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THE MICROBIOLOGY OF THE ATMOSPHERE

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PLATE 1.—Representative fields from Hirst-trap slides illustrating diverse air sporas. (Magnification: all × 1000. At this magnification 1 sq. cm. of field corresponds to 2·1 cc. of air.)

Frontispiece

(*a*) Fine-weather air spora, Ascot, Berks., 12·00 hr., 27 June 1958. Showing grass and nettle pollen, *Cladosporium*, *Epicoccum*, etc.

(*b*) Damp-air spora, Ascot, Berks., 02·00 hr., 17 June 1958. Showing spores of *Ganoderma*, *Sporobolomyces*, *Tilletiopsis*, and other hyaline basidiospores.

(*c*) Rain-type air-spora, Ascot, Berks., 04·30 hr., 13 June 1958. Showing various ascospore types, *Sporobolomyces*, soot, etc.

(*d*) Air-spora in a wheat crop at night during a thunder-storm, Harpenden, Herts., 21·30 hr., 10 August 1959. Showing *Puccinia graminis* uredospores, *Cladosporium*, and unidentified ascospore.

(*e*) Spores of *Merulius lacrymans* from air of building with timber affected by dry-rot.

From camera-lucida paintings by Maureen E. Bunce.

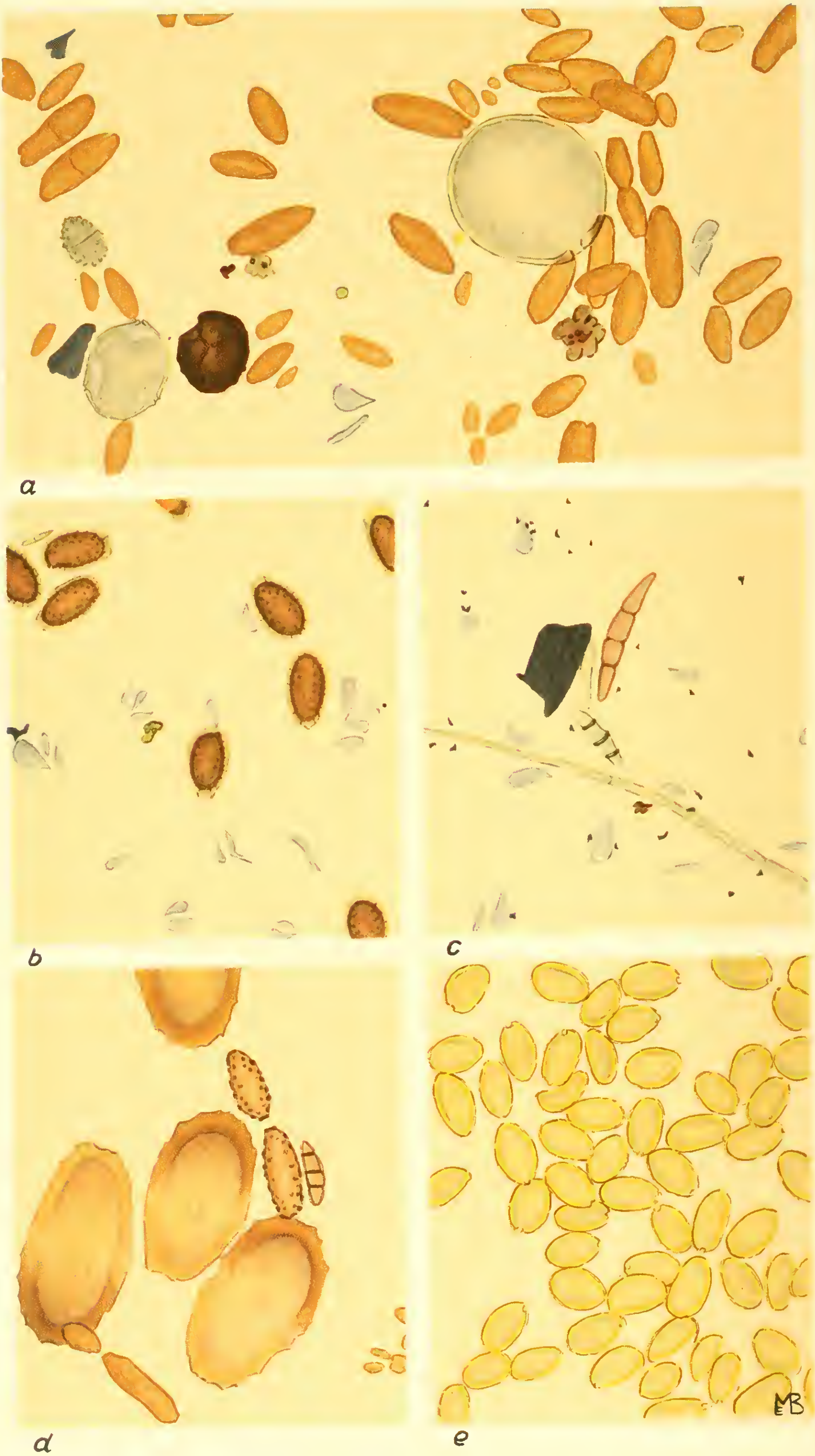

PLATE 1.—For details see preceding page.

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PROFESSOR NICHOLAS POLUNIN

THE MICROBIOLOGY OF THE ATMOSPHERE

By

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DEDICATED
to
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PREFACE

AEROBIOLOGY is usually understood to be the study of passively airborne micro-organisms—of their identity, behaviour, movements, and survival. One characteristic, which it shares with many other population studies in biology, is that the ultimate relevant unit consists of the individual cell or small group of cells. Analysis at the molecular or sub-atomic level is irrelevant to our present purpose. Like geography, aerobiology is an agglutinative study, drawing information from many kinds of scientific research. Although it already has its patron saint, Pierre Miquel, and its martyr, Fred C. Meier, aerobiology is best regarded as an activity whose material will in due course be incorporated into the main body of biological science—without, I hope, any necessity for splinter societies, journals, and international conferences.

This book amplifies and extends a course of Intercollegiate Lectures given to botanical students in the University of London in 1956. The theme, which has occupied me for over fifteen years, is as follows. Transport through the atmosphere is the main dispersal route for such organic particles as the spores of many micro-organisms. How do the properties of the atmosphere, and the properties of these particles themselves, affect their dispersal? How do the particles get into the air? How far, and in what numbers, are they dispersed? By what processes do they become grounded, so that they can continue growth? What is in the air, and how can we measure it? What are the practical consequences of this process for the micro-organisms themselves, and for man, other animals, vegetation, and crops?

Although there are one or two other books on airborne microbes, this is the first to treat the subject as a world-wide phenomenon. It is, perhaps, inevitable that it should be attempted by a mycologist. Few other biologists find their material so dominated by the atmosphere, and no other micro-organisms have so thoroughly exploited the possibilities of aerial dispersal as the fungi. One of the fascinations of the subject is the impact of facets of its knowledge on such apparently diverse topics as artificial rain-making, allergy, smoke screens, effluent of nuclear power-stations, crop protection, icing of aircraft, air hygiene, and many other topics. This book treats of the development and principles of aerobiology rather than applications; yet the stimulus to nearly all aerobiological work comes from applied science.

In this book the term 'microbe' is used freely when a general word is wanted; but, like the word 'spore', it has admittedly been stretched beyond its normal meaning. Airborne pollen of flowering plants must be included and is safely covered by the term 'spore' (botanically: 'microspore'); but are pollen grains and mushroom spores microbes? There is no other commonly accepted word that covers quite what is meant by the word 'spore' as used here: 'propagule', 'disseminule', 'biota', 'diaspore'? We have isolated part of the continuum for study but find we are not well-equipped verbally for the task of dealing with it. The microbial population of the atmosphere is referred to here as the 'air-spora', using 'spora' as a word analagous to 'flora' and 'fauna'.

Botanical nomenclature has presented some difficulties: authorities have not been given for specific names, and the names used by other authors have usually been quoted as given in the original papers—without necessarily attempting to guess what was meant, or following the nomenclature fashionable in 1960. I have converted other workers' numerical data to the metric system, and temperature to the Centigrade scale, to aid comparison, and have moreover assessed spore concentrations on the uniform basis of number per cubic metre.

Frequently, in making general statements, I have omitted safeguarding, but tedious, escape clauses: this has been done to spare the reader who will understand that biological generalizations abound in exceptions and complexities.

Interpretations in this book are mostly my own responsibility, but I am grateful for help received from many people during its preparation. In particular I offer my thanks to the following: G. Samuel and W. Buddin for introducing me to dispersal problems in the field; F. C. Bawden for encouragement in the study of aerobiology and for reading this book in manuscript; E. C. Large for advice on planning the book; D. A. Boalch (and many other librarians) for continual help with the literature; members of the British Mycological Society for named specimens of fungi, and H. L. K. Whitehouse for mosses; A. Horne, V. Stansfield, and F. D. Cowland for photography; R. Adams, G. C. Ainsworth, J. R. D. Francis, E. J. Guthrie, Elizabeth D. Hamilton, J. M. Hirst, C. T. Ingold, C. G. Johnson, F. T. Last, Kate Maunsell, T. Sreeramulu, and O. J. Stedman for discussion and help with aerobiological problems and applications; Audrey Baker, Beatrice E. Allard, and Marie T. Seabrook for clerical assistance; and Maureen E. Bunce for experimental help, revision of the manuscript, and preparation of many of the illustrations —especially the paintings for Plates 1, 5, 6, and 7. I also wish to thank authors, editors, and publishers for permission to copy illustrations which are acknowledged in the text. Finally, for the calculations involved in Figs. 24 to 27, and for those chapters needing the help of a mathematician, I have been fortunate in having the constant advice and willing help of my wife, Margaret F. Gregory, to whom I am most deeply grateful.

Rothamsted Experimental Station PHILIP H. GREGORY
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September, 1960.

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I

HISTORICAL INTRODUCTION

THE air we breathe, like our food and drink, varies in quality from time to time and from place to place. This fact was recognized many centuries before industrialized man assumed the right to pollute the atmosphere with poisonous chemicals and radioactive isotopes.

In Britain we hold that, 'when the wind is in the East 'tis neither good for man nor beast'. Some places are noted for invigorating air, and some for relaxing air; but it is not yet clear whether these properties are associated merely with differences in temperature, humidity, and movement of a gaseous mixture consisting mainly of 78 per cent nitrogen, 21 per cent oxygen, and 0·03 per cent carbon dioxide with traces of the inert gases, or whether some other factor or factors are involved.

SPECULATIONS ON THE ORIGIN OF DISEASE

Classical writers believed that the wind sometimes brought sickness to man, animals, and crops. Hippocrates, the father of medical science, held that men were attacked by epidemic fevers when they inhaled air infected 'with such pollutions as are hostile to the human race'. A rival, though perhaps not entirely incompatible, view held that epidemics were the result of supernatural agencies, and were to be warded off or cured by taking appropriate action.

Lucretius in about 55 B.C. held quite modern views. He observed the scintillation of motes on a sunbeam in a darkened room and concluded that their movement must result from bombardment by innumerable, invisible, moving atoms in the air. This brilliant intuition enabled him to account for many interesting phenomena, including the origin of pestilences. We now know that bodies which transmit human diseases through the air are larger than those which Lucretius thought of as atoms—the mosquitoes carrying malaria, for instance, or the droplets which spread the common cold and influenza viruses indoors. But in his concept of baleful particles carried in clouds by the wind, settling on the wheat or inhaled from the polluted atmosphere, Lucretius touched on some of the main problems existing in plant pathology and allergy today.

EARLY MICROSCOPISTS AND THE DISCOVERY OF SPORES

After Lucretius, more than 1,500 years passed before men even began to be aware that the air teems with microscopic living organisms.

The discovery had to wait almost until the invention of the microscope.

For a long time after Aristotle and Theophrastus, the lower plants lacking obvious seeds were believed to be generated spontaneously in decaying animal or vegetable matter. The same view was held of the origin of many of the lower animals. However, the minute 'seeds' or spores of several kinds of plants were observed in the mass long before the invention of the microscope allowed them to be identified and observed individually. What was more natural than to suppose that these minute particles were wafted about by the winds?

The discovery of reproduction of ferns is attributed to Valerius Cordus (*b.* 1515, *d.* 1564), and spores of the fungi seem to have been observed soon after this by a Neapolitan botanist, J. B. Porta, although the rusty-coloured spore deposits under bracket-fungi on beech trees must always have been familiar to the countryman.

It was P. A. Micheli (*b.* 1679, *d.* 1737), botanist to the public gardens at Florence, who first illustrated the 'seeds' of many fungi, including mushrooms, cup-fungi, truffles, moulds, and slime-moulds. Further, by sowing spores on fresh-cut pieces of melon, quince, and pear, and reproducing the parent mould for several generations, he showed that the spores of some common moulds were, indeed, 'seeds' of the fungi. He noted, however, that some of his control slices also became contaminated, and he concluded that the spores of moulds are distributed through the air (*see* Buller, 1915).

The hand-made lenses of Anton van Leeuwenhoek rendered visible the world of minute organisms whose existence had only been guessed at before, and whose significance in nature had scarcely even been imagined. He could just see bacteria, and in his letters to the Royal Society in 1680 he described some yeasts, infusoria, and a mould. From his experiments he came to doubt the current belief in spontaneous generation; it seemed more plausible to him to suppose that his 'animalcules can be carried over by the wind, along with the bits of dust floating in the air' (Dobell, 1932). The controversy over spontaneous generation was to last for a couple of centuries; but, in the second half of the eighteenth century, ideas were developed by Nehemiah Grew and E. F. Geoffrey on the function of the pollen of flowering plants. J. G. Koelreuter, in 1766, was perhaps the first to recognize the importance of wind-pollination for some plants and of insect-pollination for others. C. K. Sprengel in 1793 developed these views and concluded that flowers lacking a corolla are usually pollinated in a mechanical fashion by wind. Such flowers have to produce large quantities of light and easily-transported pollen, much of which misses its target or is washed out of the air by rain. Thomas A. Knight in 1799 reported that wind could transport pollen to great distances.

By the beginning of the nineteenth century, therefore, it was recognized that pollen of many, but by no means all, species of flowering plants, and the microscopic spores of ferns, mosses, and fungi—as well as protozoa—were commonly liberated into the air and transported by the wind. The potential sources of the air-spora had been discovered and identified in the main before the year 1800, but their role remained obscure.

CONTROVERSY ON SPONTANEOUS GENERATION *

Leeuwenhoek had come to doubt the belief, dating from Aristotle, that flies, mites, and moulds were generated spontaneously by decaying animal and vegetable matter. To him it seemed likely that animalcules could be carried by the air, and this provided an alternative explanation to spontaneous generation. J. T. Needham (*b.* 1713, *d.* 1781) had claimed that minute organisms would appear in heated infusions; but L. Spallanzani (*b.* 1729, *d.* 1799) showed, by a series of experiments, that when organic materials were subjected to sufficient heat-treatment (with various precautions against contamination) they would neither putrify nor breed animalcules *unless exposed to air.* From this Spallanzani concluded that the microbes were present in the air admitted experimentally to his sterilized vessels. A rearguard action was fought to explain away these results. J. Priestley (*b.* 1733, *d.* 1804) and L. J. Gay-Lussac (*b.* 1778, *d.* 1850) claimed that heating the vessels drove out the air and that it was *shortage of oxygen*, not lack of 'seeds', which prevented heat-sterilized materials from generating a microbial population.

Meanwhile, Appert (1810) put heat sterilization on a commercial basis by applying it to food preservation; but the controversy lingered on, even into the present century, although the experiments and polemics of Louis Pasteur were decisive. Pasteur showed that food could be conserved *in the presence of oxygen* and that preservation depends on the destruction by heat of something contained in the air. In 1859 F. A. Pouchet, of Rouen, had raised the objection that a very minute quantity of air sufficed to allow the development of numerous microbes in heated infusions, and that the air would have to be a thick soup of microbial germs.

In reply, Pasteur (1861) sterilized a series of evacuated flasks containing nutrient medium. So long as the flasks remained unopened they all remained sterile; but, even when they were opened and air was admitted, he found that one or two out of each batch would remain sterile on incubation. Pasteur replied to Pouchet, denying that only a minute quantity of air needs to gain access for a microbe population to develop and for putrefaction to take place. On the contrary, the cause of the phenomenon was discontinuous and a sample of 250 cc. of air might *or might not* contain germs.

Pasteur then showed, by opening batches of about forty such flasks in various sites, that the quantity of airborne germs differed in different places. In the open air in Paris he obtained bacteria, yeasts, and moulds;

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* *See also* Bulloch (1938) and Oparin (1957).

but some flasks remained sterile. In cellars of the Observatoire, where the temperature was constant and the air still and dust-free, many more flasks remained sterile.

On 5 November 1860, Pasteur deposited at the office of the Academy no fewer than seventy-three quarter-litre flasks, some of which he had opened to the air in batches of twenty at various heights ranging from the foothills of the Jura to high up on Mont Blanc, as follows:

Altitude	Locality where air sampled	Number of flasks Contaminated	Sterile
	Country air, far from dwelling houses, on the first plateau of the Jura	8	12
850 metres	Jura mountains	5	15
2,000 metres	Montanvert, near Mer de Glace on Mt. Blanc	1	19

The cause of this supposed 'spontaneous generation' was not only discontinuous but, moreover, its concentration decreased with height.

F. A. Pouchet had admitted that among dust particles of vegetable origin there were some spores of cryptogams, but he held that these were too few to account for the phenomena of putrefaction.

Pasteur decided that he would abandon Pouchet's method, which relied on examining spontaneous deposits of dust on the surface of objects, in favour of a new method of studying the particles by collecting from actual suspension in the air. Pouchet had drawn invalid conclusions from surface deposits because, according to Pasteur, the light air-movements which constantly play over surface deposits would pick up and remove the extremely minute and light spores of microbes more readily than they would any coarser particles. (It now appears, however, that the small numbers of the lighter bodies in surface deposits is due to the extreme slowness with which they are deposited, rather than to their preferential removal after deposition.)

Pasteur's apparatus for extracting the suspended dust in the air, for microscopic examination, was quite simple (Fig. 1). A tube of $\frac{1}{2}$ cm. diameter was extruded into the open air through a hole drilled in a window frame several metres above the ground. The rear part of the tube was packed with a plug of gun-cotton to catch particles. Air was drawn through the apparatus by means of a filter pump, and the volume of air was measured by displacement of water. Tests were made on air drawn from beside the Rue d'Ulm, and from the garden of the École Normale in Paris. During aspiration, solid particles were trapped on the fibres of the gun-cotton plug. After use, the gun-cotton was dissolved in an alcohol-ether mixture, the particles were allowed to settle, the liquid was decanted, and the deposit was mounted for microscopical examination.

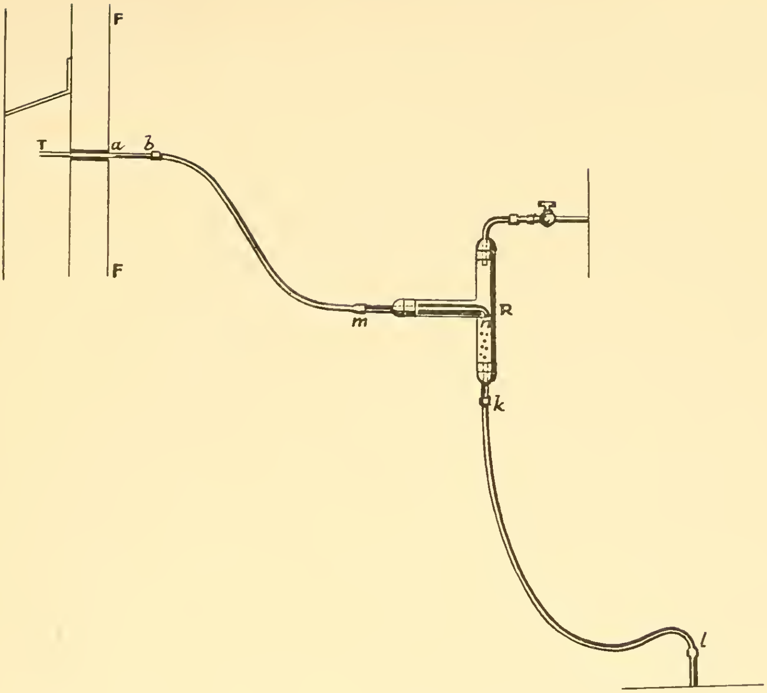


Fig. 1.—Pasteur's gun-cotton filter for airborne microbes.

a = gun-cotton plug, 1 cm. long, held in position by:
b = spiral platinum wire.
FF = window frame drilled to allow passage of:
T = tube to exterior for sampling outdoor air.
R (*m.k.l.*) = aspirator.

Pasteur, as usual, had little interest in the specific identity of his organisms; he was no taxonomist. The particles exactly resembled the 'germs' of lower organisms. They differed in volume and structure so much among themselves that they clearly belonged to very many species or even groups, including bacteria, moulds and yeasts. Their numbers contradicted the general conclusion that the smallest bubble of air admitted to a heat-sterilized medium is sufficient to give rise to all the species of infusoria and cryptogams normal to an infusion. This view was shown to be highly exaggerated, and Pasteur indicated clearly that it is sometimes possible to bring a considerable volume of ordinary air into contact with an infusion before living organisms develop in the latter.

Pasteur had demonstrated visually the existence of an air-spora, he had pointed out that it should be measured while in suspension and not after deposition on surfaces, and he had made the first rough visual measurements of its concentration in the atmosphere of the City of Paris: a few metres above the ground in the Rue d'Ulm, after a succession of fine days in summer, several thousands of micro-organisms were carried in suspension per cubic metre of air. He then abandoned the method—remarking, however, that it could doubtless be improved and used more extensively to study the effects of seasons and localities, and especially during outbreaks of infectious diseases.

The Germ Theory of Disease

We must now look back and trace the growth of the microbial theory of disease, that had been developing for more than a century.

The minute growths of fungus noticed for centuries on mildewed or 'rusted' plants were believed to be a consequence of the diseases; the dusty powder on rusted wheat was regarded as a curiously congealed exudation of the diseased plant itself. But might this not be putting the cart before the horse? Could the rust possibly be the cause of the disease instead of an effect? Perhaps the first to give reasonably affirmative evidence was Fontana (1767), who examined wheat rust with his microscope and described what he saw as a grove of parasitic plants nourishing themselves at the expense of the grain.

As further crop diseases were studied it became clear that, in some, infection is acquired by planting in contaminated soil, while others are carried on seed and still others are spread in the wind by airborne fungus spores (*see* Large, 1940).

The discovery that microbes can cause disease in man and animals came somewhat later, and the first animal pathogens to be recognized were again fungi—no doubt because they were easier to find than bacteria. In 1835, Agostini Bassi showed conclusively, by inoculation experiments, that a specific mould is the cause of the 'muscardine' disease of silkworms which was then threatening the silk industry of Piedmont. Next, historically, came the recognition of the fungi causing favus, ringworm, and 'thrush' in man, as a result of the work of David Gruby and Charles Robin.

Pasteur had demonstrated that microbes are normally abundant in the air. Many of them can cause fermentation or putrefaction when introduced into sterile organic substrates; and it was natural to speculate that others might be the causes of epidemics of some of the so-called 'zymotic' diseases whose etiology was then unknown. Medical workers soon began a systematic search among airborne microbes for the unknown causes of infectious diseases.

The search was long, and on the whole unfruitful because most epidemic diseases that attacked man were gradually traced to sources other than the outdoor air. However, in the course of the search, most of the important characteristics of the air-spora were discovered—and then forgotten. The search occupied the last thirty years of the nineteenth century and coincided with the golden age of bacteriology. Listing the dates of contemporary salient advances in bacteriology will help to give the background to this phase of aerobiology (*see* Bulloch, 1938).

Pasteur, L.	Microscopical and cultural demonstration of the existence of an air-spora, and the fermentation of urea by a *Micrococcus*	1861–62
Koch, L.	Introduction of pure-culture methods, and demonstration of spore production in bacteria. Discovery of cause of anthrax	1876
	Statement of Koch's postulates	1878
	Introduction of gelatine to solidify media	1881
Hansen, G. H. A.	Discovery of cause of leprosy	1874
Neisser, A.	Discovery of the *Gonococcus*	1879
Koch, L.	Discovery of the tubercule bacillus	1882
	Discovery of the cholera *Vibrio*	1883
Loeffler, F.	Discovery of bacillus of swine erysipelas	1885
Nicolaier, A.	Discovery of the tetanus bacillus	1885
Kitsato, S. Yersin, A.	Discovery of the bacillus of plague	1894
Ivanovski, D. Beijerinck, M. W.	Discovery of filterable viruses in plants	1892 1898

The Hygienists and their Investigation of the Air

While the causes of infectious diseases of man and animals were being unravelled in laboratories and clinics, a series of field investigations into the air-spora was in progress to find whether fluctuations in number and types of microbes present in the atmosphere were connected with outbreaks of such diseases as cholera, typhoid, and malaria.

Salisbury (1866) investigated the air-spora in connexion with malaria in the Ohio and Mississippi Valleys, by exposing sheets of glass above marshy places during the night and examining them microscopically. He observed small, oblong, Palmella-like cells singly or in groups on the upper side of the glass sheets, but never in the droplets which formed on the underside. He believed that these cells were produced from a grey mould growing on the surface of prairie soil, and were in fact its spores which were liberated at night and rose some 30 to 100 ft. in the air, none being present during the daytime. Their liberation could be prevented by covering the ground with a layer of quicklime or straw.

Some form of the 'aeroconiscope', invented by Maddox (1870, 1871), was in favour with many investigators in this period. The model used by Cunningham (1873) consists of a conical funnel, with the mouth directed into the wind by a vane, ending in a nozzle behind which is placed a sticky microscope cover-glass on which were impacted dust particles driven into the cone by the wind (Fig. 2). Cunningham's studies were made in two Calcutta gaols where cholera and other fevers were rife, and where medical statistics were available. He sampled for 24-hour periods, and illustrations of representative catches of airborne organisms, mainly fungus spores and pollens, were published in a series of splendid colour plates. He found no correlation between these micro-organisms and the incidence of fevers in the gaols. Moist weather diminished inorganic dusts, but it appeared to increase the total number of fungus spores.

The most intensive sustained analysis of bacteria and moulds in the atmosphere was made in Paris during the last quarter of the nineteenth century. Largely through the influence of the chemist, J. B. A. Dumas, the Observatoire Montsouris was launched as a State institution in 1871 to make records needed for meteorology and agriculture. The Observatoire was housed in a palace in the Parc Montsouris, about 5 km. south of the centre of Paris. One of its tasks was to be the microscopic and cultural study of the organic and inorganic dust in the air, including both Mucedineae (moulds) and bacteria.

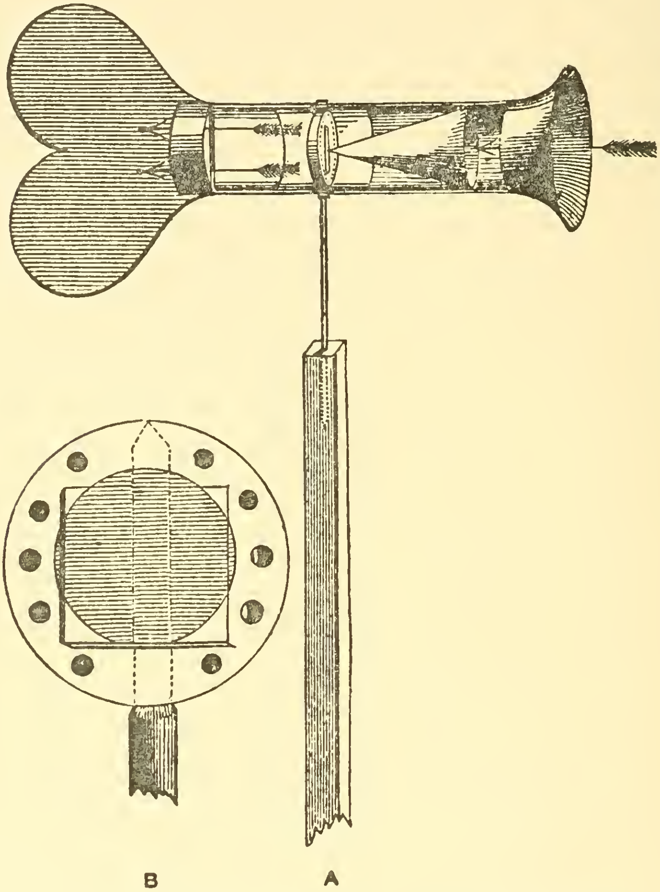


FIG. 2.—Cunningham's aeroconiscope. A = side view of apparatus (partly in section); B = face view of sticky surface behind apex of cone (on a larger scale).

Observations were started in 1875 by M. Schoenauer. He was replaced after a year or two by Pierre Miquel (*b.* 1850, *d.* 1922), the distinguished bacteriologist, who continued in charge of the work for over a quarter of a century. During the course of the survey, various methods were tested and discarded or improved; but all aimed at estimating the number of particles of various types contained in a measured volume of air. Moulds were at first estimated microscopically in a 24–28 hour deposit, obtained by impinging the air to be sampled on a glycerined glass slide which was placed horizontally 2 to 3 mm. above a downward-facing orifice. The diameter of the orifice was from 0·5 to 0·75 mm. Suction of 20 litres per hour was maintained by a water-operated pump (Miquel, 1879). Miquel found that this apparatus yielded about 100 times as many particles as the aeroconiscopes designed by Maddox and Cunningham, though for qualitative work away from the laboratory he still used a wind-operated trap of the Maddox type.

Bacteria, especially bacterial spores, could not be satisfactorily counted microscopically and Miquel was forced to estimate them by cultural methods. At first he drew known volumes of air through liquid media (sterile beef extract, etc.), partitioning the liquid either before or after exposure into 50 or 100 vessels, and adjusting the volume of air sampled so as to leave from a quarter to a half of the vessels sterile—in order to get a reliable estimate of the number of bacterial particles in the volume of air sampled. The numbers of microbes in the air varied greatly in the same place at different times, and this variation was studied in relation to season, weather, district, and altitude. Miquel was the first to make a long-term survey of the microbial content of the atmosphere by volumetric methods.

In the Parc Montsouris, out-of-doors, Miquel estimated that the mould spores averaged about 30,000 per cubic metre in summer, sometimes rising to 200,000 in rainy weather. In prolonged dry weather they decreased in number, and were only about 1,000 per cubic metre in winter, with very few indeed when snow was on the ground. While rain was falling the numbers of mould spores usually decreased considerably, but afterwards their numbers recovered quickly—in fact, much more quickly than did those of particles of inorganic dust. Resting stages (eggs) of infusoria were estimated at about 1 or 2 in 10 cubic metres of air. Pollen grains in June may make up 5 per cent of the airborne organic particles, while starch grains near habitations may account for 1 per cent. Bacterial numbers out-of-doors in the Parc Montsouris were at first estimated at about 100 per cubic metre; but improved culture media increased this figure by a factor of 7 to 10 times. The numbers of bacteria in the centre of Paris were, perhaps, 10 times as high again as in the Parc Montsouris, with larger numbers inside dwellings, and still more in crowded hospitals. The work showed signs of settling into a steady routine with the publication of Miquel's *Les organismes vivants de l'atmosphère*, Paris, 1883.

However, in 1883 and 1884 Miquel was stung into a burst of renewed activity by the intrusion of a rival centre for the study of hygiene which had been established in Berlin under W. Hesse, who used the new solid media which Miquel abhorred. With the collaboration of de Freudenrich in field work, Miquel studied the microbial population of the air at high altitudes in the Alps by volumetric methods (1884, p. 524); with the help of a sea captain, M. Moreau, the air over the sea was studied on voyages to Rio de Janeiro, Odessa, Alexandria, and La Plata; the micro-organisms brought down in rain-water were caught, precipitated, and counted; hourly variations of fungus spores and bacteria in the air were studied on improved volumetric traps with sticky slides, or on paper impregnated with nutrient media and moved by clockwork. At Montsouris, fungus spores showed a diurnal periodicity with two maxima at about 8 and 20 hours, regardless of wind velocity. When he pressed the study of changes in spore content of the air with passage of time still further, Miquel found that the hourly reading was merely a smoothing of still shorter-term variations.

Trapping airborne bacteria at Montsouris on a moving paper disc imbibed with nutrient agar, Miquel (1885) observed a regular diurnal periodicity—with two maxima at approximately 7 and 19 hours averaging about 750 per cubic metre, and with two minima at approximately 2 and 14 hours averaging about 150 per cubic metre. This periodicity was not related to wind direction, and was not altered by moderate falls of rain. In the centre of Paris the bacterial content also showed two maxima and two minima, but there the minima were about equal to the maxima at Montsouris, and the times of the maxima were closely related to activities in the city such as sweeping the street, and to the passage of horse-drawn traffic.

Miquel appears to have been overwhelmed by the richness of the information on the mould spore flora provided by his apparatus, for he promptly abandoned it, merely remarking ‘the micrographer who has the leisure could make some nice [curieuse] studies of this subject’. It was, however, not abandoned before the main elements in the mould-spora had been discovered by this excellent method.

