is understanding, and being understood, during a conversation. A letter is much more likely to be fully explicit and cogently argued. The reader may become impatient at prolixity over a point he thinks he understands, but impatience does not stop the flow of what has been written and the reader may later discover that there was something novel in the point after all. When we were reunited at Rothamsted in 1940, explanations of the detail and plan of an experiment tended to be less explicit.

Bawden had always been accustomed to work with little assistance. He himself inoculated all the plants needed for experiments in which he was involved, and counted the lesions on them. He continued this practice throughout his life, partly to maintain contact with the actual process of research, and partly as a welcome relief from paper-work—he often referred to his time in the greenhouse as 'occupational therapy'. Latterly, other commitments during normal working hours made evenings and week-ends our regular time for practical work and the experimental plan had to be carefully geared to his time-table. A frequent evening spectacle, but one that was unexpected in a large research station, was the Director skilfully managing to carry four pots of glutinosa plants in each hand through several sliding doors without damaging any of the leaves. Until 'canned music' made life there nearly intolerable, the 'local' was our usual *locale*, after he had finished inoculating the test-plants and counting lesions, for discussing results and planning the next experiment.

Bawden was made Head of the Plant Pathology Department in 1940, Deputy Director of Rothamsted in 1950 and Director in 1958. As responsibilities increased he had less time for practical work and, more important, for thinking about his research. As the list of commitments at the end of this article shows, he took on many duties outside Rothamsted. Consequently he had to work extremely hard: but he worked in a relaxed manner. After three or four days illness, he died on 8 February 1972. Had the condition of his heart been known before that illness, he would obviously have been urged to work less. Those who knew him well will wonder how effective their pleas would have been.

The art of differentiating between seriousness and solemnity came naturally to Bawden, and he seldom gave the impression that he was anxious to finish a conversation or get rid of a visitor. But when someone was being foolish, or mean, he was perfectly willing to be as blunt as was necessary to get the point across unequivocally. The distinguished position held by Rothamsted in the history of agricultural research meant a great deal to him. Before being made Director he was urged to accept directorship of another institute. When asked if he would accept, he said, 'I would rather be Head of a Department at Rothamsted than Director anywhere else. One good reason is that it is the only place every agricultural scientist knows of' (cf. Psalm 84, 10). That feeling for history may explain his refusal, in spite of his enthusiasm for clear and grammatical English, to replace the word *Experimental* in our name by *Experiment*. It could be argued that, after 130 years, we are no longer experimenting on how to run a Station.

In the 1930s Bawden was an undoctrinaire socialist; he gave useful practical and moral support to the Spanish Government during the civil war and later became a member of the Association of Scientific Workers. In 1935 he was caused some embarrassment because alphabetical listing of names caused him to head the list of those who were objecting, successfully, to the acceptance of money from Sir John Siddeley for aeronautical research in Cambridge without the assurance that there were no military strings attached. Seven of the ten 'objectors' later became F.R.Ss and it was friendship with several of them, rather than intense political conviction, that led Bawden to join in the protest. He was greatly reassured of the validity of the objection he was heading when, after an aircrash in which fire and not the crash killed the passengers, Moore-Brabazon wrote (*The Times*, 17 July 1935): 'Are we forever to prostitute the gift of flight by linking it with armaments ? Because the petrol engine has a superior performance for military machines are we to be compelled to use a similar but unsuitable prime mover because the civilian craft is supposed to be a reserve in war ?' He supported the 'Pugwash' conferences (1960d, 1962) and, having seen post-war Labour and Conservative governments in action, tended to support the Liberal Party.

In the late 1930s, people who knew, or thought they knew, the long-range policy of the Ministry and the Agricultural Research Council said that the phase of expansion at Rothamsted was over. It was to be 'kept in its place' and some even suggested that it would become an institute concerned mainly with routine soil analysis. The enthusiasm of successive directors proved more than a match for those holding these points of view. For 36 years the station has never been completely free from the inconvenient, though welcome, clutter of builders. Under Bawden's directorship the scale of building surpassed anything we had known before. Tabulation is the most convenient way to set out these developments:

1961	More space for the Statistics Department and Orion Computer. More space for the Commonwealth Bureau of Soils and the Station Canteen.
1962	Broom's Barn Experimental Station built near Bury St Edmunds. Controlled environment rooms begun at Rothamsted.
1963	New building for the Biochemistry and Pedology Departments, and the Soil Survey of England and Wales.
1965	New workshops.
1968–1970	New building for Computer and Statistics Departments.
1971–1973	New building for Botany, Nematology, Physics and Plant Pathology Departments.

Land adjacent to the Station was purchased in 1965, thus increasing the area devoted to the laboratory and farm from 240 to 330 hectares. In 1958 the staff was 471; in 1972 it was over 700 with a further 48 at Broom's Farm.

Expansion on this scale shows that Bawden was able to maintain good relations with the organizations that supplied the necessary money, and convince them that their money was being well spent. He had an equal dislike for bureaucratic methods of thinking and writing. Some of the more entertaining moments in the monthly meetings of the senior staff of Rothamsted came when he read passages from official letters connected with the work of the Station, and added: 'I think that means' and expressed the presumed meaning at a quarter the length and in shorter words. Although the Station is almost entirely financed by government funds, it is governed by the Lawes Agricultural Trust Committee and neither the Ministry nor the Agricultural Research Council is represented on the Committee. It could be argued that our autonomy exists more on paper than in practice because senior staff appointments have to be officially approved and our estimates are considered in conjunction with our recent annual reports. Nevertheless there is a measure of autonomy and Bawden guarded it fiercely; he welcomed official suggestions but discouraged official advice. His success in getting so much support in spite of his unsubservient approach probably depended on his obvious integrity and devotion to agriculture, his complete lack of pomposity, the fact that he knew just what he wanted, and his humour. The last was by no means the least important.

The capacity to discuss matters with even the more awkward members of the staff in an easy and informal way was extremely useful. Some directors act as if ensuring that the staff is adequately housed is their only function; they seem unconcerned about, or even uncomprehending of, the work done. Others try to run a dictatorship. Bawden steered an admirable middle course. He made sure that he understood the reasons for undertaking each research project and showed disapproval more by persistent questioning than direct opposition. This method often improved the project without making the scientist feel he was being bullied. When convinced that a project was likely to be scientifically illuminating, and especially if it had practical potentialities, he was an effective advocate. His own work on such themes as the nature of viruses, the control of virus and fungus infection, and the production of potato clones free from viruses, will be described later. Only a few of the lines of work to which he gave active encouragement need be mentioned here: the synthesis of relatively non-toxic insecticide analogues of pyrethrin, the rational and economical use of fertilizers and irrigation water, the unravelling of the causes of 'docking disorder' in sugar beet, and, if a personal note may be permitted, the bulk extraction of leaf protein as a food for non-ruminants. That project gained official disfavour early in its existence and the Station was told several times to discontinue it. Bawden paid no attention to these injunctions, helped to get finance from non-government sources, and wrote favourably of the project in a third of the Director's introductions to the Station annual report. Undeviating support such as that forces one to be very certain that the logical basis of a project is sound.

All directors of Rothamsted have been interested in, and knowledgeable about, the practicalities of farming. Bawden added to that an enthusiasm for the practicalities of presenting the results of research. No other Director took so much trouble over both the form and content of our papers. Like everyone concerned with language, he had a few obsessions. He would, for example, have replaced *like* in the last sentence by *as*, he would allow *case* to be used only for a container or in a legal context, and he strove to persuade his staff that the English language had adjectives other than *high* and *low* with which to express magnitude. More seriously, he was adept in detecting ambiguity. He systematically turned sentences in papers written by his staff round so that they depended on precise verbs rather than on the sloppy use of the verbs *to be* and *to have* followed by a noun, and ruthlessly pruned prolixity. These emendations were often, in his tiny handwriting, almost illegible, and the suggested new form was sometimes uncouth. But it was invariably worth while rewriting any passage he had begun to amend. He was expert at recognizing illegitimately general statements. To quote his own words (1970): ' "Was not transmitted by *Myzus persicae*" is an unequivocal statement, but is not synonymous with "Not aphid-transmitted", although it often gets so translated in general descriptions of viruses. Similarly, "The only known method of transmission is by grafting" is different from "transmissible only by grafting", and although "not mechanically transmitted" sounds positive enough, it is something that cannot be established; all that can be said is "was not mechanically transmitted between such and such plants by such and such methods".' A committee report that he edited (1962), after advocating the establishment of international science centres, continued '. . . it is important that contributing countries should know what goes on in them. This means public relations must be good and that reasons for what is being done and results achieved must be simply described. People able to write accurately about science for the general public are regrettably few. Both in their own interests and to improve the standard of scientific writing, the centres should not only employ able

[*Facing page* 27]

writers but should perhaps provide scholarships in scientific writing to be held at the centres.'

Overseas cooperation

Bawden was very well aware that the control of plant diseases was essential if the standard of living of the underfed parts of the world was to be improved. As soon as the end of the Second World War made international travel possible, he welcomed visitors to the Plant Pathology Department for training. After several years he became somewhat dissatisfied with the use that some overseas governments made of the scientists who had been trained—many were unable to get jobs in plant pathology in their own countries. He often replied to the sponsoring body, when a period of training for yet another student was proposed, that jobs should first be found for those who had already been trained. His own visits abroad did much to improve matters and establish viable research units in countries that had become aware that a disease problem existed. Awakening awareness was often the most difficult step in countries where miserable diseased plants were accepted as normal and only those that actually died were considered infected.

Personal contact with problems in tropical countries started with a visit to Ghana (then the Gold Coast) and Nigeria in 1947 to study swollen shoot disease of cocoa. The policy of destroying infected trees and their neighbours was politically controversial and some people urged a mass insecticidal attack on the mealy bugs responsible for transmission. Bawden concluded that this would not be feasible with a tree that depended on insect pollination and, in his report and in a local broadcast that was also published (1947f), he supported the 'cutting out policy'. The government formed by Nkrumah as a prelude to independence agreed. It tried a voluntary programme but was soon forced to adopt the hitherto condemned policy of compulsion. After a longer visit to West Africa in 1955 Bawden argued that there was some risk that concern about swollen shoot would become an obsession—greater loss of cocoa was caused by capsids, black pod, incomplete picking and general unthriftiness. He suggested that an important benefit to be expected from the 'cutting out policy' was that the preliminary survey would reveal the extent of other causes of loss and so lead to general reform. This attitude, that those on the spot do not always assess correctly the nature of their agricultural problems, was typical of his approach. These visits established a close connexion between the West African Cocoa Research Institute at Tafo (Ghana) and Rothamsted. For more than 10 years two members of Rothamsted staff were usually seconded there.

The effectiveness of a rogueing or 'cutting out policy' depends on early diagnosis. In 1949 Bawden visited Zanzibar to advise on the disease 'sudden death' of cloves which his colleague F. M. Roberts, who had worked with him on various problems at Rothamsted, was studying. They found that the disease was not as sudden as had been thought but that the early stages were not being recognized. Early recognition greatly improved the methods of control.

3

Bawden was a member of the London-based Advisory Committee on Agricultural Research in the Sudan and, starting in 1957, visited that country eight times, mainly to advise on problems connected with cotton. Problems arising with that crop also took him to Uganda. Of his later active concern with problems in other parts of Africa, Dr H. C. Pereira, F.R.S., writes: 'His help in Rhodesia and Nyasaland was a very gallant enterprise undertaken at a time when an avalanche of political change was sweeping away many structures useful for the future of the populations of all three countries. The disbanding of the Federation of Rhodesia and Nyasaland destroyed some fifty three-country organizations and only four remained. Among these was the new three-territory Agricultural Research Council. Fred Bawden undertook the Chairmanship with characteristic energy and directness. In spite of his heavy responsibilities at Rothamsted and his continuing work in the West Indies he found time to make a direct contribution to the agricultural research of the three small countries of Malawi, Rhodesia and Zambia. His approach to the problems was characteristic; he visited farms to meet the farmers and to gauge the standard of agriculture; at research stations he plunged into animated discussions with individual scientists about their work, but showed ill-concealed impatience with formal laboratory visits and tours. It was the ideas, not the hardware, which he wanted to discuss. He met both President Banda and President Kaunda and many of the leading farmers and scientists of Rhodesia and was particularly successful in convincing both politicians and administrators that advanced techniques of research were applicable to some urgent practical problems as well as to the agriculture of the future.

'Confidence in his support carried the Council through the stormy waters of Rhodesia's unilateral move for independence and three-country cooperative research continued for more than a year after "U.D.I.", before political stresses across the Zambesi River proved overwhelming. Again Fred Bawden's skilful Chairmanship was of great importance in achieving an orderly division of the work into national groupings.'

Although, as he pointed out (1963a), he was '. . . completely ignorant about sugar cane technology, and what little connection I have had with sugar production has been with the competing crop, sugar beet . . .', Bawden attended the 11th Congress of the International Society of Sugar Cane Technologists in Mauritius. His short paper (1963a) contains much sound advice on the general problems of agriculture, the recognition and control of disease, the need to question the efficacy of all practices—especially those that have been long in use, the importance of thinking about the whole of a crop and not being too ready to discard by-products (e.g. sugar cane leaves) as 'trash', and the folly of organizing expensive research without making sure that industry is ready to use the results.

