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MEMOIRS

Philip Herries Gregory, 24 July 1907 - 9 February 1986

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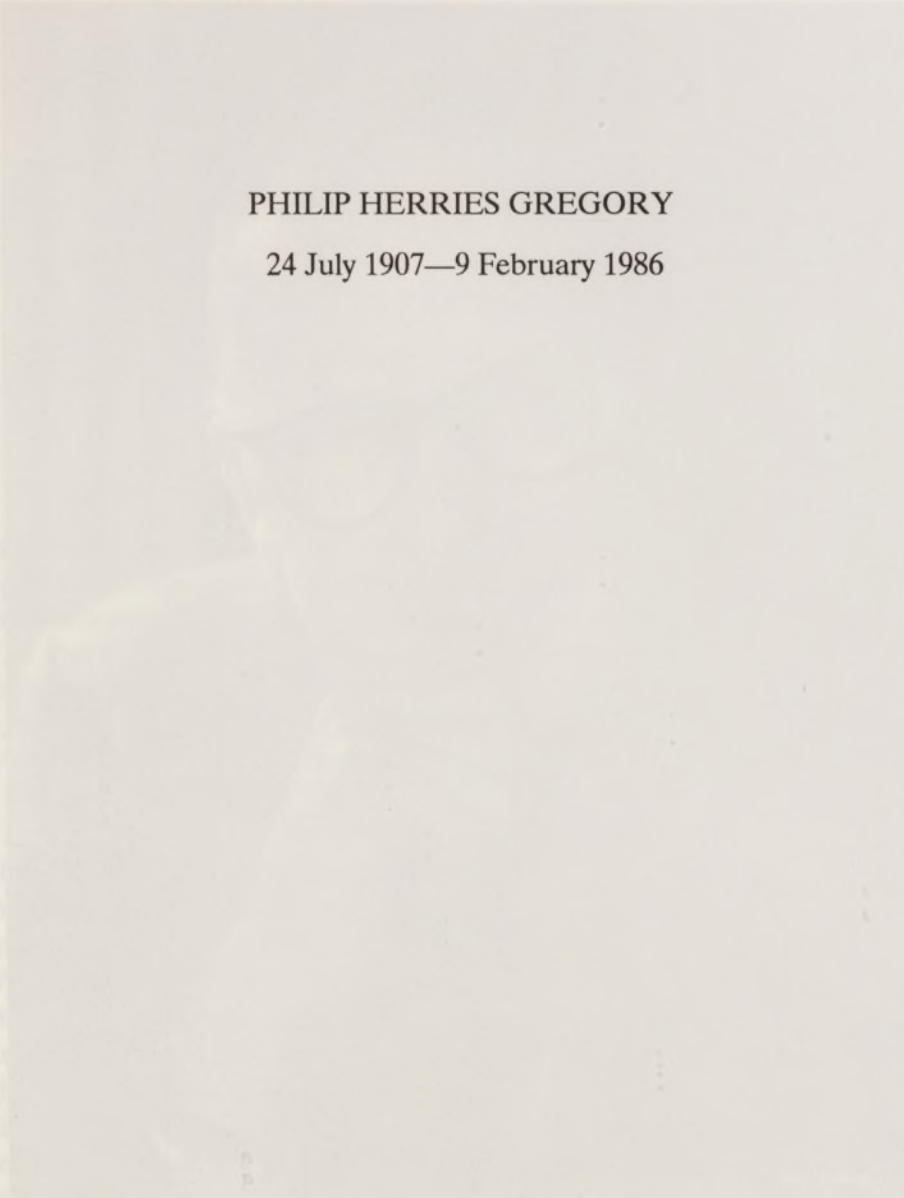

PHILIP HERRIES GREGORY

24 July 1907—9 February 1986

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Elected F.R.S. 1962

BY J.M. HIRST, D.S.C., F.R.S.

From his earliest research onward, Philip Gregory retained an interest in the liberation and dispersal of fungal spores. His work was nurtured by his personal susceptibility to respiratory diseases and by early recognition of plant disease distribution as a subject worthy of much closer study. With an enquiring mind, a love of fungi in action and experience ranging through dermatophytes, flowering bulbs, the spread of potato viruses, human allergy and cocoa diseases, Philip Gregory restored mycological aerobiology as an important scientific study.

Childhood and Education

Philip Gregory was born at Exmouth, Devon, on 24 July 1907. His ancestry traced back to Charles Gregory, a hat-band maker, a member of the Draper's Company and a Freeman of the City of London (1723). More immediately, his father, the Rev. H.S. Gregory, was a Church of England clergyman of Baptist tendencies, who ran his household along strict fundamentalist lines. As a boy, Philip was a continual sufferer of asthma, a complaint that, with others of the respiratory system, was to plague him throughout life. Asthma greatly interfered with his schooling, much of which he had to acquire, with the help of his family and visiting teachers, while in bed. Fortunately, the disease relaxed somewhat when he was 14 allowing him a more normal life and to develop other interests, especially natural history.

Being often bedridden he had become an avid reader, a skill that he used in studying biology. This led to ideas that conflicted with the religious views of his parents, but being very appreciative of his parents' feelings and care of him, he did not voice his doubts. Together with his earlier isolation, this suppression reduced his opportunities to 'learn the art of conversation'. Later he admitted that this 'sometimes made me stay silent when I ought to be expressing dissent, and then fume afterwards'. Fortunately, his health continued to improve and, his family having moved to Sussex, he was well enough to consider his future career. He thought of farming but there was little hope of finding sufficient capital; despite a strong interest in medicine, he feared he might find the course too demanding physically; so somewhat surprisingly he began studying engineering at Brighton Technical College. This cannot have satisfied him, because on learning more of careers in biology and finding good teachers in Brighton, he transferred to studying for the Pure Science External London B.Sc. degree, which he obtained in 1928, one of the early students of 'Brighton Tech.' to be on the road to the top of his chosen branch of science.