Interest in the mould-spora waned when it became clear that the devastating epidemic diseases prevalent from time to time in cities were not fungal in origin but were due to bacteria, and attention became urgently focused on drinking water as the source of many of the current epidemic fevers abounding in Paris. The laboratory at Montsouris then became the centre for the bacterial analysis of samples of drinking water sent from wells in Paris and other parts of France.

Meanwhile, in Germany, the work of W. Hesse (*b.* 1846, *d.* 1911) had proceeded along similar lines. Hesse’s apparatus for air sampling consisted of a narrow horizontal tube, 70 cm. long and 3·5 cm. wide, containing a layer of Koch’s nutrient gelatine. A known volume of air was aspirated slowly through the tube, and micro-organisms settled and grew on the medium. Most colonies developed near the entrance to the tube, and Hesse assumed that by the time the slow stream of air had reached the end of its 70 cm. course all micro-organisms had been precipitated by gravity. Hesse found that moulds penetrated much farther into his tubes than did the bacteria, and made the important deduction that mould-germs as found in the atmosphere are on the average lighter than the bacterial germs. This led him to conclude that, whereas fungus spores were usually present in the air as single particles, the aerial bacteria mostly occur in the atmosphere either as large aggregates, or attached to relatively large carrier particles of dust, soil, or debris (Hesse 1884, 1888). He also observed that most colonies consisted of a single species—bacteria usually in small colonies of pure culture, and fungi as isolated spores—and deduced that the airborne germs are not in the form of aggregates of different types.

Hesse's method was also used in London by Frankland (1886, 1887) and Frankland & Hart (1887) on the roof of what is now known as the Old Huxley Building of the Imperial College of Science and Technology, and elsewhere. Simultaneous comparisons were made between the number of micro-organisms per 10 litres (as indicated by colonies growing on Hesse's tubes of peptone gelatine) and the number deposited on horizontal dishes of the same medium, expressed as the number deposited per unit area per minute. Tests were made both outdoors and inside crowded or empty buildings. Frankland noted that the number of colonies was greater when the mouth of the tube faced the wind rather than in other directions, so he standardized his method by always turning it at an angle of 135° to the wind. A control tube facing the wind but not aspirated was always used, and sometimes it had a substantial number of colonies. Frankland seems to have been the first to realize that aerodynamic effects are of major importance in techniques for trapping the air-spora.

These methods for studying the air-spora were continued into the present century, notably by Saito (1904, 1908, 1922) in Japan, and by Buller & Lowe (1911) in the Canadian Prairies.

The Allergists

The idea that men, other animals, and plants, could become infected by microbes which set up pathological changes, had been made acceptable by the analogy of sterile organic infusions that become infected with putrefying microbes. The idea became widely accepted during the latter half of the nineteenth century and, when once the cause of the common epidemic diseases had been established, advances in hygiene and therapy began to transform the social scene. Yet there remained some diseases for which no pathogenic or parasitic invader could be found. Some of these, such as pellagra and beri-beri, have now been traced to a variety of nutritional deficiencies. Another group, the so-called allergies, were at first difficult to grasp because a peculiar condition of the patient was a complicating factor. Allergic diseases, unlike those caused by invasion of the body by a pathogenic micro-organism, are due to a changed condition of an individual patient who has become sensitive and reacts adversely to substances, often in minute amounts, which normal individuals can tolerate. The substance or allergen can be taken into the body, for example in food, or by contact through the skin, or by inhalation from the air.

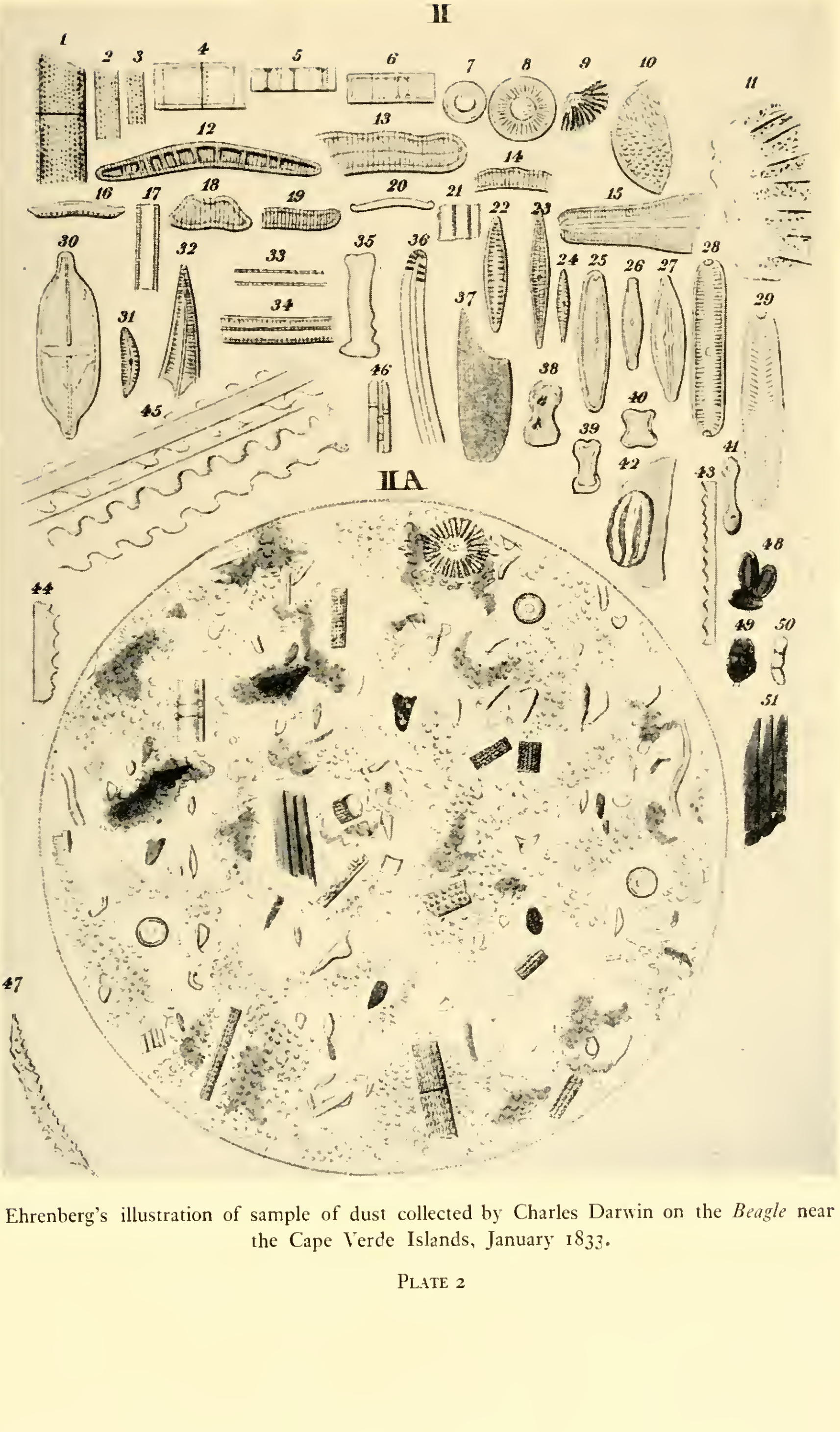
Hay fever was one of these puzzles. Long before Pasteur's epoch, hay fever had been attributed to inhalation of pollen; but it remained for Charles H. Blackley (1873), a Manchester physician, to prove by inhalation experiments on himself and others that this guess was correct, and to demonstrate by trapping methods that pollen was at times present in the air in large quantities. Blackley first tried Pasteur's gun-cotton filters and obtained some pollens, but too few to satisfy him. Finally he used four sticky horizontal microscope slides exposed under a roof supported by a square central post. The slides were placed at 'breathing level' (about 135 cm.), and he caught a maximum of 880 grains per sq. cm. per 24 hours on 28 June 1866. In 1867 his maximum was only 106, and in 1869 he placed his slides vertically in a vane shelter and gave no numerical data. He found that rain reduced the number of pollen grains caught to about 5 per cent of the number caught in dry weather. He explored the air above the ground up to 1,500 ft. by means of kites, and found that vertical slides facing the wind caught nearly 20 times as much pollen at the higher altitude as at breathing level.

Blackley showed by means of his sticky slides that the air contains enough pollen during the grass-flowering season for large quantities to be deposited on exposed surfaces. He also gave himself an attack of bronchial catarrh by inhaling *Penicillium* and *Chaetomium* spores—an experiment which he said was too unpleasant to repeat.

According to Durham (1942), after Blackley's pioneer work no progress was made with these studies until the period 1910–16, when fresh interest was aroused by the discovery that injections of pollen extracts can be used to de-sensitize patients who are allergic to pollen.

When the study of airborne allergens was again taken up in the present century, it was unfortunate that the technique chosen should have been the so-called 'gravity-slide' adopted by Blackley—a method which Pasteur had abandoned in 1861 and which Miquel had roundly condemned as 'the simplest and most defective method' of collecting airborne particles.

By the early years of this century it became possible to assess the value of the ancient belief that the wind brings disease. Many diseases of crop, but very few diseases of man, have proved to be caused by minute particles carried on the wind. The particles are not some sort of invisible atoms as Lucretius thought; indeed, among the motes in the sunbeam, he may himself have been watching some of the baleful fungus spores and pollens which cause crop disease and respiratory allergy.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Ehrenberg's illustration of sample of dust collected by Charles Darwin on the *Beagle* near the Cape Verde Islands, January 1833.

PLATE 2

Meanwhile evidence was accumulating that these particles might be carried by wind to distances vastly greater than had been imagined by the ancients. In dust deposited after transport for hundreds of kilometres by sirocco and trade winds, Ehrenberg (1849, 1872, 1872*a*) found large quantities of protozoa and plant spores, and gradually he became convinced that viable micro-organisms could survive transport through the atmosphere. When the *Beagle* was near the Cape Verde Islands, Darwin (1846) found the atmosphere hazy with dust from North Africa. In samples of this dust Ehrenberg found sixty-seven kinds of organisms—including freshwater infusoria and cryptogamic spores (Plate 2)—and Darwin at once grasped the importance of the phenomenon in the geographical distribution of organisms.

II

SEDIMENTATION IN STILL AIR

ALL the particles with which we are concerned are heavier than air. In still air they sink with characteristic and constant 'terminal velocity'.

Stillness as a quality of air is only relative. In the laboratory we can make the air as still as possible by eliminating draughts and convection currents, only to find an intense underlying activity revealed by the scintillation of motes in a beam of light. The motes are small enough to be jerked irregularly by the impact of gas molecules; but they are too large to be transported bodily by molecular diffusion, and most of the phenomena of colloidal suspensions are irrelevant to the air-spora. We shall meet some analogies with the diffusion of a gas, however, in studying the diffusion of a cloud of spores in the atmosphere.

In this study we usually ignore the underlying molecular activity of the medium, and consider a patch of air as 'still' if it is not being transported bodily at more than a certain speed. Out-of-doors this speed might be 10 cm. per sec.; in a room it might be 1 cm. per sec.; and, under carefully controlled conditions in special apparatus, a higher standard might be expected. For the present we must leave the definition vague, and simply regard air as 'still' when, in a particular context, the effects of wind, turbulence, and molecular activity are negligible. Knowledge of the properties of small particles in still air throws light on the behaviour of spores in moving air out-of-doors.

FACTORS DETERMINING VELOCITY OF FALL

One effect of its molecular activity is that the air is viscous, i.e. it resists the movement of solid particles. A small particle liberated into the air from a resting position tends to fall with an acceleration due to gravity; however, the resistance of the air increases faster than the speed of fall, and a state of balance is soon reached in which the particle stops accelerating and continues to fall through the air at a constant *terminal velocity*.

The terminal velocity of smooth spheres with diameters of between about 1 μ* and 100 μ is satisfactorily predicted by Stokes's law (for smaller particles Cunningham's correction becomes applicable, and larger particles have to be treated experimentally). Stokes's law can conveniently be given in the form:

* $\mu = \frac{1}{1000}$ mm.

$$v_s = \frac{2}{9} \cdot \frac{\sigma - \rho}{\mu} \cdot g r^2$$

where, in C.G.S. units at ordinary surface temperature and pressure:

v_s = terminal velocity (velocity of sedimentation) in cm. per sec.;
σ = density of sphere in gm. per cc. (water = 1·00);
ρ = density of medium (air = $1{\cdot}27 \times 10^{-3}$ gm. per cc.);
g = acceleration of gravity (981 cm. per sec.^{2});
μ = viscosity of medium (air at 18°C. = $1{\cdot}8 \times 10^{-4}$ gm. per cm. sec.);
r = *radius* of sphere in cm. (*N.B.* radius = $\frac{1}{2}$ diameter).

For a water droplet falling in air, $v_s = 1{\cdot}2 \times 10^{-2} r^2$ cm. per sec., when the radius is expressed in microns (μ). A fog droplet of 10 μ radius (20 μ diameter) has a calculated terminal velocity of 1·2 cm. per sec.

The pollens and spores with which we are concerned belong to the size-range where Stokes's law is valid, but they are seldom anything like smooth spheres. Stokes's law has given values of at least the right order, however, for spores whose terminal velocities have been measured experimentally. At first sight the pollen grains of some species of conifers appear to fall unexpectedly slowly, but these grains have conspicuous air sacs which greatly reduce the density of the individual particle.

The diameters of particles constituting the air-spora vary from approximately 1 μ to 100 μ or more for the largest pollens and spores (*see* Appendix I, p. 207, Plates 5–7). Some spores are filamentous, perhaps one hundred times as long as wide. Although the densities of the spores of very few species have yet been measured, there are reasons for expecting them to be much less dense than mineral particles and indeed to resemble water droplets in density. The few determinations which have been made, relative to water = 1, are as follows:

(ANGIOSPERMAE)		
Alnus glutinosa	0·752	Pohl (1937)
Betula verrucosa	0·808	”
Corylus avellana	1·008	”
Dactylis glomerata	0·981	”
Fagus sylvatica	0·713	”
Typha angustifolia	0·747	”
Typha latifolia	1·161	”
(GYMNOSPERMAE)		
Juniperus communis	0·405	”
Picea excelsa	0·550	”
Pinus sylvestris	0·391	”
Pinus montana	0·496	”
Taxus baccata	0·579	”
(PTERIDOPHYTA)		
Lycopodium sp.	1·175	Zeleny & McKeehan (1910)
(BRYOPHYTA)		
Polytrichum sp.	1·53	”

(Fungi)		
Amanitopsis vaginata	1·02	Buller (1909)
Erysiphe polygoni (conidia)	1·094	Yarwood (1952)
Lycoperdon sp.	1·44	Zeleny & McKeehan (1910)
Peronospora destructor	1·34	Yarwood (1952)
Puccinia graminis tritici	0·807 to 0·862	Weinhold (1955)
Uromyces phaseoli	1·36	Yarwood (1952)

The properties of spores are not invariable, but may alter with external conditions—sometimes enough to have a marked effect on their terminal velocity. For instance, the spores of the toadstool *Amanitopsis vaginata* were recorded by Buller (1922) as falling at 0·5 cm. per sec. when observed immediately below the gill after liberation, but they became desiccated on continuing to fall through dry air and soon slowed down to one third of their original speed. Durham (1943) gave laboratory determinations of densities of pollens, and for some the probable outdoor values which are shown in parentheses: *Ambrosia elatior*, 0·63 (0·55); *A. bidentata*, 0·56 (0·50); *Xanthium commune*, 0·52 (0·45); *Iva xanthifolia*, 0·79; *Salsola pestifer*, 1·0 (0·90); *Acnida tamariscina*, 1·0; *Zea mays*, 1·10 (1·00); *Phleum pratense*, 1·00 (0·90); *Quercus imbricaria*, 1·04; *Juglans nigra*, 0·93; *Alnus glutinosa*, 0·97; *Fraxinus americana*, 0·90.

Observed terminal velocities (v_s) of spores and pollen grains are collected in Table I.

TABLE I

OBSERVED TERMINAL VELOCITIES OF POLLENS AND SPORES

	(cm. v_s per sec.)	Author reference*
Flowering plants		
Abies pectinata	38·7	(11)
Alnus viridis	1·7	(10)
Betula alba	2·4	(10)
Carpinus betulus	2·2–6·8	(9), (10), (11)
Corylus avellana	2·5	(10)
Dactylis glomerata	3·1	(10)
Fagus sylvatica	5·5	(10)
Larix decidua	9·9–22·0	(9), (10)
Larix polonica	12·3	(11)
Picea excelsa	8·7	(10)
Pinus cembra	4·5	(11)
Pinus sylvestris	2·5	(10)
Quercus robur	2·9	(10)
Salix caprea	2·16	(11)
Secale cereale	6·0–8·8	(9)
Tilia cordata	3·24	(11)
Tilia platyphylla	3·2	(10)
Ulmus glabra	3·24	(11)
Pteridophytes		
Lycopodium sp.	1·76–2·14	(2), (5)
Bryophytes		
Polytrichum sp.	0·23	(2)

TABLE I—*contd.*

FUNGI		
Alternaria sp.	0·3	(6)
Amanita rubescens	0·15	(1)
Amanitopsis vaginata	0·29–0·61	(1)
Boletus badius	0·11	(1)
Boletus felleus	0·12	(1)
Bovista plumbea	0·24	(5)
Coprinus comatus	0·4	(1)
Coprinus plicatilis	0·43	(1)
Cronartium ribicola	2·03	(3)
Erysiphe graminis	1·2	(7)
Galera tenera	0·21	(1)
Helminthosporium sativum	2·0–2·78	(5), (6)
Lycoperdon pyriforme	0·05	(5)
Lycoperdon sp.	0·047	(2)
Marasmius oreades	0·13	(1)
Monilia sitophila	0·16	(5)
Paxillus involutus	0·11	(1)
Pluteus cervinus	0·067	(1)
Polyporus squamosus	0·10	(1)
Psalliota campestris	0·13	(1)
Puccinia coronata avenae II	1·0	(4)
Puccinia graminis secalis II	1·06	(4)
Puccinia graminis secalis I	1·02	(4)
Puccinia graminis tritici II	0·94–1·25	(4), (8)
Puccinia graminis tritici I	1·06	(4)
Puccinia triticina II	1·26	(4), (5)
Russula emetica	0·16	(1)
Tilletia tritici	1·41	(5)
Ustilago tritici	0·07	(5)
Ustilago zeae	0·3	(6)

* (1) Buller, 1909. (2) Zeleny & McKeehan, 1910. (3) McCubbin, 1918. (4) Ukkelberg, 1933. (5) Stepanov, 1935. (6) J. J. Christensen, 1942. (7) Yarwood & Hazen, 1942. (8) Weinhold, 1955. (9) Bodmer, 1922. (10) F. Knoll ex Rempe, 1937. (11) J. Dyakowska ex Erdtman, 1943.

Two methods have been used for measuring terminal velocity. The simpler method is to time the fall over a short, measured distance in a small chamber of still air by direct observation with a horizontal microscope. It was used in the pioneer work of Buller (1909), and by Yarwood & Hazen (1942). So far this method has been used only for small, slowly-falling spores, because large ones travel too fast to be timed by direct observation. The method could no doubt be extended to fast-moving spores by photographing with a flash of known duration. The technique most generally used, however, has been to release spores or pollen at the top of a column of still air in a vertical cylinder and find the time they take to arrive at the bottom. This is the method used by Zeleny & McKeehan (1910), McCubbin (1918), Ukkelberg (1933), Stepanov (1935), and Weinhold (1955).

McCubbin and Ukkelberg report results of similar type. The number of wheat-rust spores reaching the bottom of the tube in successive intervals of time showed a negative skew distribution. Ukkelberg was able to show that part of this skewness was due to the presence of clumps of spores which fell faster than single units. It is also clear that, with both uredospores and aecidiospores of rust fungi, a large number of single spores fall very slowly. Measurements are needed to test whether, within one species, the single spores arriving first at the bottom are larger than those arriving at the end of the experiment. Another possibility is that small eddies may have hastened the fall of some spores and retarded that of others. A more serious defect of the method is that a vertical circulation of air by convection in the cylinder might bias the results by introducing a systematic acceleration or retardation of fall. This drawback could be overcome by establishing a small temperature difference between the top and bottom of the column, so that the stratified air would be stabilized as in a 'temperature inversion'. A thermostat may produce artefacts from convection currents set up by rhythmic temperature changes. Buller (1909) emphasized the difficulty of reducing air to anything like stillness, even in closed beakers.

In air, spores gain or lose water rapidly and the effect of spore hydration on terminal velocity, noted earlier by Buller, is evidently complex. Weinhold (1955) showed that with uredospores of *Puccinia graminis tritici*, changes in volume and weight occurred within 3 minutes of transfer to air of different temperature and humidity. Weinhold reported that, contrary to expectation, spores *stored* at 5 per cent relative humidity fell at 1·25 cm. per sec., in spite of being smaller and less dense than spores stored at 80 per cent relative humidity, which fell at 1·1 cm. per sec. Increasing the humidity of air through which the spores fell increased the terminal velocity, which was: 1·03, 1·22, 1·23, and 1·54 cm. per sec. at relative humidities of 24, 45, 52, and 80 per cent, respectively. With increasing temperature, terminal velocity decreased from 1·06 cm. per sec. at 23·4°C. to 0·94 cm. per sec. at 39·9°C.

We still lack observations on the rate of fall of highly elongated fungus spores found in such genera as *Ophiobolus*, *Epichloë*, *Geoglossum*, and *Cordyceps*, whose unusual shape makes Stokes's law inapplicable. Falck (1927) calculated terminal velocities for a number of species with approximately elliptical spores on the assumption that the expected velocity $v_e = v_s / \sqrt[3]{(a/b)}$, where v_s is the fall velocity of a spherical particle of the same volume, and a and b are axes of the ellipse. McCubbin (1944) stressed our lack of observations on asymmetrical spores, and provisionally suggested a method of calculating terminal velocity on the assumption that surface drag accounts for most of the retardation. He showed that observed terminal velocities of most spherical and oval spores fitted the approximate formula $v_s = \frac{\text{length} \times \text{width}}{40}$, where velocity is in mm. per sec. and spore dimensions are in microns. Fusiform spores were treated as consisting of an intercalated cylinder (length = $l\mu$) between two axial cones (each of axial length = $x\mu$), v_s being again in mm. per sec.

During fall in still air, an asymmetrical particle will assume a characteristic orientation. Hydrodynamical theory requires that the orientation assumed will be that in which the resistance of the air to the motion of the particle is greatest. This phenomenon can be observed with the naked eye if minute airborne particles of fibre are watched in a beam of light in a still, darkened room.

We know very little as yet about spore orientation. Buller (1909) observed that some slightly elongated spores tend to fall with their long axis horizontal, as is to be expected for dynamical reasons. Sometimes factors other than shape seem to influence the orientation of an asymmetric spore. When Yarwood & Hazen (1942) watched the smooth conidia of *Erysiphe graminis*, measuring 32 × 20 μ, during fall in vertical glass tubes 7 mm. in diameter, they saw that half of the spores fell with the long axis horizontal and the other half with it vertical. This might indicate an uneven distribution of materials of different density in the cell contents; but, more likely, the vertical position was due to drag at the wall boundary, because if the tube is made even narrower, all the spores fall vertically. The present author has seen the filamentous ascospores of *Cordyceps gracilis* similarly oriented whilst being carried up by convection currents beside a vertical glass surface. Further, while watching the tailed spores of the puffball, *Bovista plumbea*, falling in a small chamber on the stage of a horizontal microscope, the tail was seen to trail behind the spherical spore. In Chapter VI it will be indicated that spores tend to be deposited with characteristic orientation on a surface.

Stokes's law holds for *smooth* spheres. Few pollens or spores are spheres, but a large proportion of them are microscopically smooth. Others, when highly magnified, are seen to possess warts, spines or other projections, or even to be pitted. These roughnesses would be expected to increase friction during movement through air and to retard fall, but we have as yet no experimental evidence of this.

Viewed over the whole range of spore and pollen size of, say, 4 to 100 μ diameter, and of terminal velocities of from 0·05 to 10 cm. per sec., it is clear that Stokes's law gives a good idea of terminal velocity in still air, but that asymmetry and surface roughness may play a part as yet unmeasured.

Effects of Sedimentation

The effects of spore fall in still air can be observed indoors, particularly if a room is left closed and unoccupied—a fact noted early in the study of air hygiene by workers using Hesse's horizontal tube method of air sampling, or some modification of it (*see* Chapter I, p. 10). Although all these investigations suffer from the defect of being based on highly selective culture media, all agree that wind or crowds stir up micro-organisms, and that these soon settle in buildings when the air is left undisturbed.

At the Royal Institution in London, England, Tyndall (1881) made a close study of microbes in the air in relation both to the question of spontaneous generation and to the antiseptic surgery which was being developed by Lister at that period. Tyndall showed that the air of a darkened room scattered a powerful beam of light. Gas molecules did not appreciably scatter light. Scattered light always arose from suspended *particles*, some of them too fine to be described as motes. By passing a beam of light through windows in the side walls of a glass-fronted box, he showed that, after a day or two, the air became optically empty, the particles having settled on the floor and even on the roof of the box. At the same time Tyndall found that the air, previously full of microbes, had become sterile. The ability to generate life was associated with the presence of the light-scattering particles, and the air of small spaces could be sterilized by sedimentation. Tyndall had the curious idea that microbes remained associated in the air in clouds, much as fish are associated in shoals, and he explained that some of Pasteur's flasks (pp. 3–4) must have been opened within clouds, while others were opened between clouds of floating microbes. We now think of micro-organisms as distributed in the air at random (Horne, 1935), but, under certain conditions, it may be that Tyndall was right.

Outdoors the effects of terminal velocity are usually masked by the speed and turbulence of the wind. However, conditions are sometimes tranquil enough for its effects to be detected. One example was found by Rempe (1937), of Göttingen, who made a series of aeroplane flights both by day and by night to study the distribution of tree pollen over German forests. By trapping on sticky cylinders, he obtained evidence that pollen grains of different sizes and terminal velocities differed in their relative abundance with altitude, even by day (Table II).

TABLE II

POLLEN DISTRIBUTION AT DIFFERENT ALTITUDES

(After Rempe, 1937; day flight, A 6)

Pollen	Approximate diameter (μ)	Per cent of total pollen at height 10–40 metres	2,000 metres
Betula (birch)	22	29·0	73·3
Carpinus (hornbeam)	37	55·0	10·0
Fagus (beech)	38	11·5	3·3
Others	—	4·5	13·4

By night, it sometimes happened that pollen grains were partially sorted out according to size even within a single species, as shown by the mean diameters of birch pollen on the night flight, A 10 (Table III). The size-range recorded by Rempe varied from 23 μ to 27·5 μ, so it is evident that even at night the sorting effect was not great—a difference in altitude of 1,000 metres was associated with a drop of only 4·5 μ (or 1/9th of the mean diameter), with an estimated terminal velocity differing between 1·6 and 2·3 cm. per sec.

TABLE III

SIZE OF *Betula* POLLEN AT DIFFERENT ALTITUDES

(After Rempe, 1937; night flight, A 10)

Altitude (metres)	Mean diameter (μ)	Estimated terminal velocity (cm. per sec.)
1,000	23·0	1·6
800	24·5	1·8
500	26·7	2·1
200	27·5	2·3
10–40	27·2	2·2

Quite insignificant convection currents may be enough to counteract the terminal velocity of fall of small spores. Falck (1904) believed that the fruit-bodies of the larger fungi generate sufficient heat to induce convection currents which could carry their spores upwards. The temperature of an insulated mass of *Polyporus squamosus* rose nearly 10°C. in 10 hours, and he regarded parasitism by maggots as a heat-generating adaptation favouring dispersal. Buller (1909) justly criticized this view, but field experiments are needed to determine whether the pilei of agarics modify air-flow by their own heat, by absorbing solar radiation, or by their shape generating stationary eddies in an air stream. The colours of agarics are usually considered to be functionless, but the presence of dark colours among species inhabiting burnt ground suggests that this character may have been selected during evolution. It is not impossible that both colours and shapes of agaric fruit-bodies are partly adaptive.

III

THE ATMOSPHERE AS AN ENVIRONMENT

AEROBIOLOGY is a synthesis: just as the geographer draws upon astronomy and geology, so the aerobiologist draws upon many sources. To understand the environment of the air-spora we must go to meteorology. A fuller account of the relevant features of the atmosphere than that given here can be found in works on dynamical meteorology, e.g. Sutcliffe (1940), Geiger (1950), Sutton (1953), and U.S. Weather Bureau (1955), the last including many excellent diagrams.

THE ATMOSPHERE AND ITS LAYERS

The atmosphere is usually recognized as layered; some of its main features are illustrated in Fig. 3, in which altitude is drawn on a logarithmic, instead of a linear, scale in order to allow the various layers to be represented together on one page and to illustrate vividly how the properties of the atmosphere change most sharply near the ground.

Barometric pressure, density of the air, and (as a rule) temperature, decrease with increasing height above the Earth's surface. These changes are all quantitatively important in aviation, and calculations are based on a table of an agreed 'International Standard Atmosphere'. Changes with altitude in temperature, humidity, density, and viscosity will be complex in their effect on a suspended spore, but are not likely greatly to affect its terminal velocity.

The three vertical panels of the diagram represent conditions in contrasting weather types. The central panel represents a dull, windy day, with a cloud layer shielding the ground from direct sunlight (conditions on a cloudy night are not very different). The right-hand panel represents a sunny day, and the left-hand panel a still, cloudless night. The thickness of each individual layer of air varies according to conditions; the boundaries between them vary in definiteness: sometimes transitions are imperceptible, but there is sometimes even a visible interface between layers. The layers are variously named in the literature and this may be confusing unless the following approximate equivalents are borne in mind (*see* p. 23).

It is convenient to describe these layers in the reverse order, from ground-level upwards, beginning in the troposphere with the laminar boundary layer.

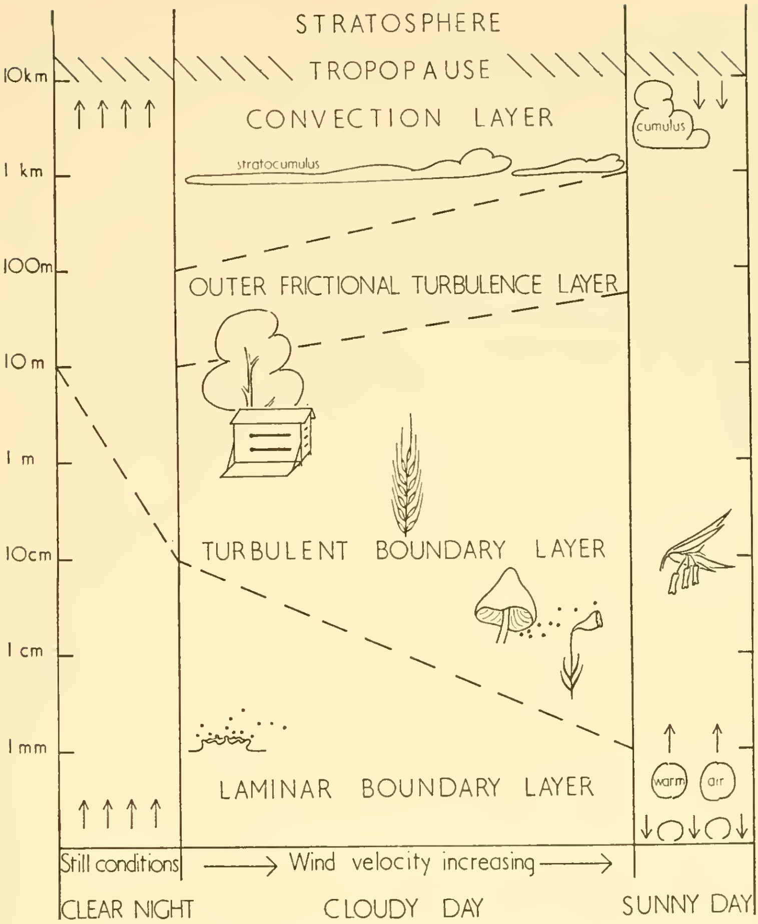

STRATOSPHERE
TROPOPAUSE
CONVECTION LAYER
cumulus
stratocumulus
OUTER FRICTIONAL TURBULENCE LAYER
TURBULENT BOUNDARY LAYER
LAMINAR BOUNDARY LAYER
warm
air
10km
1 km
100m
10 m
1 m
10cm
1 cm
1 mm
Still conditions
Wind velocity increasing
CLEAR NIGHT
CLOUDY DAY
SUNNY DAY

FIG. 3.—Diagrammatic representation of layers of the atmosphere with a logarithmic vertical scale.

Nomenclature of atmospheric layers

STRATOSPHERE			FREE ATMOSPHERE
TROPOPAUSE			
TROPOSPHERE	Convective (convection) layer		
	Transitional or outer frictional turbulence layer		PLANETARY BOUNDARY LAYER
	Turbulent boundary layer	Surface boundary layer	
	Local eddy layer		
	Laminar boundary layer		

The Troposphere

The troposphere is the name given collectively to the lower layers of the atmosphere extending from the ground to a height of approximately 10 km., and is a region characterized by a decrease in temperature with increasing height—the temperature lapse.