A visit to Ceylon and two visits to India were not primarily concerned with giving practical advice. Even so, when shown the evidence from which it had been concluded that there was no vector for leaf mosaic of jute, he was so sceptical that the matter was reopened and 'white fly' was found to be a vector in Assam. Visits to several Caribbean islands were not designed to have immediate practical results, but in Trinidad he was on the committee of the Regional Research Centre and took part in the negotiations establishing the relation between that Centre and the University faculty of Agriculture with which it is intertwined.

Bawden's concern with tropical agriculture was not limited to giving advice on specific problems, helping to improve local conditions of work, and seconding staff on a more-or-less unofficial basis from Rothamsted. He also advocated the organization of cooperation on a more formal basis. Thus in 1956 he was a member of a working party set up by the Advisory Council on Scientific Policy which recommended the creation in London of an Institute of Tropical Agriculture. This was to be concerned, not only with matters usually included in agriculture, but also with crop storage and processing: that is to say, it would have abolished what may be called the 'farm-gate hiatus'. In 1961, a committee chaired by Bawden was set up to consider methods for providing technical assistance from the United Kingdom on agriculture, animal health, forestry and fisheries overseas. The committee reported to the Secretary for Technical Cooperation in 1962 (1964c). It welcomed the establishment of supernumerary posts, in British research institutes, to be held by scientists who would spend much of their time working overseas. That plan, designed to cope with the natural reluctance of scientists to leave pensionable jobs in Britain for less predictable jobs overseas, had been advocated by Bawden for several years. The committee also recommended the appointment of agricultural liason officers to Embassies and High Commission Offices in suitable places, and suggested that better arrangements should be made for visits by senior scientists so as to dispel '. . . the sense of isolation that commonly afflicts research workers overseas'. The committee recognized the advantages of a period of training in countries such as Britain for postgraduate students from some countries, but urged the improvement of local facilities so that students could get adequate undergraduate training in their own countries.

Scientific and agricultural policy

The outbreak of war in 1939 focused Bawden's attention on the need for maximum food production. Before that, he had joked at the expense of those who spoke of agriculture as a 'way of life' and who had the delusion that farmland, compared to the heath and forest that preceded it in Britain, was in any sense more 'natural' than a factory—though undoubtedly more pleasing aesthetically. He thought, unlike many of those who had been responsible for agricultural policy, that the primary object of farming was the production of food, and that the objective should be pursued by the most efficient means possible provided the means did not cause long-term damage to farmland. He stated this point of view forcefully in a series of editorials (therefore unsigned) in *Country life*. Having given figures for the inadequate pre-war use of fertilizers, and for the experimental evidence that a three- to fourfold monetary return could be expected from judiciously increased use, he concluded (1941i): 'These figures suggest that before the war malnutrition was even commoner among our crops than Sir John Orr found it to be among our people.' He argued (1941j) that the policy of ploughing up grassland and sowing crops that could be eaten directly by people was correct only if primitive traditional methods for using grass were compared with up-to-date arable farming. In the wetter parts of the country, fertilizers could increase grass yields fourfold and, by producing protein-rich leaf, would produce silage to replace the winter feeds often grown on arable land. He also pointed out that, at a pinch, protein suitable for human food could be extracted from good quality grass. In the light of his own research interests, it is not surprising that he argued strongly for better use of the potato crop (1941k, l). He pointed out the anomaly that there was a subsidy on drying potatoes for stock-feed, but no subsidy to ensure that potatoes should be a cheaper source of human food than bread made from imported wheat, and that little more labour was needed to produce a good crop rather than a poor one—all that was needed was dissemination of existing knowledge of fertilizers, disease control and lifting date.

It is a lamentable indictment of our sanity that agriculture tended not to be taken seriously in Britain except in war-time. At the Jubilee celebrations in 1893, the Prince of Wales signed an effusive tribute to Lawes & Gilbert, but did not suggest financial help for Rothamsted. During Sir John Russell's directorship the Secretary of the Board of Agriculture said (quoted from 1965b): 'I cannot conceive the circumstances in which the Board will be at all interested in scientific work.' The first trickle of government money came to Rothamsted in 1911, but Sir John could get no government help for his appeal to save our farm in 1934. Perhaps because of the turbulent state of the post-war world, Bawden was luckier and got more ample government support. Many of those who thought about conditions in the post-war world did not, however, agree that Britain needed productive agriculture. In an editorial signed 'Rustic' (1942f), Bawden attacked *The Economist's* complacent reliance on cheap imported food; he argued that, because of war-time shipping losses, home production used less labour than importation, and that the idea of continuing cheap imports in the post-war period was illusory. Few will disagree with this point of view today.

For a time, after the end of the war, Bawden was satisfied with the progress that was being made, or that was likely, in Britain and overseas, through the actions of the various committees on which he served. As time went on, he spoke increasingly often of their dilatory and sometimes insincere ways, and this condemnation was expressed in letters and minutes that one sometimes saw, but that cannot be quoted. A 'Pugwash' meeting marked the beginning of his publicly expressed dissatisfaction. He wrote the report of an *ad hoc* group on 'International Collaboration in Science' (1962) and in it said: 'However, more than this is required, for the feeding of future populations may not be possible simply by increasing the production of conventional foods.

Dietary patterns may have to change radically and methods should be sought for making fuller use both of existing crop plants and of plants now not used at all. Much of what now goes to waste could probably be turned to good use, provided methods were discovered to separate valuable components mechanically, or convert them into valuable products by the use of animals, microbes or chemicals.

'Such work is unlikely to get the attention it deserves unless it is organized in internationally staffed institutes for applied biochemistry, which might at first be attached to some agricultural research stations in the tropics. The setting up of such institutes would most immediately benefit the developing countries, but their importance goes beyond this, for although some countries now have food surpluses, this situation cannot be relied on to continue and the continuing problem for the whole world is to ensure enough food.'

And later: 'The centres should welcome unorthodox projects. Most scientists tend to follow current trends; those who do not, often find it difficult to get support, yet some are the original minds most worth supporting. Perhaps part of the endowment of such a centre should be set aside to be assigned by assessors chosen for their unorthodoxy.'

Comments such as these are sometimes made by people who think that all that is needed is that the research should be done: application will follow automatically. Not so Bawden. He remarked (1963a): '. . . achievement has demanded two things, both equally important if an industry is to develop: (1) research to discover better methods; and (2) willingness of the industry to adopt these methods. No industry can advance without research, but research alone, however good, will not automatically benefit an industry; research is of use only when practitioners are willing and able to act on its results.' And also (1967b): 'The fact that conditions change faster in some countries than in others, and faster in some industries or activities than in others, simply reflects the differential rates at which the discoveries are being applied. That in some countries human populations are increasing faster than food production does not mean that more is known about how to improve the health of people than of crops or farm animals, but that discoveries in medicine are being applied before discoveries in agriculture.'

By an ironic twist, others, notably Lord Rothschild, F.R.S., also recognized that use is the main justification for publicly financed research, but gave precedence to the practitioners—or customers as they are now called. Before the furore over 'A Framework for Government Research and Development', usually called the 'Rothschild Report', started, Bawden had written (R.E.S. 1970) of an inquiry into soil structure and fertility presented to the Minister of Agriculture Fisheries and Food by the Agricultural Advisory Council: '*Modern farming and the soil* is rather depressing reading for research workers, because the authors seem more impressed by hearsay than by the results of controlled experiments. Thus, they seem willing to attribute poor yields to bad soil structure without ever applying any of the tests for stability that have been developed, and they give no evidence for their assumption that organic matter is so important that soils with less than a critical, and determinable, minimum will disintegrate. Also, their plea for much more research on the effects of leys seems odd to us when, after 30 years of intensive work on our ley-arable experiments, we are stopping them. Both on the light land at Woburn and the heavy land at Rothamsted, these experiments show that yields of arable crops can be as good in an all-arable six-course rotation as in a six-year rotation that includes three years of ley, provided the arable rotation is such that soil-borne pests and diseases do not become damaging and enough nutrients are given to make good what are removed in the crops.' He returned to that theme later (1972b). After the 'Report' appeared, Bawden spent much time in committee and writing memoranda discussing means for mitigating its more harmful effects. Two attacks were published (1971b, 1972a); in the second, discussing the nebulous distinction between basic and applied research in subjects such as plant pathology, out of which have come major advances in productivity, he said: 'Apparently those of us, and there are many, who have worked in such subjects and been of some practical use were sinning, for Lord Rothschild says this work had no customer and "This is wrong". Only those who are well versed in such subjects and have practical knowledge of farming conditions, do in fact know where research is needed and where it can help, despite Lord Rothschild's statement that: "However distinguished, intelligent and practical scientists may be, they cannot be so well qualified to decide what the needs of the nation are, and their priorities, as those responsible for ensuring that these needs are met." Who those responsible people are, we are not told, but presumably the proposed Chief Scientist will not be among them, unless perhaps he is undistinguished, unintelligent or unpractical.' It will be clear from these, and other, quotations that Bawden agreed with Swift's comment: 'You write with the point of a pen and not with the feather.'

Bawden's attitude was not based on a naïve yearning for continuing the existing system; on the contrary, as some of the quotations above show, he saw much that needed improvement. He was well aware that much so-called research was mere mechanical repetition. To quote again (1963a): 'When a fertilizer or pesticide is already known to give different responses in different places or years, there is little to be gained by demonstrating this again in more experiments. What is needed is to study its behaviour in detail, to find the reasons for the differences, so that the conditions in which it will be beneficial can be defined', and later: 'It is essential to know what is limiting yield, which demands study of the crop in relation to its whole environment, and to find how treatments interact, not simply what each does when applied singly. When a treatment that from general principles ought to benefit a crop fails to do so, the reason for the failure needs to be sought. Meaningful responses to fertilizers cannot be obtained where crops are being limited by pests or diseases; nor responses to disease-control measures when the prime thing limiting yield is lack of nutrients. Too often in the past valuable practices have not been adopted simply because they have been tested in conditions where they could not possibly work or produce an economic return.' In many other passages (e.g. R.E.S. 1959) he enlarged on this theme—it is important not only to find that something works, but also to find out how it works. He deplored the relative absence of interest in virus research in the universities, saying (1966a): 'This may have been understandable 30 years ago, for it was their economic importance that first attracted attention to viruses, but it ceased to be when viruses started to yield a rich harvest of results about problems basic to all biological systems. Even the fact that viruses have provided more than a substantial corner-stone in building the currently glamour subject of molecular biology seems to have left most of them unmoved.' He equally deplored (1970) the way in which so many scientists who do come into virus research, concentrate on its physico-chemical aspects rather than 'work on epidemiology, transmission, and host susceptibility that now tends to languish, although the results from this will more probably have applications in improving the health of crops'. He did not object to changes in the organization of research on principle but on the eminently practical ground that the proposed changes will make matters worse. The only people who know enough about the potentialities to plan research intelligently are those who are actually doing the work.

General outlook on pathology

While he was with Salaman in Cambridge, Bawden's work on potatoes (1932a, b; 1933, 1934) was concerned with the recognition of virus infection in crops either from the appearance of plants in the field and glasshouse, or from the reaction of extracts with specific antisera (1935a, b). The objective was clearly stated (1932a) '. . . all the recognised virus diseases may ultimately be related to a specific virus or virus complex to which a specific range of reactions will be ascribed. Hitherto our views on virus diseases of plants have either passed, or are still in process of passing, through the phase when protean reactions are mistaken for specific diseases and given special names. . . . we may be permitted to look forward to the time when the idea that names such as mosaic, mild mosaic, rugose mosaic, crinkle, streak, and the like, connote separate disease entities, instead of mere symptoms often common to the action of a number of distinct infective agents, will be consigned to the limbo of outworn hypotheses.' Writing about the viruses that cause 'top necrosis' he said (1936c): 'The disease, if any, produced by infecting a potato with a virus appears to depend almost as much on the variety of the host as on the virus. Failure to appreciate this has resulted in numerous names being given to the same virus, and similar names to different viruses. . . .' Although the papers we published on the chemical and physical properties of viruses after isolation show Bawden's general interest in the nature of virus particles, he remained essentially a pathologist. More than half of the first (1939d) and subsequent editions of *Plant viruses and virus diseases* deals with such themes as symptoms, transmission and control.

Increased dependence on home-grown food during the 1939–45 war led Bawden to consider a more extensive range of diseases. The first effects of this was a return to his old interest in fungus infections, to which he devoted a group of articles (e.g. 1941l, 1942g) and unsigned editorials in *Country life*. An awareness that food production is the primary object of agriculture was a characteristic of many of his later articles (e.g. 1951d, 1952a, 1953f, 1963a, 1969). In an autobiographical article (1970) he deplored the tendency to break up plant pathology into separate specialities concerned with funguses, mycoplasms, nematodes, viruses, etc. He was concerned with the protection of crops from all forms of damage and argued that a healthy crop was both aesthetically pleasing and financially rewarding. Academic scientists too seldom state the economic advantages or consequences of their line of work. Bawden was not one of these. For example, he (1963b) showed that for £2 an acre the occurrence of sugar-beet yellows could be delayed enough to produce extra crop worth £19–£40, and he pointed out that it cost £10M to maintain some control over potato virus diseases, which is more than it costs to operate the spectacular 'slaughter policy' for controlling foot-and-mouth disease (1956c, 1959d, 1964d). Earlier (1941h), he had vigorously defended the 'slaughter policy'—commenting that it was so efficient that it tended to inhibit research on aesthetically more satisfying methods of control.