He was introduced to mycology by Mrs Alice Bacon but what had led him toward plant pathology is not recorded. However, it was after seeking advice about this that he decided to study under Professor W. Brown, F.R.S., at the Imperial College of Science and Technology in South Kensington. Like many other of William Brown's students, he received and much appreciated, the firm foundation in methodology and techniques offered by the final year of the B.Sc. (Special) Botany Course. For research projects he was offered a laboratory subject in pectinase preparation, which he subsequently ignored in favour of a field study of *Fusarium* diseases of *Narcissus* spp. which he found much more interesting and through which he gained his Ph.D. degree and D.I.C. in 1931 (17)*.

THE BEGINNINGS OF A RESEARCH CAREER

Canada and dermatophytes

Beginning a research career at present must bear similarities to the difficulties of the financial crisis of the 1930s; but there are probably few who suffer a start as unlucky as Gregory's. On the same day, he received letters both offering and cancelling his first research grant. However, this ill-wind brought good, through a recommendation for a post as medical mycologist in Winnipeg, Canada. This appointment had two good and lasting consequences. First, it soon led to his marriage to Margaret Culverhouse to whom he had become engaged three years earlier. Second, it brought him close to Professor A.H.R. Buller, 'the best all-round mycologist I ever met', who was then leading a group thrusting forward the study of the sexuality and genetics of fungi; for example: Craigie, on sex in rusts; Hanna, on tetrapolarity in *Coprinus* spp.; the genetical work of Johnson & Newton on *Puccinia graminis*; while G.R. Bisby (155) was listing the fungi of Manitoba. However, what impressed and delighted Gregory most was their regard for fungi as active organisms, responding to all the features of their environment. He shared and never lost this view, which he found a refreshing contrast to the stuffiness of more traditional academics and fungal taxonomists.

His grant from the Banting Foundation brought him honorary posts in the Winnipeg General and Childrens' Hospitals, through this he developed a lasting interest in medical mycology. He worked closely with A.M. Davidson, a noted dermatologist. At first they surveyed Canadian human pathogenic fungi, especially the dermatophytes (1, 13, 16). In diagnosis (4, 5, 12, 14) they were aided by the development of ultraviolet fluorescence methods (2, 3). They were intrigued by the diversity of the ringworm fungi, especially in their saprobic phases, and studied their etiology and various culture methods (7, 9, 11). Work was also begun on the means of spread and control of these

* Numbers in this form refer to the entries in the bibliography at the end of the text.

fungi (6, 8).

The productiveness of this phase was indicated by publication (10) of a notable general review of the dermatophytes, within five years of the work beginning. In 1934, the studies were brought to a premature close as the Depression hit Canada and the University Bursar was gaoled for embezzling funds, so Gregory was forced to leave Winnipeg, 'the hardest break I ever made'. He returned to an uncertain future in England, but with research experience and the strength of lasting mycological friendships.

Diseases of Narcissus and other flowers

It was largely through his reputation with Professor Brown that he was able to return to studying the diseases of flowering bulbs, with the support of small grants from the Great Western Railway (21), the National Farmers Union and later from the Ministry of Agriculture. His base was at Seale Hayne College, Newton Abbot, Devon, under the guidance of Mr A. Beaumont, (then the Ministry of Agriculture and Fisheries (MAF) Regional Mycologist for the South West), but it was decreed that his field work should be done west of Truro and in the Scilly isles, to which he made almost monthly visits during five years, developing a fondness for them that he never lost.

This post made Gregory the sole researcher available to answer urgent technical needs of a specialized and isolated industry. Beaumont, his guide, advised him to concentrate on controlling the foliage diseases of *Narcissus* spp. (27, 28, 31). The series of spraying experiments, mostly with Bordeaux Mixture, revealed that the diseases caused by *Ramularia vallisumbrosae* (white mould) (18) and by *Botrytis polybastis* (Narcissus fire) (34), were more damaging than previously suspected. Good chemical control increased bulb and flower yields by 25 – 40% within a single year.

However, Gregory saw many questions that could not be answered and so studied the biology of the principal pathogens. He was intrigued to find how the organisms perennated and spread, because there was no indication that the bulb was invaded by the fungi responsible for white mould or fire. Both fungi formed resistant structures in the decaying foliage. In *R. vallisumbrosae* (25) they were small, like perithecial initials but germinated only like sclerotia to give a group of *Cercospora*-like spores. In *B. polybastis* they were genuine sclerotia but germinated to produce apothecia like a *Sclerotinia* sp., the functional connection with the latter as the sexual, teleomorphic state was then firmly established and documented (23, 26, 30, 32). The habits of both fungi suggested that scrupulous hygiene through the removal of all dead flowers and leaves should greatly assist control. Gregory would have regarded such useful practice as 'good husbandry', although it would now be glorified as a practice of 'integrated pest management'.

Again, Gregory had quickly established himself as an authority, this time on diseases affecting the production of 'bulb' crops (19, 22, 24, 29, 33). In one of the first papers (17), he gave the earliest indication of his future interest in spore liberation. In 1939, war quickly stopped commercial cultivation of flowering bulbs and although the 'phoney war' allowed Gregory to record most of the work he had done on bulbs, the course of his career had once again been changed by forces beyond his control.