Air is relatively transparent to the short-wave radiation of sunlight which therefore heats the air very little as it penetrates the lower layers of the atmosphere. On a sunny day, solar radiation falling on the Earth's surface is in part temporarily absorbed, and in part reflected back as a radiation of longer wave-length that is more readily absorbed by air. This reflected radiation now heats the layer of air near the ground and the heat later becomes diffused through the lower layers of the atmosphere from below upwards. Air temperature is thus highest near the ground and decreases with increasing height, unless a 'temperature inversion' is formed under conditions described below. The normal temperature decrease (or 'lapse rate') is about 0·6°C. per 100 metres. At the top of the troposphere is the *tropopause*—the boundary between troposphere and stratosphere.

The troposphere comprises the five following layers.

LAMINAR BOUNDARY LAYER

In contact with the surface of the earth and all projecting bodies is a microscopically thin layer of air held firmly by molecular forces. Except for molecular diffusion this layer is still and windless.

Above this windless film the atmosphere is usually in motion, set going either by pressure differences of distant origin, or by convection currents produced by local heating. The lowest layer of moving air, next to the still layer, is known as the 'laminar boundary layer' (or sometimes the 'laminar' layer). This again is a thin layer, of the order of a millimetre thick, in which there is no turbulence and the air flows in streamlines parallel to the nearest surface; heat, gases, and water vapour can move across the streamlines by molecular diffusion. Wind speed is negligible at the still surface film, and in the laminar boundary layer wind speed increases *linearly with height* (momentum being transmitted through the layer by molecular diffusion only). Particles, droplets, or spores getting into the laminar layer will sink through it, following trajectories determined by wind speed and gravity, and will come to rest at the Earth's surface.

A laminar layer also exists at the interface around any solid body, and much of the foregoing description applies equally to the air layer at the surface of a leaf or stem.

The thickness of the laminar boundary layer varies with the wind speed and with the roughness of the adjacent surface. In a high wind it may be thinned down to a fraction of a millimetre, and turbulent air from the next higher layer may reach down nearly to the surface. In very calm weather the laminar layer may thicken considerably.

In comparison with the relatively equable air at a metre or two above the surface, the eco-climate of the laminar boundary layer is violently changeable (Monteith, 1960). Unless protected by a layer of vegetation, small organisms at ground-level may be subject to extreme heat from the sun's rays by day, followed by a rapid drop in temperature as heat is lost by radiation to a clear sky at night.

The laminar boundary layer acts as a dust trap. Particles which have sunk through it and come to rest in the still or slowly moving air at the surface, are out of reach of eddies—until some unusual condition arises which thins the laminar layer enough for eddies to penetrate down and sweep away the dust particles. High winds may do this; or local heating of the surface, perhaps on a micro-scale, may set up 'dust-devils'—smaller or larger whirlwinds raising dust into the air.

LOCAL EDDY LAYER

For biological purposes we need to add the 'local eddy layer'. Even in streamlined air, local stationary eddies may exist behind small roughnesses; and, as will be shown on page 35, air-flow over a cup-shaped depression may set up a rotation pattern sufficient to throw dust up from the bowl. This layer is probably important in nature, where ideally smooth surfaces are rare. A special type of boundary at the top of a plant layer or crop has been called the 'outer active surface', or, in forests, the 'crown layer'.

TURBULENT BOUNDARY LAYER

In this layer, where flux of momentum decreases linearly with height, solid obstacles, arising at the surface in the laminar boundary layer, project into the wind and cause eddies which break away from the surface and travel downwind. A surface is aerodynamically *smooth* in conditions when the laminar layer is thick enough to submerge projections from the surface; but if the irregularities project through the laminar layer, the surface is considered *rough*. As the thickness of the laminar layer depends both on the wind speed and the stability of the atmosphere, it is clear that a particular surface such as a grass sward or a hairy leaf may be aerodynamically smooth under one set of conditions and rough under another. Each surface has a characteristic roughness parameter. Air-flow over calm water may be smooth; but, except at extremely low wind-speeds, flow over land is normally rough and disturbed by surface irregularities which cause turbulence.

Eddies of two types may occur: local or stationary eddies which may arise on both the windward and leeward sides of a bluff obstacle, and eddies which break away and travel with the wind in the obstacle's wake.

The forward velocity of a turbulent wind is thus the net result of a complex movement; the wind has vertical and lateral components as well as the horizontal movement. Further, vertical and horizontal turbulence may differ in intensity (non-isotropic turbulence).

Occurrence of mechanical or frictional turbulence depends on the wind speed being high enough, and the object large enough, to cause eddying. Whether or not flow will be turbulent can be calculated by the method of Osbert Reynolds, who found that flow is turbulent when the Reynolds number,

$$\text{Re, defined as } \frac{\text{length} \times \text{wind velocity}}{\text{kinematic viscosity}}, \text{ exceeds about 2,000.}$$

Here 'length' is taken as a characteristic dimension of the object, and kinematic viscosity for air under average surface conditions is $0{\cdot}14$ cm^2. sec.$^{-1}$ Thus for a leafy bush 100 cm. high in a wind of 100 cm. per sec. we have

$$\text{Re} = \frac{100 \text{ cm.} \times 100 \text{ cm. sec.}^{-1}}{0{\cdot}14 \text{ cm.}^2 \text{ sec.}^{-1}} = 7{,}100$$

so flow would be expected to be turbulent.

In the turbulent boundary layer, properties such as temperature, amount of water vapour, and wind velocity, change much less rapidly with increasing height than in the laminar boundary layer beneath. Eddies mix the different parts of the layer much more rapidly than do the slow processes of molecular diffusion. Particles can also be carried by eddies upwards and laterally in a manner impossible in the laminar layer. In the turbulent boundary layer the wind velocity, temperature, and amount of water vapour show a change which is *linear with the logarithm of the height.* In this layer diurnal changes of temperature are less pronounced than in the laminar boundary layer underneath, and diurnal changes decrease still further with increasing height until, at the top of the next layer, they have almost disappeared.

An increase in wind-speed increases the thickness of the turbulent boundary layer both downwards, by thinning the laminar boundary layer, and upwards, by pushing into the transitional layer as turbulence increases. The turbulent boundary layer is thinnest on clear calm nights and thickest on hot sunny days, when it may reach to a height of 150 metres.

The turbulent boundary layer is the part of the atmosphere most familiar to us. While our feet are planted in the violently fluctuating climate at ground-level, our heads, and the weather-recording instruments of the conventional Stevenson's screen, inhabit the relatively equable turbulent layer.

TRANSITIONAL OR OUTER FRICTIONAL TURBULENCE LAYER

Here frictional turbulence, generated in the layer below, still dominates vertical diffusion, but it dies out gradually until, at the top of the layer, both turbulence and diurnal temperature changes disappear. Both layers may be dusty, and the top of the transitional zone is sometimes visible as a distinct dust horizon at 500–1000 metres, marking the upper limit to which spores are raised by frictional turbulence (though much greater heights may be attained by convection).

In dynamical meteorology this zone is defined as the region where the wind structure is determined partly by surface friction and partly by the Earth's rotation.

CONVECTIVE LAYER

This layer extends from about 1 km. above the ground to the top of the troposphere at about 10 km. As in all the layers constituting the troposphere, the temperature continues to decrease with height to the top of the convective layer, though diurnal temperature variation is almost absent. Frictional turbulence does not reach here, but, as already indicated, particles from the Earth's surface can be carried into this layer by large-scale convection currents when the ground is heated by sunshine.

The height above the ground attained by a mass of heated air before it loses buoyancy, depends on the temperature gradient and water-vapour content of the air at the time, as explained in the standard works on dynamical meteorology. Ascent may be halted if there is a temperature inversion layer in the upper atmosphere. Under conditions of thermal instability, 'bubbles' of heated air may arise intermittently from areas where the ground or vegetation is being heated by the sun. These bubbles may rise to the convective layer, carrying spores and other particles as well as water vapour to the level at which cumulus clouds are formed, and at times reaching to the base of the stratosphere (Mason, 1957).

NIGHT RADIATION AND TEMPERATURE INVERSION

At night, wind speeds tend to diminish; the laminar boundary layer then becomes thicker than by day and the turbulent boundary layer may become thinner, being reduced to perhaps only 10 to 15 metres in thickness.

These changes may be carried still farther if the sky is cloudless, thus allowing radiation from the ground to escape into space. Loss of heat by radiation cools the ground and this in turn cools the air lying nearest to the ground. Thus, instead of temperature decreasing with increasing height, a 'temperature inversion' is set up: over the cold air near the ground lies air at a higher temperature—up to a certain height, the top of the inversion, above which the usual lapse rate is again encountered.

As the air is coldest and densest at the bottom of the inversion, gravity tends to prevent it from ascending and mixing with warmer air above. The air in the inversion becomes stratified according to temperature and remains very stable, in contrast to the instability that is apt to develop when the ground is heated. Such a layer of cold, heavy air may flow slowly downhill as a nearly laminar katabatic wind, filling hollows with cold air and aiding the formation of frost pockets (Geiger, 1950, p. 203).

In a temperature inversion, spores and dust particles tend to settle out, leaving the air relatively clean although the air above the inversion may continue to carry a normal spore-load.

ROLE OF CONVECTION

When the surface of the ground is heated by sunshine the lowest layer of air may be heated in turn. If a large temperature lapse-rate is established, the atmosphere becomes unstable, because the less dense ground-layer of air tends to rise and carry its load of microbes upwards, being replaced by cooler air from above. The pattern of this overturn is not yet clear. A regular 'cellular' pattern of ascending and descending air has been suggested, but more recently the ascending air has been pictured as taking the form of 'chimneys' or of 'bubbles'.

Glider pilots are familiar with the properties of warm ascending currents of air or 'thermals', as described by Yates (1953). In still air a glider sinks at about 90 cm. per sec. (about 20 times the terminal velocity of a pine pollen grain). On dull days thermals do not develop. They reach their maximum upward velocity of 3 metres per sec., or up to 25 metres per sec. in cloud, at midday in summer. Yates indicates that, depending on the type of soil, on wind strength, and on sun height, a sizeable thermal is released from an area of 1·25 sq. km. every 5 to 15 minutes in summer. At a height of 300 metres, thermals may be 300 metres in diameter, though they are probably often smaller when lower, whereas at still greater heights a diameter nearer 2 km. was reported by Ludlam & Scorer (1953). Their vertical movement may cease at a temperature inversion, or may continue to from 10,000 to 50,000 ft. The temperature in a thermal appears to average 1°–2°C. higher than the surrounding air through which it is ascending.

The theory of thermals is still a matter of controversy, but there seems no doubt that air rises from some surfaces more often than from others. Green vegetation and wet soils may be relatively cool, while a ripe cereal crop, buildings, roads, or bare rock, may heat up rapidly in the sun and become the source of rising warm air. Thermals can also arise at a cold front, and glider pilots regard hilly country as the best source of thermals.

The pattern by which cool air sinks to replace the ascending warm air is also a matter of debate. Downward draughts reported in the neighbourhood of thermal upcurrents appear to be comparatively feeble. Probably the downward movement occurs over a much wider area than the thermal, as a slow sinking of the atmosphere. The sinking speed may be comparable with that of a fungus spore (Hirst, 1959), but the local rising velocity may commonly be 100 or more times this velocity. Some bird species soar in large thermals, as do dragonflies in smaller ones near the ground. Other birds haunt thermals to prey on the insects carried upwards (Scorer, 1954).

THE STRATOSPHERE

In this region, which extends upwards from the tropopause to the limit of the atmosphere, the temperature lapse-rate, characteristic of the troposphere, is zero or may even be reversed. The height of the tropopause varies with season, latitude, and other factors. The bottom of the stratosphere may be found at an altitude of about 10 km., though under special conditions it may reach temporarily to much nearer ground-level.

The dust of the stratosphere is believed to be meteoric and to have entered the Earth's atmosphere from space. It is generally believed that terrestrial dust, including organic spores, is almost, if not entirely, confined to the troposphere—except for occasional incursions in air currents dragged up into the stratosphere by volcanic eruptions (or hydrogen bombs). However, recent studies of atmospheric circulation, discussed by Machta (1959), may point to exchange of air between troposphere and stratosphere—with rising air over the equator and descending air in middle latitudes.

CIRCULATION OF THE ATMOSPHERE

Under the influence of pressure differences resulting from solar heating, and of friction between wind and the rotating earth, a general pattern of atmospheric circulation is set up. The surface winds shown in atlases are the ground-level part of a three-dimensional system that has not yet been well explored. The pattern still being worked out shows a complex circulation, with air over the Equator ascending and flowing discontinuously to the poles, which are themselves regions of generally subsiding air (Palmén, 1951). Across the Equator there is relatively little interchange between northern and southern hemispheres.

AIR MASSES

The fact that air may have the same temperature and humidity over a wide geographical area has given rise to the concept of the discrete air mass, with properties different from adjacent air masses and separated from them by 'fronts'. When an air mass remains stationary for some time, it acquires a temperature and humidity dependent on the surface on which it rests. These characteristics will be retained for some time when the air mass moves into a new region. Air masses are classified, therefore, according to their origin, and we may have, for example: polar maritime, polar continental, tropical maritime, and tropical continental types, as well as air masses of indeterminate origin (Belasco, 1952). The different air masses interest us, not only because they bring different kinds of weather but also because they might conceivably bring an air-spora characteristic of their place of origin.

IV

SPORE LIBERATION

Up to now we have considered only the physical properties of spores and of their environment. Spores, however, are parts of living organisms whose evolution has been extensively moulded by the environment. The air-spora comes mainly from species which are highly adapted towards using wind energy for their dispersal. The physical properties of the atmosphere make dispersal possible, but also set problems to organisms using it. Adaptations for wind transport have been evolved in many widely-separated taxonomic groups.

The process of wind dispersal of spores has three principal stages. (1) *Spore liberation.* This chapter describes the processes by which pollen grains or spores 'take-off' into the air from the structure where they have been formed. (2) *Dispersion.* Chapter V describes the transport of spores by gentle air currents or strong winds, and the diffusion of an airborne spore cloud. (3) *Deposition.* Chapters VI and VII will deal with the processes by which spores leave the air and land on a surface—a necessary prelude to the germination of a pollen grain or a mould spore on its substratum.

The spore or pollen output of many species is notoriously large. For instance, Pohl (1937) estimated, for the dominant species encountered by pollen analysts, the pollen production per stamen, flower, inflorescence, and branch, revealing an annual production averaging many millions per square metre of ground covered (*see also* Erdtman, 1943). According to J. J. Christensen (1942), a field of wheat moderately affected by *Puccinia graminis* would produce at least 25 million uredospores per square metre. Buller (1909) estimated that one giant puffball (*Calvatia gigantea*) produced 7 million million (7×10^{12}) spores. The spore output of mosses and ferns is also potentially enormous.

PROBLEMS OF 'TAKE-OFF'

As described in Chapter III, the surface of the ground or plant is covered by a thin layer of still air and by the laminar boundary layer of slowly moving air; a spore will fall through this composite zone under the influence of gravity. To tap the energy of moving air for dispersal a spore must overcome the adhesive forces which tend to keep it in contact with neighbouring spores or with the substratum. It must cross the still- and laminar-air layers, at the interface between the ground or other surface and the atmosphere, in order to enter the freely moving air of the turbulent boundary layer, where it stands a chance of being carried into higher layers of the troposphere.

Many species that are distributed as spores have not solved this problem, but instead have become adapted for dispersal by some other agency such as water, insects, or other animals. There are more insect-pollinated (entomophilous) *species* of flowering plants than wind-pollinated (anemophilous) species, though in the temperate regions at least there are more wind-pollinated *individuals* because of the preponderance of grasses and anemophilous trees. We may wonder how important in practice is the occasional dispersal of a spore by some agency other than that to which it is adapted. However, it is a fundamental principle that the better a species is adapted to dispersal by one agency, the poorer are its chances of dispersal by another agency—unless, like many fungi, it produces spores of several distinct types that are specialized for different dispersal mechanisms.

If we wish to control the dispersal process, a precise knowledge of the mechanisms involved is preferable to the vague idea that the spores will get there somehow anyway! Success in colonization or fertilization depends on logistics—on getting enough material to the right place at the right time.

Energy is required to detach spores from their source. It may be an active process through which, by some explosive or hygroscopic mechanism, spores are discharged by energy operating through the parent structure. Or it may be passive, by the energy of an external agent—usually wind or the kinetic energy of falling raindrops. Seasonal development of the parent structure and maturation of the spores commonly determine what organisms are in the air at a particular time, but other factors modify this pattern. The working of the various discharge mechanisms is more or less affected by external conditions, and the result is that the output of spores of a particular species varies greatly from time to time. Conversely, all the individuals of one species in an area may behave in unison, so that the composition of the air-spora differs vastly on different occasions.

Take-off Mechanisms in Cryptogams etc.

Spore- and pollen-liberation mechanisms have formed the subject of classical researches in biology for over a century. The wealth of information in the scattered literature on land plants is reviewed by Ingold (1939), and knowledge about bacteria by Wells (1955), but for protozoa and algae I know of no comprehensive treatment. In the present connection we are concerned with those aspects of the mechanism which determine when, and under what conditions, spores get into the air.

VIRUSES

The viruses are little adapted to independent air dispersal. Some viruses infecting the animal respiratory tract are forced into the air on droplets during coughing and sneezing; but most bacterial and plant viruses, if they occur in the air at all, only get there on 'rafts' of debris or water droplets. Some of the so-called polyhedral viruses infecting insects are exceptional. Reports of outbreaks among pests of forest trees in eastern Europe speak of copious yellow deposits of the polyhedral bodies, shed by parasitized insects, which coat the surfaces of vehicles travelling through the forests. Study of air dispersal of viruses might explain some of the anomalies in the behaviour of insect viruses. To prevent contamination by an airborne infective particle of the dimensions of a virus may well require quite unusual experimental precautions.

BACTERIA

Moving air does not normally detach bacterial cells from the surface of a colony, at least when this is slimy, and in the absence of an active discharge mechanism natural processes capable of producing an aerosol of single bacterial cells are unknown. Mechanical disturbance of dust, clothing, surgical dressings, etc., however, carries into the air contaminated particles of substratum acting as 'rafts' and bearing clumps of bacteria (Bourdillon & Colebrook, 1946). Rafts of soil or dust particles are raised by wind, by 'dust-devils' when the ground is heated by solar radiation, and by animal and human activity such as cultivation of bare ground. Rain splash, breakers, and sea spray continuously throw minute, potentially bacteria-laden, droplets into the atmosphere. Droplets expelled by coughing and sneezing are important indoors (*and see* p. 158), yet processes which put bacteria into the air are still not satisfactorily known. This is also true of the yeasts whose frequent abundance in the air remains unexplained, except for the Sporobolomycetaceae which show the ballistospore discharge mechanism (pp. 37–38).

ACTINOMYCETES

The mycelial organization of this group allows the Streptomycetaceae to develop aerial hyphae bearing dry, powdery spores—the first example of the sporophore elevation device, common in more elaborate organisms, for raising the spore-producing organ above the substratum and towards the moving layers of the atmosphere. Take-off conditions in the Actinomycetes seem not to have been investigated.

MYXOMYCETES (Mycetozoa, Myxogastrales)

The slime-moulds are a group thoroughly adapted to wind dispersal. Some, such as *Reticularia*, merely expose a dry, powdery spore-mass on a cushion raised above the substratum. Others, such as *Stemonitis* and

Trichia, expose small, dry spore-masses on stalks at most a few millimetres high. The spores are set free by twisting movements of hygroscopic elaters which take place with changes in air humidity (Ingold, 1939), or, in a few species, spores may be removed by eddies from shallow wind-cups.

FUNGI

Adaptations facilitating air dispersal show more diversity in the fungi than in any other group—except, perhaps, adaptations for seed dispersal among the flowering plants. They vary from the passive but quite effective processes in the Fungi Imperfecti, to the spectacular ballistic feats of the ascus gun. The various mechanisms have been summarized by Dobbs (1942, 1942*a*) and Ingold (1953, 1960), and they formed one of the main topics of the classical work of Buller (1909–50).

In contrast, spores of many other species of fungi rarely get into the air but are carried by insects, on seeds, or in soil. Mere dispersal by insects may be relatively unimportant; but, where the insect actively inoculates the substratum or host, it is a mechanism comparable in efficiency with insect pollination of flowering plants. Passive liberation by the action of external energy depends on 'spore presentation' (Hirst, 1959).

(i) *Shedding of spores under gravity.* Stepanov (1935) concluded that spores of some *Cunninghamella* species, and of some Fungi Imperfecti, including *Botrytis cinerea*, *Monilia sitophila* and *Helminthosporium sativum*, as well as the macroconidia of *Fusarium*, could be shed under gravity. However, as he also showed that minor air currents released spores of some of these fungi, the effect remains uncertain.

(ii) *Shedding in convection currents.* Stepanov (1935) placed open Petri-dish cultures at the bottom of glass cylinders 10 to 12 cm. high in which convection currents were induced by differential heating. Sticky slides or a surface of inverted sterile medium at the top of the cylinder trapped spores which might become detached and carried aloft by convection. With temperature differences of the order of 10°C., conidia of *Monilia sitophila* and *Botrytis cinerea* were freely transferred upwards, but *Colletotrichum lini* was not. Smaller temperature differences, such as resulted from the slight heat produced by a mould culture or an electric lamp shining on the floor, were ineffective.

(iii) *Blowing away* ('deflation'). This occurs commonly with dry-spored fungi including moulds, smuts, and rust uredospores. The spores are often 'presented' on an elevated sporophore, any stem or leaf pathogen usually being adequately raised on its host tissue. Quantitative studies so far are insufficient to lead to a theory of 'deflation'. Little is known about the quantitative effect of wind-speed on liberation, but there is good evidence that the higher the wind-speed the more spores are carried away.

Stepanov (1935) was apparently the first to use a small wind-tunnel to blow spores at controlled wind-speeds. Using either cultures or plants infected with pathogenic fungi, he found that the minimum wind-speed required to remove spores varied according to the organism being tested: for *Botrytis cinerea* it was 0·36–0·50 metres per sec.; for *Monilia sitophila*, *Ustilago* spp., uredospores of *Puccinia triticina*, and *Helminthosporium sativum* it was 0·51–0·75 metres per sec.; for aecidiospores of *Puccinia coronifera* and *P. pringsheimia*, 0·76–2·0 metres per sec.; for *Cunninghamella* sp., 1·5–1·75 metres per sec. On the other hand, *Phytophthora infestans* and *Fusarium culmorum* spores were not removed at any speed tested up to 3·37 metres per sec. More spores were removed in turbulent than in streamlined wind.

A special structure facilitating blowing away is the 'wind-cup' described by Brodie & Gregory (1953). Flow of air over a cup-shaped structure produces a double eddy system which can effectively remove dry spores contained in the cup, as shown by wind-tunnel experiments with smoke and *Lycopodium* spores. Soredia were also removed from the podetia of *Cladonia* at 1·5 to 2·0 metres per sec., and spores were removed from the cupulate sporangia of certain Myxomycetes at 0·5 metres per sec.

Certain Gasteromycetes, including the puffballs *Lycoperdon perlatum* and *L. pyriforme*, and the earth-stars (*Geaster* spp.), have a 'bellows' mechanism consisting of a thin, flexible, waterproof wall covering the spore mass. Indenting this wall forces out a jet of air laden with spores. Contact with animals operates the bellows efficiently, but must be a relatively rare event in nature. Raindrops or run-off drops from trees also operate the bellows mechanism, and as one fruit-body would be hit many thousands of times in a season, rain is probably the most effective mechanism in the field (Gregory, 1949). In India W. H. Long & Ahmad (1947) find that the bellows mechanism of *Tylostoma* is operated by wind-blown sand grains in addition to raindrops.

(iv) *Mist pick-up*. This is a mechanism that has only recently been recognized. Dry, or even humid, wind fails to detach spores of some fungi which are nevertheless readily removed from their conidiophores by collision with minute droplets carried by mist-laden air. This method is known to function with two important crop pathogens, *Cercosporella herpotrichoides* (Glynne, 1953), and *Verticillium albo-atrum* (R. R. Davies, 1959), and it may play a part also in the dispersal of *Cladosporium*.

(v) *Splash dispersal*. Spores of some species are 'presented' in sticky masses to which they adhere tenaciously in wind. However, spores may become incorporated in splash droplets (Plate 3, and Fig. 4) which are thrown up from the impact of a falling raindrop, or a drip from a leaf, hitting a liquid film containing spores (Gregory *et al.*, 1959). Rain splash is thus another passive mechanism, quite different from mist pick-up by which slime-spored fungi may become airborne in the smaller droplets. Experiments suggest, however, that the larger splash-droplets, over 50 or

100 μ in diameter, carry most of the spores which are dispersed in this fashion, and these droplets are massive enough to follow definite trajectories without being truly airborne.

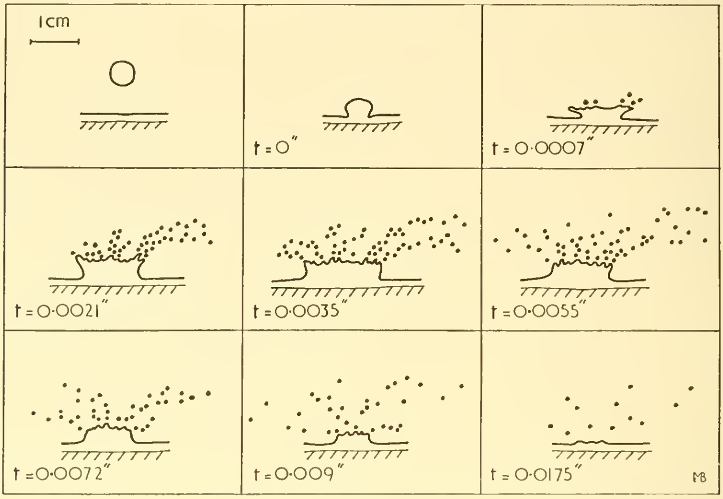


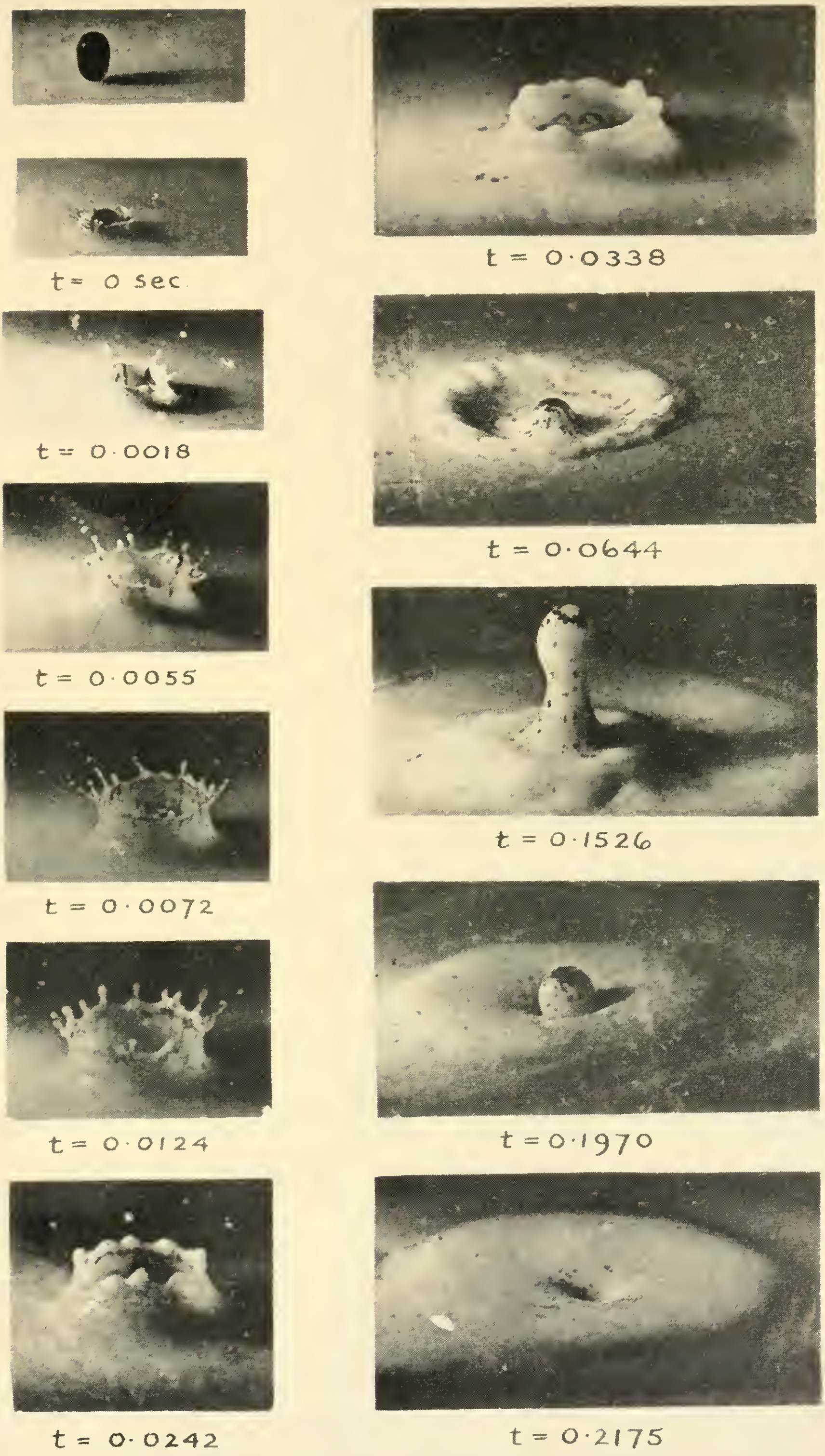
FIG. 4.—Splash from impact of water drop (5 mm. diameter) falling with velocity of 440 cm. per sec. on a thin film of water (drawn from stills from ultra-high-speed film made by Mr. E. D. Eyles at Kodak Research Laboratories, Harrow).

(vi) *The splash-cup mechanism.* This is a device, studied particularly by Brodie (1951, 1957), which is widespread among lower as well as higher plants, by which the energy of falling raindrops throws relatively large bodies to distances of several feet. Examples are the peridioles of the birds-nest fungi (Nidulariaceae), the gemmae of *Polyporus conchatus*, and droplets bearing spermatozoids of the Bryophytes. However, the projectiles scarcely become airborne, for they follow a definite trajectory.

(vii) *Hygroscopic movements* of conidiophores, which may result in detachment of spores during violent twisting, occur in a number of Fungi Imperfecti and Phycomycetes. The effect depends on rapid changes in atmospheric humidity and is often most marked in the morning hours.

All active mechanisms for spore liberation depend on the fungus having sufficient water-supply. The more ephemeral fruit-bodies develop after rain and discharge spores for a short period only. More durable fungi can be dried but will discharge spores again when re-wetted; others again can draw on an extensive mycelium deep in the substratum and may be almost independent of the weather. Distances of ejection vary and have been compiled by Spector (1956, p. 153).

(viii) *Squirt-gun mechanism.* This is found in many Ascomycetes in which the ascus, which contains the ascospores, typically swells at maturity



t= 0 sec

t = 0·0018

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t = 0·0072

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t = 0·0338

t = 0·0644

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t = 0·2175

Photographs by Worthington & Cole (1897) showing splash of a water drop weighing 0·2 gm. (coated with lamp-black) falling 40 cm. into a mixture of milk and water. Mag. $\frac{3}{4}\times$.

PLATE 3

and finally bursts at the tip, projecting the spores into the air to a distance varying from a fraction of a millimetre to several centimetres. The larger the projectile, the further it tends to be shot (Ingold, 1956*a*; Ingold & Hadland, 1959).

Four clearly-distinct types of liberation are recognized in the Ascomycetes by Ingold (1953), as follows:

'1. In the *Discomycete* type the spore-producing surface, consisting of asci intermixed with parallel paraphyses, is more or less exposed, most often as a lining to a shallow cup-shaped apothecium. The extensive exposed hymenium allows opportunities for 'puffing'—the simultaneous bursting of numerous asci.

'2. In the *Pyrenomycete* type the asci are contained in a small flask-shaped structure (perithecium) which opens to the outside by a minute ostiole. Before each ascus can discharge the spores, its tip must reach the ostiole, and the canal of the neck is usually so narrow that normally only one ascus can emerge at a time.

'3. In the *Erysiphales* type the fruit-body is a cleistocarp. This is rather like a perithecium but is completely closed; there is no ostiole. In this type the swelling asci must first burst the wall of the cleistocarp before they can emerge and discharge their spores.

'4. In the *Myriangium* type, though the hymenium is exposed in a structure like a small apothecium, the spherical asci are embedded in a plectenchymatous tissue and are free to discharge only when this gradually undergoes gelatinization.'

Some Ascomycetes which lack explosive asci may liberate spores in slime to be dispersed by rain-splash. Other species, again, may be either explosively or slime-dispersed, according to the conditions obtaining. With still others, such as *Chaetomium* whose spores are regularly found in the air, the spore discharge mechanism is unknown.

(ix) *Squirting mechanisms*, which propel spores violently into the air, occur among Phycomycetes in *Pilobolus*, *Basidiobolus*, and *Entomophthora muscae*, as well as in the imperfect genus *Nigrospora* (Webster, 1952).