The need for more pathologists is a recurrent theme. Bawden realized sooner than most scientists that improvements in agricultural technique, if not directed specifically at the control of pests and diseases, tended to increase the risk from disease. Pathogens spread more readily in lush, uniform crops, and, although a well-nourished crop may sometimes be a little more resistant to infection, when infected it supplies more inoculum than a less vigorous crop would have done (1955a, 1957c). He had summed this up (1950j): '. . . it will be obvious that the conditions of agriculture are much more favourable for the rapid increase of disease than the conditions obtaining in most natural habitats. The growing of large areas of the same plant is an unnatural procedure. Under most natural conditions, there is a mixed and varied flora. If a plant of one species becomes diseased, it is likely that its immediate neighbours will be different species and immune from its particular trouble. The next susceptible plant may be a considerable distance away, and, whether the inoculum is carried by wind, rain or insects, its chances of becoming infected from its unfortunate relative are slight. How different is the position in a crop, where the infected plant is surrounded by other susceptible plants, so that there is good opportunity for most of the inoculum to fall in conditions where it can cause infection.'

He argued (e.g. 1951d, 1952a) that widespread mild infections, often unnoticed by unskilled people, caused greater total loss than localized devastating epidemics: even in an environment as rich in pathologists as Rothamsted, the importance of the fungus causing eyespot (*Cercosporella herpotrichoides*) passed unnoticed for many years. As he saw it, the most useful job for a pathologist was diagnosis in the field and measurement of the probable extent of loss. That would impress farmers and officials with the need for crop sanitation: he stressed the need for legal enforcement when control measures had been discovered (1951d, 1969) and pointed out that such enforcement was no more undemocratic than compulsory sanitation and vaccination.

As the last two paragraphs show, Bawden fully supported all effective measures for controlling the spread of diseases. He doubted the efficacy and political wisdom of many attempts to control the spread of diseases from country to country. To quote (1950i): 'There is little doubt that many quarantines have been costly to operate and valueless as disease-control measures. In some countries embargoes have been used for economic rather than biological reasons, for they provide a convenient alternative to a tariff wall and are more effective than tariffs in excluding imports that might interfere with the sale of home-produced crops. When quarantines and embargoes are based on sound biological knowledge of the pathogen and host plants concerned, there is everything to be said in their favour, and they are an obvious first measure of protection. On the other hand, when (as has happened) they are brought into force against pathogens that already exist in the importing country, against those which have ample means of entering other than in the excluded materials, or against pathogens that could not thrive in the importing country, then quarantines and embargoes are only laughing-stocks.'

Although he supported academic research enthusiastically, he emphasized the seeming paradox that control did not necessarily depend on it (1969); thus little is known about the chemical and physical properties of leaf roll virus and it can be effectively controlled in the field, whereas there is more information about tobacco mosaic virus (TMV) than any other nucleoprotein but we know little about its natural dispersal, and control is inadequate. The reciprocity between symbionts, or pathogens, and their hosts fascinated him (e.g. 1957c). Each adapts to the environment created by the other, and the adaptations can be beneficial, harmful or apparently neutral.

About 15 years ago, public disquiet over the dangers from testing nuclear bombs began to be replaced by disquiet over the possibility that people, animals and plants would be deliberately exposed to infection in time of war. In spite of the adaptability of pathogens, and the consequent possibility that more pathogenic variants could be selected or made, Bawden doubted the efficacy of the malign use of plant diseases, and thought that concern about them tended to be a 'red-herring' diverting attention from the more serious threat from nuclear weapons. He attended a Pugwash Conference to put this point of view; a shortened version of his paper was published (1960d). Such devastating outbreaks as potato blight in the 1840s or coffee rust at the end of the century, depended, in his opinion, on rather unusual climatic and other circumstances. His own experience with infections deliberately introduced into a crop, made in the course of experiments on the control of the spread of infection, led him to conclude that plant diseases were too unpredictable for use in warfare.

The control of virus infections

Bawden's primary interest was to ensure that healthy and productive crops could be grown when and where a farmer wished. As he put it (1970) '. . . people seem to think I will be pleased to see a diseased crop. Interested yes, but pleased no, and especially not when the disease is one for which control measures are known. Some moments of the greatest pleasure for me recently have been to contemplate the perfectly uniform stands of plants in crops of virus-free King Edward potatoes and compare them with memories of the uneven crop of 40 years ago, when not only every plant inevitably had paracrinkle virus, but many also had leaf roll or virus Y, and some had all three.' His work on the chemical and physical properties of viruses was an important step towards that primary interest because it made him well known when young to all plant pathologists and so ensured opportunities to develop his real bent, but work along those lines remained a peripheral interest. To quote his own words again (1970): 'There is nothing easier than to put a virus through the current range of standard machines, some automatic or semiautomatic, that will purify it, photograph it, measure it, and analyse it, with a paper at the end containing the canonical measurements and pictures editors of journals readily accept, even though in essence it contains nothing new. It is much to ask someone to give up this easy approach to publication and tackle the more difficult problems of pathology.'

By the time we had begun to regard virus infection as a general disturbance of host metabolism (1952b, 1953c) rather than as the multiplication of an invading organism in an essentially inert host, several parts of the picture of the influence of virus infection on crop yield were beginning to fit into place. We already knew (1939c) that the extent to which a plant was crippled by a disease bore no relation to the amount of virus that the plant contained. This was a point that Bawden emphasized in many later papers. Viruses did not seem to cripple plants merely by sequestering nutrients; they seemed rather to act by interfering specifically with part of the mechanism of metabolic control. If they acted in this specific manner, it seemed possible that they could be inhibited specifically. The control of bacterial infections in people and animals by penicillin and other antibiotics suggested that a similar suppression of infection in plants might be possible. Many substances were known that destroyed infectivity *in vitro*, or that prevented infection in the highly artificial conditions of rubbing on to a leaf along with a virus. But those that did not injure the plant were not curative or prophylactic. Bawden & Freeman (1952d) studied some components of *Trichothecium roseum* and found that one of them had some inhibitory action even a day after infection. However, it was phytotoxic and, in a review of the subject (1952b), we concluded that chemical methods for curing virus infections were not likely to be effective in practical agriculture. Bawden later (1955b, 1958b, 1959d, 1966a) excepted tree crops from this discouraging forecast because, if cured, they could live long enough to recover from debilitation.

Although treatments that would cure an infected crop seemed improbable, methods for curing an individual plant that would later be used as material for producing an uninfected clone had been known since 1923. Heat was the agent most often used. Bawden surveyed the literature on heat therapy in several reviews (e.g. 1955b, 1966a) and suggested (1964d) that, in the plains of India, leaf roll in potatoes may be being controlled by inadvertent heat therapy because of the high temperature at which the seed-tubers are stored. When he, with Kassanis, F.R.S., & Nixon (1950c), had shown that there is nothing mysterious about the presence of paracrinkle virus in the whole clone of King Edward potatoes, the possibility of producing a virus-free clone excited him greatly. Heat therapy had failed (1950c), but Kassanis (*Ann. appl. Biol.* **45**, 422, 1957) managed to grow a potato plant from a fragment of apical meristem into which the virus had not yet penetrated. This was still a King Edward potato but virus-free. All certified stocks of King Edward grown commercially in Britain are now part of the clone descended from that fragment of apical meristem and they produce about 100 000 tons more tubers annually than the original King Edwards would have done on the same land. His pleasure at this outcome shows clearly in a review of the subject (1965a) and in many references elsewhere (e.g. R.E.S. 1966).

Vegetative propagation has many merits, but it greatly increases the probability of virus infection becoming widespread or even universal. In several articles (e.g. 1952a) Bawden pointed out that, because of infection, the clones of cassava usually grown in East Africa gave only one-sixth the yield that virus-free clones gave in the same situation. For obscure reasons (1959e, 1966a), true seeds are usually uninfected (legume seeds are the main exception); true seed is, as a rule, used to start a new variety even of species that will later be propagated vegetatively. The material planted may initially be healthy but gets infected in the field. Bawden therefore encouraged research on the spread of virus infection and devoted more space in his later writings to this subject than any other. At first he paid most attention to spread by vectors moving above ground, but latterly stressed the importance of those below ground such as eelworms and funguses (1960e).

An early attempt to limit the spread of infection in potatoes and sugar beet by killing aphids with nicotine was a catastrophic failure. This happened because (1946a, 1952a, 1954e), although the aphids considered purely as a pest were eliminated, the survivors were irritated into mobility and spread infection more widely than a much greater number of quiescent aphids would have done. In all later articles (e.g. 1969) on protecting crops Bawden stressed the importance of detailed investigation into the habits of vectors—where they came from, when they moved, how long they fed and from what parts of the plant, when they acquired the ability to transmit infection, and how long they retained it. Until then the study of points such as these was often regarded as somewhat academic; Bawden argued forcefully that it was fundamental to a rational use of insecticides to control virus infection. Killing insects after they have infected a crop is mere revenge. The important thing is to kill them before they can infect or, better still, to deter them from entering the crop, or to kill them on the plants from which they are bringing infection. Having this aim, he actively encouraged the organization of the sugar-beet 'spray warning' scheme to farmers when aphid infestations seemed likely to spread beet yellows virus. It started in 1957, by 1959 more than 95% of the total beet acreage was sprayed in response to it, and the net increase in income as a result was about £5M in that year (1963a). Since then the spray warning scheme has continued and, in conjunction with other control measures, has effectively restricted the incidence of yellows. Spraying is so often obviously beneficial that he feared crops were sometimes sprayed unnecessarily and emphasized the importance of keeping '. . . an indispensable practice from becoming an established ritual' (R.E.S. 1962).

Although well aware of the potential hazards to people and other animals of the indiscriminate use of insecticides, he remained firmly convinced that use was essential (e.g. R.E.S. 1962). To encourage proper use he accepted presidency of the British Insecticide and Fungicide Council and the British Crop Protection Council. He was naturally delighted by the development at Rothamsted of synthetic analogues of the pyrethrins. They are cheaper and more stable than the natural products and, like them, are relatively harmless to mammals and birds.

All plants are immune to most diseases. Plant breeders, having produced varieties that are temporarily immune to many fungus infections, hoped for similar success with virus infections. Bawden argued (1946a, 1948c) that this was unlikely because, in the virus infections that matter most in agriculture, an infection at one point on a leaf ultimately pervades the whole plant whereas a plant that is resistant to a fungus may merely be localizing the attack. Furthermore, immune varieties give only a short respite (1951d) because pathogens continually mutate and produce variants able to attack the immune variety; he argued that because the number of virus particles in an infected plant was very much larger than the number of fungus spores, the breakdown of immunity to virus infection would probably be quicker because there would be more opportunity for mutation. He was equally doubtful about the long-term value of tolerant strains which he regarded as reservoirs of infection for their more susceptible neighbours. He thought (1946a, 1948c, 1969) that breeding hypersensitive plants would be the most useful approach. They are killed abruptly by infection so that a crop of them is, in effect, self-roguing. Hypersensitivity, though catastrophic for the individual plant, is beneficial to a community of plants because it gets rid of a focus of infection. This concept—that the welfare of the community may not coincide with the apparent welfare of the individual—is emphasized in several other articles. It also applies at the cellular level. An infection so virulent that it killed the infected cell quickly would probably never be noticed (1952b, 1972c); a less virulent infection causes a necrotic local lesion that does not spread; it is the still less virulent type of infection that is able to pervade the plant.

THE CHEMICAL AND PHYSICAL PROPERTIES OF VIRUSES

In 1934, filtration through nitrocellulose membranes had assigned approximate dimensions to several viruses too small to be resolved by u.v. microscopy. Schlesinger had shown that TMV could be sedimented slowly at 20 000 *g* (an intense centrifugal acceleration at that date) and that preparations of a more easily sedimented bacterial virus contained deoxyribonucleic acid. That was about the sum total of knowledge about the intrinsic properties of viruses. There was a vast body of information, or lore, about the treatments that led to loss of infectivity: this was not directly interpretable. Enzyme preparations were grossly unspecific. In 1936, the most active ribonuclease preparation was 'crystalline' trypsin. The more cautious virus workers realized that loss of infectivity when a crude extract was heated, or exposed to alcohol or extremes of pH, was as likely to be caused by entrainment of virus on unspecific precipitates as by a change in the virus itself.

Until the mid-1930s, viruses were usually studied by animal or plant pathologists most of whom thought of them as small bacteria. They had therefore little incentive to attempt purification, in the chemical sense. At that date it was even rare to find published figures for the chemical composition of whole bacteria. It is more surprising that those who understood, or thought they understood, Beijerinck's curious concept of the *contagium vivum fluidum* did not get further with purification. Two important reasons may be suggested. Instead of using the conventional methods that had been used succesfully to fractionate proteins and other large molecules for 50 years, novel and bizarre methods were tried that have not remained popular; people were loth to believe that a virus could be a prominent component of an extract such as plant sap, the fractions they discarded probably contained a greater proportion of the virus they sought than the 'purified' fraction they retained.

The viruses that Bawden studied in some chemical and physical detail are arranged in this section more or less in the sequence in which he worked on them, but he usually worked on several at the same time. His work on paracrinkle virus is mentioned in the section on the control of infection, on clover mottle virus in the section on photochemical studies, and on cucumber viruses 3 and 4 in the section on classification.