Epidemiology of potato viruses

Faced with food shortages and fear of invasion, the Ministry of Agriculture, Fisheries & Food (MAFF) was concerned that supplies of potato 'seed' tubers from Scotland might be insufficient to provide the larger requirement needed as a consequence of the rationing of other foods. Gregory was 'directed' to join a team being assembled under Mr Geoffrey Samuel to examine the possibility of producing healthy seed potatoes in England. The team, based in Harpenden, comprised two components: one at the MAFF Plant Pathology Laboratory and the other in the Plant Pathology Department at Rothamsted Experimental Station, then one of the few centres of knowledge about plant virus diseases. Gregory recalled that one of his lecturers at Brighton mentioned Rothamsted's history and contributions but he never expected to be sent there to work, let alone on viruses and with an entomologist, Dr J.P. Doncaster (and later Dr L. Broadbent), to study how the spread of potato viruses by aphid vectors might be prevented.

The results of their work were not fully published until after the War (39), but they and those who later joined the team made important contributions to knowledge and policy, by demonstrating the, then insuperable, problems preventing the original aim being achieved. Much of the spread of potato virus Y (severe mosaic) and of potato leaf roll virus (37) was shown to be by mobile winged aphids very soon after the plants began to emerge, even before the plants from infected tubers showed symptoms. Although roguing had proved effective in Scotland, secondary infections were too many and too widespread in England for this to give effective control (38, 43). No more success could be achieved by early lifting or by early haulm destruction. Nevertheless, the work subsequently influenced work on potato virus diseases in U.S.A., Canada, The Netherlands and elsewhere in Europe, and Gregory's advice continued to influence Rothamsted's studies of the epidemiology of virus diseases of other crops.

The work (39) proved very valuable in other ways, because it added scientific justification to the effective health certification schemes (40) and to some empirical practices of the seed potato producers, while it stressed the importance of 'groundkeepers' (tubers inadvertently left in the soil over winter) as virus sources in short rotation areas. The laborious series of periodic liftings and date-of-planting experiments clearly showed the penalties in disease (44) and yield (36, 39) usually associated with incorrect manuring and late planting.

For Gregory, the work had different but very important consequences. He had become interested in the progress and distribution of virus infections in crops (41, 42). It was through the drudgery of making routine virus counts (on Holbeach Marsh) in a very large potato crop grown from healthy seed, that Gregory realized that his counts showed that the frequence of new virus infections rapidly decreased with increasing distance from the edge of a crop planted partly with infected, 'once-grown' tubers. He later wrote that he gradually became convinced that 'infection gradients and their causes represented a first-rate general problem in plant pathology, that so far as I then knew no one had previously formulated'.

Small diversions

Before embarking on an account of Philip Gregory's major researches concerned with aerobiology, it is convenient to mention several brief episodes.

When he could be spared from the War-time potato virus field work, Gregory felt the need for an opportunity to catch up on laboratory research. One of the most active and fascinating new mycological projects concerned the production of the antibiotic penicillin by *Penicillium notatum*. He obtained a one year secondment to join the ICI team in Manchester. His arrival was a little late because a research student was already well advanced toward showing that penicillin was released from germinating spores, Gregory confirmed this and studied spore formation (101) before returning to Rothamsted.

As a result of depression and war, Philip Gregory was still dependent on a sequence of grants, even though approaching 40, and naturally he sought a more permanent appointment. The publicity and hopes of the East African Groundnuts Scheme led him to apply for a post as plant pathologist. Although promised the appointment and having resigned from the Agricultural Research Council (ARC) post at Rothamsted, he was turned-down on health grounds within three weeks of his expected departure. To his great relief and fortunately for aerobiology he was immediately offered a reinstatement at Rothamsted.

At about this time (1948) an Essex naturalist, Mr S. Waller living in the suburban area of Wanstead, about five miles north of the docks in East London, helped draw Gregory's attention to many unexplained deaths of sycamore trees in a local park (45,47). Although the fungus associated was new in England, the disease appeared identical with one previously recorded in North America. The rapidity of killing, the proximity to the docks and the commonness of sycamore suggested that this could be the start of a serious epidemic. Fortunately this proved untrue and circumstantial evidence suggests that the pathogen may have been less able to attack healthy trees than those struggling against pollution in the London suburbs. Nevertheless, Gregory derived much satisfaction from unravelling the taxonomy of the pathogen - *Coniosporium corticale*, which necessitated its transfer to a new genus as *Cryptostroma corticale* (46) and describing the complex symptomatology of the disease. In view of Gregory's other interests it is odd that this fungus is also known in N. America as the cause of 'maple-bark stripper's disease', a respiratory allergy.

Preparing for the rebirth of mycological aerobiology

Study of the movements and significance of airborne fungi was very erratic, and his brief history (89) shows that after early classic studies, the subject received very little attention until the late 1930s when the title 'aerobiology' was created. Methods and understanding were often of a low order for long periods, until the researches that Gregory led renewed interest not only among mycologists but in plant pathology, allergy, palynology and environmental health, and assisted study of the movements of atmospheric pollutants.