(x) *Rounding-off of turgid cells* acts as a discharge mechanism when the flattened double walls between two turgid cells suddenly separate. By this means spores of some Phycomycetes can be ejected up to a centimetre into the air. The same mechanism operates to eject aecidiospores when aecidia of rusts become moistened. Discharge of all these types is favoured by high humidities, and indeed aecidiospores of the rust fungi are discharged under conditions unlike those favouring dispersal of uredospores.

(xi) *Basidiospore discharge*. This is a highly characteristic process which is found with the same essential features almost throughout the Basidiomycetes. The basidium is a cell producing one or more sterigmata, at the end of each of which one basidiospore is formed asymmetrically. Typically, when the spore is mature, a drop of water is excreted at the hilum end of the spore and almost immediately the spore is shot off to a distance of a fraction of a millimetre or more. In species which form the basidia on exposed surfaces, as in many lower Basidiomycetes, the spore after discharge has a chance of being picked up by an air current.

The higher Basidiomycetes often show great elaboration of a stalked fruit-body with the basidia lining the vertical surfaces of folds, gills, pores or spines. Here, in cavities protected from wind and adverse conditions, the basidiospores are discharged into still air and fall under the influence of gravity into the moving air-current below the cap-shaped or bracket-shaped fruit-body. Spore discharge in the higher Basidiomycetes often goes on continuously throughout almost the entire life of the fruit-body—to all appearances little affected by wind, temperature, or humidity, though it must be emphasized that accurate quantitative studies on the effects of these factors are lacking. Just how a basidiospore is shot off the sterigma remains a major puzzle of mycology; several explanations have been advanced, but none seems entirely satisfactory. Nevertheless the process is highly efficient and basidiospores are a conspicuous component of the air-spora.

The same mechanism occurs in the mirror-yeasts (Sporobolomycetaceae), which may possibly have evolved from lower Basidiomycetes (unlike the Saccharomycetaceae, which are clearly Ascomycetes). To avoid prejudging the issue by calling the spores of the mirror-yeasts 'basidiospores', the term 'ballistospores' has been coined to include all spores showing the drop-excretion discharge mechanism. A moist substratum is necessary for spore discharge in the Sporobolomycetaceae.

LICHENS

The fungus component of lichens discharges ascospores from typical apothecia or perithecia, or basidiospores from basidia. Fragments of the thallus including both fungal and algal components are blown about freely. Rounded groups of algal cells surrounded by fungal hyphae, separating off from the lichen thallus as soredia, are also blown away; but we know little as yet about the relative importance of these various modes of reproduction.

ALGAE

Adaptations facilitating take-off into the air are unknown in the algae, though some of the simpler types of algal cells get into the air regularly. Pettersson (1940) suggested that *Chlamydomonas nivalis* is carried away from its habitat on snow-fields and glaciers in melt-water and becomes airborne by splash in mountain torrents. Lichen soredia may possibly aid the dispersal of algae when they become grounded in a habitat moist enough for the algal component to dominate the fungus, and where the resulting colony will be an alga instead of a lichen. Again, some terrestrial and epiphytic algae may crumble and blow away.

BRYOPHYTES

Spores of mosses and liverworts are formed in sporangia which are typically raised on stalks above the substratum, but the structure of the sporangium is quite different in the two groups. The moss sporangium is a firm 'box' opening at the top, whereas the liverwort sporangium breaks open completely, exposing the spores in a mass of stiff threads (elaters).

In the simpler liverworts the spores may be blown away by wind from the mass of elaters, or the elaters may twist hygroscopically, actively throwing spores into the air. In most leafy liverworts, however, a spring mechanism released by water-rupture in the drying elaters throws the spores into the air (Ingold, 1939, 1956), while in *Frullania* the sporangium explodes by an efficient spiral spring mechanism which also is released on drying.

The mosses liberate spores from the stalked sporangium (capsule) by two principal methods. *Sphagnum* has an 'air-gun' mechanism (Ingold, 1939). An air space below the spore mass is compressed by transverse contraction of the drying sporangium wall, internal pressure increases and, finally, the top of the sporangium breaks, ejecting a spore cloud to a height of 15 or more centimetres.

Most of the other mosses have flask-shaped sporangia, which open gently at the top when mature. In some genera the mouth of the sporangium is surrounded by one or more rows of triangular teeth which move hygroscopically, closing the mouth at high humidities. To what extent spore liberation in nature depends on shaking of the sporangium in the wind, and what role is played by hygroscopic movements of the teeth in actively throwing out the spores, is still a matter of controversy; but evidently spore liberation is checked by high humidities and low wind-speeds.

PTERIDOPHYTES

Spores of Pteridophytes (ferns and their allies) are formed on the fronds within a closed sporangium, from which they are dispersed into the air by a 'sling' mechanism depending on water-rupture under great tension as the maturing sporangial wall dries (*see* Ingold, 1939). Pettersson (1940), in Finland, found that effective scattering of fern spores takes place out-of-doors only when the relative humidity of the air falls to 76 per cent, or even to 60 per cent, according to the species.

Pollination of Phanerogams

Insects and wind are the chief agents of cross-pollination in flowering plants. Other pollinating agents that are effective in a far smaller number of species include water and humming-birds. There are probably ten times as many entomophilous (insect-pollinated) as anemophilous (wind-pollinated) species of flowering plants in the world as a whole.

The characteristics of wind-borne pollen become clear when contrasted with insect-borne pollen (Table IV). There are many exceptions to the generalizations in this table and, in particular, some plants make the best of both methods. Both anemophilous and entomophilous plants often protect their pollen from the rain, and many store it within the flower for some time after shedding from the anthers. Anemophilous pollen is not generally shed into very calm or very damp air.

TABLE IV

TYPICAL CHARACTERISTICS OF ANEMOPHILOUS AND ENTOMOPHILOUS PLANTS

	Wind-pollinated	Insect-pollinated
Flowers	Lack conspicuous and attractive petals, scent, and nectar.	Often with bright colours, scent; nectar attractive to insects.
Flower position	Projecting into air: hanging from bare branches before leaves open (catkins); on erect stalks (grasses, etc.); or at ends of branches (conifers).	Tend to be exposed to view, but not exposing anthers to wind. Flowers usually maturing when plant in full growth and insects abundant.
Prevention of self-fertilization	Male and female organs often in separate flowers or inflorescences, or on separate plants. If flowers hermaphrodite, one sex commonly matures before the other, or, if sexes are in separate inflorescences, the female is often above the male.	Flowers usually hermaphrodite, with structural or genetic barriers to selfing.
Pollen	Often shed into the air in vast quantities.	Usually restricted pollen production with little shedding.
	Shape rounded, often nearly spherical or ellipsoidal.	Shape very variable.
	Size-range narrower than entomophilous pollen and seldom less than 15 μ.	Size very variable, 3 to 250 μ, but often less than 15 μ.
	Surface typically smooth as seen under the microscope, non-sticky, easily separating into single grains in air.	Surface typically rough, spiny or warted, often oily or sticky, tending to adhere in clumps.

GYMNOSPERMS

Conifer pollen, instead of being formed in stalked anthers as is that of Angiosperms, is produced in two or more pollen sacs on the lower side of the male cone-scales. The pollen grains are large and often bear two conspicuous air-filled bladders which decrease the density of the particle and so retard its fall under the influence of gravity.

In *Pinus*, cone-scales of the erect male cone separate as they mature, and pollen shed from the paired sacs falls into small hollows on the upper surface of the cone-scale below. From these hollows the pollen is blown away when the wind reaches sufficient velocity. Some other conifers have hygroscopic mechanisms protecting their pollen from rain and allowing its release only in dry weather. In *Taxus*, *Thuja*, *Cupressus*, and *Juniperus*, the pollen is not winged. In *Juniperus* the expanded ends of the cone-scales interlock closely in damp weather, separating again in dry air and allowing pollen to be blown out.

ANGIOSPERMS

Details of flowering-plant pollination mechanisms are given by Marilaun (1895), Knuth (1906), Erdtman (1943, 1952, 1957), Wodehouse (1945) and others.

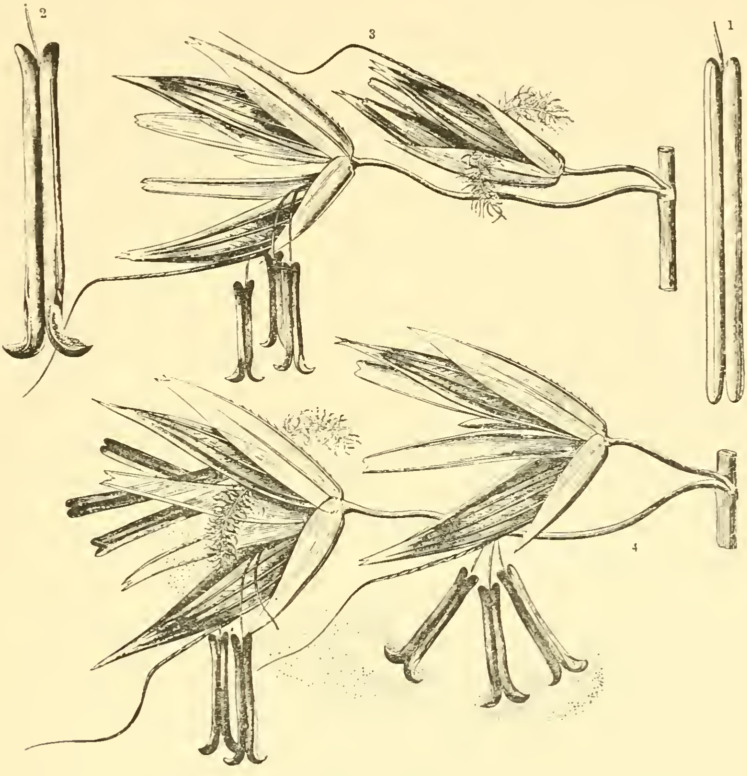


FIG. 5.—Anthesis of false oat-grass (*Arrhenatherum elatius*): (1) closed anther; (2) open anther; (3) spikelets on a calm day; and (4) spikelets in a wind. (Reproduced from Marilaun's: *Natural History of Plants*, by permission of Messrs. Blackie & Son, Limited.)

(i) *Grasses, rushes, sedges and their allies.* The Gramineae, Cyperaceae, Typhaceae, and Juncaceae are typically wind-pollinated. From the raised inflorescences of grasses, the anthers are extruded on long filaments to which they are so lightly attached that they vibrate in the slightest wind. Often, as in *Arrhenatherum*, the end of each pollen-sac bends up (Fig. 5), forming a spoon into which pollen is shed from a slit, and where it accumulates until blown away by the wind. Either damp or very dry weather may delay both extrusion of the stamens and splitting of the anthers. Except for rye and maize, most cultivated cereals are self-fertilized and shed little pollen, but pasture grasses are free shedders.

In central Europe, Marilaun (1895) found that different grasses flowered for brief periods of only 15 to 20 minutes daily, and at characteristic times of the day:

hours	
04–05	*Poa*, *Koeleria*, *Avena elatior.*
05–06	*Briza*, *Deschampsia caespitosa*, *Triticum*, *Hordeum.*
06–07	*Secale*, *Dactylis*, *Andropogon*, *Brachypodium*, (*Bromus?*), *Festuca* spp., *Holcus* (1st anthesis).
07–08	*Trisetum*, *Alopecurus*, *Phleum*, *Anthoxanthum.*
08–09	Exotic types in Europe: *Panicum*, *Sorghum.*
09–10	*Setaria italica*, *Gynerium* (*Cortaderia*) *argenteum.*
11–12	*Agrostis* spp.
12–13	*Melica*, *Molinia*, *Nardus*, *Elymus*, *Sclerochloa*, some *Calamagrostis* spp.
14	A few *Bromus* spp.
15	A few *Avena* spp.
16	*Agropyrum.*
17–18	*Deschampsia flexuosa.*
19	*Holcus* (2nd anthesis).

This timetable does not necessarily apply elsewhere, and, in Nebraska, Jones & Newell (1946) found a less precise timing and showed that anthesis is determined by temperature. They distinguish cool-season from warm-season grasses. Cool-season grasses include: *Festuca elatior* (anthesis at 13.30–15.00 hours); *Agropyrum* spp. (14.00–18.30 hours); *Bromus inermis* (14.30–19.00 hours); *Poa pratensis* (during the night); *Secale cereale* (02.30–11.30 hours, maximum 06.00–08.30 hours). The warm-season group includes: *Bouteloua gracilis* (03.00–09.00 hours, maximum 04.30–05.30 hours during darkness); *Buchlöe dactyloides* (06.30–13.00 hours, maximum 07.00–08.30 hours); *Panicum virgatum* (10.00–12.00 hours, delayed in cool season); *Zea mays* (07.30–16.00 hours, maximum 08.30–11.00 hours).

Hyde & Williams (1945, p. 89), from the cooler climate of Wales, report both discrepancies and agreements with Marilaun's timetable: *Holcus lanatus* (04.00–06.00 hours, but mainly at 14.00–19.00 hours); *Cynosurus cristatus* (05.00–06.00 hours); *Arrhenatherum* (07.00–08.00 hours); *Trisetum flavescens* (before 08.00 hours); *Festuca pratensis* (08.00–14.00 hours).

(ii) *Aquatic monocotyledonous herbs* include a few other wind-pollinated plants, for example *Triglochin* and *Sparganium*, while in the genus *Potamogeton* some species are pollinated by wind and others by water.

(iii) *Entomophilous herbs and low shrubs* include some species in which the phase of insect visitation is followed by an opportunity for wind-pollination, the anthers first shedding pollen within the corolla; but as the flower matures, the elongating filaments protrude and scatter pollen in the wind. These types include the semi-parasites *Bartsia* and *Lathraea*

(Rhinanthaceae), and the heaths *Calluna* and *Erica*—but not *Rhododendron*, which has very sticky pollen.

(iv) *Tropical and sub-tropical trees* include few anemophilous species, but *Casuarina* and *Myrothamnus* are wind-pollinated, and some of the palms, although entomophilous, shed a good deal of pollen, which may be carried by the wind.

(v) *Nettles and their allies* form an anemophilous group which do not store pollen after dehiscence of the anthers. The anthers dry as they mature, tissue tensions are set up, and suddenly, as the pollen sacs burst, the filaments uncoil, throwing pollen into the air. The process can be watched on a still, dry day when small puffs of pollen appear as the nettle flowers explode, but in damp air dehiscence of the anthers is inhibited. The mechanism occurs in *Urtica*, *Parietaria*, *Morus*, and *Broussonetia*. A sifter mechanism similar to that of the grasses occurs in *Cannabis* and *Humulus*.

(vi) *Herbs with inflorescences elevated* above the general level of the foliage include a number of anemophilous types such as *Mercurialis*. In *Plantago* and *Globularia* the anthers, which are exposed in cups, close their slits in moist weather but shed their pollen in dry air. Upward-facing cups occur also in *Poterium* and *Sanguisorba*. Sifter mechanisms occur in some species of *Rumex* and *Thalictrum*. Other conspicuous pollen shedders occur in the Chenopodiaceae (*Beta*, *Salsola*, *Chenopodium*) and in the Amaranthaceae, and also in some groups within the Compositae—especially *Ambrosia* and *Artemisia*.

(vii) *Deciduous trees* of temperate regions form a biological group. Typically the male flowers are aggregated into pendulous catkins, usually appearing shortly before the leaves expand. In *Alnus*, *Betula*, *Castanea*, *Corylus*, *Fagus*, *Juglans*, *Populus* (*Salix*, like *Tilia*, is both insect-pollinated and a wind shedder), and *Quercus*, pollen is protected from rain after shedding while temporarily stored on the upper scales of the flower standing underneath—until it is blown away by wind in a manner reminiscent of *Pinus*. *Platanus* closes its catkins by a hygroscopic mechanism, so that pollen is not merely protected from rain but can be blown away only in dry weather. *Hippophaë* pollen is shed into the base of the flower while this is still in bud. At maturity the perianth lobes remain united at the top but separate at the base, leaving slits through which pollen can be removed by the wind. In another group, including *Fraxinus*, *Buxus*, *Phillyrea* and *Ulmus*, the anthers project as upward-facing cups from which pollen is removed by wind.

The take-off mechanisms briefly sketched in this Chapter, with others (doubtless including some still undiscovered), are not mere curiosities of natural history. On the contrary, they are highly efficient processes that restrict spore liberation to limited meteorological conditions. Pollen and spores of mosses and ferns tend to be shed into dry winds. Ascomycetes and lower Basidiomycetes are more likely to discharge spores when the substratum is wet. Spore shedding in higher Basidiomycetes is less affected by air humidity and wind speed. Spores of some Fungi Imperfecti may depend on wind for removal, or on changes in humidity for hygroscopic movements, or on rain for splash dispersal. Soil- and dust-borne bacteria and protozoa are probably borne aloft in high winds from heated or mechanically disturbed ground. The nature of the 'take-off' mechanism profoundly affects the occurrence of different kinds of spores or pollens in the atmosphere—with consequent significance for hay-fever patients, seed-crops, plant diseases, evolution, and geographical distribution.

V

HORIZONTAL DIFFUSION

We have now described the particles composing the air-spora and the relevant properties of the atmosphere. What happens to the particles after they have been launched into the atmosphere? Common-sense tells us that they become dispersed—in the sense that their concentration per unit volume of air decreases with increasing distance from the point of liberation.

Tyndall (1881) believed that airborne microbes float through the atmosphere in miniature clouds. He explained Pasteur's demonstration of non-continuity in the spontaneous generation controversy by postulating that Pasteur sometimes opened his flask in the midst of a bacterial cloud and obtained life, and sometimes in the interspace between two clouds and obtained no life. In hospital practice, opening a wound during the passage of a bacterial cloud would have an effect very different from opening it in an interspace between clouds.

It was not necessary to draw this conclusion, however, as Pasteur's results could be explained equally well if microbes were randomly distributed in the air. Evidence for random distribution was obtained by Horne (1935), who applied Fisher's χ^2 test to catches on 1,000 or more Petri dishes of sterile media which had been exposed in Kentish orchards by N. W. Nitimargi. The observed frequencies of total bacteria or total moulds, or of any genera or species tested separately, did not depart significantly from the Poisson distribution. Horne concluded that micro-organisms are distributed at random in the air, and that, for making valid comparisons between populations of airborne microbes at different places and times, analysis of variance could legitimately be applied to plate counts.

Dispersion of the Spore-cloud

It is still convenient to speak of clouds of spores—not, indeed, keeping together in the manner of locust swarms, but tending to become dispersed while suspended passively in the atmosphere. Sampling a region small enough in relation to the size of the cloud may then reveal a random distribution of particles.

Dispersion of the spore-cloud can be deduced from early observations on the distribution of rust on rye by Windt (1806), who observed that rust was severe near barberry bushes which are now known to be the alternate hosts for the fungus: 'the effects are striking and desolating in the distance of ten to twelve paces, I have also perceived them visibly at 50, 100, 150 paces and a final attack at above 1,000 paces.' Similarly, dispersion of the pollen cloud made it possible for Blackley (1873) to advise his hay-fever patients to keep away from grass fields during the flowering season of the grasses. Attempts to formulate the process of spore dispersion through the atmosphere have been based on geometrical, empirical, or meteorological considerations.

The geometrical approach is suggested by analogy with the laws of radiation. Nägeli (1877) stated that the amount of dust which comes on an air current from one place falls off with the inverse square of the distance, whereas E. Fischer & Gäumann (1929) stated that, with linear increase of the distance, the chance of infection by rust spores decreases in cubic progression. Kursanov (1933) stated that, in the absence of wind, the number of fungus spores would fall off inversely as the cube of the distance from the source. The ideas that underlie the geometrical approach are simple. Spores travel away from the point of liberation: at greater distances the volume of air which they can occupy increases as the *cube* of the distance or, alternatively, the surface of the ground on which they could fall increases as the *square* of the distance. A third possibility would be a simple inverse relationship with distance, as the areas of successive annuli around a point increase in arithmetical progression.

The geometrical method is unsatisfactory because, although in a general way it illustrates the features of dispersion, it is not clear why spores should travel and spread out in the manner predicted. The particles interesting to us here are passively borne and do not behave like radiations, because the air which carries them is not in process of being continuously generated at some point in the atmosphere; consequently some totally different concept is needed.

The approach by empirical curve-fitting has been based on field records of dispersal gradients, such as the scatter of seeds or seedlings on the ground, contamination of seed crops by foreign pollen, or the incidence of plant diseases. Using such data, a curve is fitted to the observed points, either graphically or by the statistical method of least squares, and an attempt is made to find an empirical formula to fit the curve. These methods will be referred to in detail in Chapter XIII, after the subject of spore deposition has been discussed. In general the empirical method has the advantage that an equation can usually be obtained, containing at most three parameters, which gives a good fit to any one set of field data. On the other hand, it is difficult to compare results obtained by different workers. The parameters are calculated from the data and correspond to no obvious natural phenomena; consequently it is difficult to use empirical formulae to predict a dispersal pattern under conditions differing from the original one.

In the long run a more ambitious approach seems essential, with the aim of developing formulae whose parameters correspond to factors of the environment, and which take into account the total number of microbes liberated (if known), allow for variations in weather, and use a standard unit of distance.

Diffusion as a Result of Atmospheric Turbulence

Watching the drift of smoke from a bonfire or factory will convince the observer that wind, instead of having a steady streaming motion, is characteristically turbulent as described in Chapter III. According to Brunt (1934), large numbers of small-scale eddies, whose periods are of the order of 1 second, are usually present in the turbulent boundary layer, and at least two-thirds of the eddying energy is associated with eddies of less than 5 seconds. The action of these very numerous eddies of varying size on the very numerous spores produced from plant sources, makes some regularity in the dispersal pattern possible.

The study of eddy diffusion has proved difficult, but it provides the most promising approach to the elucidation of dispersal. Before describing the methods in detail, a few general notions—familiar to physicists, but mostly unfamiliar to biologists—must be introduced.

We are attempting to discover laws governing spore diffusion in the atmosphere. In nature this is often a complex process, as there are obstacles preventing the free flow of air. We therefore use a device familiar to physicists—making a simplified model in the hope that, if we can understand the process of diffusion under simple conditions, we shall be able to attack the more complex situations found in nature. The assumptions we have to make for a simplified model are as follows.

(i) *The field.* Diffusion is assumed to be taking place in three dimensions in the atmosphere over a plane surface which is of indefinite extent, free from topographical irregularities—not necessarily 'smooth', but, if aerodynamically rough, then uniformly so.

(ii) *Co-ordinates.* To describe movement over the plane surface we need a system of co-ordinates. Their origin, 'O', is conveniently taken to be the point of liberation of the pollen or spores. The 'x'-axis is horizontal and positive in the down-wind direction, and the 'y'-axis is also horizontal but at right-angles to the direction of the wind. Lengths above and below the origin are measured on the vertical 'z'-axis.

(iii) *Sources.* Particles are liberated from a source. The simplest form of source is a 'point source', and this may either liberate a number 'Q' of spores at a single instant (an 'instantaneous point source'), or it may be a 'continuous point source' emitting Q spores per second.

Instead of a point source we may have a 'line source'. For simplicity we assume that the line is horizontal, and is emitting Q spores per centimetre of its (effectively) infinite length. The line source in turn may be instantaneous or continuous. Furthermore, we may have an 'area source' (emitting Q spores per square centimetre), or a 'volume source'. Real sources in the field that correspond approximately to these ideal sources would be a single plant (point), a hedge (line), a ground crop (area), and an orchard or forest stand (volume). The dimensions of the source must be treated as relative to their distance: thus a field would be regarded as effectively a point source when considered from distances many times its own width.

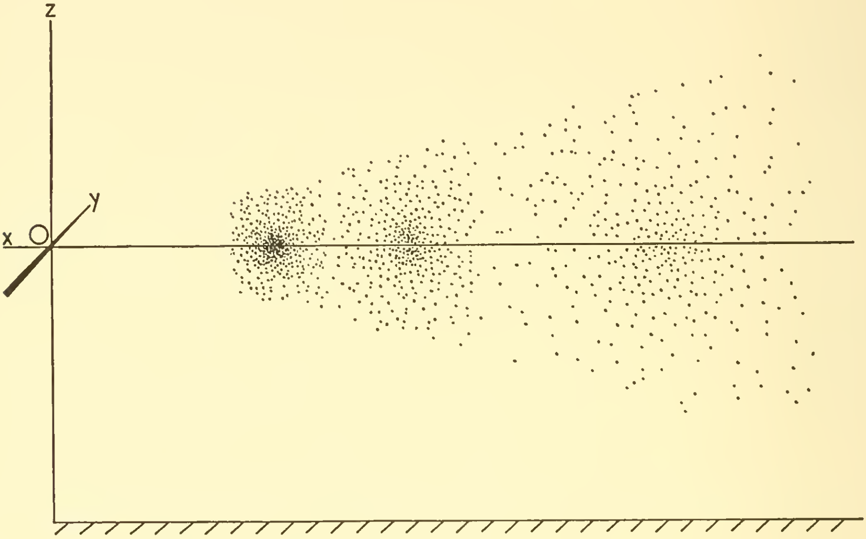


FIG. 6.—Diffusion of spore-cloud during horizontal travel in wind. O = origin of co-ordinates at source of liberation; x, y, z = down-wind, cross-wind, and vertical axes, respectively. Growth of cloud is measured by increase in standard deviation after the centre of the cloud has travelled to three positions down-wind.

All these sources may be instantaneous or continuous. The cloud from an instantaneous point source is a puff or spherical cloud, whereas the conical cloud arising from a continuous point source is familiar in the smoke plume from a chimney. A continuous point source can be viewed as made up of a succession of overlapping instantaneous emissions.

(iv) *Standard deviation.* Suppose that a 'puff' of spores has been liberated at an instant from a point source into a wind and has become subject to the action of atmospheric eddies which move individual spores apart at random. After a short time the particles composing the cloud will show a *scatter* around their origin (Fig. 6). At any instant such a cloud has two characteristics which we could compute if we had all the data: (1) the *mean position* of the particles, i.e. the centre of the cloud, which can be expressed as a point on the system of x, y, and z ordinates; and (2) the standard deviation, σ, of the particles from their mean position. When the cloud has travelled farther down-wind it will have a new mean position, and during the time the cloud has been travelling it will have been further diluted by eddies, its particles will have got farther apart, and consequently their standard deviation will have become larger.

The next problem is to find a relation between the standard deviation and the distance travelled. How does σ grow as x grows? This is a problem that has excited the interest of many workers since the First World War, who were attempting to predict the concentration of gas clouds, smoke screens, smoke trails, and crop pathogens.

The pioneer in the subject was the Austrian meteorologist, Wilhelm Schmidt (1918, 1925), who put forward a theory similar to those being developed almost simultaneously in Britain by G. I. Taylor and L. F. Richardson. Schmidt supposed that, with a given state of turbulence of the air, diffusion of particles proceeds like the diffusion of heat in a solid, but with an atmospheric turbulence coefficient A/ρ replacing the coefficient of thermal conductivity. He showed that for these conditions

$$\sigma^2 = 2(A/\rho)t, \text{ where } t = \text{time.}$$

His work is now mainly of historical interest, but we should note one interesting feature: according to Schmidt the standard deviation squared is proportional to the *time* during which diffusion has been taking place, so that on his theory the standard deviation will not be constant at a given distance, but will depend on the time taken to reach that distance, i.e. upon the speed of the wind.

Schmidt also assumed that the particles in the diffusing cloud are brought to ground-level by their fall under gravity, and he used measured values of terminal velocity to fix dispersal limits for various organisms (cf. Table XXVII).

Sutton (1932) recognized that diffusion in the atmosphere differs from molecular diffusion of heat in a solid in one important respect. Diffusion in a solid is constant (depending on the mean free path of the molecules) however long the diffusion has been going on. Diffusion in the atmosphere is much more complex, because atmospheric eddies are of a vast range of sizes, varying from a centimetre or so up to eddies that we recognize as fluctuations in wind direction, and even to cyclones and anticyclones. Sutton realized that the size of eddy effective at a given moment in *diluting* a cloud is of the same order as the size of the cloud itself at that moment. Thus a 1–cm. eddy would not effectively dilute a cloud 1–metre in diameter, and a 1,000–metre eddy would merely carry a 1–metre cloud around bodily without diluting it. The eddy that dilutes a 1–metre cloud is itself of the order of 1 metre. This led Sutton to an equation for the standard deviation which is fundamentally different from that of Schmidt:

$$\sigma^2 = \tfrac{1}{2}C^2(ut)^m,$$

where t = time; u = wind-speed; 'C' is a new coefficient of diffusion with dimensions $(L)^{\frac{1}{8}}$; and '*m*' is a number varying between 1·24 in extremely stable, non-turbulent wind, and 2·0 under conditions of extreme turbulence. The value for normal overcast conditions with a steady wind is $m = 1{\cdot}75$.

Because wind-speed multiplied by time equals distance we can write Sutton's formula: $\sigma^2 = \frac{1}{2}C^2x^m$. This suggestion that σ^2 is a function of the distance, x, is not unreasonable, because the surface roughnesses which generate eddies are spread out along the distance travelled by the cloud. It is moreover a tempting theory, because we need not know the wind-speed under which dispersal takes place.

Values of C decrease with height because conditions at great heights are unfavourable for the formation of eddies. Values for *m* appear to increase with longer sampling periods, and Sutton suggests that *m* itself is a function of time. In making continuous observations over a long period on the density of a cloud, he suggests that the random element may become smoothed out, so that, over a sufficiently long period, $m = 2$. These possibilities should be borne in mind when the density formulae described below are applied to some biological data where the sampling period is very long.

In practice it is found that near ground-level, diffusion takes place faster on the x- and y-axes than on the vertical z-axis. Turbulence is then said to be 'non-isotropic', and C has to be represented by its components: C_x, C_y, and C_z.

The number *m* is an indicator of the degree of turbulence of the air and is, as a first approximation, independent of the mean wind-velocity. It is primarily affected only by those factors which tend to damp out or increase turbulence, such as the vertical temperature gradient and the roughness of the ground. For conditions of spore dispersal tests it seems appropriate to assume values of $C_y = 0{\cdot}5\text{–}1{\cdot}0\ (\text{metre})^{\frac{1}{8}}$, $C_z = 0{\cdot}1\text{–}0{\cdot}2\ (\text{metre})^{\frac{1}{8}}$, and $m = 1{\cdot}75\text{–}2{\cdot}0$.

Expressions for the concentration of particles in a cloud emitted from various types of source were deduced by Sutton (1932), and are analogous to heat-conduction equations, as follows:

(i) *An instantaneous point source*, such as a puff of Q grams of smoke, or a number Q of spores emitted at an instant of time. Here the concentration in the cloud is given by

$$\chi = \frac{Q}{\pi^{\frac{3}{2}}C^3x^{\frac{3}{2}m}}\exp\left\{-\frac{r^2}{C^2x^m}\right\},$$

where 'r' = distance from the centre of the puff or cloud.

(ii) *A continuous point source*, such as a factory chimney emitting Q particles per second. Here, to obtain an integral that can be handled conveniently, the assumption is made that the spread of the cloud laterally and vertically is small compared with its spread down-wind. When emission has continued long enough for the distribution to reach a steady state, the concentration is given approximately by

$$\chi = \frac{Q}{\pi C^2 u x^m} \exp\left\{ -\frac{y^2+z^2}{C^2 x^m} \right\}.$$

The cross-wind concentration shows a 'normal' distribution of particles. On the axis of the cloud ($y = z = O$) the concentration is given by the simpler expression

$$\chi = \frac{Q}{\pi C^2 u x^m},$$

and because, according to the theory, m cannot exceed 2·0, the fall-off in concentration on the axis of a point-source cloud cannot be more rapid than the inverse square, no matter how turbulent the wind may be.

(iii) *A continuous line source at right-angles to the mean direction of the wind*, emitting Q particles per second per centimetre, and assuming the line to be of infinite length

$$\chi = \frac{Q}{\sqrt{(\pi)} C u x^{\frac{1}{2}m}} \exp\left\{ -\frac{z^2}{C^2 x^m} \right\}.$$

Values obtained by Sutton suggest that, as a rough and ready rule, a finite line source behaves as a line of infinite length for distances of travel of the cloud up to 4 times the actual length of the line. For points on the xOy plane

$$\chi = \frac{Q}{\sqrt{(\pi)} C u x^{\frac{1}{2}m}}.$$

Sutton's statistical method does not exhaust the possible approaches to the problem of atmospheric diffusion, and attempts to find a still more useful model continue (*see* H. L. Green & Lane, 1957). From the theory of T. von Kármán, Calder (1952) developed an equation which is said to give better predictions than Sutton's theory up to distances of 100 metres, but not for greater distances. It is also difficult to apply Calder's equations except to point sources. Another theory of dispersion, based on fluctuations in wind direction, is outlined by Sheldon & Hewson (1958), and a recent theory by Clarenburg (1960) will have to be taken into account.

FIELD EXPERIMENTS ON DIFFUSION OF SPORE-CLOUDS

Several experiments have now been reported that give data from which it is possible to test the applicability of eddy diffusion theories to diffusion of the spore-cloud in a horizontal direction.