Potato virus X

While Bawden worked at the Potato Virus Research Station (Cambridge), attention had to be concentrated on viruses that attacked potatoes. We found (1936a) that preparations made by differential pH precipitation lost infectivity, and precipitability with antiserum, when incubated by trypsin, pepsin and papain activated by KCN, but not by papain or KCN separately. From this we concluded that '. . . protein is an essential part of virus X, but there is no evidence that other equally important substances may not also be present'. By the same fractionation procedure, we made a similar, but inactive, material from uninfected leaves. Two years later (1938a), having acquired more skill in handling leaf extracts, we made liquid crystalline preparations consisting mainly of ribonucleoprotein from both a severe and a mild strain of virus cultivated on three different host species. It was difficult to get preparations colourless and they had a disconcerting tendency to become insoluble. This is still a troublesome virus to work with. It deserves more attention than it gets because it differs in several interesting ways from other rod-shaped viruses such as TMV. Potato virus X particles are flexible, carry little electric charge at neutrality, and the protein moiety reaggregates into amorphous rather than rod-shaped particles (1951c, 1959g).

Perhaps because of the readiness with which it becomes insoluble, little extra virus was released from leaf fibre by fine grinding, but virus was released by fibre-digesting enzymes from snail gut (1947d). Conveniently, although this virus is relatively unstable, it is not readily attacked by that enzyme mixture. The virus is also precipitated by pancreatic ribonuclease and the precipitate, like the ones that form spontaneously, slowly redissolves in borate (1948b).

Tobacco mosaic virus

The restriction of research to viruses attacking potatoes disappeared with Bawden's move to Rothamsted in 1936. Plant virus workers had realized many years earlier that tobacco mosaic, which had unequivocally been shown to be a virus infection in 1898, was the disease best suited to laboratory study. Bawden had already (1935a) used crude preparations of TMV to demonstrate the specificity of antisera made against potato virus X, he now devoted most of the glasshouse space available to him to the cultivation of plants infected with TMV. Although sap from infected plants will transmit infection after great dilution, we calculated from the approximate dimensions of TMV (deduced from filtration and centrifugation) that the concentration of virus in sap could be so small that large volumes would be needed to prepare enough virus for chemical study. That calculation depended on the false, but general, assumption that only a few particles were needed to infect a plant.

In a few weeks, using methods that had been standard in protein chemistry for 50 years, we made gram quantities of liquid crystalline nucleoprotein from plants infected with three strains of TMV. The liquid crystallinity, and the curious 'herring bone' pattern that appears when a drop of TMV solution is allowed to dry, intrigued us greatly and we realized that our product was ordered to an extent that should make it amenable to study by X-ray diffraction. We therefore took some preparations to J. D. Bernal, F.R.S., and published jointly (1936d) with him. We had difficulty in persuading Bernal to accept the last paragraph of the paper. It pointed out that the substance was intrinsically interesting and would become even more interesting if we could demonstrate that it was the virus and that it had not been modified in the course of isolation. Bernal measured the width of the particles and we calculated their length (1937c) from the concentration at which a solution became liquid crystalline—we followed Staudinger in assuming that at that concentration each particle was free to rotate in either a cylinder or a sphere. The particle mass so deduced showed definitely that many thousands were needed to cause an infection: hence our caution.

The physical properties of the material we had isolated from virus-infected plants excited considerable interest, partly because our biological outlook led us, at a Royal Society soirée, to demonstrate anisotropy of flow by using a goldfish and seahorse to stir a dilute solution, placed between 'polaroid' sheets, rather than a more conventional stirring mechanism. The presence of nucleic acid excited no interest at all; for two years it was strenuously opposed. Nucleic acids were not fashionable at that date and no other authentic nucleoprotein—that is to say, a preparation in which nucleic acid and protein remained associated when in solution—was known. The 'tetranucleotide hypothesis' was widely believed in. If nucleic acids had been tetranucleotides, there would clearly be little scope for specificity in them. But anyone reading the literature on nucleic acids at that date could see that the hypothesis was baseless. Chemical evidence did no more than make it unnecessary to assume the presence of more than four nucleotides, it had no bearing on the question of whether four was the limit; it was obvious from their physical properties that nucleic acids were large. We regarded the presence of nucleic acid as a not unexpected fact rather than as a matter of philosophical import.

The properties that we attributed to TMV differed radically from those that Stanley had attributed to it in 1935. During the next few years he incorporated most aspects of our description into his. This unanimity helped to speed virus research, but leaves unanswered the question of what it was that he isolated in 1935.

Because virus in fresh sap differed from purified preparations in filterability, the character of the precipitate with antiserum, and the readiness with which anisotropy of flow could be demonstrated, we postulated an aggregation during purification. Electron micrography later suggested that we exaggerated the extent of aggregation but it is now generally agreed that there is some aggregation when purification is rigorous enough to remove the more obvious host components from the preparation. The effects we noticed were partly the consequence of aggregation of genuine TMV, partly of aggregation of non-infective material serologically related to TMV, and partly of the removal of interfering contaminants present in sap from both uninfected and infected plants (1945g). Many years elapsed before there was agreement that infection with TMV leads to a general derangement of metabolism which produces proteins serologically related to TMV but without the nucleic acid.

Recognition of the variety of particles produced in the course of TMV infection led us to wonder whether material related to TMV remained associated with the fibre. By fine grinding, and incubation with trypsin and snail gut enzymes, we released as much TMV from the fibre as was present in the original sap (1946b): this made it the predominant protein in an infected leaf. Work on these aspects of the problem was confused by imprecise repeatability of experiments after intervals of a few years. When we returned to the study of anomalous proteins produced along with TMV (1956a) changes in the virus strain, the variety of host plant, or the conditions in which the plants were grown, had altered the relative proportions of the various serologically related fractions. The subject is still confused.

Although the three strains of TMV with which we habitually worked caused strikingly different symptoms on infected plants, they resembled each other closely in chemical and physical properties. Bawden studied (1956d, 1958c) another strain, derived originally from leguminous Nigerian plants. Preparations cultured on beans differed from preparations cultured on tobacco in electrophoretic mobility, amino acid composition, serological behaviour, symptoms when they were compared on the same test-plant, and appearance under the electron microscope. He described in detail the steps taken to exclude the possibility that he was working with a mixed culture and that the two hosts favoured the multiplication of different components in it. The point should be unequivocally established. It is well known that fragments from the host are associated with many viruses but the changes that Bawden claimed were unusually profound. His claim is disputed but he reiterated it (1961a, 1964d).

Bawden's dissatisfaction with the common tendency automatically to accept orthodox opinion on the mechanism of nucleic acid and protein synthesis was also shown by his argument (1959h, 1964b) that the variant forms of TMV that appeared in plants infected with virus that had been nearly completely robbed of its infectivity by treatment with nitrous acid were not necessarily the consequence of mutation rather than selection of a pre-existing resistant variant. His main arguments were: that no variant had at that time been produced that was not already known in the type strain of TMV, and that the aucuba strain, which presumably undergoes the same chemical changes on treatment with nitrous acid, does not produce variants. This question also is still unsettled.

Even if it should turn out that Bawden's interpretation of the phenomena observed with the legume strain of TMV was wrong and that his doubts on the interpretation of the nitrous acid results were unnecessary, the stress that he put on the potential variability of viruses was salutary. As he put it (1964d): 'Single cells infected with tobacco mosaic virus may contain more than 10^6 virus particles and a local lesion more than 10^9. An error rate in assembly of only one in a million could give a thousand aberrant (mutant) particles in one local lesion. With such possibilities for new variants in these immense populations, it is the stability of bulk cultures rather than their variability that seems more cause for surprise. This stability can be attributed to natural selection, for few variants will be better fitted than their parents to survive in the conditions for which their parents have already long been selected, and the more they depart from their parents the less likely are they to be able to supersede their parents in these conditions. In constant conditions natural selection will operate mainly as a stabilizing factor, but when conditions change it will operate to select any variants with extreme properties that are better fitted to survive in the new conditions. The evolutionary value of great variability is mainly in increasing the survival chances when the environment (host plant or growing conditions) is changed; its small value otherwise is shown by the fact that none of the variants yet obtained as single-lesion isolates from tobacco mosaic virus competes successfully with the type strain in tobacco plants grown under usual conditions.'

Tomato bushy stunt virus

The flood of metaphysical balderdash that was released by the observation that TMV, which some people wished to regard as an organism, had quasi-crystalline properties, would have been very much greater if we had happened to work first on bushy stunt virus. On precipitation with ammonium sulphate it formed unequivocal rhombic dodecahedral crystals (1938d, 1943b). Those who were worried by what they regarded as the antithetical properties of TMV could solace themselves with the thought that it was not 'really' crystalline. No such escape was possible with bushy stunt virus. Some observations on its liberation from leaf fibre and on methods that rob it of infectivity without loss of serological activity or crystallizability will be summarized later.

Tobacco necrosis viruses (*TNV*)

Bawden & van der Want (1949c) found that a TNV caused bean stipple-streak which is important commercially in the Netherlands. Otherwise, most of the early work on this group of viruses was undertaken for purely academic reasons. The main point of interest at first was the similarity in the symptoms produced by distinguishable cultures: a striking feature of other plant virus infections is the diversity of symptoms caused by closely related strains. In animals, different viruses often cause similar symptoms, but this phenomenon was rare in plants. Another interesting point was the widespread occurrence of TNVs in the roots of apparently healthy plants and, later, the discovery of their transmission by vectors in soil. Bawden began to disentangle the group (1941a) by separating two serologically unrelated cultures that produced indistinguishable symptoms. We then (1942e) sought further TNV cultures, both from other institutes and from the roots of apparently healthy potato and tobacco plants. Five, some of which would not now be called TNVs, were serologically distinct and all but one crystallized in obviously different forms. The crystals of two were birefringent but the serum precipitates were of somatic type. This suggests that the particles are only slightly anisometric. They have not, apparently, been investigated further. These crystals were made by adding ammonium sulphate until the solution was just opalescent at room temperature and cooling it quickly to 0 °C; crystals separated when the solution was slowly warmed, for these viruses, like bushy stunt virus, are more soluble cold than hot. The culture that failed to crystallize when treated thus, crystallized when ultracentrifuged from water (1945f). The crystals were accompanied by amorphous material and it was this that was infective; it also sedimented more rapidly on ultracentrifugation. We suggested that the crystalline component was a breakdown product of the amorphous one and that only the intact form was infective. This was plausible because these TNV preparations lost infectivity on aging and during the process crystals separate slowly. But Kassanis showed that the culture contained two unrelated viruses: the crystalline material was not, when alone, infective; the amorphous one was, and in its presence the crystalline one multiplied. This was the beginning of the phenomenon of 'satellitism'.

No host was known which was systemically infected by TNVs. We thought that this might be a consequence of rapid inactivation of virus as it moved from the point initially infected into adjacent cells. We tried to get evidence on the matter by studying the conditions in which our amorphous culture lost infectivity. Extracts made from leaves frozen while intact were less infective than those made from frozen pulp, and ultracentrifuge sediments made quickly from chilled sap were less infective than those made from sap aged at room temperature (1950e, f). We thought that was evidence for activation but later (1957e) found that gentle treatment stabilized leaf mitochondria and that these then inactivated the virus. We also found (1950e) that leaf ribosomes were more effective than the other substances we tested as adsorbents for separating the infective from the non-infective component of our preparations. We collected a great deal of information on what might be called the Natural History of a virus infection, but did not manage to fit the facts into a coherent picture. As we remarked (1950e): 'Our results do not simplify knowledge of viruses; rather the reverse.'

Insect-transmitted viruses

The physical and chemical uniformity of the first group of viruses that we studied—potato X, TMV, bushy stunt and TNV—could have arisen because we selected for study viruses that were stable in sap and that were mechanically transmissible. We thought that viruses that differed biologically from the group already studied might have different chemical properties. Insect-transmitted viruses were the obvious choice, but it would have been difficult, if not impossible, to assay viruses transmitted only by insects. However, potato virus Y and Hyoscyamus virus 3 can be mechanically transmitted although readily transmitted by aphids in the field (1939c). Because of the instability of these viruses, the small amount in sap, and the small capacity and speed of our centrifuge, they were troublesome: but we isolated anisometric nucleoproteins of doubtful purity. There are many strains of virus Y, and host strains differ in their response to each of them (1946c, 1947c): perhaps we chose both strains badly.

The mild and severe tobacco etch viruses are in many ways similar to the two just discussed; Bawden & Kassanis (1941b) discussed a possible classificatory relationship, and pointed out (1945d, 1951e) that different conclusions would be reached if most attention were paid to serology rather than antagonism within the host. Their study of partially purified preparations suggested that these viruses were anisometric.

The distribution of broad-bean mottle virus, which is unrelated to the four discussed above, suggests (1951f) that it has an insect vector. Purified preparations consisted of isometric particles resembling bushy stunt virus in composition but less easily precipitated by ammonium sulphate. Both in sap and in purified preparations, unusually large amounts of virus had to be used to transmit infection, and there was some evidence that the properties of this virus depended on the host from which it came. These properties may be connected with the persistence with which polyphenol oxidase accompanied the virus through cycles of ultracentrifugation.