The study of dispersal gradients

Gregory's observations of disease gradients in potato crops had led him to recognize a general problem, studying the components and mechanisms of which could allow him to integrate all his diverse biological interests and experience. He began this new quest with characteristic enthusiasm and thoroughness, later writing: 'The problem then, as now, was how to search the literature for a nonproblem. There is still no real substitute for library browsing and talking to colleagues. 'It was indeed thus that he found clues to several obscure, but to him important, papers. One (Stepanov 1935) occupied 56 pages of Russian. Undaunted, Gregory sold his grandfather's gold watch to buy a course of Russian language gramophone records. After spending many of the uneventful nights of his War-time Air-Raid Warden duties with these, he eventually produced a translation. He agreed with Stepanov's experimental observations but was disappointed that they did not help to explain the rapid initial decreases in deposition or dispersal gradients. His persistence eventually led him to study the attempts to define meteorological dispersion in mathematical terms by an Austrian, Wilhelm Schmidt (1925), and a British meteorologist, O.G. Sutton (1932). The latter he found the more acceptable because it incorporated a diffusion constant that increased with time.

However, neither of these treatments closely simulated the infection gradients that Gregory had then observed in crops. Eventually he concluded that, being designed to predict the behaviour of smoke or gas clouds, they took no account of particulate deposition on the ground or on vegetation (or of insect behaviour in the case of vector-borne plant viruses). With the help of his wife, a mathematician, an exponential deposition term was inserted into Sutton's equations. This became widely used, after further modification by A.C. Chamberlain (1956), often to predict the deposition of radioactive products and other pollutants (49), although Gregory was the first to admit it remained imperfect.

These theoretical stages of the work were undertaken while Gregory was still fully engaged with the epidemiology of potato viruses. After the War he had more freedom to select his research subjects. He had found the work on potato viruses both fascinating and inspiring; had become concerned that the spread of pathogens between experimental plots challenged the validity of the statisticians' assumption (based on manurial experiments) that neighbouring plots were independent of one another. However, his heart lay in mycology and he was relieved to be able to study the dispersal processes with 'passive fungus spores' rather than 'behaviour-plagued aphids'!

The development of better measurements

His first need was for facts with which to test his theories, but these quickly led to doubts about the seemingly simple methods then used to trap airborne spores. The first comparison of sticky slides, cylinders, a petri dish and as a volumetric standard, a cascade impactor (May 1945) were done (1948) with spores liberated after working hours into the natural draught along the corridor of the Plant Pathology building at Rothamsted. These results suggested that deposition might vary greatly depending on particle size, windspeed, the dimensions and configuration of the trap surfaces.

Among the revelations of later work was the extreme selectivity for spore size of many of the freely exposed sticky surface traps, so that large spores were often over-represented, whereas smaller particles were almost entirely missed. Both routine trapping and dispersion experiments needed new methods of greater and less variable efficiency. New principles and better standards were provided by studies, initially for defence against poison gases, but latterly conducted at the Microbiological Research Establishment at Porton Down. These introduced the principle of isokinetic air-sampling and designs that deposited even the smallest particles collected on slides where they could be assessed, rather than failing to retain them or depositing many on other internal surfaces. Thus the cascade impactor, operated isokinetically, became the standard of comparison.

It soon became clear that reproducible quantitative experiments required the construction of a small wind tunnel (52) within which, with the help of O.J. Stedman, there were long series of tests to measure the efficiency of deposition on exposed sticky surfaces of particles of different sizes, carried in winds differing in speed and turbulence; first using cylinders (51, 52) and then plane surfaces varying in size and orientation (55). Few such factors had previously been studied by biologists, to whom the work also introduced new measures of spore frequence such as: 'concentration' (number per cubic metre) of air; 'efficiency of deposition' on traps or other surfaces and the 'area dose' of particles to which they had been exposed. The work soon showed the imperfections in methods that had been used for many years and hence cast doubt on many of the conclusions from results obtained using them. The work with cylinders also provided the impetus for the development in U.S.A. of the valuable and initially secret 'rotorod' sampler (Perkins 1957).

Realizing which spores had been missed led directly to efforts to develop less selective, quantitative methods of measuring the airborne spore flora (or 'air spora' as Gregory (54) christened it) and relating changes to weather. The four years during which Gregory, Stedman, F.T. Last and I shared the same laboratory at Rothamsted, proved to be a stimulating and constructive period for all of us. In preparation for my appointment, Gregory had made preliminary observations of numbers of sporangia of *Phytophthora infestans* caught daily on sticky cylinders above a blighted potato crop. These catches bore no relation to infections, thus suggesting that need for much more accurate estimates made each hour, so that numbers could be related to weather favouring infection. Some of the needs were met with the automatic volumetric spore trap (later commercial models were known as the Hirst and Burkard Traps) (Hirst 1952), which adopted a modified second stage orifice from the cascade impactor, behind which the sticky trap slide was moved to deposit spores in positions that could be related to time.

The much wider spectrum of spores caught by suction impactor traps and the ability to relate concentrations to time and weather, clearly fascinated Gregory as it revealed the air spora in operation. His broad mycological knowledge helped us to identify many of its previously recognized components (54), while others could then only be placed in broad 'form-groups' with little presumption of origin or function. Gradually we identified many spores, showed many effects of seasonal, diurnal or episodic meteorological periodicities in air (Hirst 1953). Also that their responses to weather could often be related to their biological form and function (53, 56). Slowly some of the 'nick-named' spores were assigned to respectable taxonomic epithets and to established roles in biology, pathology or allergy and it became possible, albeit crudely, to reconstruct recent weather and even the vegetation surrounding the trap from the composition and changes in the air spora. Although initially developed with plant pathology as the beneficiary, the new methods and wider understanding that they brought found applications to many other human problems, involving other scientific disciplines.