Stepanov (1935) used artificial sources of spores that were liberated at a point in the open air. He trapped the spores on glass slides, coated with glycerine jelly, placed on the ground at various distances from the source and in various directions relative to the wind. At the end of the experiment cover-glasses were placed on the slides, and the number of single spores per unit area was counted (spore clusters were disregarded).

In Experiment 1 (28 July 1933), on a lawn near the Middle Neva River, Elagin Island, Leningrad, approximately $1{\cdot}2 \times 10^9$ spores of *Tilletia caries* were disseminated into the air through gauze, at a height of about 80 to 120 cm. above the ground. According to anemometer readings the wind varied from 0·5 to 4·0 metres per sec., but sometimes fell to a complete calm; its direction was also variable. Two glass slides were placed at each trapping position, the numbers of spores trapped being shown in Table V.

TABLE V

RESULTS OF DISPERSAL OF SPORES OF *Tilletia caries*, Experiment 1 (Stepanov, 1935)

Number of spores per cover-glass 18 × 18 mm. (average of 2)

Angle of slide to wind	At 5 metres from place of dispersal of spores	At 10 metres from place of dispersal of spores	At 15 metres from place of dispersal of spores	At 20 metres from place of dispersal of spores
− 20°	204	23	4	0
− 10°	435	45	19	8
+ 30°	964	212	207	49
+ 45°	1198	587	87	142
+ 55°	659	123	77	15
+ 65°	341	24	26	7
+ 75°	365	5	26	53
+ 85°	20	10	9	14

Experiment 2 (5 September 1933) was made at the same place as the previous one. This time a mixture of spores of *Tilletia caries* and *Bovista plumbea* was disseminated through a small sieve at a height of about 150 cm. Scattering of the spores occupied 15 minutes, after which 30 to 35 minutes were (perhaps unnecessarily) allowed to elapse for the deposition of the spores. During this period the wind mostly varied from 2·3 to 3·0 metres per sec., but was sometimes calm. As shown in Table VI, three slides were placed at each trapping position. Approximately $1{\cdot}8 \times 10^9$ spores of *Tilletia* were used but those of *Bovista* were unfortunately not estimated.

Stepanov's results led him to an empirical law of spore dispersal which was expressed as: $y = C + a/sx$, where 'y' = the distance at which the spores were trapped, x = the number of spores deposited per unit area of trap surface, s = area of trap surface, and 'C' and 'a' are parameters dependent on the conditions of the experiment. The number of spores deposited is thus regarded as varying inversely as the first power of the distance from an origin of co-ordinates that is not coincident with the source.

It will be shown later that Stepanov's formula, which is the first-fruits of the experimental approach to the problem, needs modification if it is to describe spore dispersal over a wide range of conditions (Gregory, 1945). First it will be necessary to re-examine Stepanov's results in the light of present knowledge of eddy diffusion.

TABLE VI

DISPERSAL OF MIXED SPORES OF *Tilletia caries* AND *Bovista plumbea*, Experiment 2 (Stepanov, 1935)

Number of spores per cover-glass 18 × 18 mm. (average of 3)

	Tilletia				*Bovista*			
Angle	5 m.	10 m.	20 m.	40 m.	5 m.	10 m.	20 m.	40 m.
− 45°	3·0	0·3	0·7	0·0	0·3	0·0	0·0	0·0
− 30°	128·0	2·3	0·3	0·0	7·0	0·3	0·0	0·0
− 15°	43·3	54·7	4·7	0·3	7·0	4·0	0·0	0·0
0°	206·0	204·0	5·3	8·3	17·0	0·0	1·7	0·0
+ 15°	623·0	115·3	31·3	1·3	46·0	16·0	0·7	0·0
+ 30°	877·7	216·7	49·0	7·0	81·3	20·3	6·3	0·0
+ 45°	911·7	89·7	207·0	9·3	70·0	10·7	7·3	2·7
+ 60°	245·7	48·0	3·0	2·3	27·7	17·3	0·7	0·0

Stepanov's observational data enable us to test whether the standard deviation, σ, of the spores from their mean position agrees with Sutton's form: $\sigma^2 = \frac{1}{2}C^2x^m$, or with the older diffusion theories where $\sigma^2 = 2Kt$. The data also allow us to estimate the parameters m and C, which can then be compared with values obtained by meteorologists for similar conditions. Examination of Tables V and VI shows that the spores at any one distance do not lie in a smooth normal frequency distribution, but are significantly clumped. This is probably because the duration of the dispersal operation was insufficient to smooth out the action of a few large-scale eddies.

The standard deviations of spores lying at each distance from the source have been calculated for Table VII, where for convenience the deviations from the mean position at each distance were measured along the arc with the point source as centre. The standard deviation at each distance was calculated from the usual formula, $\sigma = \sqrt{[(x - \bar{x})^2/(n - 1)]}$. This is not strictly legitimate, because the trapped spores are a systematic instead of a random sample of the population and should be regarded as estimates of the ordinate of a normal frequency curve. However, the formula clearly gives a useful approximation—which would have been better if the traps had extended farther laterally and if data for some of the intermediate radii had not been missing.

Both experiments were done in the same place, and with comparable wind velocities, and when values for log σ are plotted against log x the points are found to lie reasonably close to a straight line. The slope of this line is not unity, as it would have been with the older diffusion theories, but corresponds with Sutton's formula for σ, where C = 0·64 (metre)$^{\frac{1}{8}}$, and m = 1·76. Sutton's work was apparently unknown to Stepanov when these experiments were done, and so the data could not at the time be analysed in terms of eddy diffusion. However, the agreement between experiment and theory provides evidence that spore dispersal in air is mainly controlled by eddy diffusion of the type postulated by Sutton (*see* Table VII). The values for C and m obtained from Stepanov's experiments agree well with those found in spore dispersal tests by other workers (Table VIII), and with comparable data obtained by Richardson (1920) for dispersal of smoke from a point source over distances of tens of metres, where C = 0·6 (metre)$^{\frac{1}{8}}$, and m = 1·75.

TABLE VII

CALCULATION OF PARAMETERS FOR SUTTON'S DIFFUSION EQUATION FROM STEPANOV'S DATA (1935)

Expt. No.			*Distance in metres*				
			5	10	15	20	40
1	*Tilletia*		2·25	2·97	5·03	6·64	—
		log	0·3522	0·4728	0·7016	0·8222	—
2	*Tilletia*		1·81	3·62	—	4·87	14·79
		log	0·2577	0·5587	—	0·6875	1·1699
	Bovista		1·790	3·673	—	5·343	—
		log	0·2529	0·5651	—	0·7277	—
	log distance (metre)		0·6990	1·0000	1·1761	1·3010	1·6021

Equation for regression line:
a = 0·5971 (S.D. 0·02), b = 0·88$_{12}$ (S.D. 0·072), $y = 0{\cdot}5971 + 0{\cdot}88_{12}\,(x - \bar{x})$.
Whence C = 0·637 (metre)$^{\frac{1}{8}}$, and m = 1·76

E. E. Wilson & Baker (1946) liberated *Lycopodium* spores at 7·5 ft. above ground-level and caught them, not on glass slides on the ground as Stepanov had done but, because they were interested in diseases of fruit trees, on vertical sticky slides placed on three vertical posts at 1·5, 3·0, and 5·1 metres down-wind from the source, and at thirteen heights above ground at each distance; seven tests were done at wind speeds ranging from 1·7 to 7·2 metres per sec. Other tests measured the horizontal dispersion. Wilson & Baker calculated the standard deviation of the spores deposited at each distance in each test, and from their values for σ we can now estimate the parameters for Sutton's equation. In a few individual experiments their values obtained for m lay outside the limits of 1·24 and 2·0 postulated by Sutton. But their mean value is m = 1·74—thus agreeing well with Sutton's theory (m = 1·75) and with Stepanov's experimental value (m = 1·76). Though their values for C_z agree well with Sutton's findings, those for C_y are much higher, but agree with those of Gregory, Longhurst & Sreeramulu (*unpublished*).

Values for C and *m* calculated from various spore-dispersal tests are shown in Table VIII. Evidently for microbiological work we must use high values of C_y, perhaps because we are concerned with longer sampling periods than Sutton. We shall therefore choose $C_y = 0{\cdot}8\ (\text{metre})^{\frac{1}{8}}$, and $C_z = 0{\cdot}12\ (\text{metre})^{\frac{1}{8}}$, as standard in Chapter XIII where deposition gradients are considered in detail. There seems to be little in favour, however, of adopting $m = 2{\cdot}0$ instead of $m = 1{\cdot}75$.

TABLE VIII

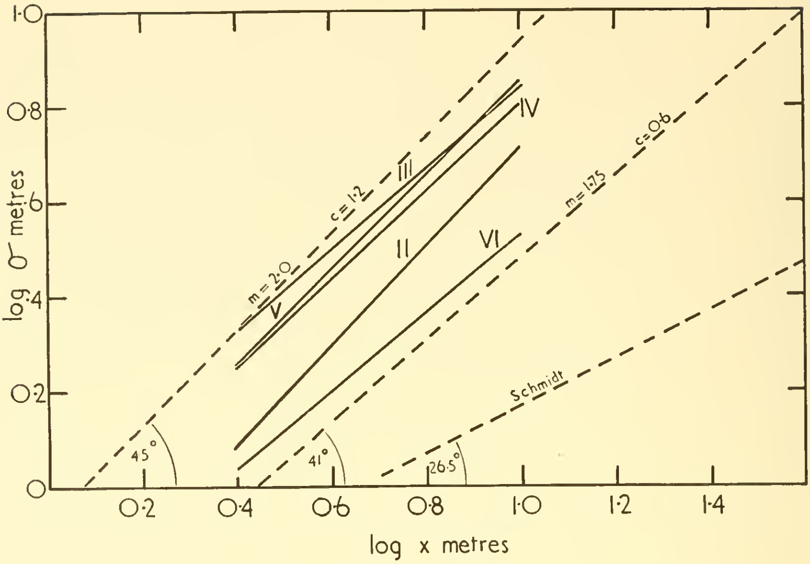
OBSERVED VALUES OF PARAMETERS IN SUTTON'S DIFFUSION EQUATION FROM EXPERIMENTS ON SPORE DISPERSAL

	C_z vertical $(\text{metre})^{1/8}$	C_y horizontal $(\text{metre})^{1/8}$	*m*	
Stepanov, 1935				
Tilletia spores I	—	1·67	1·49	
Tilletia spores II	—	0·35	1·90	
Bovista spores	—	0·89	1·65	
Wilson & Baker, 1946				
Lycopodium spores				
Wind speed 1·7 metres/sec.	0·20	0·66	1·70	1·51
2·7	0·11	4·26*	1·97	0·88*
3·2	0·22	0·30	1·75	1·64
4·6	0·12	0·40	1·86	1·74
(mean of 7 experiments)	0·15	—	1·92	—
Gregory, Longhurst & Sreeramulu (*unpublished*)				
Lycopodium spores				
Wind speed 0·4 metres/sec.	—	0·97	1·80	
1·05	—	0·28	2·12	
1·28	—	0·58	1·99	
1·63	—	0·89	1·66	
2·64	—	1·40	1·71	
Gregory (*unpublished*)				
Lycopodium spores	—	0·68	1·98	
	—	0·26	1·94	

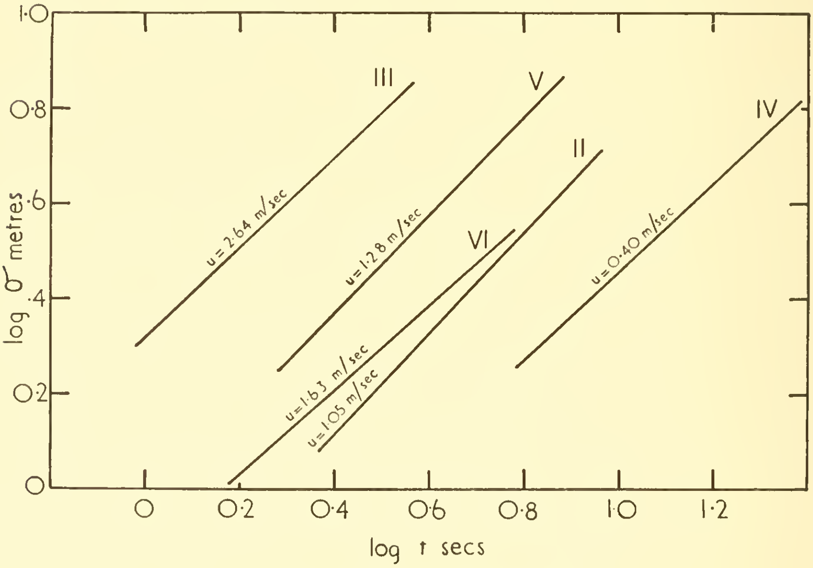
* abnormal values.

COMPARISON OF THEORIES OF W. SCHMIDT AND SUTTON

According to Schmidt's theory, $\sigma^2 = 2At/\rho$, so, because $t = x/u$, we have $\log \sigma = \frac{1}{2} \log x + \frac{1}{2} \log (2A/\rho u)$. If this relation holds true in field tests, plotting experimental data for $\log \sigma$ against $\log x$ should give a line



(*a*) Graph of log σ against log x.



(*b*) Graph of log σ against log t.

Fig. 7.—Test of agreement of W. Schmidt's and Sutton's diffusion theories with experiments using *Lycopodium* spores liberated over grass field at Imperial College Field Station, Ascot, Berks. (Gregory, Longhurst & Sreeramulu, *unpublished*)

of slope $\tan^{-1}\frac{1}{2}$, that is 26°34′. However, according to Sutton's theory $\sigma^2 = \frac{1}{2}Cx^m$, therefore

$$\log \sigma = \frac{m}{2} \log x + \tfrac{1}{2} \log (\tfrac{1}{2}C^2)$$

If this holds true, plotting the observed values of log σ against log x should give a line of slope $\tan^{-1}\frac{m}{2}$. For values of Sutton's m between 1·75 and 2·0, the line should slope at an angle between 40° 36′ and 45°.

Field tests with *Lycopodium* spores liberated over short grass by Gregory, Longhurst & Sreeramulu (*unpublished*) allow a direct comparison to be made of the theories of Schmidt and Sutton. Spore-cloud concentrations were measured near ground-level at distances up to 10 metres simultaneously at 24 points. Results plotted in Fig. 7*a* show the lines sloping at angles varying between 40° and 46°. This is incompatible with Schmidt's theory which requires a slope of 26°34′. Furthermore, if log σ is plotted against log t (calculated from the distance and mean wind speed) according to Schmidt's theory σ should be the same after a given *time* whatever the wind speed, but this is not so (Fig. 7*b*). On Sutton's theory at a given distance log σ varies only over a comparatively narrow range of values depending on the parameter m. The results of these experiments are compatible with Sutton's theory which requires a slope of 40°36′ for $m = 1{\cdot}75$, and 45°0′ for $m = 2{\cdot}0$.

In biological applications we are usually interested in the relation between diffusion and distance rather than between diffusion and time. As we often lack measurements of the variable wind velocities in which dispersion has occurred, Schmidt's theory would be inconvenient to handle. On Schmidt's theory σ varies with time, on Sutton's σ varies with distance travelled. Sutton's theory not only fits experimental results well, but is also convenient because it does not require a knowledge of wind speed.

VI

DEPOSITION PROCESSES

We have now considered airborne micro-organisms as diffusing clouds. Before we can discuss processes by which they are deposited in the complex outdoor environment, we must deal with deposition processes under simplified, ideal conditions. The word 'deposition' is used in a general sense to include all processes by which airborne particles are transferred from aerial suspension to the surface of a liquid or solid. One form of deposition, the impaction of droplets or particles on surfaces, has been extensively studied both theoretically and in wind-tunnel experiments. It is highly relevant to the problems of spore deposition in nature and of sampling techniques which form the topics of Chapters VII and VIII.

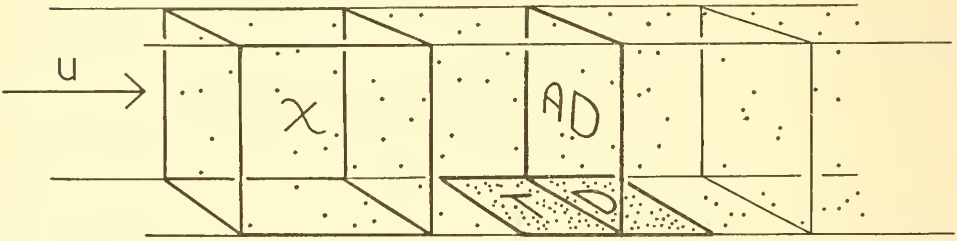


Fig. 8.—Diagram showing relation between concentration (χ = number of spores per unit volume); wind-speed = u; area dose (A.D. = number of spores passing through frame of unit area); and trap dose (T.D. = number of spores deposited on unit area of surface).

The relation between concentration of the spore-cloud, χ, and deposition on the surface (T.D. = trap dose) over which the spore-cloud travels, is illustrated in Fig. 8, together with the concept of 'area dose' (A.D. = the number of particles flowing through an imaginary frame of unit area cross-section at right-angles to the direction of the wind). Concentration of the cloud (χ = number of spores per cubic metre) is the more fundamental measurement, and the one of greatest interest to the allergist, whose patients inhale volumes of air. The trap dose, which measures deposition on a surface, is of more interest to plant pathologists, plant breeders, and pollen analysts. The area dose is a useful concept in passing from the one measurement to the other. For a given concentration of particles per unit volume of air, the area dose must increase with wind-speed, but whether the trap dose will also be affected is a matter for experimental investigation. With a continuous source emitting during a limited time, the area dose will be the same as if the same total quantity of particles, Q_0, had been liberated in a number of successive instantaneous puffs arriving in a series of greatly fluctuating concentrations.

We can conveniently express the percentage efficiency of a trapping surface as

$$E = \frac{\text{Trap dose per sq. cm.}}{\text{Area dose per sq. cm.}} \times 100.$$

This convention expresses the efficiency with which a surface clears the spore-cloud to a height of one centimetre above the surface. Deposition on a surface takes place in several ways, including impaction and sedimentation, for sedimentation seldom acts alone.

MECHANISM OF IMPACTION

When a bluff object such as a cylinder is placed in wind, the oncoming air-stream has to flow around the obstruction, but airborne particles will be carried some distance towards it by their own momentum before they are in turn deflected by the wind flowing around the obstacle (Fig. 9).

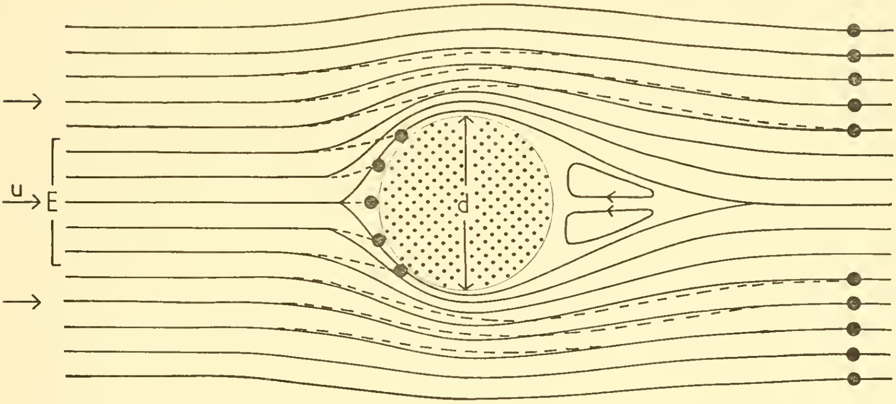


FIG. 9.—Streamlines of air and particle trajectories around a cylindrical obstruction (vertical cylinder seen in plan). E = streamlines carrying spores towards cylinder; d = diameter of cylinder; arrows on left show direction of wind of velocity = u.

If all those particles were impacted whose trajectories in the free wind-stream would have passed through the obstruction, impaction efficiency would be 100 per cent, but apparently in practice it never is. The distance travelled by the particle towards the cylinder before being deflected by the air streamlines flowing around the cylinder is related to both the momentum of the particle and the size of the object disturbing the air-flow. Another effect, collection by direct interception, becomes important when the diameter of the particle is an appreciable fraction of the diameter of the cylinder. With low wind-velocities and with particles smaller than spores, Brownian diffusion may play a major role in deposition.

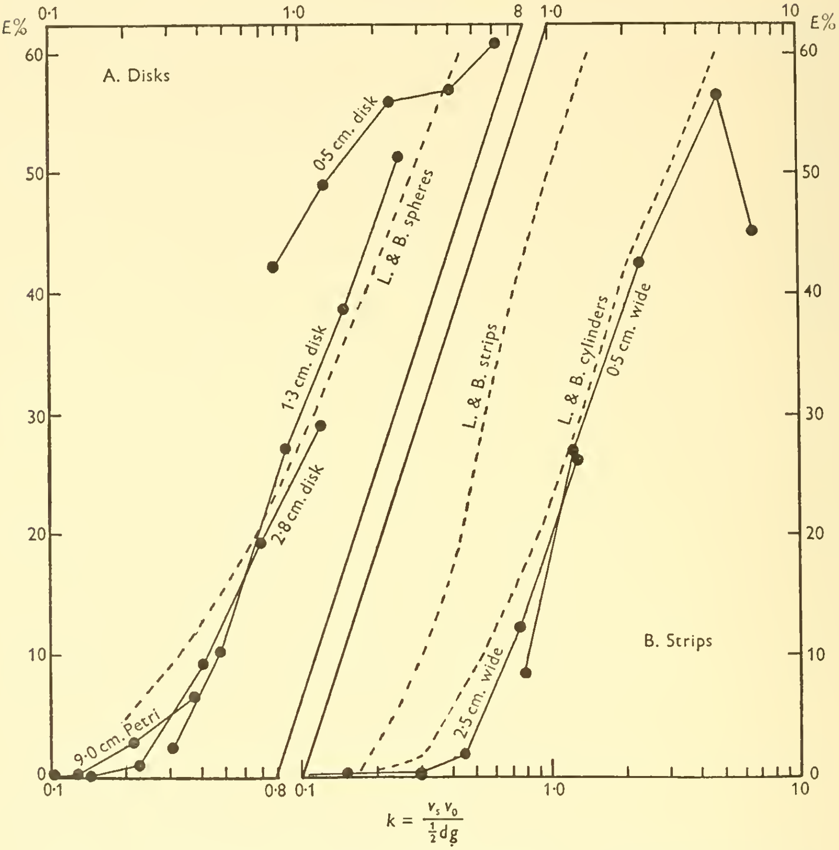


FIG. 10.—Observed relation between E per cent and $k = v_s u/\frac{1}{2}dg$. Solid lines from Gregory & Stedman (1953). Broken lines = values for spheres, strips and cylinders as predicted by Langmuir & Blodgett (1949), for $\phi = 10^3$. (Reproduced by permission from the *Annals of Applied Biology.*)

The general principles of impaction have been made clear by Sell (1931) in connection with dust filtration. From aerodynamical considerations Sell postulated that the efficiency of impaction, E, is related to a non-dimensional constant, which may be written in a form convenient to us as

$$k = v_s u/\tfrac{1}{2}dg,$$

where: v_s = speed of fall of particle in still air; u = speed of wind; d = diameter of cylinder, strip, etc.; and g = acceleration due to gravity.

Sell derived the relation between E and k by observing the trajectories of uniform droplets of Indian ink on paper bisecting a vertical cylinder in a small wind-tunnel. It is not clear from Sell's paper what range of conditions he tested.

Efficiency of impaction on spheres, cylinders, and strips has attracted two distinct types of investigators—theoretical and experimental. There have been large discrepancies between the conclusions of different theoretical workers and again between wind-tunnel studies, but in more recent papers substantial agreement is evident between theory and experiment. Deposition on cylinders has been studied by: Sell (1931), Glauert (1946), Langmuir & Blodgett (1949), Johnstone *et al.* (1949), Chen (1955), Wong *et al.* (1956), La Mer & Hochberg (1949), and Landahl & Herrmann (1949). Deposition of cloud droplets on rotating multicylinders was studied, both theoretically and in flight, by Brun *et al.* (1955). A theory of particle deposition on cylinders, showing reasonably good agreement with the observed data of Gregory (1951) and of Ranz & Wong (1952), has been developed by C. N. Davies & Peetz (1956). Deposition mechanisms other than impaction still await a coherent theory, and we must rely on experimental values. (Fig. 10.)

WIND-TUNNEL STUDY OF IMPACTION

The following account is based on work with a small, low-speed wind-tunnel built at Rothamsted Experimental Station in 1949 (Gregory, 1951; Gregory & Stedman, 1953) and includes some hitherto unpublished data.

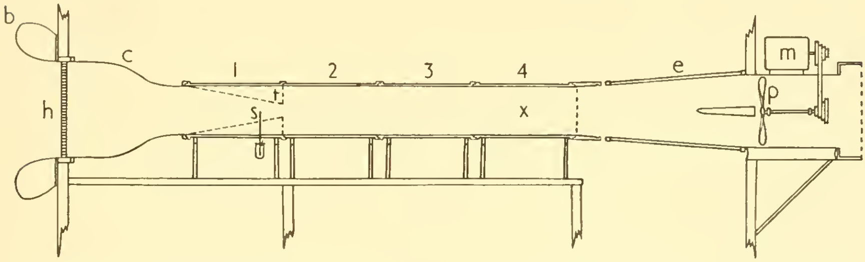


FIG. 11.—Diagram showing small wind-tunnel used in deposition study at Rothamsted Experimental Station, elevation view.

1–4, 'Perspex' working sections; b, bell-shaped intake; c, contraction to smooth flow; e, expansion and conversion from square to circular cross-section; h, paper-honeycomb straightener; m, motor; p, propeller; s, spore input; t, removable constriction to generate turbulence when required; x, trapping position.

The wind-tunnel consists of a horizontal square duct (Fig. 11). The two ends of the tunnel project through the end walls of a small building which forms a laboratory traversed by the eight-feet-long working section of the tunnel. The tunnel uses outdoor air which is passed through once only and not re-circulated. A four-bladed wooden propeller absorbing 0·56 horsepower at 2,850 r.p.m. in the exit draws air down the tunnel. An expansion section converts the 29 cm.-square working section to the 46 cm.-circular diameter at the fan. The flared intake-end is of 51 cm.-square cross-section, contracts to a bell shape, and contains a paper honeycomb 'straightener' to remove eddies and produce streamlined flow; but if turbulent flow is needed a constriction is inserted in the first part of the working section (indicated by dotted lines at t in Fig. 11).

Spores under test are injected or otherwise liberated, usually on the tunnel axis near the constriction. Spore trapping equipment, plants, etc., can be inserted farther downwind through removable panels in the walls of the working section. Wind-speeds of from 0·5 to nearly 10 metres per second are obtained by changing pulleys on the belt drive between the constant-speed electric motor and the fan, and by inserting screens across the tunnel to increase its resistance. The lower wind-speeds are best obtained by increasing the resistance of the tunnel, rather than by slowing the fan, because outdoor wind movement disturbs the flow less when the tunnel resistance is high than when it is low.

Most tests of spore dispersal or deposition in the wind-tunnel involve knowledge of the time-mean spore concentration of the air. The Cascade Impactor (K. R. May, 1945; *see also* Chapter VIII), operated isokinetically (i.e. with the orifice facing the wind and with suction adjusted to draw air in through the orifice at the same speed as the wind) is taken as standard to estimate the mean number of particles per cubic metre of air during the period of the experiment. With this information, and knowing the wind-speed, we can calculate the area dose (A.D. $= \chi ut$). The trapping efficiency of any surface exposed to the spore-cloud in the wind-tunnel can then be determined by estimating the number collected per square centimetre of trap surface, and expressing it as per cent of the area dose.

Liberation of one million *Lycopodium** spores at a point on the central axis of the tunnel produced a conical cloud. At a sampling point on the central axis of the tunnel, 1·4 metres downwind, the area dose was about 4,500 spores per sq. cm. under turbulent condition at wind-speeds of from 5·75 to 9·7 metre per sec. Under streamline conditions the dispersal cone was visibly narrower and the area dose nearly double at these wind-speeds. At 1·1 metre per sec., however, streamline conditions gave a much lower area dose because the cloud was displaced downwards under gravity. On the whole, efficiency of impaction was not much affected by whether the flow was turbulent or streamlined.

IMPACTION ON CYLINDERS

The efficiency of impaction on vertical sticky cylinders is *increased* by: (1) increasing wind-speed; (2) increasing the mass of the particle (by increase in size or density); and (3) decreasing the diameter of the cylinder (except that large particles, such as *Lycopodium* spores, tend to blow off narrow cylinders at high wind-speeds, whereas small spores, such as those of *Ustilago perennans*, do not). As will be shown later, similar relations hold for impaction on surfaces of other shapes, such as spheres, disks, strips (ribbon) and—in the field—leaves, stems, and stigmas. The value for E depends also on the shape. The order of decreasing efficiency is probably: spheres, disks, cylinders, and strips (other conditions being equal, including radius or half-width).

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* Spores of *Lycopodium clavatum* are convenient for experimental work. They can be bought easily; they separate readily from one another when blown into the air. They are not smooth spheres, but their mean diameter is about 32 μ, density 1·175, and terminal velocity estimated as 1·76 to 2·14 cm. per sec.; the number per gram is 9·39 to $9{\cdot}4 \times 10^7$.

Wind-tunnel results confirm the conclusion of C. N. Davies & Peetz (1956), that under extreme conditions efficiency of impaction can be zero; for example the very small spores of the puffball, *Lycoperdon* (*Calvatia*) *giganteum*, were not impacted under any of the conditions tested. The slightly larger spores of the smut fungus, *Ustilago perennans*, however, showed appreciable efficiencies—but probably because they often travel through the air in clumps which effectively behave as heavier particles than their component single spores.

The deposit is not uniform over the cylinder, but is densest on the part of the circumference projecting farthest forward into the wind; this is the so-called 'stagnation line'. The density of the deposit falls off towards the sides of the cylinder, and there is a spore-free zone on the shoulders where the air-flow is more or less tangential to the surface. Usually there is no deposit at the back or downwind side of the cylinder, but with *Lycopodium* spores (32 μ diameter) a narrow line of deposit has been observed down the back of cylinders of less than 0·1 cm. diameter at wind-speeds of 1 metre per sec. or less. Deposit on the side opposite to the oncoming wind is negligible or zero under most conditions tested. The angle subtended by the deposit on the upwind side was less than 180° in both turbulent and streamline air. Other things being equal, the angle subtended at the centre of the cylinder by the deposit was increased by increasing the wind-speed and by decreasing the cylinder diameter—increasing efficiency of the whole cylinder evidently runs parallel with increase in the angle subtended by the deposit. The low efficiency of wide cylinders and slow winds shows both as a narrower trace, and thinner deposit per unit area.

The decrease of efficiency with increasing cylinder size was first noticed in field tests. Per unit length, a large cylinder 12 cm. in diameter may collect no more pollen grains or spores than a cylinder 1 cm. in diameter, and per unit area of surface it may collect many fewer (Gregory, 1951).

IMPACTION ON A ROTATING STICKY CYLINDER

Rotating the cylinder at a peripheral speed comparable with the wind-speed would be expected to reduce the thickness of the boundary layer on the surface, to induce the well-known Magnus effect, and to produce a local rotation of air round the cylinder itself. It was not obvious whether these effects would alter impaction efficiency.*

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* This experiment was suggested by Mr. J. R. D. Francis, of the Civil Engineering Department, Imperial College of Science and Technology. I am indebted to him for advice and the loan of equipment for the tests, the results of which have not been published hitherto.

Tests were accordingly made in the Rothamsted wind-tunnel, with a 15·5 cm.-square constriction upwind to generate turbulence. *Lycopodium* spores (32 μ diameter) were blown in at a point on the axis 18 cm. upwind of the constriction, and, after a diffusion path 63 cm. long, the spore-cloud reached the trapping section where a stationary and a rotating cylinder, each 0·5 cm. in diameter, were exposed simultaneously. The rotating cylinder, which was placed vertically across the axis of the tunnel, consisted of a steel rod mounted in a ball-race secured flush with the floor of the tunnel at one end, and connected by a sleeve of stout rubber tubing to the spindle of a 225-watt 'Universal' motor mounted on the roof of the tunnel. The stationary cylinder was 2 cm. to one side and 2 cm. upwind of the rotatable cylinder, and both carried adhesive coatings of cellulose film which, after exposure, were removed and scanned under the microscope to measure the deposit. Speed of rotation of the cylinder was controlled by a 'Variac' transformer and was measured by a stroboscopic lamp. The range of speeds that could be tested was limited by the steel rod which began to bend at speeds above 7,000 r.p.m.

With a wind of 1·1 metres per sec., efficiency was substantially unchanged until the peripheral speed of rotation attained approximately the speed of the wind; at higher rates of rotation the efficiency decreased rapidly, reaching zero before the peripheral speed of the cylinder reached twice that of the wind. At a lower wind-speed of 0·68 metre per sec., efficiency of the cylinder, when rotating at 0·4 times the wind-speed, fell to 53 per cent of the stationary cylinder, and to 24 per cent at 0·82 times the wind-speed. These results suggest that the centrifugal effect is sufficient to decrease impaction to zero. The phenomenon would be interesting to explore at a wider range of cylinder diameters and wind-speeds (the work of Brun *et al.* refers to much higher wind-speeds than these).