Virus multiplication

Even in the 1950s, some microbiologists still thought of viruses as very small bacteria that had become obligate parasites because of an unusually extensive loss of the enzymes necessary for saprophytic growth. This had been the orthodox point of view a decade earlier and it still mars some textbooks that refer to viruses as the simplest form of 'life'. Alongside those who held this orthodox view, there were those who thought that the host was not a simple culture medium but played an active role in virus multiplication. Sanfelice, Bordet, Muller, Johnson, Mulvania, Wollman and Lwoff were prominent among the heterodox during the period from 1914 to 1936. In the first edition of *Plant viruses and virus diseases* (1939d), Bawden expressed considerable sympathy with the heterodox point of view. He did not adopt this attitude because we had found that some viruses could form crystals or paracrystals. We had commented (1937c): '. . . phrases such as "lifeless molecules" have been increasingly applied to viruses, and much has been made of the idea that there is an essential incompatibility between the living and the crystalline states. As this is obviously an aesthetic rather than a scientific incompatibility it is necessary to be clear about the aesthetic connotations of the word crystalline. We have already suggested that the virus "crystals" might more accurately be described as fibres, and we doubt whether it is profitable to say that these viruses can be crystallised, or to apply the word crystalline to them without some qualification. Writers who find this incompatibility usually assume that a crystalline material must consist of a single definable chemical substance; this, however, is by no means necessarily true, for whenever groups of superficially similar substances are studied mixed crystals are found. The proteins form such a group, and, although it has been shown that the haemoglobins often do not form mixed crystals, the point has been so inadequately studied that it cannot be asserted that even true protein crystals are necessarily homogeneous. Structures such as plant fibres, hairs and muscle are fully as crystalline as the solid virus preparations have yet been shown to be, and the organisation in suspensions of rod-shaped bacteria (or even shoals of fish) closely resembles that in the liquid crystalline virus preparations. A state of organisation that is often described as crystalline is necessarily taken up by any collection of rods of equal cross-section when flowing or when packed tightly, and such states are widespread in nature. Using crystallinity in this sense there is obviously no incompatibility between the living and the crystalline states, and it is only in the sense that any regularity in the arrangement of particles gives that arrangement some of the attributes of a crystalline substance that this term can be applied to the virus preparations. It is, however, unprofitable to attempt to apply the words living and dead to viruses. . . .' Bawden worked on the assumption that viruses could more properly be thought of as being made by the host than as multiplying in the host, not because he thought that we had demonstrated that they were particularly simple, but because of his extensive knowledge of the processes of infection and the differences between virus infection and infection by bacteria and funguses.

Leaves are unsuitable material on which to study the first phases of infection and multiplication because, when uninjured, they are not penetrated by viruses. The consequences of the treatments needed to ensure penetration are therefore inextricably mixed up with the consequences of the infection. However, once inside a susceptible leaf, viruses spread to varying extents from cell to cell. The responsiveness of the leaf to changes in environmental and cultural conditions is a troublesome complication when reproducible results are sought and uniform starting material is needed. This very responsiveness makes plants particularly suitable hosts in which to study factors influencing the reactions between viruses and cells, because it allows them to be studied under a much wider range of conditions than can be used with many other kinds of organism.

Bawden pointed out in several articles (e.g. 1964b) that apparent susceptibility to infection seemed to follow no rational rules. A virus able to multiply in a leafhopper and a flowering plant may be unable to multiply in closely related leafhoppers or plants, and viruses, each of which can multiply in many different species, may share few hosts. Even within one host species, differences in weather and the conditions of husbandry to which crops are exposed in commercial practice have long been known to affect susceptibility to infection. In his books, and in many papers (e.g. 1952a), he tried to clarify thinking by distinguishing three distinct facets of susceptibility: the ease with which infection is initiated, the severity of host reaction to infection, and the quantity of virus produced. He emphasized that these processes were so unlike that it was improbable that a physiological difference between two sets of plants would affect all the processes in the same sense. Furthermore, it is seldom possible to tell whether differences in the physiological state of the plant, the composition of the inoculum, or the technique of inoculation, are affecting the number of entry points, the rate of multiplication, or the movement from cell to cell. If there were no movement, infection would not be recognized, for the death of a single cell would be unnoticed.

A series of papers (1947b, 1948d, 1950b, 1950d), with Roberts and Kassanis, reported that the number of necrotic lesions produced by an inoculum was increased by shading before inoculation. Shading after inoculation had little effect, or even diminished the number of lesions. Shading obviously interferes with one aspect of a plant's nutrition. By contrast, suboptimal use of fertilizers such as nitrogen, phosphorus and potassium diminished both the number of lesions on a host giving local lesions, and the quantity of virus produced in a systemically infected host. The effects of fertilizer were largely the result of differences in plant size. In plants with tobacco mosaic, the percentage of the dry matter of the leaf accounted for by virus could however reach surprising levels when growth was heavily restricted by potassium deficiency coupled with abundant nitrogen and phosphorus. Some years later (1960c), he summarized this work, and work by others, and pointed out the importance of distinguishing the amount of virus in a plant from the amount in each infected cell. This distinction is particularly important when the effects of temperature are considered. Exposure to temperatures around 36 °C often favours the spread of virus from cell to cell but not the multiplication within each cell. That is favoured by keeping the plants, after infection, at a lower temperature. We had earlier (1953c) discussed the more chemical aspects of knowledge about virus multiplication and concluded that it differed in no characteristic respect from other types of synthesis. We chose protein synthesis as the paradigm, and ended the review thus: '. . . we have related our argument to protein synthesis, because, although ideas about it are still nebulous, they have attained more form than ideas about nucleic acid synthesis. Only recently has it been generally recognized that variations in nucleotide sequence permit extensive isomerism of nucleic acids: not perhaps the gratuitous isomerism that protein structure theoretically permits, but still amply sufficient to cover the amount of specificity for which there is evidence. We might, indeed, with more aptness, have considered the whole problem in terms of the synthesis of nucleic acid, because transmissible nucleic acids are known.'

Our attitude of mind sprang partly from the 'law of parsimony', variously attributed to Duns Scotus, Occam and Dante, according to which one should not unnecessarily invoke a novel mechanism, and partly from our observation (1945g, 1956a) that plants infected with TMV contained several types of protein serologically related to TMV. We argued (1950h) that an understanding of virus infection depended on studying all its consequences and that attention should not be restricted entirely to those products that were able to transmit the disease to hosts inoculated in conventional ways. Our observations and attitude gained little acceptance at first but later gained popularity (references in 1957a and 1960c).

Opinion on virus multiplication underwent a radical change with the discovery, in other institutes, that little of the protein in some bacterial viruses entered a bacterium during infection, and that a fraction from disrupted TMV, consisting predominantly of nucleic acid, could infect tobacco plants. We were, at first (1957a especially in the discussion at that meeting; 1957d, 1957g) sceptical, not because we thought there was anything unreasonable in nucleic acids being infective, we had already (1953c) commented on the possibility that it was a vehicle of specificity, but because we doubted the cogency of the evidence that was being presented for the infectivity of 'pure' TMV nucleic acid. We also pointed out that the protein fraction from disrupted TMV inhibited infectivity and that this complicated the interpretation of experiments purporting to show that TMV could be reconstituted from its fragments. Furthermore, some of the treatments that inactivated the infective nucleic acid fraction from TMV (1959j) were not, at that date, known to modify nucleic acid. It could be argued, by hindsight, that we were too sceptical: scepticism and objectivity are near neighbours.

By analogy with observations on the processes by which bacterial viruses infected their hosts, it was widely assumed that plant viruses also were dismantled during the first phases of infection. Bawden stressed (1957a, 1960c, 1964b) the absence of direct evidence for this though his own work on photoreactivation (which will be discussed later) and on the appearance of small molecules containing ^{32}P in extracts from plants infected with labelled TMV, was compatible with dismantling. He pointed out the unreliability of the evidence that lesions, or new virus, appeared more quickly after infection with nucleic acid rather than intact TMV (1964b). His observations showed that inocula that would ultimately produce the same level of infection produced it at the same rate, but that nucleic acid must act quickly if it is to act at all (because of the instability of nucleic acid on the leaf surface) whereas TMV from the inoculum could persist longer and start the infective process later. However, working on the assumption that nucleic acid rather than intact TMV was the material responsible for the spread of infection from the cell(s) initially infected in an inoculated leaf, we thought that differences in the apparent susceptibility of plants in different physiological states might be explained by differences in the movement and survival of TMV nucleic acid in them.

The basic problem in studies on the initiation of infection is to distinguish failure of a putative infective agent to multiply at the initial site, from failure to move from that site so that infection becomes apparent, and from destruction by what we called 'scavenging processes' (1953c). We argued that no copying process was likely to be error-free so that normal synthesis in an uninfected host is likely to produce some false-copies, most of which will be destroyed. A virus is a copyable entity able to evade this scavenging. According to that picture, virus infections would be expected very occasionally to arise *de novo*. A somewhat similar hypothesis attributes normal ageing to the accumulation of unscavenged copyable false-copies.

The infectivity of the nucleic acid fraction from dismantled TMV is so easily destroyed that we thought it possible that differences in the susceptibility of leaves in different physiological states might be correlated with differences in the quantities of those inactivating agents that were known to be normal leaf components. We found (1959j) that physiological differences had a much greater effect on the apparent infectivity of nucleic acid than of intact TMV and that differences in the amount of inactivating or inhibiting agents, e.g. leaf ribonuclease(s) and calcium, were in the right sense. But quantitatively the differences seemed inadequate to explain the observed differences in susceptibility. In the course of that work we found some other conditions in which the nucleic acid fraction was inactivated which did not seem compatible with the then known properties of a nucleic acid if that term were rigidly defined. The next 12 years were at first frustrating, partly because our work was constantly interrupted by other activities, partly by the great variability in the number of lesions given by an inoculum on leaves ostensibly in the same physiological state, and partly by striking inconsistencies between separate experiments. It is unlikely that a statistician would have agreed with most of the tentative conclusions on which we planned further experiments, but we did not think the importance of the theme, and the amount of time we were able to devote to it, justified vastly increased expenditure on test-plants. Bawden indeed often referred to the routine inoculations he did during most of this period as 'occupational therapy'—a welcome spell in the glasshouse rather than at his desk—and he insisted that our work on this subject should be planned in such a way that he could manage all the inoculations himself.

In our main series of experiments, we compared the infectivities of extracts made in various ways from tobacco leaves infected with TMV, and uninfected leaves to which purified TMV was added, all finally treated with phenol to disrupt the TMV. We concluded (1972c, d) that, when mature leaves were used, nucleic acid became firmly attached to the insoluble parts of the leaf in the presence of several leaf components (e.g. Ca^{2+}, nicotine and spermine) if the system was protected from oxidative or autolytic damage. We suggested that sequestration of nucleic acid by this system, or a system analogous to it, might be responsible for the failure of nucleic acid to move from a site of initial infection so as to form a visible lesion. The involvement of Ca^{2+}, and therefore of metabolites able to chelate with it, could explain the effects of the physiological state of a host on its apparent susceptibility. But for Bawden's untimely death, we would have tried to elucidate the mechanism more fully; we had however agreed the wording of most of the two papers and it seemed better to publish them as they stood rather than continue the work.

Photochemical studies on virus multiplication

Photoreactivation, the reversal by exposure to visible light of damage done by u.v. light, had been observed with a bacterium, a bacterial virus, a fungus and sea urchin eggs—none of them systems using light in their economies. Comparable processes could reasonably be expected in leaves. First, Bawden & Kleczkowski, F.R.S. (1952c) showed that a level of exposure to u.v. light that killed leaves kept in the dark after exposure did not do so if the leaves were illuminated, that is to say, the leaf itself is a photoreactivable system. Secondly, some viruses seemed to have been robbed of their infectivity by irradiation with u.v. light when assayed on plants kept in the dark, but were apparently little affected if the assay plants were illuminated. The damage done to the virus was not reversed if it was illuminated *in vitro*. These characteristic effects of irradiation and photoreactivation were used (1953d, 1955d, 1960a) to analyse some stages in the initiation of infection.

TMV, and some other viruses, though inactivated by u.v. are not photoreactivated. Bawden & Kleczkowski (1959b) found that nucleic acid made from TMV inactivated by u.v. was also not photoreactivable, but that nucleic acid inactivated by u.v. after being separated from normal TMV was photoreactivated. They suggested that in intact TMV the nucleic acid is combined in such a manner that it is protected from the type of u.v. damage that is reversible, but undergoes more radical irreversible damage. They pointed out that there is evidence that TMV reconstituted from its components *in vitro* is more easily damaged by irradiation than normal virus—perhaps because the protective link is not formed.

After being damaged by irradiation, the machinery in the leaf that supports virus multiplication takes some time to be restored to activity by light. Intact virus can survive during this time and so remains ready to initiate infection when the machinery has recovered from damage. Nucleic acid is a more vulnerable inoculum and starts an infection only if it finds the synthetic machinery already functional (1960a). The systems in the leaf that are responsible for the initial fixation and (possibly) modification of the virus seemed to be unaffected, or less affected, by u.v. irradiation than those concerned with synthesis.