Developing an aerobiological overview

Philip Gregory was one who always thought long and hard on and around work that he enjoyed. It was therefore almost to be expected that he would in time become the acknowledged expert in his field and in great demand as an exponent of its capabilities and problems. The process required missionary zeal and occupied more than a decade. It also involved four years (1954-58) when Gregory occupied the Chair of Botany, formerly held by his early mentor, Professor W. Brown, in the Imperial College of Science and Technology of London University and ten months (1956–57) when he underwent major surgery. Characteristically, Philip recognized some benefits of the new circumstances but these were mixed with the trials of ill-health so it was clear that these were not his happiest or most successful years. In 1958 he returned to Harpenden as the Head of the Plant Pathology Department at Rothamsted. In the succeeding paragraphs, scientific continuity is emphasized in preference to chronology or contemporary circumstance.

Gregory's 1951 Presidential Address to the British Mycological Society (138), entitled 'Fungus spores', had revealed much of his approach and the depth of his thinking. Surprisingly, this Address seems not to have been remembered as often as it should have been, perhaps because so much that was new, was so skilfully introduced and argued that it was accepted as 'common sense'. He began by revealing his devotion to fungi in action; 'I can never accept the verdict of the authority on a group who stated frankly: "these fungi are best studied dead"' He continued by admitting his fascination with the variety and success of the spore production and liberation mechanisms adopted by fungi (50, 96), which Ingold (1971) had so consistently and successfully studied. He admitted that he believed a modicum of innocent teleology was often stimulatory to the search for understanding and later he used it to hypothesize how differences between large 'impactor' spores and smaller 'penetrators' would confer selective ecological advantages to their parent fungi. The impactors would be better suited to leaf pathogens needing to be deposited on foliage, whereas the penetrators would be more able to negotiate vegetation canopies to reach the soil. He also drew attention to the probable importance of spore shape, surface chemistry and of redistribution processes (see also 71, 88).

Gregory's list of publications contains many references to what may seem to have been isolated studies but some of which satisfied his curiosity (56, 61, 73, 91, 96); represented a useful contribution completed during the stay of a visiting researcher (57, 76, 108); recorded enquiries to answer questions arising during the examination of trap catches (60, 76, 104) or described methods or answers to specific problems (59, 65, 83). One such study (104, 140), gave Gregory especial pleasure and satisfied his love of the 'whodunnit' approach to such investigation, it remains unique as the first British national record of a fungus (*Pithomyces chartarum*) initially recognized in a spore trap catch. By progressive air sampling up a dispersal gradient it was later tracked to its source, isolated and identified conventionally. Although such small studies continually added to knowledge, the three predominant themes during the period 1954–58, were splash dispersal, dispersal gradients and allergy to fungus spores. Excellent work continued with close collaborators but Gregory was disappointed with the contributions he was able to make through research students. Doubtless the record indicates only a little of the help he gave to most of his students, because he would consent to be a co-author of publications from a thesis only where he had indeed played a major part. Partly this dissatisfaction with university life may have been due to the fact that Philip's charisma more often showed through close personal collaboration than as an extrovert impressing an audience; also partly because the research he wanted to pursue seldom fitted well into the life and facilities available to university students.

Splash dispersal

Water plays many diverse roles in the dispersal of fungi, only some of which rank for a place in aerobiology, but rain splash certainly does. The immediate interest came through E.J. Guthrie's studies of the apple fruit rot caused by *Gloeosporium perennans*, splashing water seemed certain to be involved in spreading the sticky spores but scarcely any facts were known about the splash process.

The single publication (66) again typifies Philip Gregory's determination to begin with a study of principles. Although largely physical, the work clearly showed that under optimal conditions there might be up to 5000 products ('splash droplets') from some collisions, almost half of which might contain spores that were originally included either in the 'target film' or in the 'incident drop'. The results provided an understanding and philosophy for important later work on diseases of cocoa and gave others a most valuable basis for tests out of doors, which involved the carriage of splash droplets in wind and their evaporation to leave contained spores subject to dry air dispersal

Dispersal processes and deposition gradients

Gregory went to Imperial College knowing that later publications had supported the theoretical prediction he had made in 1945 (49, 64) that in normal turbulence probably about 90% of spores would have been deposited within 100 m of a near-ground source. Despite strong (and justified) convictions, he then had no effective answer to the paradox that this seemed inconsistent with much evidence of very long distance transport.

For many years Gregory and A.C. Chamberlain (1967) had been engaged in friendly but independent study of the deposition of particles on ground and vegetation close to near-ground sources, the latter having the advantages of radio-tagging (89, p.110). At Imperial College, Gregory and co-workers (68) used spores both of *Lycopodium clavatum*, 32 m dia. and *Ganoderma applanatum*, 10 x 6 m to compare surface deposition with airborne concentration over distances up to 20 m from the source. Sadly, making the extensive sampling array, the time available and Philip Gregory's indisposition limited the volume of results. One possibly weak point in the calculations was the difficulty of measuring accurately the terminal velocity of spore fall in air. It had long been known that the Stokes velocity was inadequate and would be inapplicable to non-spherical spores, some of which would also be subject to variable degrees of hydration depending on atmospheric humidity. It was very difficult to produce really still air in which to make accurate direct measurements of the terminal velocity of spore fall. Accordingly, Gregory and colleagues endeavoured to make accurate indirect measurements based on turbulent air and impaction efficiency (93, 99) and also to make preliminary studies of possible effects of electrostatic charges on spore deposition (61).