IMPACTION ON PLANE SURFACES AT VARIOUS ANGLES TO WIND

The interest in deposition on narrow horizontal and vertical strips lies in the widespread use of microscope slides for routine trapping of fungus spores and pollen.

The theory of gravity deposition assumes that the air flowing past the surface contains a large population of particles distributed at random. The particles fall at their terminal velocity, v_s cm. per sec., and the wind blows horizontally at u cm. per sec. A plane surface of area 1 sq. cm. faces the wind, making an angle θ with the horizontal plane, as shown in Fig. 12. Then only particles contained in the rectangular skew prism ABCD EFGH, have trajectories in the free air which would carry them to the surface during time t secs. The volume of this prism is given by

$$V = t(u \sin \theta + v_s \cos \theta) \text{ cc.}$$

If $\theta = 90°$, then $v_s \cos\theta = 0$, and hence the number of particles with trajectories cutting a vertical surface should be independent of the terminal velocity of the particles but will depend on the wind-run. (Deposition will in practice be reduced below this value because the air-stream is deflected by the surface itself, and efficiency of collection depends on u (Langmuir & Blodgett, 1949; Gregory, 1951).)

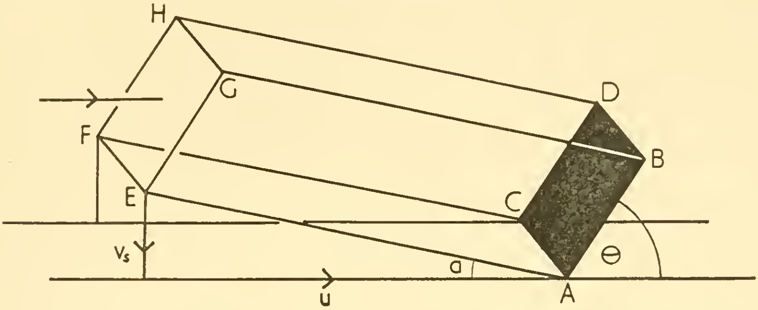


FIG. 12.—Diagram illustrating gravity theory of particle deposition. ABCD = trap surface; u = wind velocity; v_s = terminal velocity of particle; ABCDEFGH = rectangular skew prism containing particles whose trajectories would bring them to rest on trap surface; θ = presentation angle; tan a = v_s/u.

If $\theta = 0°$, then $u \sin\theta = 0$, and deposition under the influence of gravity should depend on the terminal velocity, v_s, so that for a horizontal trap the volume of air sampled should be independent of wind-speed, and should depend only on the terminal velocity of the particles. From a cloud of uniform concentration, most trajectories should pass through a surface inclined at an angle θ, when $\tan\theta = u/v_s$ ($\theta = 45°$ when $v_s = u$).

If the time-mean density of the spore-cloud $= \chi$ spores per cu. metre, it will be apparent that the area dose A.D. $= \chi v_s$—from which, if the deposition is by gravity as assumed, the expected area dose $= (100/u)v_s$. Comparison of observed results with the expected value will give a convenient test of the validity of the theory.

Our wind-tunnel experiments show that deposition on a horizontal flat surface is a fairly complex process depending on several factors besides the simple resultant of gravity and wind. The surface studied in greatest detail has been the 76 × 25 × 1·3 mm. glass microscope slide, as this has been extensively used in routine spore trapping. Experiments with other plane surface traps are reported in more detail than given here, by Gregory & Stedman (1953).

The slide was placed with its long axis at right-angles to the wind and held by clips, placed at the two ends to avoid disturbing the air-flow. Its surface was orientated at various angles to the wind in different experiments, the convention adopted being: presentation angle 0° = parallel with the wind; 45° when the leading edge was lower than the trailing

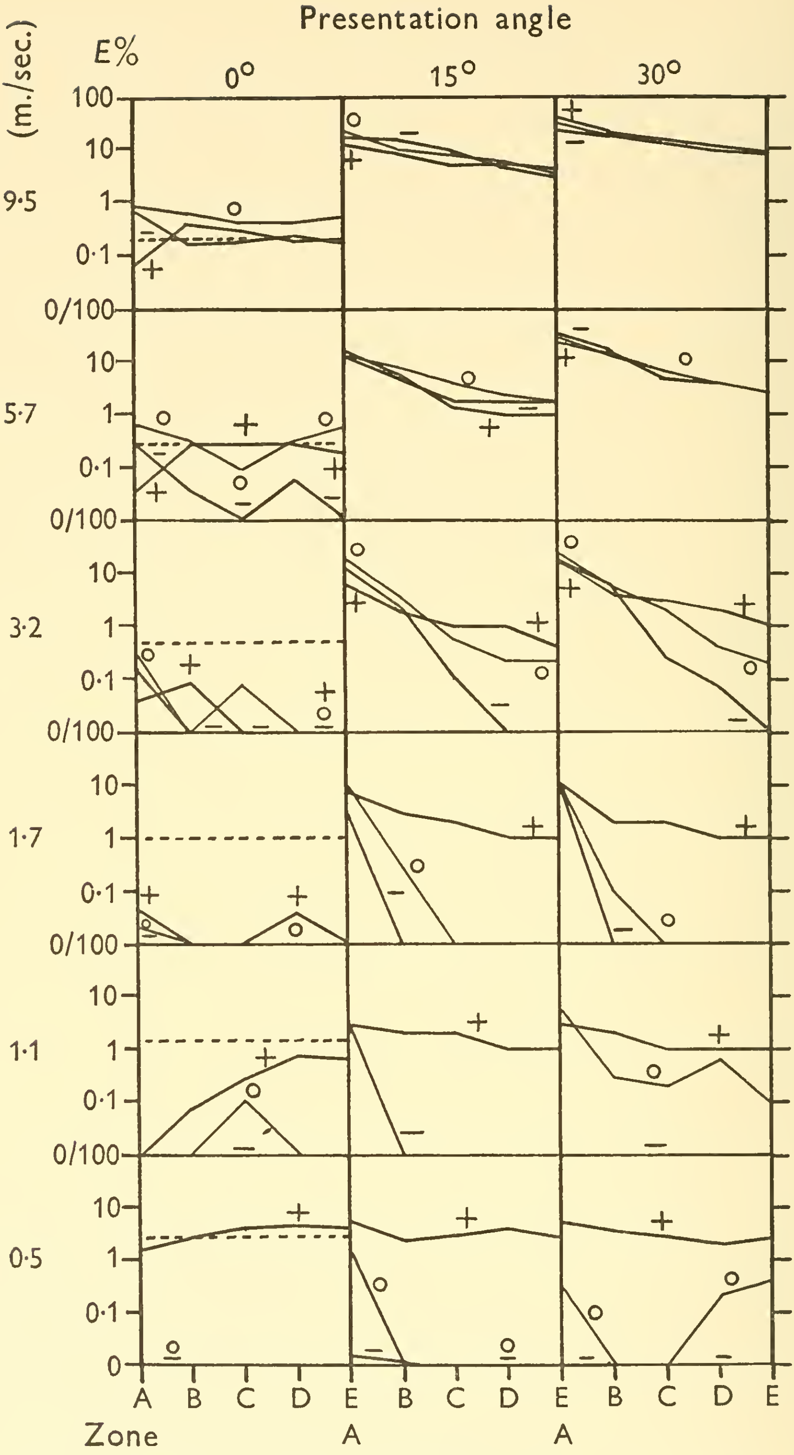
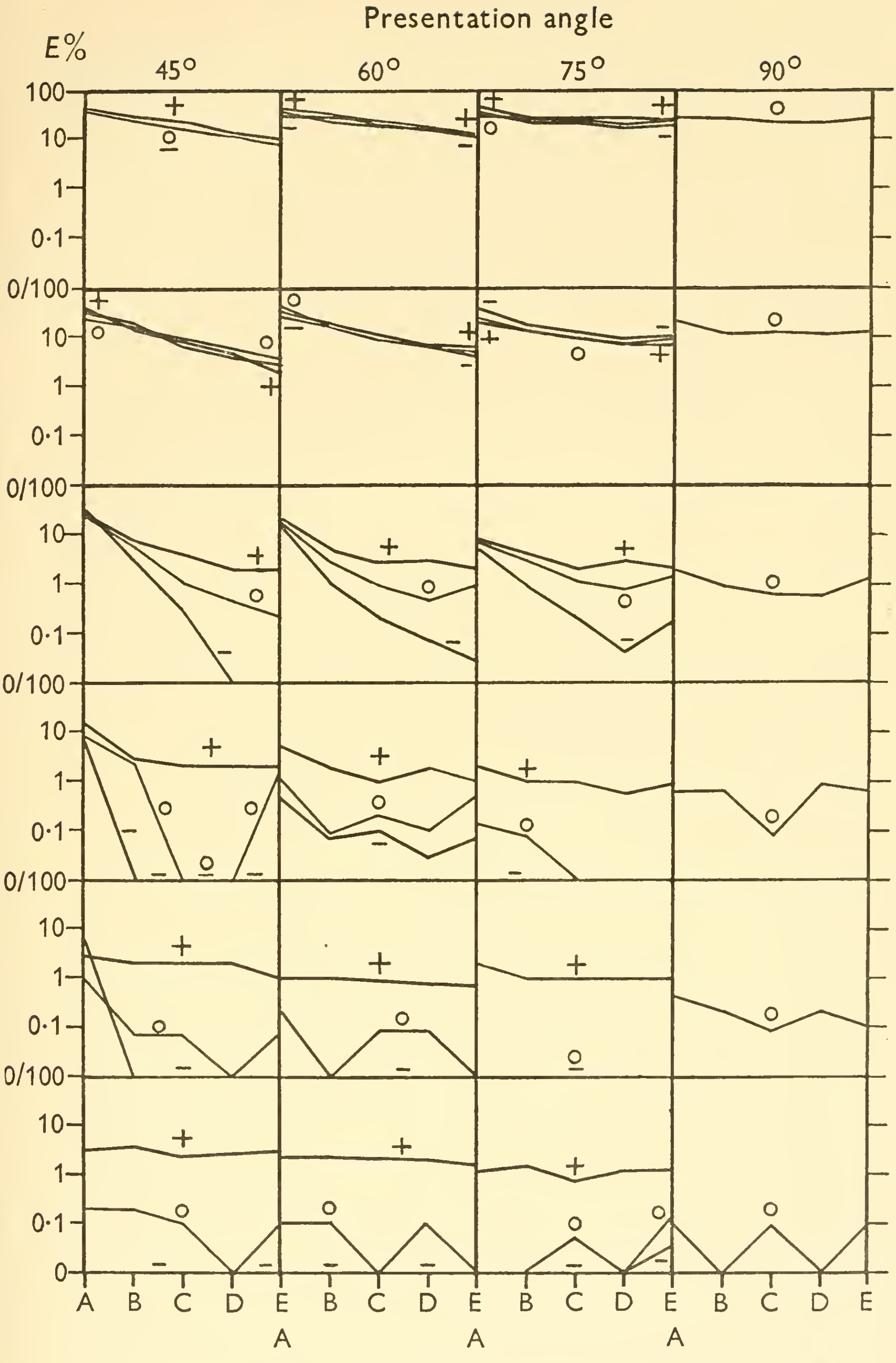


FIG. 13.—Efficiency of deposition of *Lycopodium* spores on zones across glass microscope slide at presentation angles from 0 (left side of left-hand figure) to 90 (right side of right-hand figure) degrees as observed in wind-tunnel experiments. *F*% = efficiency as percentage area dose; A, B, C, D, E = successive half-centimetre



zones across slide from leading edge (A) to trailing edge (E); + = gravity positive; o = gravity neutral; — = gravity negative (*from* Gregory & Stedman, 1953). Reproduced by permission from *Annals of Applied Biology*.

edge; and 90° at right-angles to the wind. (Presentation angle so defined differs from the aeronautical 'angle of incidence' in which at 45°, for example, the leading edge is higher than the trailing edge.)

The effect of gravity was studied in two sets of experiments. In one set, with the long axis of the slide vertical (parallel with the z-axis) and the surface making various angles with the x, z-plane, the effect of gravity on deposition must be neutral. In the other set, with the long axis of the slide horizontal (parallel with the y-axis) and the surface making various angles with the x, y-plane, the effect of gravity must be positive at angles from 0° up to less than 90°, neutral at 90°, and negative at angles greater than 90° and up to 180° (gravity condition denoted by g_+, g_0, and g_-, respectively). Angles greater than 180° represent the back of the slide.

Preliminary tests showed that trapping efficiency varied in different parts of the slide. Accordingly the slide was divided into five $\frac{1}{2}$-cm. zones, denoted: A, B, C, D, and E, respectively, from the leading to the trailing edge (Fig. 13).

Results of the main series of tests are plotted in Fig. 13, where the efficiency of deposition expected on the gravity theory at 0° for each wind-speed, taking v_s for *Lycopodium* as 1·76 cm. per sec., is indicated by dotted lines. The observed values below $E = 0{\cdot}1$ per cent are unreliable, but are given to show the trend. Values below $E = 0{\cdot}01$ per cent, including zero, are all plotted as 0·01 per cent as they cannot reasonably be distinguished with the data available.

The curves obtained probably result from the interaction of several deposition mechanisms: sedimentation, impaction, turbulence, and edge effects. In certain sets of conditions, one or other of the mechanisms can be found acting singly; but for the most part deposition is interpreted as resulting from the simultaneous action of several mechanisms.

DEPOSITION ON HORIZONTAL SLIDES

(i) *Deposition by sedimentation*, under the influence of gravity alone, is seen on the upper surface of a horizontal slide at the lowest wind-speed tested (conditions denoted by: 0°, 0·5 metres per sec., g_+). Here deposition over the slide as a whole was very close to the expected value predicted by the gravity theory ($E = v_s/u \times 100 = 1{\cdot}76/50 \times 100 = 3{\cdot}5$ per cent), but even at this low wind-speed the bluff edge of the slide, 1·3 mm. thick, caused some edge shadow, shown as a reduced deposition just behind the leading (upwind) edge. That deposition was solely caused by gravity is shown by the absence of deposit on the underside of the horizontal slide, and on either side of a vertical slide held parallel with the wind (0°, 0·5 metres per sec., g_-, and g_0).

At the wind-speeds more usual outdoors of between 1·0 and 2·0 metres per sec., a surprising effect developed in these wind-tunnel experiments. With gravity positive, the bluff edge of the slide produced an edge shadow deflecting a large proportion of the approaching spores;

at 1·1 metres per sec. the part of the surface behind the leading edge was almost free from deposit, and efficiency reached about 50 per cent of the expected value only on the rearmost zone. At 1·7 metres per sec. efficiency was almost zero over the whole slide. With gravity neutral or negative, efficiencies were also almost zero.

(ii) *Turbulent deposition.* As the wind-speed was raised still further, the efficiency of the horizontal slide recovered; but deposition cannot have been due to gravity sedimentation, because at 9·5 metres per sec. the amount deposited was almost the same on the under-side (g_-) as on the upper-side (g_+) of a horizontal slide, and also on the two sides of a vertical slide held parallel with the wind (g_0). At this speed turbulent deposition is seen in its almost pure condition. As indicated below, there is some evidence that this deposition may result from turbulence generated by the bluff edge of the slide itself.

At 0° (horizontal slide) and higher wind-speeds, although deposition was turbulent, gravity appeared to interact with the process in some way that is at present obscure. With gravity neutral (g_0) and wind-speeds of 5·7 and 9·5 metres per sec., deposition was higher at the leading and trailing edges than in the middle of the slide. With gravity negative (g_-) at 9·5 metre per sec., however, the leading edge showed an anomaly, having a deposit 8 to 10 times that found with gravity positive. With gravity negative at 5·7 and 3·2 metres per sec., deposition behind the leading edge was negligible.

DEPOSITION OF *Lycopodium* SPORES ON INCLINED PLANE SURFACES

Deposition on a horizontal microscope slide is best regarded as a special case of deposition on an inclined plane with the presentation angle 0°. A number of possible angles ranging from 0°, through 90° (vertical slide) to 180°, were tested in the turbulent wind-tunnel, and results are also shown on Fig. 13.

(i) *Impaction.* Deposition by impaction should be zero at 0°, but it would be expected to occur to some extent at all other presentation angles, as at these angles the surface subtends the oncoming air-stream. With the slide vertical (90°), the gravity effect should be neutral, and at low wind-speeds of 0·5 to 1·1 metres per sec. the slide would not be expected to generate turbulence. Deposition under these conditions should be due to impaction only. In the tests, as wind-speed was increased (90°, 1·7 to 9·5 metres per sec.), deposition increased over the whole surface and was more uniformly distributed; but even at the highest speed tested the deposit at the margin exceeded that at the middle. In this respect impaction on a plane surface contrasts strikingly with that on cylinders, where the centre of the trace is always denser than the edges.

(ii) *Edge drift.* The effect of the bluff edge of the slide in 'shading' the leading edge has been referred to above. Behind the edge shadow, a region of greater deposition caused by an edge drift might be expected.

Fig. 13 shows that at 0° this edge drift fell behind the trailing edge, but that when the slide was inclined at 15° or 30° to the wind, the edge drift impacted on the slide. This is shown by the deposit on the leading edge which greatly exceeded the expected value over the range 15° to 60°, 1·7 to 9·5 metres per sec.

(iii) *Mixed effects.* Over most of the range of zones, presentation angles and wind-speeds, the deposition was from a mixture of two or more mechanisms whose relative importance can be roughly assessed from the empirical results shown in Fig. 13.

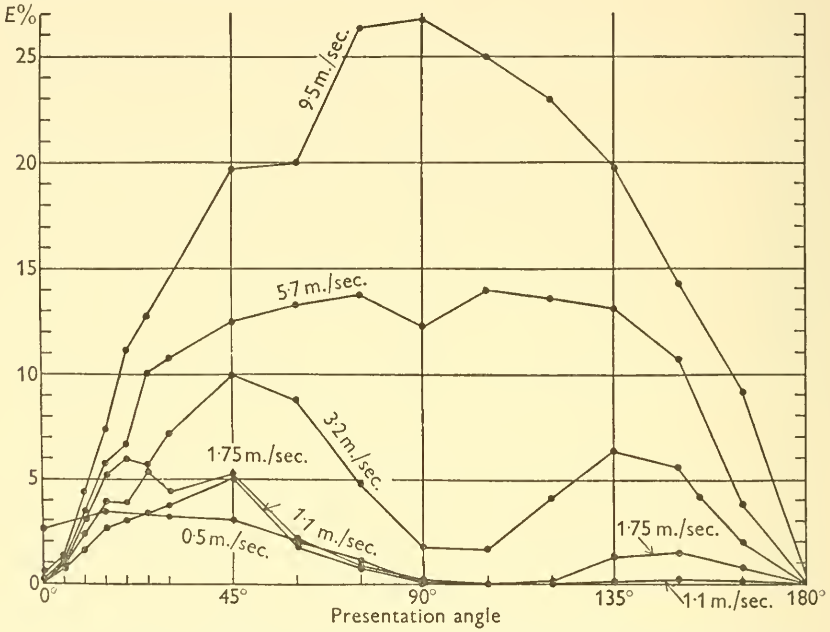


FIG. 14.—Mean efficiency of deposition of *Lycopodium* spores on glass microscope slide (all zones) at presentation angles of 0° to 180°. E = efficiency as percentage area dose (Gregory & Stedman, 1953). Reproduced by permission from *Annals of Applied Biology.*

MEAN DEPOSIT ON INCLINED SLIDES

In the foregoing paragraphs, efficiencies of various arrangements of a microscope slide, acting under different conditions as a spore trap, have been measured and interpreted in terms of different deposition mechanisms acting on different surface zones of the slide. In practice, when scanning a slide (or Petri dish trap), we usually need a mean value of efficiency for the whole sampling area. Mean efficiencies for a microscope slide with its long axis parallel to the y-axis, orientated at different presentation angles to the x, y-plane (i.e. g_+, or g_-), are given in Fig. 14. They are taken from the same results as were used in the preceding figure. Each point of Fig. 14 represents values obtained in from one to eight experiments.

The values used for Fig. 14 were obtained with highly turbulent wind. Partially streamlining the flow, by removing the turbulence-generating obstruction from the tunnel, had little effect on the deposit—except with presentation angles between 0° and 10°, and with wind-speeds below 5 metres per sec., when efficiency of deposition was reduced, being least with the horizontal slide (0°).

Efficiency of deposition on the back of the microscope slide was usually less than 1 per cent.

Decreasing the width of the slide from the customary 2·5 to a mere 0·5 cm., increased efficiency most at the lowest wind-speeds. This narrow trap was most efficient at 5·5 metres per sec. and 90° presentation angle (vertical), and a fall in efficiency at 9·5 metres per sec. and 90° was comparable with the anomalous reduction in efficiency with very narrow cylinders at higher wind-speeds (Gregory, 1951).

TABLE IX

EFFICIENCY (E %) OF DEPOSITION ON INCLINED SLIDES IN TURBULENT WIND-TUNNEL (Gregory & Stedman, *unpublished*)

Presentation angle	Wind-speed (metres/sec.)					
	9·5	5·5	3·2	1·7	1·1	0·5
Lycoperdon (*Calvatia*) *giganteum* (c. 4 μ)						
0°	0·07	1·1	0·6	1·2	5·6	3·3
90°	0	0	0	0	0	0
180°	0·04	1·1	1·7	1·1	6·1	2·2
Ustilago perennans (c. 6 to 8 μ)						
0°	0·2	0·2	0·2	0·1	0·02	0·09
45°	0·3	0·4	0·3	0·04	0·1	0·1
90°	0·3	0·2	0·6	0·2	0·01	0·03
135°	0·4	0·2	0·4	0·09	0·04	0·04
180°	0·2	0·2	0·2	0·02	0·02	0
Erysiphe graminis (conidia c. 25 × 12 μ)						
0°	0·25	0·13	0	0	0·05	0·92
45°	7·7	3·70	1·48	0·93	0·86	1·39
90°	2·70	0·77	0·06	0	0·07	0
135°	4·10	1·83	0·18	0	0	0
180°	0·72	0·19	0	0	0	0
225°	0·28	0·78	0·31	0·22	0·25	1·16
270°	0·39	0·14	0·12	0	0	0
315°	0	0	0	0	0·07	0
360°	0·72	0·19	0	0	0	0

DEPOSITION OF OTHER SPORES ON INCLINED PLANE SURFACES

Lycopodium was studied in greatest detail because it is easily handled and has relatively large spores. Less detailed tests were also made with the smaller spores of *Lycoperdon* (*Calvatia*) *giganteum*, with *Erysiphe graminis* conidia, and with spores of *Ustilago perennans* (Table IX). In general it may be said that impaction efficiency on a microscope slide held at right-angles to the wind is low, but might be as high as 25 per cent with grass pollen or rust uredospores in winds of 9 metres per sec.

EFFECT OF THICKNESS OF SLIDE

Deposition on a horizontal or inclined surface is evidently complex and may be disturbed by edge shadowing. Tests were therefore made with both thicker and thinner slides, and with thick plates, 10 cm. wide, having a double-bevelled edge.

With a horizontal plate 6·4 mm. thick, the edge-effect was present, and at medium wind-speeds edge-shadow became pronounced. At 1·1 metres per sec. nearly the whole surface was in the shadow of the leading edge, and at 3·2 and 5·5 metres per sec. there was almost no deposit on the slide. At 9·5 metres per sec., however, there was some turbulent deposition on both upper and lower surfaces, both in the turbulent and streamlined wind-tunnel.

When the leading edge of the plate, 6·4 mm. thick, was sharpened with a double bevel to form a 45° edge facing the wind (as used by Landahl & Herrmann, 1949), a very different effect was observed. In a wind of 0·5 metres per sec. there was a very even deposit over the whole upper surface, but at 1·1 metres per sec. an edge-shadow developed and spread across the whole surface as the wind-speed increased, until at 5·7 metre per sec. deposition was negligible. There was no recovery by turbulent deposition at higher wind-speeds, and at 9·5 metres per sec. the thick, bevelled trap under-estimated spore concentration by a factor of 200 times.

Thin horizontal surfaces, on the contrary, gave efficiencies much nearer to the expected values for gravity sedimentation. However, edge-shadow and turbulent deposition occurred—even with an edge 0·016 cm. thick (a microscope cover-glass). A double-edged 'wafer' safety razor-blade gave uniform deposits on the upper surface, which were close to expected values—except at 9·5 metres per sec., where the deposit was three times that expected.

ORIENTATION OF SPORES

Lycopodium spores showed different orientations in different parts of the deposit. Gregory (1951) stated that, on the stagnation zone upwind of a vertical cylinder, the spores lie with the rounded distal surface uppermost, and that spores settling in air under the influence of gravity come to rest in the same position. Further observation shows that this contention was incorrect, and that in the stagnation zone or its equivalent the spore lies with the rounded distal surface touching the sticky cylinder. Evidently the spore becomes orientated with the point trailing as it moves through the air. Orientation with the point upwind is therefore characteristic of *Lycopodium* in the stagnation zone.

Microscopic observation of deposits showed that, as was expected, when the glass slide was horizontal the stagnation zone was on the edge, and when the slide was vertical this zone was in the middle of the slide. At intermediate presentation angles, seen most clearly at angles near 90°, the stagnation zone shifted, at 115° occupying zone B, and reaching zone A at about 120° at the higher wind-speeds. At lower wind-speeds, orientation was less definite.

Deposition on 9 cm. Diameter Petri Dish

The Petri dish trap, extensively used in aerobiological mould surveys, was tested horizontally after pouring with 15 cc. of 2 per cent water agar (tests showed that deposition and retention on this medium were similar to those on glycerine jelly). Mean deposition efficiencies (per cent A.D.) for 1 cm. square zones on the agar surface are given by Gregory & Stedman (1953). At all wind-speeds, narrow edge drifts occurred behind the rim of the leading edge and in front of the rim of the trailing edge. Efficiency at 0·5 metres per sec. was low, but at 1·1 and 1·7 metres per sec. efficiency was high, apparently because of the large contribution to the total made by the front and back edge drifts. At 3·2 metres per sec. and above, efficiency fell off substantially below expectation—apparently because the sampling surface was almost entirely shadowed by the 1 cm. high rim of the dish. Efficiencies were somewhat higher at 9·5 metres per sec.

Effects produced by the rim of the Petri dish were nearly eliminated by placing the dish at the bottom of a metal cylinder 13 cm. deep and 11·5 cm. in diameter, sunk below a horizontal flat surface consisting of a square cardboard platform cutting the central axis of the wind-tunnel. The cardboard fitted flush with the mouth of the cylinder and extended 11 cm. up- and downwind.

The Petri dish was also tested in a vertical position. At 9·4 and 5·5 metres per sec., the deposit was four times as great in the central zone of 2·5 cm. radius as it was in the peripheral centimetre around the rim. At, and below, 3·2 metres per sec. the difference was reversed, with nearly 75 per cent more spores just inside the rim of the dish than elsewhere.

Retention and Blow-off From Clean Surfaces

Experiments showed that there is no appreciable loss of *Lycopodium* spores from the deposit on the surface of a slide with a sticky coating of glycerine jelly at any of the wind-speeds tested. Blow-off from a non-sticky glass surface, however, depended on the wind-speed and the angle of incidence of the wind. Clean microscope slides were placed in a spore-cloud at 0·5 metres per sec. to obtain a deposit, and were then placed successively in winds of increasing speeds. Tests were made at angles of 0°, 45°, and 90°. The percentage of the original deposit that was retained after 1 minute at each wind-speed was estimated by counting. At the highest wind-speed, 9·5 metres per sec., slight traces of grease on the slide greatly increased retention when the slide was horizontal, and, unless the surface was carefully cleaned before use, erratic results were obtained under these conditions.

With the slide vertical (90°), blow-off was nearly linear with wind-speed, 98 per cent being retained at 1·1 metres per sec., and 60 per cent at 9·5 metres per sec. Blow-off was least at 45°, and at this angle retention was 100 per cent at wind-speeds up to 5·5 metres per sec., and 95 per cent was retained even at 9·5 metres per sec. By contrast, blow-off was greatest with the surface horizontal (0°), when 77 per cent was retained at 1·7 metres per sec., and only 26 per cent at 9·5 metres per sec. These results illustrate the way the laminar boundary layer acts as a dust trap (p. 25), but the actual values probably have little application to plant surfaces.

Deposition and Retention on Potato and Bean Leaves

The tests described in the preceding sections were all on artificial surfaces, approaching ideal conditions, and gave information on principles of particle deposition from air. This is useful in devising apparatus for sampling airborne particles. We now need to ask how relevant this work is to spore deposition on plant surfaces, especially on leaves which, though rough, are not particularly sticky, and which flap in the wind.

To imitate natural conditions, shoots of potato (*Solanum tuberosum*) with rough leaves, and broad bean (*Vicia faba*) with smooth leaves, were placed in the turbulent wind-tunnel and exposed to clouds of *Lycopodium* spores in the usual manner. The petiole of the leaf was clamped and the leaflets allowed to flap freely, trailing the leaf-tip downwind. After exposure, the leaf surfaces were examined under the microscope and the deposit was counted on zones across the tip, middle, and base of the lamina (upper and lower surfaces), the deposition efficiency being calculated (Table X).

Considerable differences from deposition on a rigid, sticky horizontal slide are apparent. Turbulent deposition either failed to develop at the higher wind-speeds, or the spores were shaken off again in the wind. Deposit on the undersides of the leaves was small at all wind-speeds, but on the upper side it was up to 5 per cent of area dose at winds of 0·5 to 1·0 metres per sec.—both on potato leaves and on the still smoother broad-bean leaves. At low wind-speeds the deposit was similar to that expected from sedimentation under the influence of gravity; but potato leaves had more spores at the base, and broad-bean leaflets had more at the tip.

TABLE X

EFFICIENCY (E %) OF DEPOSITION OF *Lycopodium* SPORES ON UPPER AND LOWER SURFACES OF POTATO AND BROAD-BEAN LEAFLETS IN TURBULENT WIND-TUNNEL (Gregory & Stedman, *unpublished*)

	Wind velocity (metres/sec.)						
Part of leaf	9·4	5·3	3·0	1·6	1·3	1·1	0·6
Potato leaflet							
Tip (upper)	0·0	0·16	0·17	0·68	—	0·42	0·0
(under)	0·0	0·06	0·04	0·19	—	0·89	0·0
Middle	0·06	0·24	0·30	1·34	—	1·62	3·20
	0·0	0·0	0·02	0·28	—	0·0	0·0
Base	0·0	0·12	0·47	1·10	—	8·7	5·8
	0·04	0·0	0·0	1·06	—	0·0	0·0
Broad-bean leaflet							
Tip (upper)	0·06	0·0	0·15	—	1·4	2·82	5·20
(under)	0·0	0·0	0·0	—	0·0	0·02	0·0
Middle	0·0	0·0	0·46	—	2·0	3·52	6·0
	0·0	0·0	0·0	—	0·0	0·06	0·0
Base	0·0	0·0	0·35	—	2·2	1·31	2·0
	0·0	0·0	0·02	—	0·03	0·05	0·0
Horizontal slide	0·42	0·32	0·05	0·09	—	0·29	0·6
	0·36	0·05	0·02	0·01	—	0·004	—
Theoretical	0·20	0·34	0·57	1·05	1·35	1·6	3·45
(sedimentation)	0·0	0·0	0·0	0·0	0·0	0·0	0·0

There is reasonable agreement between observation and the theory of impaction, but other forms of deposition are impure and complex. Efficiency of a collecting surface as an impactor spore-trap increases as the wind-speed and particle size increase, and as the size of the collecting surface decreases. Deposition on horizontal trap surfaces and leaves can be predicted in terms of sedimentation under gravity at low wind-speeds, but edge effects can easily predominate as wind-speed increases, and at 5 to 10 metres per sec. turbulence may result in deposition upwards against gravity.

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VII

NATURAL DEPOSITION

HAVING become airborne and been transported by the wind, the spore must quit the turbulent layers of the atmosphere and re-cross the boundary layer before coming to rest in the still layer of air on a solid or liquid surface, which may or may not prove favourable to growth. Some characters of spores seem to have been evolved in response to problems of take-off, while others may well have been evolved as adaptations for deposition.

Little was known about deposition processes until the development of wind-tunnel techniques—originally for research in aerodynamics—made it possible to experiment on the behaviour of spores in controlled winds in the laboratory. The principal methods of spore deposition in nature can now be tentatively suggested: impaction, sedimentation, boundary-layer exchange, turbulent deposition, rain-washing, and electrostatic deposition.

MEASUREMENT OF DEPOSITION

The relation between χ, the cloud concentration, and 'd', the surface deposition, has been little studied, although it is a relation of considerable biological importance—for instance in pollination, and in epidemics of plant diseases and their control by protectant dusts and sprays. With wind flowing across a smooth surface, it would be possible to calculate deposition directly from a knowledge of concentration, wind-speed, and terminal velocity. However, it is not clear what factors dominate the situation under the complex conditions obtaining in nature, and so the problem must be approached experimentally. With some insight, obtained from Chapter VI, into deposition under relatively simple conditions in a wind-tunnel, we can better understand the complex factors of deposition in nature. In wind-tunnel studies, and in calibrating spore-traps, it is convenient to use percentage efficiency of deposition, $E = (\text{Trap dose}/\text{Area dose}) \times 100$.