These results were compatible with the idea that an early stage of infection is the release of nucleic acid from the invading virus in a form that is vulnerable to leaf enzymes; that after about 30 min in an undamaged leaf this vulnerable phase is succeeded by a phase in which stable virus is synthesized; but that in the damaged leaf the vulnerable phase persists. The results with red clover mottle virus, and nucleic acid derived from it, were similar (1961b). In that study, the effects of working at different temperatures were included and seemed to show that the mechanism involved in dissociating protein from nucleic acid was inactive at temperatures greater than 32 °C.

Interpretation was complicated by differences in the results with different viruses and hosts and by the possible effects (1955e) of irradiation and recovery on the synthesis of substances absorbing strongly around 260 nm which could act as protective screens from u.v. irradiation. These experiments ramified in several directions and included comparisons with the effects of inhibitors and inactivators such as ribonuclease, of repeatedly rubbing leaves in simulated inoculation, and of different ambient temperatures. The results cannot therefore be summarized succinctly, but they will repay close scrutiny by anyone embarking on a study of the first phases of virus infection.

Immunological research

Soon after Bawden started working with Salaman, several papers appeared on the production of specific antibodies by rabbits injected with sap from virus-infected plants. Salaman's medical background made him quick to see the importance of these observations and he suggested that Bawden should collaborate with Spooner in the Department of Pathology (Cambridge). They made (1935a) sera that precipitated with extracts from plants infected with potato virus X regardless of the host species, that did not precipitate with

TMV, and that fixed complement. They noticed the loose, flocculent, character of the antigen: antibody precipitate. Spooner was familiar with this type of precipitate as a feature distinguishing bacterial flagellar from somatic antigens: he commented, 'Your viruses have tails'. The serum precipitation end point of fresh leaf extracts, and partly purified material, paralleled their infectivities closely. When infectivity was destroyed by heating, antigenicity was destroyed also, but antigenicity survived the destruction of infectivity, whether measured by precipitation or the ability to induce antibody formation on injection into rabbits, after treatment with formaldehyde or nitrite (1935b, 1936b). This dissociation of loss of infectivity from loss of antigenicity is observed with many other viruses and the production of some vaccines depends on it. We got the same effect by treating potato virus X and TMV with alkali, hydrogen peroxide, X-rays and u.v. light (1937c, 1938a, 1940d). Some dissociation of the two activities is possible on heating tomato bushy stunt virus (1943c), and, surprisingly, on freezing it in carefully defined conditions. In general, treatments that did not affect antigenicity, had little effect on the physical properties or crystalline form of viruses. In discussion with those concerned with the manufacture of vaccines against animal diseases we often commented on the unreasonably small range of disinfecting agents tried.

Potato virus X is only partially resistant to proteolytic enzymes, the other viruses with which we worked seem to be completely resistant, it may be for this reason that they are exceptionally good antigens. Normal leaf proteins cause much less antibody formation; hence the possibility of making a virus-specific antiserum by injecting unfractionated leaf sap. The antigenicity of normal protein can however be shown by the anaphylactic response (1937e). We concluded that TMV preparations contained antigens characteristic of normal tobacco unless they had been subjected to treatments that altered the physical properties of the TMV. Those who prepare TMV merely by centrifugation seem to have lost sight of this point—but it has not been controverted. Treatments that remove normal leaf components, also enhance the 'flagellar' character of the precipitate with antiserum. Similar treatments convert into 'flagellar' type antigens some components of infected sap which initially give only a 'somatic' type of precipitate (1945g). More brutal treatment, e.g. exposure to alkali (1940d, 1957g, 1959g), have the opposite effect; TMV and potato virus X pass through the phase of 'somatic' type antigenicity before losing antigenicity altogether.

Several different factors are probably involved in these phenomena. We interpreted an increasingly 'flagellar' type of precipitation as the consequence of linear aggregation and the final disappearance of precipitability as the consequence of dispersion of the virus particles into pieces too hydrophilic to be made insoluble by antibody. The latter state can be attained in other ways. Extracts are usually made from virus-infected leaves by mincing, or grinding by hand in a mortar, and squeezing. By grinding the fibrous residue from tomatoes infected with bushy stunt virus very finely, we extracted more virus, part of which was associated with other leaf components and did not precipitate with antiserum until these had been removed (1944b). The effect was partly the result of absorption of antibody by virus associated with chlorophyll-containing protein; this protein, after coagulation, and if made from infected plants, specifically absorbed anti-virus antibodies. Plants infected with potato virus X gave somewhat similar results (1947d). It remains an open question whether these complexes exist *in vivo* or are made during the very fine grinding.

Comparable complexes, which are indubitable artefacts, are made when viruses are heated with some other proteins. Thus TMV or bushy stunt virus loses the ability to precipitate with antiserum if heated with unspecific serum proteins, but not if heated to the same extent and then mixed with serum proteins (1941c). Though there is no precipitation with specific antibody, complement is still fixed. The complex made between bushy stunt virus and rabbit serum albumin elicited in rabbits the formation of antivirus antibodies seemingly identical with those made against untreated virus (1942c). If attention is confined to precipitation, rather than to complement fixation, one has here the unusual situation of an antibody that does not precipitate with the eliciting antigen but only with a related antigen.

At one phase in the development of immunological theory, it had been suggested that antibodies were modified antigens. Support for this idea came from an apparent correlation between the stability of antisera and the stability of the eliciting plant viruses. Bawden & Kassanis (1945d) showed that the idea was baseless and that the apparently unstable sera were simply much weaker initially.

Many plant viruses not only induce antibody formation very effectively, they also precipitate with antisera at great dilutions—those with elongated particles usually give visible precipitates at 1 mg per litre and often at one-fifth of that concentration. Plants infected with potato virus X cannot be reliably identified by field inspection. With Kassanis & Roberts (1948a), Bawden explored serology as a quicker means for identifying infected tubers than rubbing the cut tubers on test plants and waiting for signs of disease to develop. Extracts from whole tubers gave unreliable results, extracts from peel were better, and extracts from sprouted 'eyes' were reliable. Serology had already (1944a) been used to differentiate viruses causing visually similar lesions in potatoes, and to recognize infections that could diminish yields by 20% without so affecting the foliage that field recognition was easy.

Classification of viruses

Biologists, from the time of Aristotle or even earlier, have seen that the classification of species raises problems. Is it arbitrary, depending on convenience and the use to which the species are put; or are fundamental relations being recognized? After Linnaeus there was agreement that a fundamental, 'natural', system was possible. The reason was not recognized until Charles Darwin, F.R.S., wrote: 'Our classifications will come to be, as far as they can be made, genealogies; and will then truly give what may be called the plan of creation.' Zoologists, having fairly adequate fossil sequences, soon adopted that point of view. Botanists knew that they were as often erecting phylogenies on the basis of present-day apparent relations as vice versa; many of them tended therefore to regard classification as an art in its own right and not dependent on evolution. By 1930, so many virus diseases of plants were known that unequivocal labelling became a serious problem. Botanists were therefore the first to be confronted with the problem of virus classification and it can be argued, by hindsight, that their preconception explains the length of time it took them to distinguish between classification and labelling.

In the first (1939) edition of *Plant viruses and virus diseases* Bawden distinguished clearly the immediate desirability of having a set of agreed labels, from the more remote prospect of being able to design a classification. He suggested that host range was a much less satisfactory basis for classification than serology. He had already (1934) suggested a serological classification of the potato virus X group and we (1937d) proposed one for the strains of TMV and discussed where, within it, cucumber viruses 3 and 4 would fit. He and Kassanis returned to that theme later (1968a). Misleading 'classifications', based mainly on host range, continued to appear and he attacked them with both argument and ridicule. After again arguing for an agreed list of names he wrote (1941g), 'Such a list, however, should make no pretence to classify. In the matter of classification it is probably better to go nowhere at present rather than to go to the wrong place. To be the Linnaeus of plant viruses is no doubt a laudable desire, but . . . those who have ideas [should] refrain from renaming viruses *en bloc*.'

He criticized systems that gave prominence to the host in which infection had first been recognized. When it was established that some plant viruses multiplied in their insect vectors, and are even transmitted through their eggs, he argued (1954e, 1957b) that they would logically be classified as insect, rather than plant, viruses because the trivial symptoms produced in insects suggested such a prolonged association that insects may well have been the original hosts.

Bawden was particularly critical of binomial labelling systems because their form suggested that classification was intended. He wrote of one such system (1953b): 'Not only do viruses, about whose intrinsic properties nothing is known, get the same generic name (at least this does not conflict with knowledge), but so do many viruses that are known to differ widely, both in their intrinsic properties, such as morphology, chemical constitution, and physico-chemical behaviour, and in properties that may or may not be intrinsic, such as methods of transmission, host range, and pathogenicity.' And later: 'A Latin translation of a common name may sound more learned and exact than the original, but it is still a common name. On what appears to be the main principle by which binomial names have so far been applied to viruses, cow parsley and cow oak would probably find themselves in the same genus. . . .'

This antagonism arose partly because of the notoriously unsatisfactory working of the binomial system with bacteria, and partly because there is good reason to think that viruses do not have a phylogeny in the Darwinian sense. Their nearest analogues are the normal macromolecules of their hosts: satisfactory classification will not be possible till these have been classified. As he put it (1955c): 'Indeed, it is even doubtful whether viruses are suitable objects for attempting to arrange in the kind of groups that are used to classify organisms; the determination of such groups depends on sexual reproduction and phylogeny, criteria that could hardly be less appropriate for classifying clones about whose origin we have not the slightest idea.'

Bawden's own early work shows that he was well aware of the importance of information about the composition and organization of viruses: what he attacked was the assumption that a useful system of classification would necessarily emerge from that knowledge and that the time of people trained in plant pathology was well spent in gaining it. As he put it (1970): 'However, many pathologists seem still imbued with the faith I have lost, for how else to explain the increasing numbers being attracted to studying the detailed physical and chemical structure of virus particles ? It surely cannot be only that the sophisticated and expensive equipment needed for the work has an irresistible glamour, although it is curious that taxonomy should be fashionable with viruses, whereas it seems to be languishing in mycology and in other parts of botany where it is more simply studied. For, of course, it is in taxonomy rather than pathology that the results of work on such things as size and shape of virus particles, number and arrangement of protein subunits, or position of nucleic acid and ratios of nucleotides, are likely to be useful. Taxonomy is a worthy subject, but I hope it will not attract too many virus workers from pathology, which is even worthier, especially as few pathologists will be likely to contribute as much new information as those already skilled in biochemical and biophysical techniques.'

It is probably largely because of Bawden's obduracy that virus nomenclature remains chaotic—but has not become misleading. With justifiable satisfaction he wrote (1966a): 'Fortunately most virus workers are neither politicians nor administrators and so could not be persuaded to change types of names without supporting objective evidence, because any change they might have made, like many made by politicians or administrators, would almost certainly have been for the worse.'

Intracellular structures

Before the virus category of infective agents was recognized, characteristic 'inclusion bodies' had been seen in the cells of animals suffering from some infections. With the recognition of the virus category it became clear that they were found only, though not invariably, in virus infections of animals and plants. They were found in both nucleus and cytoplasm. In plants there are two types, crystals and lumps, now often called X-bodies, that float round in the streaming cytoplasm and tend to coalesce when they collide. From the beginning of his research career, Bawden was fascinated by these structures. He complemented his early descriptions of the appearance of infected plants to the naked eye (e.g. 1932a, 1934) and infrared camera (1933), with histological observations (1932b); he also commented on the apparent absence of X-bodies, but the presence of crystalline deposits, in the leaves of potatoes infected with several viruses. When we made paracrystalline complexes between clupein and TMV, and some other viruses (1937c, d), we suggested that they might be analogous to inclusion bodies; protamines and histones were plausible cell components and the conditions in which the complexes formed were physiological. We used our failure to get any true crystals with TMV preparations *in vitro* as supporting evidence for our suggestion that viruses were modified in the course of purification (1937c, f). Continuing that line of argument (1940d) we commented on the similarities between the complexes that TMV formed with nicotine, and some other bases, and some types of inclusion. Evanescence was one feature. The complexes formed slowly *in vitro* in undisturbed solutions and dispersed completely on shaking: the abundance, or even presence, of inclusions depends on undefined conditions of plant growth. Thus there were more X-bodies than crystals in plants infected with the aucuba strain of TMV in the early 1930s, more crystals a few years later, and intricately coiled structures appeared in the 1940s (1939b, 1964d). This variability in the behaviour of viruses and their hosts complicates research—but increases its interest.

The behaviour of inclusion bodies gives information of a sort about what is happening within the infected cell. We made abortive attempts to generalize phenomena of this type by searching for virus-like substances in extracts from toothwort (*Lathraea* spp.), because it contains crystalline inclusions similar to those in infected cells, and for inclusions in *Arum maculatum*, because the black patches resemble the early stages of some virus lesions. Bawden & Sheffield (1939b, 1944a) worked more productively. They described in detail the manner in which the character and abundance of inclusions depended on the strain of virus and host used and the type of visible symptom produced by the infection. It had been suggested that there were more inclusions when virus concentration was greatest; they did not agree. They found fewer late in infection and suggested that the substance(s) responsible for the precipitation of viruses from cellular fluids in which they would have been expected to be soluble were specific products of the early stages of virus infection. They also found, with virus X, that inclusions appeared in potato varieties that showed no external signs of infection. The suggestion that the substance(s) responsible for the formation of inclusions was not a normal leaf component gained support from Bawden & Kassanis' comparisons (1941b, 1945d) of mild and severe etch viruses alone, mixed, and in the presence of some related viruses. Infection with severe etch produced more inclusions, especially of the crystalline type, but not to an extent compatible with the idea that the inclusions were the cause of the more severe symptoms. The amount of space devoted to inclusion bodies in the various editions of *Plant viruses and virus diseases* shows the importance that Bawden attached to this method of getting evidence on the extent to which virus infection must be regarded as a general derangement of host metabolism. Recent research has added to the complexity of the picture, and has shown relations between X-bodies and other organelles, but it leaves the essentials of the picture unaltered.