Fungus spores and other airborne causes of respiratory allergy

As a sufferer of chronic respiratory problems and having an abiding interest in medical mycology, it was natural that Gregory would pay particular attention to relating these two subjects. He had been quick to notice that both coloured and hyaline ballistospores (basidiospores) formed important and persistent contributions to the air spore, with *Sporobolomyces* spp. and related genera often forming the dominant component at night (53). Spores provide important taxonomic characters among many of these fungi, so they may often be identified at least to genus by the spores alone. One of the first practical tests of the new methods of spore trapping was therefore to try to reveal the presence of small ballistospores of the dry rot fungus *Serpula (Merulius) lacrimans* in bomb-damaged London houses, where patients were reporting asthmatic symptoms (56). Large concentrations, probably of freshly released spores, were found not only close to fructifications but throughout affected buildings. Such work and Gregory's persuasiveness convinced many allergists, early among whom were Dr K. Maunsell, Dr A.W. Frankland, Dr D.A. Williams and Dr R.S. Bruce Pearson, that fungi were worth testing as possible provokers of unexplained symptoms of respiratory allergy. Sometimes there was an evident suspect, for example, *Fulvia fulvum* (tomato leaf mould) for those affected in glasshouses; other searches were fruitless, as were the many inspections of fungi in house dust. However, his (1961) correspondence with Dr Maunsell shows that he had found mites prevalent in this dust and believed their possible role in 'house dust allergy' should be investigated. Later, others proved a relationship with the mite *Dermatophagoides pteronyssinus* and he returned to the problem (112) to emphasize the great importance of mite faeces and how the danger could be decreased by vacuum cleaning. In later years fungal material might be provided for provocation tests, but often the search was initially directed only by a location, a season or time of day associated with the onset of symptoms as recorded by patients (63, 90, 116) or even had to be sought among general seasonal surveys conducted in town or country (62, 89, p. 152). Through such collaboration with clinicians many allergens were revealed, enabling sufferers to be treated or to attempt avoidance.

Sometimes long-established practices were strongly defended by their protagonists because of familiarity or some particular convenience. For example, American allergists had long used horizontal ('Durham') slide exposures, while palynologists relied on harsh methods of microscopic preparation to improve identification of pollen grains. Persuading experts to change accepted practices often required much patient discussion or presenting new facts to audiences unfamiliar with them (102, 113, 114, 115). Nowhere was this skill of Philip Gregory better illustrated than in his modest leadership of the team work described in the following section. Concerning this, one eminent clinician wrote, '...the medical doctors poured scorn on the idea that botanists could solve the problem of Farmer's Lung. It was only when they had wrongly blamed *Aspergillus fumigatus* that they finally, I believe, had to turn to Philip.

Further medical mycology and the cause of 'farmers lung' disease

Having established an interest and reputation in medical mycology during his Canadian work, Philip Gregory was invited to attend a M.R.C. meeting in May 1943. This recommended forming an M.R.C. Committee on Medical Mycology (Ainsworth 1978) and that Gregory be its Secretary, the latter proposal being vetoed by the then A.R.C., for whom he was working. Relations between the two Councils later became more cooperative and from 1953 to 1964 Gregory contributed regularly to meetings of the Committee, which led ultimately to the formation of the British Society for Mycopathology.

In 1957, prompted by Mr P.K.C. Austwick, the Committee resolved: 'That mouldy hay appears to constitute a major source of infection for various pulmonary and systemic mycoses and to be involved in several disorders of uncertain etiology affecting both man and animals... knowledge of the origin and development of the mycoflora of hay is needed for a rational approach to the etiology and epidemiology of these diseases...' and it recommended that the ARC and MRC jointly support a grant.

Although first named in 1932, and gradually associated with mouldy hay, 'farmer's lung' gained little prominence until 1957, because farmers had then become less cautious following the introduction of the pick-up baler which had lessened the risk of spontaneous rick fires from hay made while still too moist. The ARC gave Philip Gregory a grant for the investigation while he was still at Imperial College but allowed its transfer to Rothamsted in 1958. He approached the problem like a systematic detective directing his force: first to examine suspect hays; then to attempt to reproduce them experimentally and finally, immunologically, to implicate particular constituents or products in causing the disease. The Rothamsted arm of the team comprised Maureen Bunce (now Lacey, who transferred from Imperial College), aerobiologists, microbiologists, biochemists and farm staff. The medical arm, led by Professor Jack Pepys (Institute for Diseases of the Chest (now the Cardiothoracic Institute) Brompton) was greatly strengthened by modern immunological capability. The teamwork was most effective and, as a result, the research prospered and made best use of some good fortune.

Trial hays revealed (103, 109, 111) the microbial successions, temperature and pH reached in experimental hays made with different initial water contents. To simulate what might be inhaled, it was decided to standardize the sampling of dust from hays using dry methods, so weighed amounts of hay were tumbled under standard conditions in the small wind tunnel (52, 74). Two sets of simultaneous air samples were collected, one for visual examination with a cascade impactor. The other to identify the catch in culture, first unsatisfactorily with alginate filters, then successfully with a recently acquired Andersen sampler (106). Both methods retained the smallest spores and concurred that thermophilic fungi and actinomycetes were particularly prevalent in suspect hays. Culture plates from the Andersen sampler (105, 108) were most impressive because dry collection avoided most bacteria and incubation at 60° C restricted growth selectively to thermophilic actinomycetes, many with spores in the 1 m size range and so capable of being respired into lung alveoli.

The combination of these techniques and immunological tests quickly and confidently implicated the thermophilic actinomycete *Faenia rectivirgula* (at the time *Thermopolyspora polyspora*) as a principal source of farmer's lung antigen (107, 114, 115). It develops optimally in hays containing more than 35% water when baled and which heat to 65 C. It perhaps grows more on the mycelium of thermophilic fungi that grew earlier in the microbial succession than directly on hay grasses and is thus a product of very special ecological processes. Such work led Gregory's colleagues to the identification of a family of clinically similar diseases caused by different organisms but now known collectively as extrinsic allergic alveolitis or hypersensitivity pneumonitis (Lacey & Crook 1988). Knowledge had certainly been advanced since the start of the investigation when, having arranged for the delivery from a patient of a bale of hay for microbiological examination, Gregory commented 'What a pity he sent such a good bale', to receive the farmer's reply 'What use to anyone is a bad bale'!