For field conditions, two expressions have been used for deposition on the ground. The 'deposition coefficient', $p = d/n$ (where 'd' = number of spores deposited per sq. cm. of surface, and 'n' = number suspended per cc. of air), measures the thickness of the slice of cloud cleared while travelling over unit length of ground surface (Gregory, 1945).

Under a given set of conditions, p is assumed to depend only on concentration, though we do not yet know how it is affected by wind-speed, turbulence and other factors. The 'velocity of deposition', introduced by Chamberlain (1956), was defined as

$$v_g = \frac{\text{amount deposited per sq. cm. of surface per second}}{\text{volumetric concentration per cc. above surface}}$$

If p is assumed to be independent of wind-speed, it will be apparent that, in our notation,

$$p = v_g/u.$$

MEASUREMENT OF DEPOSITION COEFFICIENT, 'p'.

The first attempt to evaluate p by Gregory (1945) was based on experiments by Stepanov (1935), whose results were tested against Sutton's (1932) eddy-diffusion theory.

Sutton's formulae had been developed for calculating the concentration of a cloud of particles whose deposition was negligible—the number of particles in the cloud, Q_0, remaining constant throughout the diffusion. In our problem, although the effect of gravity on *dispersion* has been neglected, the quantity of spores remaining in suspension is steadily diminishing owing to a relatively large deposition from that part of the cloud which is in contact with the ground, so that Q_x, the total quantity remaining in the cloud when its centre has moved to a distance x, is less than the original Q_0. It has been shown* that Q_x will decrease exponentially with increasing distance, according to the equation:

$$Q_x = Q_0 \exp.\left[-\frac{2px^{(1-\frac{1}{2}m)}}{\sqrt{(\pi)}\ C(1-\frac{1}{2}m)}\right].$$

Values of Q_x and d for two values of the parameter *m* have been calculated, and it is now possible to test the theory against Stepanov's results. In each of his experiments the total number of spores liberated differed, so that the data had first to be put on a comparable basis by equating the mean deposition, d, at 5 metres, to 100 per cent, and then expressing the deposition observed at greater distances by relative percentages. The logarithms of the observed relative depositions were plotted against the logarithms of the distances in centimetres. The expected depositions when $p = 0{\cdot}05$, $0{\cdot}025$, and zero, respectively, were also plotted, and the line calculated for $p = 0{\cdot}05$ was seen to approach most clearly to the observed values (Gregory, 1945). A deposition coefficient of $p = 0{\cdot}05$ means that, in travelling across 1 sq. cm. of surface, the entire cloud would deposit a quantity of spores approximately equivalent to the number contained in a slice half-a-millimetre thick through the axial plane of the cloud. This value of p was estimated from experiments in winds of about 1 metre per sec.

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* By Margaret F. Gregory (*see* Appendix *in* Gregory, 1945).

The problem was next taken up experimentally by Chamberlain (1956), who made *Lycopodium* spores radioactive by steeping them in a solution of iodine-131 in carbon tetrachloride. When dry, they were liberated at a height of 1 metre above a grass field. The concentration of the spore-cloud was measured 20 metres downwind by using sticky cylinders 0·65 cm. in diameter at 30, 60, and 90 cm. above ground-level. The wind-speed at each height was measured and, from the known impaction efficiency of cylinders, the dosage at each height could be estimated (dosage did not vary much with height at this distance). The radioactivity of the grass turf just in front of each sampling position was measured to give an estimate of deposition. 'Velocity of deposition', v_g, and deposition coefficient, p, were then calculated from these two measurements (Table XI), the results giving some support to the idea that p is independent of wind-speed.

TABLE XI

DEPOSITION ON GRASS OF *Lycopodium* SPORES ACTIVATED WITH IODINE-131 (data of Chamberlain's, 1956) AT 20 METRES FROM POINT WHERE LIBERATED AT 1 METRE ABOVE GROUND-LEVEL

Wind velocity at 1 metre above ground-level cm./sec.	v_g cm./sec.	p
815	2·07	0·0025
310	1·07	0·0035
160	0·50	0·0031

Further information was obtained by Gregory, Longhurst & Sreeramulu (*unpublished*) from experiments in 1956-57 at the Imperial College Field Station, Ascot, England. Spores of *Lycopodium*, and the much smaller spores of a bracket fungus, *Ganoderma applanatum*, were liberated a short distance above ground-level in a field of short, rough grass. Cloud concentration and deposition, measured at a number of positions simultaneously, enabled p or v_g to be estimated at various distances up to 10 metres from the point source (Table XII). (Two additional recent estimations at 1 metre from the source, with *Lycopodium* spores on a smooth lawn at Rothamsted Experimental Station, gave $p = 0·05$ and 0·09, and $v_g = 3·1$ and 5·3 cm. per sec., respectively.) A remarkable phenomenon, evident from Table XII, is that both v_g and p vary with distance, decreasing with distance from the source.

Much more experimental work is needed before the relation between χ and d can be established, but meanwhile it appears that, at 10 metres or so from the source near ground-level, v_g nearly equals the terminal velocity of the particle, whereas closer to the source the value may be up

TABLE XII

DEPOSITION OF SPORES ON GROUND, FROM SIMULTANEOUS MEASUREMENTS OF χ AND d BY VISUAL COUNTS UNDER MICROSCOPE.
(Gregory, Longhurst & Sreeramulu, *unpublished*)

Height of liberation	Mean wind-speed metre/sec.	Distance from source 2·5 m. p	2·5 m. v_g cm./sec.	5·0 m. p	5·0 m. v_g cm./sec.	10·0 m. p	10·0 m. v_g cm./sec.	20·0 m. p	20·0 m. v_g cm./sec.
Lycopodium spores									
1·0 metre	1·98	0·01	2·3	0·02	3·6	0·02	3·4	—	—
	0·83	0·02	1·2	0·05	3·8	0·06	5·1	—	—
	0·62	—	—	0·09	5·5	0·05	2·9	0·03	1·7
	0·40	0·44	17·6	0·05	2·1	0·02	1·0	—	—
0·25 metre	1·28	0·05	6·9	0·03	4·4	0·02	2·7	—	—
	1·10	0·07	7·2	0·01	1·5	0·02	1·7	—	—
	1·09	0·13	13·7	0·04	4·5	0·02	1·8	—	—
	Mean:	0·12	8·16	0·042	3·64	0·029	2·8	0·03	1·7
Ganoderma spores		1·0 m.		1·5 m.		2·5 m.		5·0 m.	
0·25 metre	1·70	—	—	—	—	0·003	0·44	0·0008	0·14
	0·91	0·022	1·97	0·006	0·56	0·005	0·46	0·004	0·34
	0·76	0·015	1·13	0·006	0·43	0·003	0·24	0·001	0·08
	0·61	0·014	0·83	0·010	0·61	0·006	0·34	0·005	0·29
	Mean:	0·017	1·31	0·007	0·53	0·004	0·37	0·003	0·21

Summary

	Mean of all values p	Mean of all values v_g	Mean at selected distance p	Mean at selected distance v_g
Lycopodium *c.* 32 μ dia. v_s = 1·76 cm./sec.	0·057	4·35	0·03	2·7 at 10 metres
Ganoderma *c.* 10 × 6 μ v_s = 0·18 cm./sec.	0·007	0·56	0·004	0·37 at 5 metres

to 5 times as great. (On theoretical grounds, Schrödter (1954, 1960) deduced that the 'probable final velocity' of a spore is *half* the terminal velocity.) For a deposition theory based on sedimentation under the influence of gravity, it seems reasonable to accept observed terminal velocities of the particles as measuring their velocity towards the ground; but for a ground-level source, allowance will have to be made for exceptionally large deposition during the first few metres of travel. Data are not sufficiently extensive to bar the use of the coefficient of deposition, p, which assumes that, for a particle of given size, the deposition depends on the distance travelled, rather than on the time taken to travel that distance. If p turns out to be independent of wind-speed, the parameters p and v_g would stand contrasted in a manner recalling the different treatments of σ by Schmidt and Sutton (Chapter V).

Ground deposition conforms better to a sedimentation theory than does deposition on the horizontal microscope slide in the wind-tunnel recorded in Chapter VI. For comparison with ground deposition, Table XIII shows wind-tunnel values, calculated in terms of p and v_g, for deposition on a horizontal slide.

TABLE XIII

OBSERVED VALUES OF p AND v_g FOR *Lycopodium* SPORES ON HORIZONTAL MICROSCOPE SLIDE IN WIND-TUNNEL (TURBULENT AND STREAMLINED CONDITIONS)

	Wind-speed cm./sec.					
	950	575	320	170	110	50
Turbulent wind						
p	0·0043	0·0029	0·0005	0·0009	0·0050	0·026
v_g cm./sec.	4·10	1·7	0·10	0·15	0·55	1·3
Streamlined wind						
p	0·0042	0·0013	0·00008	0·00002	0·0004	—
v_g cm./sec.	4·0	0·75	0·025	0·004	0·004	—
p expected for $v_g = 1·75$ cm./sec.	0·00185	0·003	0·0055	0·01	0·0016	0·035

Loss by Deposition from Spore-cloud

To judge from outdoor values of p and v_g, a spore-cloud liberated near ground-level must lose an important fraction of its original number by deposition on the ground in the early stages of its diffusion. Relevant field measurements are incomplete, but we have attempted to make minimum estimates of ground deposition from the experiments of Stepanov (1935) and Gregory, Longhurst & Sreeramulu (*unpublished*), where Q_0 is known and where deposition was measured at several distances along lines radiating from the point of dispersion. Each experimental value was plotted to scale on graph paper, points were joined, and the total number of spores deposited within the area sampled was estimated by integrating areas under the curves (Table XIV). It is clear that spores must also have been deposited on each side of the area sampled,

TABLE XIV

PERCENTAGE OF TOTAL SPORES (Q_0) LIBERATED NEAR GROUND-LEVEL THAT WERE ESTIMATED TO HAVE BEEN DEPOSITED ON GROUND IN OPEN-AIR TESTS

Wind-speed metre/sec.	Height of liberation	Dimensions of sector of annulus		Estimate of percentage of spores recovered on test area
		Distance limits	Angle	
Stepanov (*Tilletia caries*)				
	metre	metre	deg.	
0·5–4·0	0·8–1·2	5–20	105	11·2
2·3–3·0	1·5	5–40	105	8·55
Gregory, Longhurst & Sreeramulu (*Lycopodium*)				
	metre	metre	deg.	
1·01	0·25	2·5–10	120	24·4
0·40	1·0	2·5–10	100	18·1
1·28	0·25	2·5–10	120	14·5
0·83	1·0	2·5–10	120	13·5

and the values are therefore underestimates; they were made without extrapolation, except that, where the number of radii on each side of the axis of dispersion was unequal, a symmetrical dispersion was assumed. With liberation at 0·25 m. above ground-level, from 14 to 24 per cent of the spores liberated were deposited within 10 metres' radius in winds of little over 1 m. per sec.

Deposition Mechanisms Outdoors

BOUNDARY-LAYER EXCHANGE

Observations on deposition out-of-doors are still meagre, but values for v_g obtained with plant spores of two widely different sizes and fall velocities, *Lycopodium clavatum* (1·75 cm. per sec.) and *Ganoderma applanatum* (0·18 cm. per sec.), suggest the following picture of deposition.

Deposition on the ground tends to remove spores from the base of the cloud. The concentration of the cloud near ground-level is then restored by diffusion—either horizontal diffusion from a near-by source, or downward vertical diffusion from a reservoir of particles overhead, when the atmosphere itself is acting as a source. Diffusion thus brings particles down to the boundary layer, and here they settle-out mainly under gravity. This is why, when v_g is estimated from χ as measured just above ground-level, it numerically approaches the Stokesian terminal velocity. This process which has been called 'boundary layer exchange', continually replenishes the ground layer of still air in which even minute spores can sediment-out.

The demarcation between the laminar surface layer and the turbulent wind-stream is not sharp. From time to time, spore-bearing eddies break into the laminar layer which is being cleared by sedimentation, removing spore-free air and leaving, in exchange, small volumes of spore-laden air. These spores sediment at terminal velocity under the influence of gravity and are soon out of reach of further eddies. In boundary-layer exchange, turbulence has a great effect in bringing spores down to the layer where they can slowly sediment under the influence of gravity.

SEDIMENTATION

As we have seen, the effect of gravity is usually negligible on vertical distribution in the atmosphere. Still air, as Tyndall (1881) found long ago, soon becomes purified because microbes settle out from it under gravity—a process which we call sedimentation. Out-of-doors the air is almost never still—except within about a millimetre of the surface. In the turbulent air-layer above the ground, the effects of gravity are slight and difficult to demonstrate; but Rempe (1937) demonstrated gravitational effects with tree pollen near Göttingen (*see above*, p. 21). Under stable conditions on clear nights, when air at ground-level is cooled by radiation, the laminar layer may extend to a height of several metres. This zone may be nearly cleared of pollen by sedimentation, while above it a much larger spore and pollen concentration may be retained in the turbulent layer.

Sedimentation, we may therefore suppose, is only noticeable in the laminar layer which normally extends only a few millimetres above the surface but, under exceptional conditions at night, may reach several metres. Wind-tunnel experiments confirm that the effect of sedimentation is slight at wind-speeds of 2 m. per sec. and upwards.

IMPACTION

When a small surface, such as that of a leaf or twig, projects into the wind, spores may be deposited by impaction on its windward side. Wind-tunnel experiments confirm that impaction is inefficient when small spores approach large obstructions at low wind-speeds. Conversely, impaction is more efficient when large spores are blown towards small objects at high wind-speeds. So it seems that large spores, in addition to carrying a bigger food reserve, have the advantage of a favourable size for impaction on surfaces. Dry-spored, airborne leaf-pathogens usually have comparatively large spores (e.g. uredospores, aecidiospores, *Phytophthora*, *Helminthosporium*, etc.).

On the other hand, dry-spored soil inhabitants are characterized by small spores, unsuitable for impaction (e.g. *Penicillium* and *Aspergillus*). Among vegetation, where the wind-speed normally reaches an upper limit of about 2 metres per sec., spores of *Lycoperdon perlatum* 4–5 μ in diameter would not be impacted at all, even on objects as narrow as 1 mm.; and it can be calculated that spores of this size would require a wind of about 25 metres per sec. to be impacted with only 10 per cent efficiency on a blade of grass. Evidently we must look to processes other than impaction to deposit minute spores such as those of puffballs, earthstars, *Ustilago*, and the common moulds. The loose smuts of cereals, *Ustilago* spp., with spores in the 7–9 μ range, would not be impacted efficiently on leaves and stems; but on narrow surfaces such as glumes and stigmas of grasses, they would be expected to reach an efficiency as high as 50–75 per cent.

Agaricus (*Psalliota*) *campestris* has spores of about 7 × 6 μ, which should be near the lower limit of size for impaction on grass leaves and stems, at the limiting wind-speed in closed vegetation of about 2 metres per sec. Uredospores of *Puccinia graminis* and conidia of *Erysiphe graminis* would impact on a leaf of wheat with efficiences near 40–60 per cent. *Botrytis polyblastis*, a leaf pathogen of *Narcissus*, with spores up to 90 μ diameter, comes into the same group of pathogens that are relatively efficiently impacted on leaves and stems.

The difficult problem of impaction on objects as wide as the trunk of a tree seems to have been solved by some of the lichens. *Pertusaria pertusa*, as I have myself observed, can shoot single ascospores, measuring some 150 × 50 μ, to a record horizontal distance of 40 mm. Extrapolation from wind-tunnel data suggests that, once launched into a wind of only 2 metres per sec., these giant spores (nearly the largest in the fungi) would impact on a tree-trunk of 8 inches diameter with about 50 per cent efficiency.

Although a high impaction efficiency may be necessary for fungi which attack leaves and stems, it may be positively disadvantageous for spores produced among dense vegetation. Johnstone *et al.* (1949) point out that the ability of an airborne particle to penetrate close vegetation is the inverse of its impaction efficiency. In close vegetation a high impaction efficiency would reduce the chances of a spore getting very far from its point of liberation. It is possible that the 10 μ-diameter spore represents a working compromise between the conflicting requirements of dispersal and deposition, evolved under the normal range of winds encountered among vegetation. The large-spored leaf- and stem-pathogens appear to be specialized *impactors*, while the minute-spored puffballs and moulds appear to be specialized *penetrators*—perhaps normally deposited by processes other than impaction.

TURBULENT DEPOSITION

Turbulent deposition has been observed in the wind-tunnel and on artificial spore-traps in the open air. Spore-laden air flowing over horizontal surfaces will deposit spores at rates much greater than those calculated for sedimentation under the influence of gravity. In the wind-tunnel turbulent deposition increases with increasing wind-speed and, at 5 to 10 metres per sec., deposition may be as great on the underside of a horizontal surface as it is on the upper-side—an effect which clearly cannot be caused either by impaction or by sedimentation under gravity. The effect has been noted on pollen traps by Durham (1944, p. 233), who found the catch on the lower surface of a horizontal slide to be as high as 50 per cent of the upper surface. Rishbeth (1959) found that spores of *Fomes annosus* and *Peniophora gigantea* can be deposited on the undersurface of pine stem sections exposed a few metres above ground-level.

Turbulent deposition in the open air is also illustrated by experiments with *Lycopodium* spores liberated just above short grass at Rothamsted Experimental Station (Table XV). Deposition was recorded on the upper and lower surfaces of horizontal traps held clear of supports on long pins projecting from a wire frame. Catches shown in Table XV are for traps at the same level as the spores were liberated (h + 0), and at 25 cm. above this level (h + 25), in a downwind direction. The dimensions of the traps were 18 × 18 × 4 mm. in the x, y, and z directions, respectively.

The greater deposit on the undersurfaces of traps at 25 cm. above the level of emission, together with the unexpectedly large deposition on ground near the source as shown in Table XII, is evidence of factors near the source of a diffusing cloud which still remain to be elucidated.

TABLE XV

NUMBER OF *Lycopodium* SPORES DEPOSITED ON UPPER AND LOWER SURFACES OF HORIZONTAL TRAPS, $Q_0 = 10^8$ SPORES LIBERATED NEAR GROUND-LEVEL (Gregory, *unpublished*)

	Height of trap (cm.)	Distance downwind of source (cm.) 25	50	75	100	105	130	155	180
11 Feb. 1948									
	h + 25	12	5	4	3	—	—	—	—
		19	19	8	15				
	h + 0	7640	1915	659	353	—	—	—	—
		208	238	88	27				
30 April 1948									
	h + 25	0	4	4	7	30	0	0	4
		0	11	4	22	55	0	0	60
	h + 0	1000	3500	730	520	540	320	120	166
		18	0	0	7	0	7	4	4

Conditions	Wind-speed at 2 metres (μ)	Height of liberation (h)
11 Feb. 1948	3·7 metres/sec.	5 cm.
30 April 1948	3·9 metres/sec.	7 cm.

ELECTROSTATIC DEPOSITION

The basidiospores of the cultivated mushroom and some other fungi were shown by Buller (1909) to carry small electric charges when falling in air. Little is known about the phenomenon, and its effect is probably negligible—except when the spore is within about a millimetre of another body. The origin of the charge, its effect over very short distances, and its relation to the vertical potential gradient in the atmosphere, which is said to average about 150 volts per metre, might repay future investigation.

Ingold (1957) suggested that in polyporous fungi with long and narrow, vertical hymenial tubes, electrostatic forces may keep a basidiospore in the middle of the tube, preventing deposition on the walls of the tube, while the spore is slowly falling under gravity. Gregory (1957) showed that basidiospores of *Ganoderma applanatum* usually carry a positive charge when allowed to fall between two condenser plates which are charged + and − 200 volts with respect to earth potential. In one test the average deflection of the spores from the vertical was 12°, indicating a velocity component towards the plate of 0·036 cm. per sec. in a field of 400 volts per cm.

The ascospores of *Lophodermium* [*pinastri*], the cause of pine leaf-cast disease, are shot into the air from fruit-bodies on fallen pine-needles. Rack (1959), using a potential difference of 75 volts in an apparatus resembling ours, but without earthing the battery, claimed that immediately on ejection from the ascus the spores carried a negative charge, but that, at a height of 1·0 to 1·6 metres above ground-level, from 93 to 99 per cent of the spores carried a positive charge. He concluded that this interesting phenomenon might aid adhesion of spores to healthy pine-needles on the tree.

In the normal, fine-weather electrical field of 1 volt per cm. over a flat surface with the Earth negatively charged, a *Ganoderma* spore would gain a negligible addition of 0·05 per cent to its terminal velocity. Ranz & Johnstone (1952) have shown that aerosol particles 0·5 μ in diameter could easily carry charges by which their deposition or suspension would be controlled by the Earth's field rather than by gravity. Whether such comparatively large particles as fungus spores or pollen grains are repelled from the ground or, alternatively, attracted to projecting surfaces such as leaves and tree tops, is as little known as are the causes of changes in the Earth's field itself. Clearly this phenomenon is worth further investigation.

MINOR DEPOSITION MECHANISMS

It is also known that small particles tend to move down a temperature gradient (Cawood, 1936; Watson, 1936), and that forces exist which cause particles, at least up to 2 μ in diameter, to be repelled by a hot surface and attracted by a cold one. Smoke particles and *Lycopodium* spores are also known to move away from light in the phenomenon of 'photophoresis' (Whytlaw-Gray & Patterson, 1932).

RAIN-WASHING ('Scrubbing', 'rain-out', 'wash-out')

Natural raindrops vary in size up to a maximum diameter of about 5 mm., above which they become unstable and break up during fall into two smaller drops. They have terminal velocities of fall varying from 2 to 9 metres per sec. (Best, 1950; *see also* Gunn & Kinzer, 1949).

The pick-up of small spheres in the path of falling raindrops was studied theoretically by Langmuir (1948) in connection with artificial rain-making in Hawaii. To judge from Langmuir's figures, the minute spores of *Lycoperdon* and of the soil-inhabiting Penicillia would fail to be collected at all by drops much below 1 mm. in diameter, and efficiency of collection would rise to a maximum of about 15 per cent with droplets about 2 mm. in diameter, decreasing again with still larger drops. Basidiospores of *Agaricus* (*Psalliota*) *campestris* should begin to be collected by raindrops over 0·2 mm. in diameter, reach a maximum of 30 per cent efficiency with raindrops of 2·0 mm. in diameter, and decrease slightly with drops of larger diameters. Spores of *Tilletia caries*, *Puccinia* uredospores, and conidia of *Erysiphe graminis*, could be collected by any possible raindrop, and collection would reach a maximum of about 80 per cent efficiency with drops 2·8 mm. in diameter.

The optimum size of spore for deposition in rain varies with the size of the prevalent raindrops. As we have seen, spores of *Lycoperdon perlatum* would not be collected by drops less than 1 mm. in diameter, and I have shown that drops of less than this diameter do not operate the bellows mechanism of this species (cf. p. 60, and Gregory, 1949). According to Langmuir, collection efficiency is at a maximum with drops of about 2 mm.

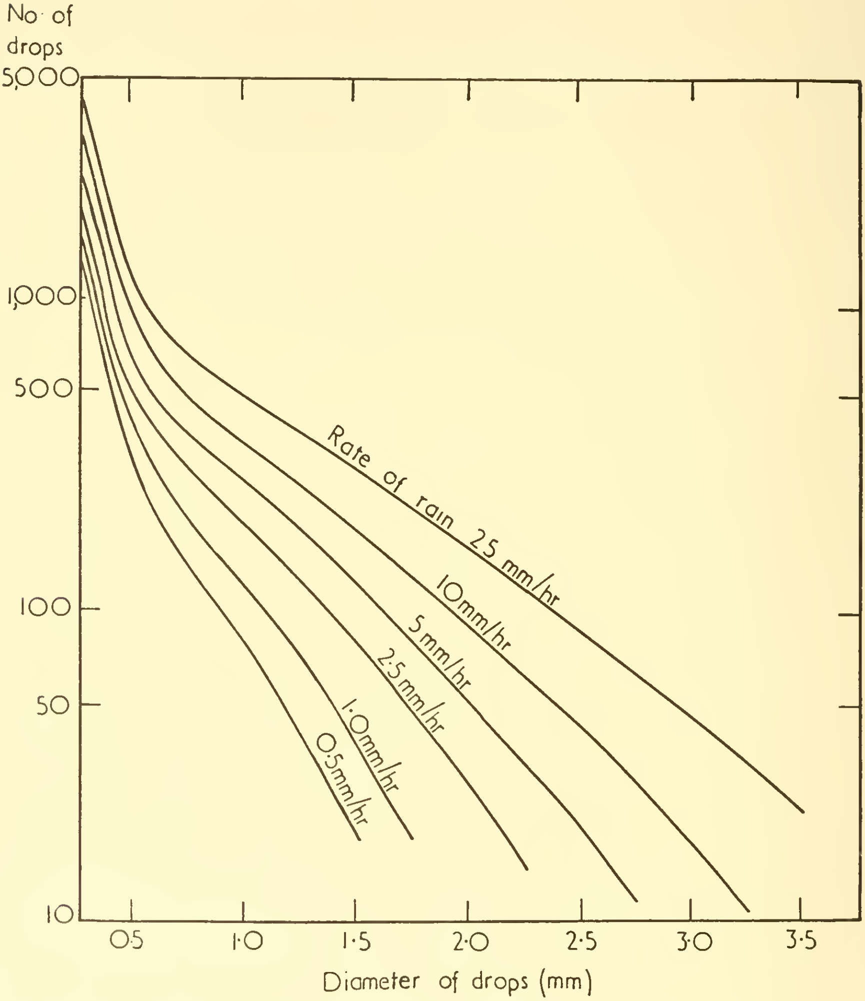

FIG. 15.—Number of raindrops of various diameters passing per second through 1 sq. metre (horizontal), with rainfall of intensities varying from 0·5 to 25 mm./hour. (Smoothed curves from data of Best, 1950).

in diameter for all spore sizes, and is then about 25 per cent for spores 4μ in diameter, and 80 to 90 per cent for spores 20 to 30 μ in diameter.

Nothing is known of the pick-up of non-spherical spores and how properties other than size or terminal velocity affect collection by raindrops. The spores of *Ustilago perennans*, although not easily wetted by water, are evidently readily collected by rain. The work of Burges (1950) suggests that, when non-wettable spores reach the ground, they remain in the upper layers of the soil. For the leaf- and stem-parasites, removal from the air by rain is possibly unfavourable, while for small-spored soil inhabitants as well as for smuts and other fungi that infect seedlings, it may be the normal method whereby they come to ground.

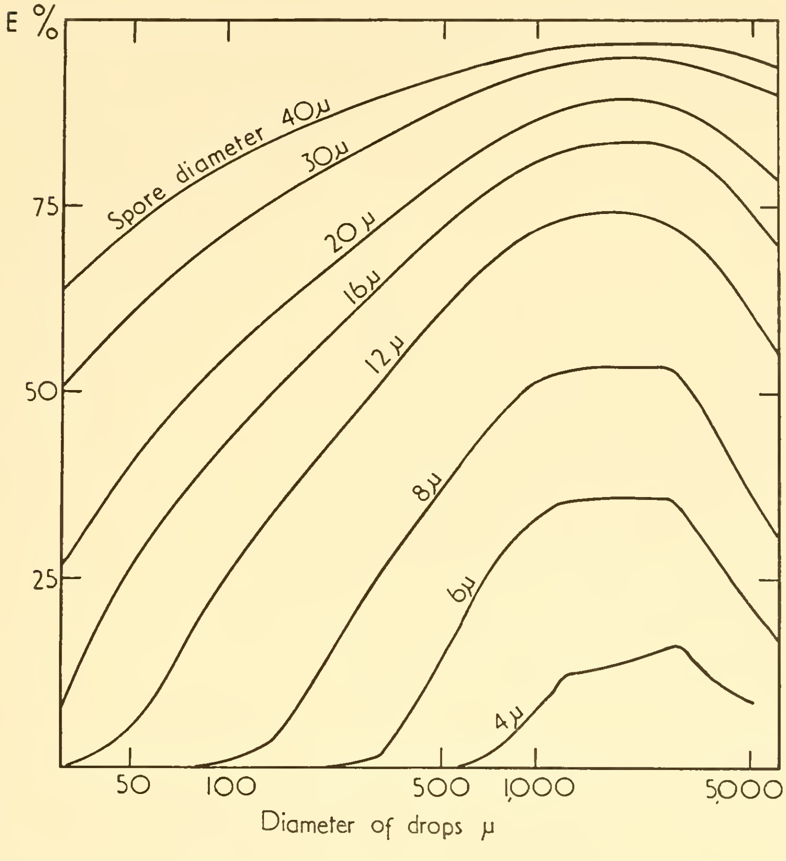

FIG. 16.—Collection efficiencies of spores of diameters 4 to 40 µ by raindrops of diameters 0·03 to 5·0 mm. (Smooth curves drawn through values computed by Langmuir, 1948.)

Figs. 15 and 16, compiled from the data of Best (1950) and others, show the proportion of raindrops of various sizes occurring in natural rainfall, and the collection efficiencies of such drops (E per cent) as given by Langmuir (1948).

Most relevant to our problem is the theoretical study by Chamberlain (1956), who used Best's (1950) results to calculate that, if other causes of diminution of the spore-cloud concentration are neglected, rainfall at the rate of 1 mm. per hour would deplete an aerosol of *Lycopodium* spores according to the equation

$$\chi_{(t)} = \chi_0 \exp. (-3{\cdot}3 \times 10^{-4}t).$$

This implies that after one hour the concentration will be reduced to one third of its initial value. Chamberlain applies the concept of v_g to rain wash-out and shows that, the greater the height of the spore-cloud through which rain falls, the greater the rate of wash-out. The study was continued experimentally at Harwell by F. G. May (1958), who found good agreement with Chamberlain's theoretical values when tested with *Lycopodium* spores marked with iodine-131. When testing thundery showers, May also obtained good agreement with values calculated by Langmuir (1948) and by Mason (1957)—but the predominantly smaller and more variable droplets of frontal rain removed particles faster than had been predicted by theory. McCully *et al.* (1956) reported highly efficient removal of fluorescent dusts by rain from the air in both laboratory and field tests.

May (1958) points out that, in addition to removal by impaction, raindrops can act as electrostatic collectors by means of two effects—the coulombic attraction between oppositely-charged spores and raindrops, and by induced attraction. He estimated that capture by coulombic attraction in thunder rain might equal capture by induced attraction, and that both together could amount to 20 per cent of the total wash-out. On the other hand, May suggests that for frontal rain coulombic collection can be neglected.

RELATIVE IMPORTANCE OF DEPOSITION MECHANISMS

With Q_0 spores liberated into the air from a source, the number of spores remaining in suspension will be reduced during travel in the wind by the action of various deposition processes and, at a distance x from the source, the number remaining in suspension will be Q_x (Chapter XIII).

The relative importance of the deposition processes can now be seen to differ in different positions. Close to a source liberating spores near ground-level, the mechanisms of impaction and boundary-layer exchange will be the dominant factors in depleting the cloud. Near to the source, rain-wash will have a relatively slight effect, because the height and breadth of the cloud are small. But, as the cloud diffuses to its maximum height, rain will have an increasingly large effect. With the still smaller particles of radioactive dust, pushed into the stratosphere by megaton bombs and falling back into the troposphere, rain-wash appears to be the most important mechanism of removal. The level of strontium-90 in soil at Antofagasta, Chile, in rain-free desert, is only 1 per cent of that general for places in the same latitude with normal rainfall (Libby, 1956).

Measurement of deposits on leaves in the field are few, but Rishbeth (1959) has used surface microflora of conifer needles and leaves of birch, etc., as a measure of infection-potential of forest contamination with spores of *Fomes annosus* and *Peniophora gigantea*. Studies on the rate at which spores accumulate and disappear in East Anglia, showed that there was no continued increase, and that the rate of deposition was roughly equivalent to the rate of disappearance.

Rain-washing of air, when it occurs, rapidly ends the process of spore dispersal, and seems to be effective with small spores which are deposited only slowly and ineffectively by other processes.

VIII

AIR SAMPLING TECHNIQUE

Knowledge of the air-spora has depended on developing sound techniques for air sampling. Smoke and many industrial dusts can be studied satisfactorily with the ultra-microscope (*see* Green & Lane, 1957, p. 218), but direct microscopic examination of spores suspended in air is scarcely ever practicable. All convenient methods depend on apparatus to remove the spores to a surface where they can be examined—either directly under the microscope or after growth in culture.

Early methods of air sampling were summarized by Cunningham (1873). Developments during the next seventy years were reviewed by the Committee on Apparatus in Aerobiology of the National Research Council, Washington, D.C. (1941), and again by duBuy *et al.* (1945) of the United States Public Health Service. Now that deposition efficiencies are better understood, sampling methods can be reviewed once more.