Bawden was knighted in 1967. He became a Fellow of the Royal Society in 1949, served on many of its committees and on Council. He was appointed Acting Treasurer after the illness and death of Lord Fleck, F.R.S., in the summer of 1968; the appointment was ratified at the Anniversary Meeting that year. Of his treasurership Sir David Martin writes: 'During his period as Treasurer he supervised the finance of the introduction to the Society of its own catering service, the great increase in the Society's exchange programmes with other countries, and the undertaking of major expeditions including the setting up of a research station on the island of Aldabra. His experience of overseas agricultural activities was especially valuable. He was a valuable ambassador to many overseas countries and he chaired the Society's committee concerned with overseas visiting research professorships, as well as the Travelling Expenses Committee. In a period of expansion of the Society's activities in increasing directions, Bawden as Treasurer kept a wise and firm grip on financial policy but always placed the promotion of the Society's scientific aims as the first priority in the formulation of that policy.'

Besides service on the various bodies already mentioned, Bawden was a member of the Natural Environment Research Council, and the Research and Development Committee of the Potato Marketing Board, he was on the Scientific Advisory Committee of the Commonwealth Agricultural Bureaux, the Cotton Research Corporation, the Tea Research Institute of Ceylon, the Research Committee of the Forestry Commission, and the International Sugar Research Foundation. He was president of the Society for General Microbiology, the Institute of Biology, the Association of Applied Biologists, and the First International Congress of Plant Pathology; he was chairman of the Agricultural Advisory Panel of the British Council, and of the Board of the Council of Science and Technology Institutes. Although never involved in regular teaching, he was visiting professor in Imperial College of Science and Technology, a member of the University of London Science Advisory Committee on Relationship with Research Institutes, a member of the Court of the University of Surrey, of the Governing Body of Hatfield Polytechnic, and had honorary degrees from Hull, Bath, Reading and Brunel Universities. The New York Academy of Sciences and the Indian Botanical Society made him a Life Member, the Indian Phytopathological Society and the Indian Academy of Sciences made him an Honorary Fellow, and the Royal Netherlands Academy and the All-Union Academy of Agricultural Sciences of the U.S.S.R. gave him Foreign Membership.

The first photograph is by W. Bird, and the second by P. H. Gregory, F.R.S.

Bibliography

Citations in the form R.E.S. and a date refer to the Director's Introduction to the Rothamsted Experimental Station Annual Report.

1930 The distribution and perennation of cereal rusts. Thesis for Diploma in Agricultural Science, Cambridge.

1932 a (With R. N. Salaman) An analysis of some necrotic virus diseases of the potato. *Proc. R. Soc. Lond.* B, **111**, 53.

b A study on the histological changes resulting from certain virus infections of the potato. *Proc. R. Soc. Lond.* B, **111**, 74.

1933 Infra-red photography and plant virus diseases. *Nature, Lond.* **132**, 168.

1934 Studies on a virus causing foliar necrosis of the potato. *Proc. R. Soc. Lond.* B, **116**, 375.

1935 a (With E. T. C. Spooner) Experiments on the serological reactions of the potato virus 'X'. *Br. J. exp. Path.* **16**, 218.

b The relationship between the serological reactions and the infectivity of potato virus 'X'. *Br. J. exp. Path.* **16**, 435.

1936 a (With N. W. Pirie) Experiments on the chemical behaviour of potato virus 'X'. *Br. J. exp. Path.* **17**, 64.

b (With N. W. Pirie & E. T. C. Spooner) The production of antisera with suspensions of potato virus 'X' inactivated by nitrous acid. *Br. J. exp. Path.* **17**, 204.

c The viruses causing top necrosis (acronecrosis) of the potato. *Ann. appl. Biol.* **23**, 487.

d (With N. W. Pirie, J. D. Bernal & I. Fankuchen) Liquid crystalline substances from virus infected plants. *Nature, Lond.* **138**, 1051.

1937 a (With N. W. Pirie) Liquid crystalline preparations of cucumber viruses 3 and 4. *Nature, Lond.* **139**, 546.

b Plant viruses. *Biology*, **3**, 349.

c (With N. W. Pirie) The isolation and some properties of liquid crystalline substances from solanaceous plants infected with three strains of tobacco mosaic virus. *Proc. R. Soc. Lond.* B, **123**, 274.

d (With N. W. Pirie) The relationships between liquid crystalline preparations of cucumber viruses 3 and 4 and strains of tobacco mosaic virus. *Br. J. exp. Path.* **18**, 275.

e (With N. W. Pirie) A note on anaphylaxis with tobacco mosaic virus preparations. *Br. J. exp. Path.* **18**, 290.

f (With N. W. Pirie) Liquid crystalline preparations of plant viruses. *Congrès du Palais de la Découverte*, p. 377. Paris: Hermann et Cie.

g (With J. Henderson Smith, A. S. McFarlane, C. H. Andrewes, J. D. Bernal & L. P. Garrod) Discussion of recent work on heavy proteins in virus infection and its bearing on the nature of viruses. *Proc. R. Soc. Med.* **31**, 199.

1938 a (With N. W. Pirie) Liquid crystalline preparations of potato virus 'X'. *Br. J. exp. Path.* **19**, 66.

b Crystalline and liquid crystalline viruses. Contribution to A discussion on new aspects of virus disease. *Proc. R. Soc. Lond.* B, **125**, 297

c (With N. W. Pirie) A plant virus preparation in a fully crystalline state. *Nature, Lond.* **141**, 513.

d (With N. W. Pirie) Crystalline preparations of tomato bushy stunt virus. *Br. J. exp. Path.* **19**, 251.

e (With N. W. Pirie) A note on some protein constituents of normal tobacco and tomato leaves. *Br. J. exp. Path.* **19**, 264.

f. Virus diseases of potatoes: mosaic, crinkle and leaf-drop streak. *Ministry of Agriculture and Fisheries Advisory Leaflet* no. 1396.

g (With N. W. Pirie) Plant viruses 1: Serological, chemical and physico-chemical properties. *Tabul. biol.* **16**, 355.

h. (With N. W. Pirie) Contribution to Aggregation of purified tobacco mosaic virus. *Nature, Lond.* **142**, 842.

1939 a Some recent work on plant viruses. *Emp. J. exp. Agric.* **7**, 1.

b (With F. M. L. Sheffield) The intracellular inclusions of some plant virus diseases. *Ann. appl. Biol.* **26**, 102.

c (With N. W. Pirie) The purification of insect-transmitted plant viruses. *Br. J. exp. Path.* **20**, 322.

d *Plant viruses and virus diseases*. Leiden, Holland: Chronica Botanica Co.

1940 a The sizes of plant viruses. *Chronica Bot.* **6**, 13.

b Some properties of plant viruses. *Chemy Ind.* **18**, 788.

c (With N. W. Pirie) The inactivation of some plant viruses by urea. *Biochem. J.* **34**, 1258.

d (With N. W. Pirie) The effects of alkali and some simple organic substances on three plant viruses. *Biochem. J.* **34**, 1278.

1941 a The serological reactions of viruses causing tobacco necrosis. *Br. J. exp. Path.* **22**, 59.

b (With B. Kassanis) Some properties of tobacco etch viruses. *Ann. appl. Biol.* **28**, 107.

c (With A. Kleczkowski) Some properties of complexes formed when antigens are heated in the presence of serologically unspecific proteins. *Br. J. exp. Path.* **22**, 208.

d (With A. Kleczkowski) Non-precipitating protein antigens. *Nature, Lond.* **148**, 593.

e Problems in breeding for disease resistance. *Chronica bot.* **6**, 247.

f. Virus diseases of the dahlia. *Dahlia Yb.*, p. 20.

g *Nomina ad infinitum. Chronica Bot.* **6**, 385.

h To slaughter or not to slaughter. *Country Life*, 15 March, p. 229.

i Fertilisers can give us much more food. *Country Life*, 22 March, p. 246.

j The use of grassland. *Country Life*, 29 March, p. 268.

k Potatoes and policy. *Country Life*, 21 June, p. 534.

l How to check potato blight. *Country Life*, 28 June, p. xvi.

1942 a Crystallography and plant viruses. *Nature, Lond.* **149**, 321.

b Potato virus diseases. *Nature, Lond.* **150**, 476.

c (With A. Kleczkowski) The antigenicity of non-precipitating complexes. *Br. J. exp. Path.* **23**, 169.

d (With A. Kleczkowski) The effects of heat on the serological reactions of antisera. *Br. J. exp. Path.* **23**, 178.

e (With N. W. Pirie) A preliminary description of preparations of some of the viruses causing tobacco necrosis. *Br. J. exp. Path.* **23**, 314.

f Cheap food and prosperity. *Country Life*, 2 Jan., p. 30.

g Plant diseases and their cure. *Country Life*, 10 July, p. 84.

1943 a Some properties of the potato viruses. *Ann. appl. Biol.* **30**, 82.

b (With N. W. Pirie) Methods for the purification of tomato bushy stunt and tobacco mosaic viruses. *Biochem. J.* **37**, 66.

c (With N W Pirie) The inactivation of tomato bushy stunt virus by heating and freezing. *Biochem. J.* **37**, 70.

d *Plant viruses and virus diseases* (2nd ed.). Waltham, Mass., U.S.A.: *Chronica Botanica Co.*

e Plant diseases. *Mon. Sci. News*, **24**, 6.

1944 a (With F. M. L. Sheffield) The relationships of some viruses causing necrotic diseases of the potato. *Ann. appl. Biol.* **31**, 33.

b (With N. W. Pirie) The liberation of virus, together with materials that inhibit its precipitation with antiserum, from the solid leaf residues of tomato plants suffering from bushy stunt. *Br. J. exp. Path.* **25**, 68.

c The nature of plant viruses. *Proc. Linn. Soc. Lond.* **155**, 241.

1945 a Plant viruses and virus diseases. *Nature, Lond.* **155**, 156.

b The nature of viruses. *Scient. Mon.* **60**, 48.

c (With A. Kleczkowski) Protein precipitation and virus inactivation by extracts of strawberry plants. *J. Pom. hort. Sci.* **21**, 2.

d (With B. Kassanis) The suppression of one plant virus by another. *Ann. appl. Biol.* **32**, 52.

e The potato and its ailments. *Sch. Sci. Rev.* **27**, 62.

f (With N. W. Pirie) Further studies on the purification and properties of a virus causing tobacco necrosis. *Br. J. exp. Path.* **26**, 277.

g. (With N. W. Pirie) The separation and properties of tobacco mosaic virus in different states of aggregation. *Br. J. exp. Path.* **26**, 294.

1946 a Virus diseases of plants. *Jl R. Soc. Arts*, **94**, 136.

b (With N. W. Pirie) The virus content of plants suffering from tobacco mosaic. *Br. J. exp. Path.* **27**, 81.

c (With B. Kassanis) Varietal differences in susceptibility to potato virus Y. *Ann. appl. Biol.* **33**, 46.

d Virus diseases. *Farming*, July–August, p. 72.

1947 a (With B. Kassanis) *Primula obconica*, a carrier of tobacco necrosis viruses. *Ann. appl. Biol.* **34**, 127.

b (With F. M. Roberts) Influence of light intensity on the susceptibility of plants to certain viruses. *Ann. appl. Biol.* **34**, 286.

c (With B. Kassanis) The behaviour of some naturally occurring strains of potato virus Y. *Ann. appl. Biol.* **34**, 503.

d (With E. M. Crook) Some properties of potato virus X in leaf extracts made in different ways. *Br. J. exp. Path.* **28**, 403.

e Planternes virusstoffer. *Naturhistorisk Tidende*, **11**, 52.

f Swollen shoot being an infectious disease must be treated as such. *African Morning Post*, 1 Jan.

1948 a (With B. Kassanis & F. M. Roberts) Studies on the importance and control of potato virus X. *Ann. appl. Biol.* **35**, 250.

b (With A. Kleczkowski) Variations in the properties of potato virus X and their effects on its interactions with ribonuclease and proteolytic enzymes. *J. gen. Microbiol.* **2**, 173.

c Some effects of host-plant physiology on resistance to viruses. *Proc. R. Soc. Lond.* B, **135**, 187.

d (With F. M. Roberts) Photosynthesis and predisposition of plants to infection with certain viruses. *Ann. appl. Biol.* **35**, 418.

e *Plant diseases*. Edinburgh: Nelson.