Spreading the gospel

As a dedicated applied scientist, Philip Gregory wanted his work to be used and did not consider it completed unless its threats or benefits had been made known. As an agriculturist and a chronic respiratory sufferer he was particularly interested to take his findings to the notice of his fellows or final customers. This principle had been consistently applied in his early work on dermatophytes, on diseases of flowering bulbs, and would be in later work on cocoa black pod disease but here we are concerned with the major aerobiology component.

Although during War little (36) of the work on potatoes could be published, no similar restriction then affected the generality of his first aerobiological papers (48, 49). As his knowledge and evidence accumulated he was invited to speak at many international conferences and produced a long succession of more general accounts for the benefit of particular or general scientific audiences (70, 75, 79, 80, 85, 94, 97, 100, 102, 113, 114, 115, 138, 141, 143); these were accompanied by equally authoritative contributions intended for wider interests (58, 67, 77, 81, 92), special importance attached to his 1970 Leeuwenhoek Lecture to the Royal Society (87) and always to his thoughts on dispersal gradients, their limits and processes (72, 84, 86, 95, 98, 128).

All of these, both contributed to and gained from, the long preparation of Philip Gregory's book *The microbiology of the atmosphere* (69); a work that fully satisfied his wish to complete a major resource through which mycological aerobiology would be firmly established and able to develop further. In a philosophical mood he wrote, 'I spent 10 months in hospital, which was lucky because I had the leisure to plan and start writing my book', after great effort it was finished in 1960 following his return to Rothamsted and, despite its quality, there were many of his staff who wished it could have been earlier. Nevertheless, the book achieved its purpose by creating a subject where previously there had been little but fragments. It was very well received and Philip took it as a great compliment when it was translated into Russian and edited by K.M. Stepanov (78), whose paper he had earlier taken such pains to translate. As it soon became clear that the first edition would sell out and he wanted to correct some imperfections, he began preparing a second edition (89) which contained much new material and went far to balancing the botanical bias of the first edition with additional microbiology, more closely to fit the book's broad title.

Cocoa diseases

Although outwardly Philip remained cheerful, continuing ill health added to the growing strains of contemporary research management must have made work feel in increasing burden. Consequently, he decided to retire in 1967 at the age of 60. However, very shortly afterwards, to the general amazement and delight of his friends, he added a further, productive and demanding phase to a career that already had much variety. This seems to have been possible as a result of improved medical treatment that enabled him to undertake the arduous duties of an international consultant on cocoa diseases; he travelled widely and was particularly pleased when he had the opportunity to return from South America by *Concorde*.

It had been Dr E.E. Cheesman who had suggested to the Cocoa, Chocolate and Confectionary Alliance, that the recently retired P.H. Gregory would be just the right person critically to appraise past and present research on black pod disease; and to visit the major cocoa growing areas and suggest needs for further research and where this should be situated. The industry hoped for a 'fresh view' from an experienced pathologist. Having so little experience in plantation crops, the tropics or of *Phytophthora* spp., apart from *P. infestans* (which was to prove irrelevant, if not misleading) this was a prescription that Philip could not avoid. He relished the new challenge, which he began in May 1968, and his comprehensive report (117), delivered in September 1969, recorded visits and enquiries in a dozen countries. It described the fungus *Phytophthora palmivora*, then held responsible for the destruction of a tenth of the crop worldwide; its genetics; how it was affected by environment, crop management and fungicides. The Report recommended pooling world knowledge in an International Advisory Black Pod Research Committee and strengthening existing research in epidemiology, fungicidal control, genetics and breeding. It emphasized the large gaps in knowledge, the needs for fundamental study and for its results to be made available to small countries which could not afford to undertake such research themselves. While supporting resistance screening, it cautioned that tests might stress short-lived (monogenic) resistance and emphasized the care necessary to prevent international carriage of strains of the pathogen. Characteristically, he separated the factual bulk of the report from an appendix containing his own opinions and speculations, in 'Black pod epidemiology: a personal interpretation'.

The recommendations of the Report were largely implemented as described in the Final Report of the International Cocoa Black Pod Research Project (130) which was financed by the International Office of Cocoa and Chocolate and established at the Cocoa Research Institute of Nigeria between 1973 and 1980. Nigeria was chosen because of the generous offer of good facilities, the associated cocoa research and an intermediate severity of black pod. The project aimed to identify sources and modes of spread of the pathogen at the weakest stage of the disease cycles, and relied heavily on difficult analyses of three dimensional infection gradients (made more difficult by slight knowledge of various possible mechanisms of dispersal, save that airborne dispersal seemed unusual). Philip Gregory very successfully accomplished the awkward role of 'non-playing captain', recruiting a young and able team whom he visited only annually but, from Harpenden, constantly advised and helped, as 'father confessor'. The task was very challenging, the outcome excellent.