1949 a Some implications and limitations of recent work on plant viruses. *Proc. 4th Int. Congr. Microbiol. Copenhagen*, 1947, p. 58.

b Les variations chez les virus des plantes. *Colloques int. Cent. natn. Rech. scient. Unités biologiques douées de continuité génétique*, no. 8, Paris, 1948, p. 79.

c (With J. P. H. Van Der Want) Bean stipple-streak caused by a tobacco necrosis virus. *Tijdschr. PlZiekt.* **55**, 142.

d Some factors affecting the susceptibility of plants to viruses. *Proc. 5th Int. Congr. Comparative Pathology, Istanbul.*

1950 a Research on plant viruses and virus diseases. *Br. agric. Bull.* **2**, 347.

b (With B. Kassanis) Some effects of host nutrition on the susceptibility of plants to infection by certain viruses. *Ann. appl. Biol.* **37**, 46.

c (With B. Kassanis & H. L. Nixon) The mechanical transmission and some properties of potato paracrinkle virus. *J. gen. Microbiol.* **4**, 210.

d (With B. Kassanis) Some effects of host-plant nutrition on the multiplication of viruses. *Ann. appl. Biol.* **37**, 215.

e (With N. W. Pirie) Some factors affecting the activation of virus preparations made from tobacco leaves infected with a tobacco necrosis virus. *J. gen. Microbiol.* **4**, 464.

f (With N. W. Pirie) Some effects of freezing in the leaf and of citrate *in vitro*, on the infectivity of a tobacco necrosis virus. *J. gen. Microbiol.* **4**, 482.

g Interference phenomena with plant and bacterial viruses. In *Viruses, 1950* (ed. M. Delbruck), p. 30. California Institute of Technology. Pasadena, U.S.A.

h (With N. W. Pirie) The varieties of macromolecules in extracts from virus-infected plants. In *Viruses 1950* (ed. M. Delbruck), p. 35. California Institute of Technology. Pasadena, U.S.A.

i *Plant Diseases* (rev. ed.). Edinburgh: Nelson.

j *Plant viruses and virus diseases* (3rd ed.). Waltham, Mass., U.S.A.: Chronica Botanica Co.

1951 a The multiplication of viruses. *Sci. Progr.* **39**, 1.

b Viruses: molecules or organisms ? *Discovery*, **12**, 41.

c (With H. L. Nixon) The application of electron microscopy to the study of plant viruses in unpurified plant extracts. *J. gen. Microbiol.* **5**, 104.

d Growing healthier crops. In *Four thousand million mouths* (ed. F. Le Gros Clark and N. W. Pirie), p. 74. Oxford University Press.

e (With B. Kassanis) Serologically related strains of potato virus Y that are not mutually antagonistic in plants. *Ann. appl. Biol.* **38**, 402.

f (With R. P. Chaudhuri & B. Kassanis) Some properties of broadbean mottle virus. *Ann. appl. Biol.* **38**, 774.

1952 a The control of plant viruses diseases. *Int. Conf. Crop Prot. Problems in World Agriculture, June 1951*, p. 76. London. Plant Protection Ltd.

b (With N. W. Pirie) Physiology of virus diseases. *A. Rev. Pl. Physiol.* **3**, 171.

c (With A. Kleczkowski) Ultra-violet injury to higher plants counteracted by visible light. *Nature, Lond.* **169**, 90.

d (With G. G. Freeman) The nature and behaviour of inhibitors of plant viruses produced by *Trichothecium roseum* Link. *J. gen. Microbiol.* **7**, 154.

e Virus and its interaction with the host cell: biochemical aspects. *Pap. Discuss. 2nd Int. Polio. Conf. Copenhagen, 1951*. Philadelphia: Lippincott.

f Reducing losses from virus diseases. *Gdng ill.* **69**, 163.

g The control of plant diseases. *Listener*, **48**, 294.

h J. Henderson Smith, M.B., Ch.B. *Br. med. J.* 3 Jan., p. 47.

1953 a Some properties of the tobacco necrosis viruses. In *Proc. 7th Int. bot. Congr. Stockholm, 1950*, p. 705.

b Criticism of binominal nomenclature as applied to plant viruses. *Ann. N.Y. Acad. Sci.* **56**, 538.

c (With N. W. Pirie) Virus multiplication considered as a form of protein synthesis. In *The nature of virus multiplication. Symp. of the Society for General Microbiology*, **2**, 21. Cambridge University Press.

d (With A. Kleczkowski) The behaviour of some plant viruses after exposure to ultraviolet radiation. *J. gen. Microbiol.* **8**, 145.

e The initiation and development of virus infection. In *Symposium: Interaction of viruses and cells. 6th Int. Congr. Microbiol., Rome*, p. 3.

f Controlling plant diseases. *Agriculture, Lond.* **59**, 451.

1953 g The control of plant diseases, In *Research for plenty*, p. 35. London: Geoffrey Bles.

1954 a (With B. KASSANIS) Some effects of thiouracil on virus-infected plants. *J. gen. Microbiol.* **10**, 160.

b (With B. M. G. HAMLYN & M. A. WATSON) The distribution of viruses in different leaf tissues and its influence on virus transmission by aphids. *Ann. appl. Biol.* **41**, 229.

c Inhibitors and plant viruses. *Adv. Virus Res.* **2**, 31.

d Cellular metabolism and virus growth. In *Int. Symp. on the dynamics of virus and rickettsial infections* (ed. F. W. Hartman and others), Detroit, 1953, U.S.A., p. 59. Detroit.

e The development of knowledge on plant viruses & virus diseases. *J. scient. ind. Res.* (*India*), **13A**, 106.

f Tom Goodey, 1885–1953 (obituary). *Biogr. Mem. Fellows R. Soc.* **9**, 141.

g Combating plant diseases. *Financial Times*, 15 Nov.

1955 a The spread and control of plant virus diseases. *Ann. appl. Biol.* **42**, 140.

b Virus diseases of plants. *Jl R. Soc. Arts*, **103**, 436.

c The classification of viruses. *J. gen. Microbiol.* **12**, 362.

d (With A. KLECZKOWSKI) Studies on the ability of light to counteract the inactivating action of ultraviolet radiation on plant viruses. *J. gen. Microbiol.* **13**, 370.

e (With B. D. HARRISON) Studies on the multiplication of a tobacco necrosis virus in inoculated leaves of French-bean plants. *J. gen. Microbiol.* **13**, 494.

1956 a (With N. W. PIRIE) Observations on the anomalous proteins occurring in extracts from plants infected with strains of tobacco mosaic virus. *J. gen. Microbiol.* **14**, 460.

b The impact of viruses on society. *Impact Sci. Soc.* **7**, 85.

c Research on viruses and virus diseases. *Jl R. agric. Soc.* **117**, 75.

d Reversible, host-induced, changes in a strain of tobacco mosaic virus. *Nature, Lond.* **177**, 302.

e Cure and prevention of virus diseases in plants. *Wld Crops*, **8**, 393.

f In A discussion on immunological tolerance. *Proc. R. Soc. Lond.* B, **146**, 58.

1957 a The multiplication of plant viruses. In *The nature of viruses, Ciba Fdn Symp., 1956*, p. 170. London: Churchill.

b The transmission of plant viruses by insects. In *Biological aspects of the transmission of disease* (ed. C. Horton-Smith), p. 87. Edinburgh: Oliver & Boyd.

c The role of plant hosts in microbial ecology. In *Microbial ecology. Symp. Soc. Gen. Microbiol.*, **7**, 299. Cambridge University Press.

d Tobacco mosaic virus. In *Cellular biology, nucleic acids and viruses* (ed. O. v. St. Whitelock), *Spec. Publs N.Y. Acad. Sci.* **5**, 249.

e (With N. W. PIRIE) A virus-inactivating system from tobacco leaves. *J. gen. Microbiol.* **16**, 696.

f (With A. KLECZKOWSKI) An electrophoretic study of sap from uninfected and virus-infected tobacco plants. *Virology*, **4**, 26.

g (With N. W. PIRIE) The activity of fragmented and reassembled tobacco mosaic virus. *J. general Microbiol.* **17**, 80.

h The nature of plant viruses. *Outl. Agric.* **1**, 244.

1958 a Gradations and transitions between pathogenicity and commensalism in infections with plant viruses. In Symposium on *Latency and masking in viral and rickettsial infections, 1957*, p. 80. Wisconsin: Burgess Publishing Co.

b Viruses and virus diseases. *East Malling Research Station Report for 1957*, 37.

c Reversible changes in strains of tobacco mosaic virus from leguminous plants. *J. gen. Microbiol.* **18**, 751.

1959 a The establishment and development of infection. In *Plant pathology: problems and progress, 1908–1955. Golden Jubilee Volume of the American Phytopathological Society*, p. 503. University of Wisconsin Press.

b (With A. Kleczkowski) Photoreactivation of nucleic acid from tobacco mosaic virus. *Nature, Lond.* **183**, 503.

c Rothamsted Experimental Station. *SPAN*, **2**, 6.

d Viruses. In *Vistas in botany* (ed. W. B. Turrill), p. 291. London: Pergamon Press.

e Physiology of virus diseases. *A. Rev. Pl. Physiol.* **10**, 239.

f Evolution and viruses. In *Symposium on evolution, Duquesne University, Pittsburgh*, p. 9.

g (With A. Kleczkowski) Some properties of decomposition products of potato virus X. *Virology*, **7**, 375.

h Effect of nitrous acid on tobacco mosaic virus: mutation or selection? *Nature, Lond.* **184**, 27.

i Viruses: retrospect and prospect. *Proc. R. Soc. Lond.* B, **151**, 157.

j (With N. W. Pirie) The infectivity and inactivation of nucleic acid preparations from tobacco mosaic virus. *J. gen. Microbiol.* **21**, 438.

1960 a (With A. Kleczkowski) Some effects of ultraviolet radiation on the infection of *Nicotiana glutinosa* leaves by tobacco mosaic virus. *Virology*, **10**, 163.

b Plant viruses: what they are and what they do. *Proc. R. Instn Gt Br.* **38**, 50.

c The multiplication of viruses. In *Plant pathology: a treatise on basic principles* (ed. J. G. Horsfall & A. E. Dimond), p. 71. New York: Academic Press.

d Plant diseases. *Bull. atom. Scient.* **16**, 247.

e Soil-borne viruses. *Agriculture, Lond.* **67**, 387.

1961 a Some effects of changing environment on the behaviour of plant viruses. In *Microbial reaction to environment. Symp. Soc. Gen. Microbiol.* **11**, 296. Cambridge University Press.

b (With R. C. Sinha) Effects of ultraviolet radiation on infection by intact and phenol-disrupted red clover mottle virus. *Virology*, **14**, 198.

c The susceptibility of *Rhoeo discolor* to infection by tobacco mosaic virus. *J. biol. Chem.* **236**, 2760.

1962 International collaboration in science. *Proc. 10th Pugwash Conf.* London, 1962, p. 241.

1963 a The role of research in the development of modern agriculture. In *Proc. 11th Congr. Sug. Cane Technology Mauritius 1962*, p. 17.

b Plant viruses: their nature and control. *SPAN*, **6**, 88.

1964 a Viruses in the soil. *Land*, **17**, 11.

b Speculations on the origins and nature of viruses. In *Plant virology* (ed. M. K. Corbett & H. D. Sisler), p. 365. Gainesville: University of Florida Press.

c *Technical assistance from Britain in agriculture, animal health, forestry and fisheries, overseas.* Cmnd 2286. London: H.M.S.O.

d *Plant viruses and virus diseases* (4th ed.). New York: Ronald Press Co.

1965 a (With B. Kassanis) The potato variety King Edward VII and paracrinkle virus. *Rothamsted Experimental Station Report for 1964*, p. 282.

b Sir John Russell, O.B.E., F.R.S. *Nature, Lond.* **207**, 1031.

1966 a Some reflexions on thirty years of research on plant viruses. *Ann. of appl. Biol.* **58**, 1.

b Rothamsted Experimental Station. *Jl R. agric. Soc.* **127**, 54.

c John Bennet Lawes, Joseph Henry Gilbert: biographical sketches. *J. Nutr.* **90**, 1.

1967 a Science and agriculture: the contribution of Harold H. Mann. Introduction to *The social framework of agriculture: India, Middle East, England* (ed. D. Thorner). Bombay: Vora and Co. Reprinted as: 'Dr Mann's contribution to science and agriculture'. *Economic and Political Weekly, Bombay*, **2**(13), 2.

b Trends and prospects from the standpoint of natural scientists. *Int. J. agr. Aff.* **5**, 115.

1968 a (With B. Kassanis) The serological relationship between tobacco mosaic virus and cucumber viruses 3 and 4. *Virology*, **34**, 174.

b Healthier, heavier harvests. *New Scientist*, **39**, 136.

1969 Plant virus research. In *Proc. Symp. on Potentials in Crop Protection*, p. 33. New York: Cornell University.

1970 Musings of an erstwhile plant pathologist. *A. Rev. Phytopath.* **8**, 1.

1971 a Alfred Alexander Peter Kleczkowski (obituary) 1908–1970. *Biogr. Mem. Fellows R. Soc.* **17**, 431.

b Rothschild report on control of funds for research. *Times*, 31 Dec.

1972 a Bringing Rothschild down to earth. *Nature, Lond.* **235**, 7.

b Some factors affecting soil fertility. *Rep. 26th Oxford Farming Conf.*, p. 40.

c (With N. W. Pirie) Factors affecting the amount of tobacco mosaic virus nucleic acid in phenol-treated extracts from tobacco leaves. *Proc. R. Soc. Lond.* B, **182**, 297.

d (With N. W. Pirie) The inhibition, inactivation and precipitation of tobacco mosaic virus nucleic acid by components of leaf extracts. *Proc. R. Soc. Lond.* B, **182**, 319.