In a final paper (133) the achievements and some afterthoughts were summarized and made to seem much easier than in reality. The theory proposed differed radically to previous thinking, it applies particularly to Nigeria and needs confirmation elsewhere. Several factors aided the work immeasurably. First, a new species *Phytophthora megakarya* was discovered to be more common in Nigeria than *P. palmivora*; it seldom caused persistent infections of flower cushions and so displayed simpler dispersal patterns. Second, the understanding of splash dispersal that Gregory had pioneered (66) pointed the way to means of analysing the distribution of 'initiator' (primary) pod infections in an area where all visibly infected pods were removed daily. This produced evidence of a single vertical disease gradient originating at ground level. This was explained on the basis of infections occurring below 70 cm resulting predominantly from spore-bearing droplets moving in ballistic trajectories from the splash; whereas the many fewer infections at greater heights were attributed mostly to spore-bearing splash droplets behaving as aerosol particles. The resulting gradient incriminated the ground as the persisting source but failed to explain how it operated. Third, the team studied many possibilities but rested their main emphasis on the discovery that *P. megakarya* frequently infected the shallow feeder roots of cocoa trees. It was speculated that, on these infected roots in suitable conditions, sporangia were produced, which characteristically for the genus, could again germinate to produce motile zoospores. Three alternative fates confronted the zoospores; they could reinfect nearby roots to which they show positive chemotaxis; they might temporarily encyst until more favourable conditions recurred or with suitable soil moisture and away from roots they display negative geotaxis to reach surfaces where they might be available for splash dispersal. Philip Gregory hoped that further studies in Nigeria would verify these speculations.

As usual, Gregory made sure that the research was brought to general notice and in many countries, for which some duplicate publication was excusable, indeed most praiseworthy (118, 119, 120, 121, 122, 123, 124, 125, 129, 131, 132, 133, 134), and also cautioned researchers and the industry about the benefits of protective international quarantine (126, 127, 128). The cocoa industry had indeed chosen well, both for its the reviewer of the black pod problem and for the team that progressed the research then suggested, so far and in such unexpected directions.

Personal interests and assessment

Philip Gregory had many interests beyond his work and family, he read widely and was always enquiring. His recuperation in hospital during 1957 gave him not only the chance to begin his book but an opportunity, as occupational therapy, to test his skill as an artist. Oil painting became a hobby from which he continued to gain a great deal of pleasure and satisfaction, and from which resulted some delightful and sensitive work. He continued his boyhood interest in natural history, although the fungal component attracted most public notice. He was a frequent attender and sometimes leader at the forays of the British Mycological Society, regularly contributed notes on the fungi of Hertfordshire (135, 137, 139, 145) as well as serving as the president of the Hertfordshire Natural History Society (142). He was awarded the D.Sc. degree of London University in 1949, was a Fellow of the Institute of Biology and a loyal supporter of several scientific societies. Although he did not often accept office, he was prominent in proposals to remodel societies. For example, the formation of the Federation of British Plant Pathologists, the British Society for Plant Pathology, the British Society for Mycopathology and the International Association for Aerobiology. Of the last two and of the British Society for Allergy and Clinical Immunology he was created an Honorary Member.

Through these pursuits, as well as in all aspects of his work, Philip created many strong friendships, some of which he had the task of completing with an obituary (153, 154, 155, 156, 157, 158, 160, 161, 162). He helped many beginners to find their feet, because he had a knack of introducing his knowledge through conversation rather than delivering it as the expert he often was. At one time he seemed shy in public but gained in confidence and skill of presentation as increased demands gave practice. Later, to hold the attention of an audience, he took a somewhat puckish delight in being unorthodox or challenging their preconceptions (141, 142, 148, 149). In addition to these titles he contributed a good deal of general comment and new thinking to mycology (143, 144, 146, 147) and in the year before he died, launched into the fungal mycelium as a topic new to him (150, 151, 152).

Philip would have been the first to acknowledge the debt that he owed to Sir Frederick Bawden (158, 159) who, having recognized his merits, had twice enabled him to return to Rothamsted at critical times. He would also have praised the succession of his support scientists who worked long and hard because he involved them in the planning and publication of the work they shared, notable among these were John Stedman, David Henden and Maureen Lacey. Philip devoted much of one of his later papers (94) published in the *Annual Reviews of Phytopathology*, to give an insight as much into the modes of his career, his motivations, the importance of chance meetings (luck well-used) and its underlying purposes, as to recalling the actual advances that he achieved. Unusual though such published statement are, they are very revealing and this one helps to explain why he was the man we knew. Always kindly, modest, willing to listen to all with a genuine interest and patient with novices, but there were stronger threads within his personality which occasionally showed an underlying determination. When pursuing a cause he considered just he could be very persistent, sometimes stubborn, but he much preferred that persuasion based on evidence should bring agreement. He was equally keen to correct errors, in print if necessary, whether they were his own (60, and a list of minor corrections to his 2nd edition, 89, offered in a letter to the Editor of the *International Aerobiology Newsletter*, no.11, November 1979, ISSN 035704512) or of others (73). However, his generosity often prevented public correction if it could be avoided. I recall several distinguished scientists leaving red-faced but unrevealed, having mistaken the origin of 'mystery bodies' usually pollens or coloured spores that, like Fleming's *Penicillium*, had come through the window to be deposited and mounted as parts of their histological preparations.

His many personal contacts with research workers and students were supported by warm hospitality from his family. His wife Margaret was used to welcoming visitors to lunch, often at short notice, and in the evening. Many of the visitors, especially those from overseas, became lifelong friends of the whole family. His children, Andrew and Rachel, shared in the hospitality. They also both absorbed the atmosphere of scientific enquiry, and both graduated in natural sciences.

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It is symptomatic of the regard in which Philip Gregory was held that, besides his family, so many friends have helped me with information and often checked the accuracy of my script. I am indebted to them all but especially to, Dr G.C. Ainsworth (mycology and medical mycology), Mr E.T.

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