The various sampling techniques that are now possible have different advantages and limitations. The following questions have to be answered before a technique is chosen for a particular job. Is an assessment of the total air-spora wanted, or is the study concerned only with a few groups or a single species? Is a continuous day-and-night record needed, or will short and regular or occasional samples suffice? If changes in the air-spora are being studied, what time-intervals are necessary: would a 24-hour mean suffice, or must an accuracy of ± 1 hour be attained, or again, is an instantaneous cut-off needed to give a time-discrimination of minutes or seconds? The size of the sample must be decided upon, and the choice made between the volumetric or deposition methods. Allergists are normally interested in the number of particles (dead or alive) in a given volume of air, whereas plant pathologists and plant breeders are more interested in the deposition of viable spores or pollen grains.

Spore trapping requires apparatus, and many questions have to be asked about this. What are its capital and running costs? (It is uneconomic to use the time of a trained scientist with a good microscope on inefficient sampling methods.) Does it need a power supply? Must it be portable? Is it to be operated by a skilled staff or must it be robust and foolproof? Does its efficiency vary with wind-speed?

When the spore has been caught it has to be identified—but is this to be done visually or by cultural methods? Visual methods (using various forms of microscopy) should give the complete picture of the air-spora with spore-aggregates as well as inorganic particles, whereas cultural methods allow the most accurate taxonomic determinations—but they will only show viable micro-organisms that can grow on the media chosen. Visual pollen identification can be carried to species level in many genera; but whereas spores of a few pathogenic fungi can be recognized with certainty, the identification of spores and cells of bacteria, actinomycetes, and most of the smaller fungi, is tentative in the extreme (see Appendix I, p. 207).

To economize description in the following account, the various kinds of apparatus for sampling the air-spora are grouped according to the physical processes by which they remove particles from the air and deposit them on surfaces for examination. Many of the techniques can be adapted to give either a deposit for visual examination under the microscope or cultures on artificial media.

Gravity Sedimentation Methods

SEDIMENTATION FROM STILL AIR

A simple box, developed by Alvarez & Castro (1952) for the study of airborne fungi, had two hinged sides and a covered tray at the bottom for inserting a microscope slide or Petri dish. To take an air sample, the two hinged sides were raised horizontally and wind was allowed to blow through the box. Closing the hinged sides trapped a box-full of air and the entrapped spores then sedimented under gravity.

In theory the result is not affected by wind velocity or particle size. Sampling is discontinuous, only a small volume of air being sampled at a time, and there will be losses on the walls and roof of the box due to convection and diffusion (*see* Tyndall, 1881; Green & Lane, 1957, p. 229).

SEDIMENTATION FROM WIND

The method of examining the deposits on a freely exposed, horizontal surface such as a glass microscope slide was used by Pouchet in his controversy with Pasteur, but can be traced back to van Leeuwenhoek.

(i). *The 'gravity slide'* has been the routine method for investigating the pollen and spore content of the air since the early days of hay-fever studies. Scheppegrell (1922) used ordinary 76 × 25 mm. microscope slides exposed without protection from rain. Most workers, however, e.g. Blackley (1873), Wodehouse (1945), Durham (1946), Hyde & Williams (1950), and Hyre (1950), have exposed the slides horizontally, with the sticky slide facing upwards in some form of shelter—open to the wind but giving protection from rain. The adhesive coating of the slide is usually glycerine jelly or petroleum jelly. A slide is commonly exposed for a period of 24 hours, and slides are changed daily throughout a season.

The gravity slide is cheap, simple, and operates continuously, but has serious defects as a quantitative method of air sampling out-of-doors, giving a highly distorted picture of the air-spora because it preferentially selects the larger particles. Terminal velocity increases as the square of the spore's radius (Chapter II), and terminal velocities are such that under ideal conditions, while for example a slide is receiving the puffball spores in a layer of air 0·5 mm. thick, it also receives rust uredospores from a column 10 mm. thick, and grass pollen from a layer 50 mm. thick. A volume of air containing puffball spores and grass pollen in equal concentration would be recorded by the gravity slide as having 100 times as many grass pollen grains as puffball spores. To correct this distortion Scheppegrell (1922) tried to calculate the volumetric concentration from gravity-slide deposits using a formula based on particle *diameter*, which was later corrected by Cocke (1937) to particle *radius*.

Because of edge effects and turbulent deposition at high wind-speeds (Chapter VI), the gravity-slide catch is very difficult to interpret; but in spite of these defects it has been widely used and has contributed much of our still meagre knowledge of the air-spora.

(ii) *The gravity Petri dish.* A few workers have exposed Petri dishes horizontally in outside air, to provide pollen deposits for visual examination (Hesselman, 1919; Ludi & Vareschi, 1936).

More commonly, Petri dishes of sterile media are exposed in the open air for periods of from 1 to 10 minutes to investigate the cultivable bacterial or mould flora of the atmosphere. (Some workers expose empty sterile dishes and pour the medium on returning to the laboratory.) Indoors, the method is subject only to distortion owing to the sedimentation rate. Out-of-doors, however, the method is also subject to aerodynamic effects from the edge of the dish—unless the dish is sunk below a plane surface (p. 73). For sampling out-of-doors the method has been used in tests by: P. F. Frankland & Hart (1887), Saito (1904, 1908, 1922), ZoBell & Mathews (1936), Dye & Vernon (1952), Menna (1955), Richards (1954, 1954*a*, 1954*b*), Werff (1958), and many others.

Apart from convenience and economy, the method is valued for the precision with which organisms can be identified in resulting cultures. Its defects are: sensitivity to particle size, wind-speed, and aerodynamic effects (p. 73); also the small volume of air sampled intermittently. Continuous sampling is impracticable and diurnal changes of the air-spora are not revealed. Its restriction to viable and cultivable particles may be developed with advantage to a high degree of selectivity when sampling is aimed at a limited group of organisms. With pleomorphic fungi, positive growth in culture may still leave the origin in some doubt; a *Phoma* or a *Fusarium* culture might have arisen either from a conidium or an ascospore—a detail which it is sometimes important to resolve.

(iii) *Conical funnels* have been exposed for trapping conidia of downy mildew of the vine (*Plasmopara viticola*) by Savulescu (1941), for forecasting mildew outbreaks in Rumania.

SEDIMENTATION FROM ARTIFICIALLY MOVING AIR

Hesse's method of sedimentation in long horizontal tubes has been described in Chapter I. Cocke (1938) used the same principle for visual microscopic examination of airborne pollen. A small chamber was lined top and bottom with eight glass slides, leaving a passage of only 1–2 mm. between floor and roof. With 1·4 cu. metres of air per 24 hours drawn between the slides, Cocke reported good agreement with the gravity slides exposed simultaneously out-of-doors.

Similar in principle are the funnel device (Hollaender & Dalla Valle, 1939), in which air enters the stem of an inverted conical funnel suspended 3 mm. above a Petri dish of medium, and the bottle device of Scharf (in duBuy *et al.*, 1945), in which air plays from the end of a tube onto the surface of a culture medium in a horizontal medical-flat bottle. As the volume of air sampled in a given time is often inconveniently small, and they are not easily made quantitative, none of these methods has passed into routine use.

INERTIAL METHODS

In the 'inertial methods' the particles may be retained on filters, on flat surfaces, or in liquids. The air may operate by being drawn through a jet or tube, or by being spun to produce centrifugal separation; or, alternatively, the apparatus may move the trap surface through the air as in the whirling arm devices, or in sampling from aircraft. The grouping adopted below is convenient rather than fundamental.

IMPACTION USING WIND MOVEMENT

(i) *Vertical and inclined sticky microscope slides* have been used for catching pollen in hay-fever research and spores in cereal rust studies. Blackley (1873) exposed four slides at a time, facing different points of the compass; but commonly a single slide is exposed for 24 hours in a pivoted vane shelter which swings to face the wind—cf. Craigie (1945), Clark (1951), and Mehta (1952). Slides were fixed in trees, in positions comparable with leaves, in order to trap spores of *Hemileia vastatrix*, a rust fungus devastating coffee, in Ceylon by Ward (1882) and in India by Mayne (1932).

Various methods are used to test for the spore liberation period of a green plant or fungus, but this is a different problem from air sampling (Pettersson, 1940; Oort, 1952; Hopkins, 1959).

Vertical slide traps have been sent aloft fixed to kites, first apparently by Blackley (1873). A variety of such devices were used by Mehta (1933, 1940, 1952) in his extensive studies of rust dissemination in India. During 1930–32 he used free hydrogen balloons to carry vertical slides, the cylinder containing the slide being opened and closed again by burning fuses after about 5 minutes at the right altitude (Chatterjee, 1931); but this method was discontinued in favour of sticky slides attached to kites which could be kept aloft in the wind for 2 or 3 hours. It is now obvious that when carried by a free balloon (contrary to a kite or captive balloon), even if the slide faced the wind, its trapping efficiency would be low as there would be little or no movement of the slide relative to the air.

Sampling from aeroplanes in the early days was by sticky microscope slide or Petri dish, exposed at right angles to the line of flight. The wooden paddle and bottle devised by Stakman *et al.* (1923) was also used by Mehta (1952) and others, and, at aircraft speeds, should be a reasonably efficient collector except for the smallest spores. Newman (1948) claimed an increase in efficiency by placing a leading wire in front of the slide, to break the stagnation zone when sampling from aircraft.

(ii) *Vertical cylinder.* A removable sticky coating applied to a vertical cylinder was apparently first used by Rempe (1937) for studying airborne pollen at Göttingen. To measure pollen 'drift', cellulose film coated with petroleum jelly was wrapped around the surface of small brass tubes, 14 mm. wide by 45 mm. long. These tubes were hung vertically from trees or on stakes at the required height. Rempe compared pollen 'drift' with pollen 'deposition' (which he measured on horizontal slides 1 cm. above the ground), and found that drift was usually greater than deposition. At 100 metres horizontal distance from a *Corylus* bush, and at a height of 3 metres, the drift was 25 times as great as the ground deposition. Day and night values for a whole month were obtained on the level roof of the Göttingen Botanical Institute. The vertical sticky cylinder (0·5 cm. in diameter) has also been used by Turner (1956) for field studies on cereal powdery mildew (*Erysiphe graminis*).

The lower limit of cylinder diameter, and at the same time the maximum efficiency, is probably reached in the glass fibres of Kordyum & Bobchenko (1959), and in the 'flag sampler' of Harrington *et al.* (1959). This latter consists of a miniature wind-vane of cellulose tape folded over a pin which rotates in a low-friction bearing.

Sticky-surface traps have usually been scanned visually but they can be used to provide cultures. Thus Martin (1943) showed that spores can be picked off an exposed slide by Hanna's (1928) wet-needle method.

Sticky gravity slides, vertical slides, and cylinders, are all convenient and cheap. Their defects are: (1) theoretically a zero catch of large particles in still air and of small fungus spores even at ordinary wind-speeds; and (2) very great changes of efficiency with wind-speed (*see* Fig. 10).

Landahl & Herrmann (1949) claimed that the amount of aerosol 'deposited on a vertical slide does not change much if it is oriented at various angles within 30° of the wind'. Our results indicate that with *Lycopodium* spores this is true only at wind-speeds of about 5 metres per sec. Rotating the slide from 90° to 60° increases the efficiency by 10 times at 1·1 and 0·75 metres per sec., and by about 5 times at 3·2 metres per sec., whereas at 9·5 metres per sec. the efficiency is decreased by one quarter.

The use of the 7·6 × 2·5 cm. microscope slide at angles intermediate between 0° and 90° would increase trapping efficiency at the wind-speeds normally experienced in the open air near the ground. Hyre (1950) observed that a slide with a presentation angle of 45°, exposed in the field, caught more sporangia of *Pseudoperonospora cubensis* than either a vertical or a horizontal slide at wind-speeds of up to 2·4 metres per sec.—a result easily explicable from wind-tunnel work (cf. Fig. 14). It ought to be possible to orientate a slide at 5° to the oncoming wind which should give an efficiency varying only between 0·6 and 1·4 per cent over the range of 1 to 10 metres per sec.; or at 10°, when its efficiency would vary between 1·5 and 4·5 per cent over the same range of wind-speeds. An alternative approach would be to make the slide tilt, according to the wind's force, over the range of angles 10° to 30° as the wind-speed decreases from 10 to 1 metres per sec.—over which range it would have a nearly constant efficiency of 4 per cent with *Lycopodium.*

The vertical 7·6 × 2·5 cm. slide, widely used for research in plant pathology, is an impactor trap; it suffers from the defects of being relatively inefficient as an impactor at low wind-speeds and of being highly sensitive to changes in wind-speed. To avoid wrong conclusions and to be able to translate deposit into time-mean concentration, it is necessary to know the wind-speed under which deposition took place and to make the necessary correction. This may be illustrated by considering the deposit received from a cloud containing 10,000 *Lycopodium* spores per cubic metre, using wind-tunnel data for two wind-speeds. At 1·0 metres per sec. impaction at 5 per cent efficiency would deposit about 20 spores per sq. cm. per hour. With an increase in the wind-speed to 9·4 metres per sec., the deposit would increase to about 9,000 spores per sq. cm. per hour—a 450 times increase in deposit without change in the number of spores per cubic metre of air. A further source of error is that at low wind-speeds the efficiency is low, and as the catch is therefore small it has to be multiplied by a large factor, and the error of estimation becomes great.

(iii). *Aeroconiscopes*, used first by medical workers and later by plant pathologists, are now mainly of historical interest. They seem first to have been used by Salisbury (1866) in the Mississippi Valley, but were developed more fully by Maddox (1870, 1871) and Airy (1874) in England, and by Cunningham (1873) in India (Chapter I).

Aeroconiscopes of the Maddox and Cunningham type (Fig. 2) have been used in plant pathological investigations by Christoff (1934) in Bulgaria, and by A. A. Shitikova-Russakova (*see* Stepanov, 1935) in

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[*] The word 'aeroscope' has been used with some ambiguity, referring either to this type of instrument or to bubblers of the type described by Rettger (cf. p. 97).

Russia. Such wind-operated aeroconiscopes or aeroscopes* are essentially qualitative and there is no information on their efficiency. Finding an organism means that it was certainly present in the air, but gives no information about its numbers. When wind-speed is low, failure to find an organism does not necessarily mean that it was not present.

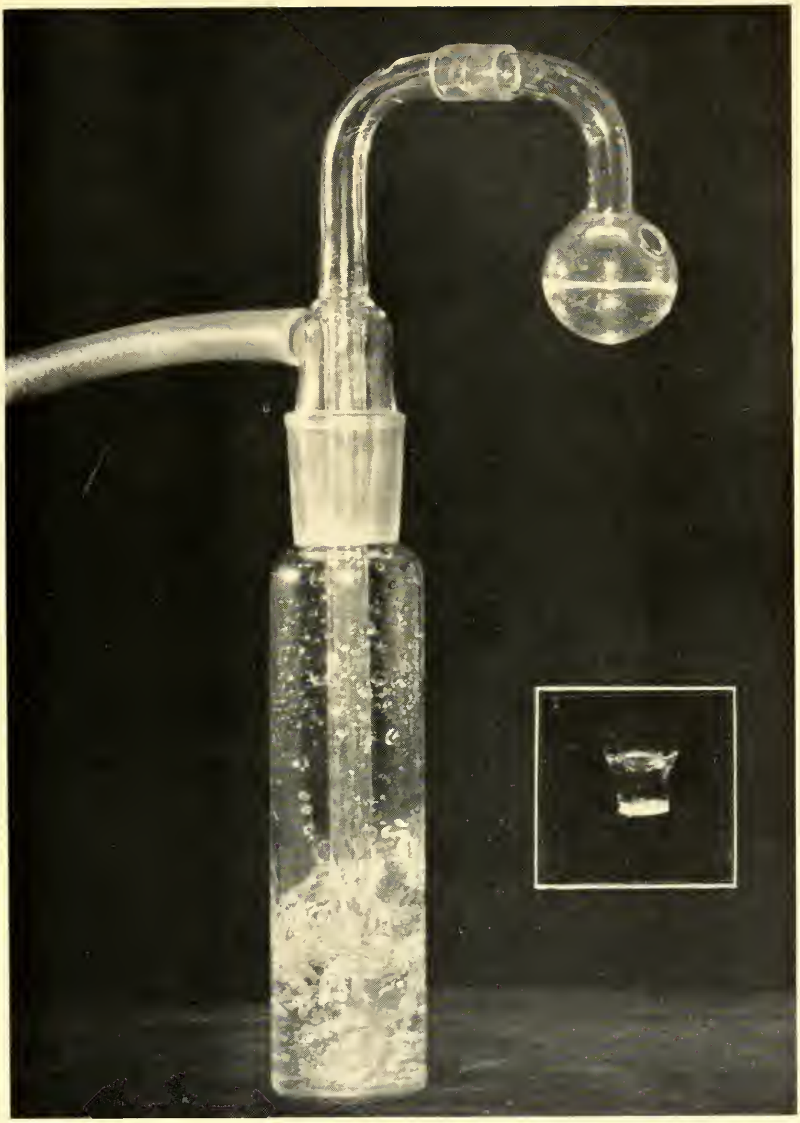
FORCED AIR-FLOW IMPACTORS

Samplers through which air is drawn by pumps, fans, or aspirators, can be made relatively independent of changes in wind-speed and differences in particle size, and they can accordingly give a volumetric reading under field conditions.

For sampling clouds of inorganic particles, which are often present in high concentration in closed spaces, various forms of koniometer have been developed (e.g. the Kotze koniometer, the Owen jet dust-counter, and the Aitken nucleus counter). None of these is well suited to the requirements of aerobiology; because of the small volume of air sampled, they are suitable only for high concentrations, and their aerodynamic features make isokinetic operation impossible (also, aggregates are shattered by a high speed of impact). Their efficiency has been tested by C. N. Davies *et al.* (1951), and their advantages and drawbacks are well summarized by Green & Lane (1957). As was emphasized by K. R. May (1945), a true sample of moving air 'is only obtained by isokinetic sampling, that is, when the sampling tube, with a feathered leading edge, faces upstream with suction applied at such a rate that the air velocities in the tube and main airstream are equal'. Many of the devices extensively used in biological work are satisfactory for sampling bacterial aerosols consisting of single bacterial cells or mould spores in *still* air, but fall far short of the ideal isokinetic sampling when used for bacteria carried on 'rafts', and larger fungus spores or pollen grains in *moving* air.

The main errors in impactor traps operated by suction are: (1) *collection errors* due to failure of the spore to enter the orifice (these errors may be reduced by isokinetic sampling with the orifice facing the wind, *see* Watson, 1954); and (2) *retention errors* due to failure to deposit spores in the correct place, either because they are lost on the walls of the trap or because they pass through the trap. Splash-borne spores, travelling mostly in droplets of 150–600 μ diameter, are not yet satisfactorily collected by any existing equipment.

(i). *Sieving filters.* Drawing air through a filter with pores too small for the organisms under investigation to pass through, is a simple technique which is, however, relatively little used as it is difficult to get a sufficiently high rate of air-flow through small pores. Filter-paper has been used by Frey & Keitt (1925) for *Venturia* spores, by Chamberlain (1956) in wind-tunnel tests with *Lycopodium*, by Gordon & Cupp (1953) for *Histoplasma*, and for pollen collection on Atlantic liners by Erdtman (1937). Membrane or 'Multipore' filters of re-precipitated cellulose can



Rosebury-Henderson Capillary Impinger in operation, with air entering first through a May & Druett Pre-impinger. (Inset shows the capillary in still conditions.)

PLATE 4

now be bought with pores from 0·8 to 5·0 μ in diameter which allow flow-rates adequate for some air sampling (First & Silverman, 1953; Goetz, 1953; Haas, 1956). After exposure these membranes can be placed directly on the surface of solid media in a Petri dish to allow growth on the membrane; or they can be shaken in water and the suspension plated out; or the membrane can be mounted as a transparency and examined directly under the microscope.

(ii). *Impaction filters* differ from sieving filters in consisting of a deep layer of fibres or granules separated by relatively wide air-spaces. Airborne particles are subjected to repeated encounters and are impacted in the foremost layers of the filter substance. Pasteur's air filter (*see* p. 5) was packed with a nitrocellulose plug which, after sampling, was dissolved in an alcohol-ether mixture and the particles were examined microscopically. As this treatment killed the trapped organisms, P. F. Frankland (1887) substituted powdered glass which was washed, diluted, and plated out after exposure. Because of the difficulty of washing organisms off a solid filter, many workers have preferred a completely soluble filter medium such as sodium sulphate (Miquel, 1890). Buller & Lowe (1911) substituted a plug of powdered sugar; Richards (1955) introduced the sodium alginate-wool filter, and others have used ammonium alginate (Hammond, 1958), which is soluble in water, or calcium alginate, which is soluble in Ringer's solution or in sodium hexametaphosphate.

For many years the standard technique for trapping airborne microbes was that of Petri (1888) or modifications of it (e.g. Weinzerl & Fos, 1910). Air was drawn through a sterilized tube 9 cm. long and 1·6 cm. wide, containing two columns of sand separated by wire gauze. These two sand filters were plated-out separately, the rear portion acting as a control. Equipment for exposing a set of five such tubes from aircraft during flight is described by Overeem (1936).

A simplified, wind-operated filtration method has been developed by Rishbeth (1958, 1959) to study fungus pathogens of coniferous forests. Butter-muslin squares (20-cm. sides), dry-sterilized in paper envelopes at 100°C., are put on a wire frame exposed either at right-angles to the wind (with the frame clipped to a stick, commonly at 2 metres above ground-level) or mounted on a moving vehicle. Exposures may last from minutes to hours; when they have been completed, a 10-cm. square of muslin is cut out, shaken in water, and the suspension plated out. 'Plating' on freshly-cut slices of pine trunks gives a sensitive and extremely selective method of detecting spores of two species of fungi, *Fomes annosus* and *Peniophora gigantea*.

(iii) *Liquid scrubbing devices* remove particles suspended in air, as it bubbles through a liquid, by various combinations of impaction, sedimentation, and diffusion. A simple 'aeroscope' bubbler devised by Rettger (1910), consisting of an inlet tube ending in a submerged perforated bulb, appears to be the prototype of a practicable method. Another simple form is described by Gilbert (1950). Improved forms of bubbler have been described by Wheeler *et al.* (1941), by Moulton *et al.* (1943) who added an atomizer stage before the bubbler, and by duBuy *et al.* (1945).

(iv) *The Rosebury-Henderson capillary impinger* (Plate 4) differs somewhat in principle from the bubblers. A small flask carries a wide inlet tube, and the inner end of the tube is fused to a short length of capillary tubing which dips at least 5 mm. below the liquid but remains at least 4 mm. above the bottom. The diameter of the capillary tubing acts as a limiting orifice, controlling the air-flow rate under suction (for example at 2–3 litres per min., or even up to 20 litres per min.) (Rosebury, 1947). This impinger has been tested and found to have a high retention-efficiency in work on experimental airborne infection of animals. If used to sample clouds containing large particles, however, substantial wall-loss may occur at the bend of the inlet tube. This can be prevented by adding a pre-impinger, originally devised by K. R. May & Druett (1953) to collect particles over 8 μ in diameter.

(v) *Centrifugal samplers.* Centrifugal impaction is used in the Wells (1933) air centrifuge, in which 30 to 50 litres per min. of air are drawn through an agar-lined glass cylinder rotating at 3,500 to 4,000 r.p.m.; this makes the air rotate and throws all suspended particles onto the wall of the cylinder by centrifugal force. After exposure the cylinder is incubated, and colonies developing on the agar-coated walls give a direct volumetric reading of the organisms present—so far as these are cultivable on the medium used. This apparatus has been used very extensively for routine bacterial sampling (e.g. Pincus & Stern, 1937; Wells, 1955). Its disadvantages include the difficulty of examining the catch inside the curved tube, and a deposition efficiency falling from 100 per cent with 2·3 μ particles to 50 per cent with 0·77 μ particles (Phelps & Buchbinder, 1941). Wells has also illustrated a model of the air centrifuge for collecting pollen for microscopic identification (*see* Committee on Apparatus in Aerobiology, 1941).

A more elaborate development is the 'conifuge', designed for microscopic study of size-distribution of particulate clouds (Sawyer & Walton, 1950; Green & Lane, 1957). It appears to be ideal for comparing terminal velocities of spherical with irregularly-shaped particles, but has the disadvantage that it samples only 25 cc. of air per minute.

Different in appearance, but essentially similar in principle, are the cyclone dust-collectors extensively used in industry for removing dust from air, and which have the advantage of allowing a large through-put with small pressure-drop. Small cyclone dust-collectors have been used by Tervet (1950), Tervet & Cherry (1950), and Ogawa & English (1955), to collect large quantities of rust spores for inoculation experiments, and we have found them satisfactory for the much smaller spores of *Ustilago*. (For the design of cyclone dust-collectors, *see* C. N. Davies, 1952).

(vi) *Impaction samplers.* 'Impactor' samplers use suction from a pump to accelerate air through an orifice to a speed at which deposition efficiency becomes high (80–100 per cent) and airborne particles are deposited on a solid surface.* The prototypes of these are a series for the study of industrial dusts and atmospheric nuclei, such as the Owen jet dust-counter, the Aitken nuclei counter, and various forms of koniometer (*see* p. 96). These instruments are not very suitable for microbial work, but Durham (1947) found such a pump effective for spot samples of pollen clouds in high concentration. Power-driven prototypes for aerobiological study include the impactor of Hawes *et al.* (1942).

(vii) *The slit sampler* (Bourdillon *et al.*, 1941) was designed primarily for indoor studies with bacteria. A stream of air is drawn through a narrow slit placed just above the surface of sterile medium in a slowly rotating Petri dish. Particles, spores, etc., are impacted on the medium and, after a few minutes' running time, the Petri dish is removed and incubated so that colonies may develop and be counted. The 'duplex radial-jet air sampler' of Luckiesh *et al.* (1949) is similar in principle and allows sterilization by autoclaving. Retention in the slit sampler is good; identification is made in culture; the apparatus is suited for occasional or regular 'spot' samples, but not for continuous use. It is best used indoors as it is not suitable for isokinetic sampling, and collection errors would be high when sampling large particles in a wind.

(viii) *The Cascade Impactor* (K. R. May, 1945) is a highly efficient suction trap. Used isokinetically, it serves as the standard of reference against which other devices may be calibrated. The Cascade Impactor consists of a folded tube through which the air to be sampled is drawn by suction. During its passage, the air is accelerated through a series of four progressively narrower jets, and airborne particles are impacted on sticky slides placed close behind the jets. The first jet (the intake orifice) faces the wind. In the original model, at the sampling rate of 17·5 litres per min., the speeds through the four jets are: 2·2, 10·2, 20·4, and 34 metres per sec., permitting 50 per cent of the particles whose diameters are 12 μ, 4 μ, 2 μ, and 1·1 μ to penetrate the respective jets. Later models give good retention down to 0·5 μ.

The Cascade Impactor thus fractionates the catch into four sizes and it avoids breaking up clumps. It is ideal for short sampling periods, but if used for sampling the air-spora out-of-doors in summer in England the trace becomes dense after an hour or two. A model of the Cascade Impactor with moving slides was developed by K. R. May (1956) to overcome this kind of difficulty and to give time-discrimination. A five-stage Cascade Impactor has been designed by Wilcox (1953).

(ix) *The automatic volumetric spore-trap* (Hirst, 1952) is a power-driven trap designed for operating continuously in the field (Fig. 17). It consists essentially of a single impactor slit (actually this has the same dimensions

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* Impaction and impingement are nearly synonymous. In the context of air sampling, devices putting particles into a liquid are distinguished as 'impingers'.

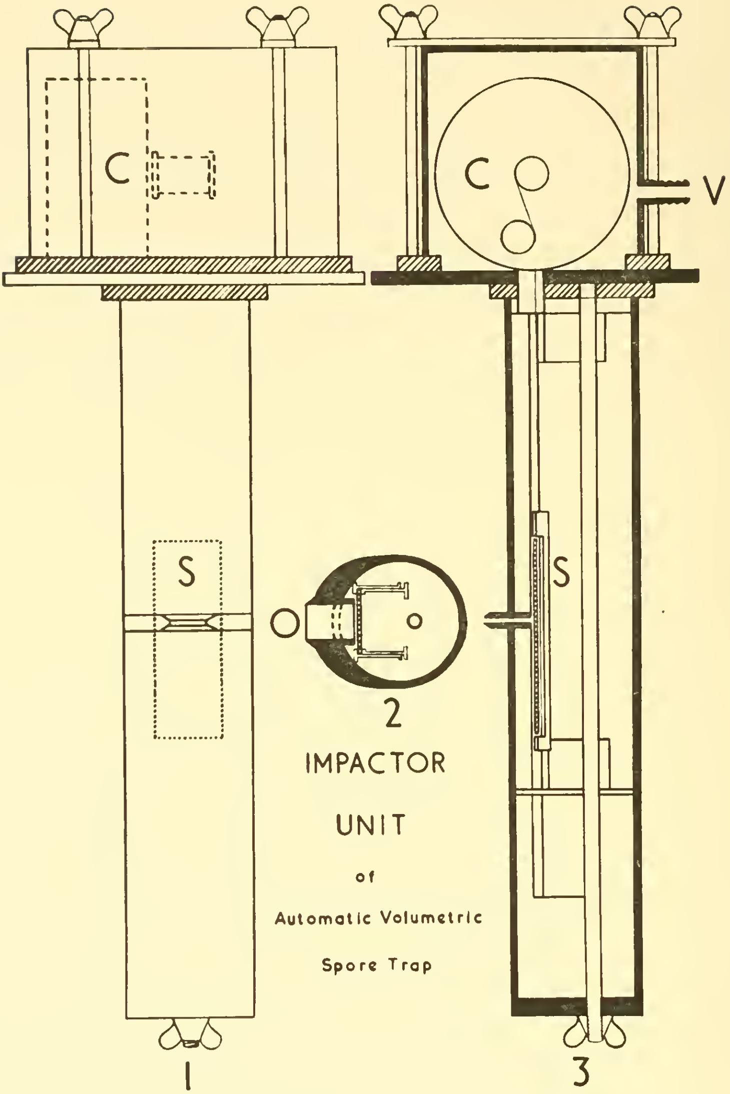

FIG. 17.—Diagram of the Hirst automatic volumetric suction-trap: 1, elevation facing wind; 2, plan of section through orifice; 3, elevation in side view; C, clockwork drive for raising slide; O, orifice facing wind, with slide in holder moving up past orifice; V, to vacuum pump. (Wind vane and cap to protect orifice from rain are not shown.) (Illustration by permission of J. M. Hirst.)

as the second jet of the Cascade Impactor), behind which is placed a sticky microscope slide moving at 2 mm. per hour. In the course of twenty-four hours a trace is deposited in a band 48 mm. long. This can be scanned under the microscope longitudinally to obtain a daily mean, or it can be scanned transversely at intervals of 4 mm. to get a reading corresponding to every two hours throughout the day and night.

The Hirst trap is ideal for survey work, and it is a useful compromise over many conflicting requirements. It is power-driven; sampling is approximately isokinetic; identification is visual under the microscope, and time-discrimination is obtained to ± 1 hour or better. The advantages of the Hirst trap are its robustness, simplicity, and continuous operation with a few minutes attention every 24 hours. Its disadvantages are capital cost, power requirement, and its unsuitability both for identification in culture and for trapping splash-dispersed spores. Pady (1959) has described a modified Hirst trap with intermittent hourly movement replacing continuous movement of the slide. Panzer *et al.* (1957) devised a battery-driven spore collector for continuous operation, but its description suggests that its collection and retention efficiencies are probably small.

Scanning slides under the microscope is tedious unless the deposit is dense. Hirst (1959) reports a comparison of mean density of spore deposit on horizontal slides, vertical cylinders, and Hirst trap slides (Table XVI), exposed for four summer months in the open air. Small spores, which almost entirely escape the vertical cylinder and horizontal slide, are caught in rewarding numbers in the Hirst trap deposits.

TABLE XVI

AVERAGE DENSITY OF SPORE DEPOSIT FROM THREE TYPES OF TRAP 2 m. ABOVE GROUND, HARPENDEN, ENGLAND, JUNE TO SEPTEMBER 1951.
(Hirst, 1959)

	Spores per sq. cm.			Ratio	
	a	b	c	b/a	c/a
	Hirst spore-trap	Vertical cylinder 5 mm. dia.	Horizontal slide		
Smuts	621	15	3	0·024	0·005
Alternaria	156	58	3	0·372	0·016
Cladosporium	8,930	376	59	0·042	0·007
Erysiphe	100	69	2	0·690	0·018
Pollen $< 20\ \mu$	206	377	8	1·830	0·038
Pollen $> 20\ \mu$	181	490	13	2·707	0·072

Examples of deposits obtained with the Hirst trap are shown in Plate 1 (Frontispiece), and some results of its use are described in the next chapter.

(x) *The Portable Volumetric Spore-trap* (Gregory, 1954) samples 10 litres of air per minute, with suction obtained by turning a light, sliding-vane pump by hand. The apparatus weighs about 10–12 lb. Its advantages are cheapness and portability; time-discrimination is accurate to seconds if desired; it is suitable for work in the less accessible places and for short-time samples (5–10 min.). However, it is fatiguing to use, and being unsuitable for continuous operation, it cannot conveniently be used to trace diurnal or weather effects on the air-spora. Brook (1959) has developed essentially similar equipment for sampling the air-spora of pastures in New Zealand.

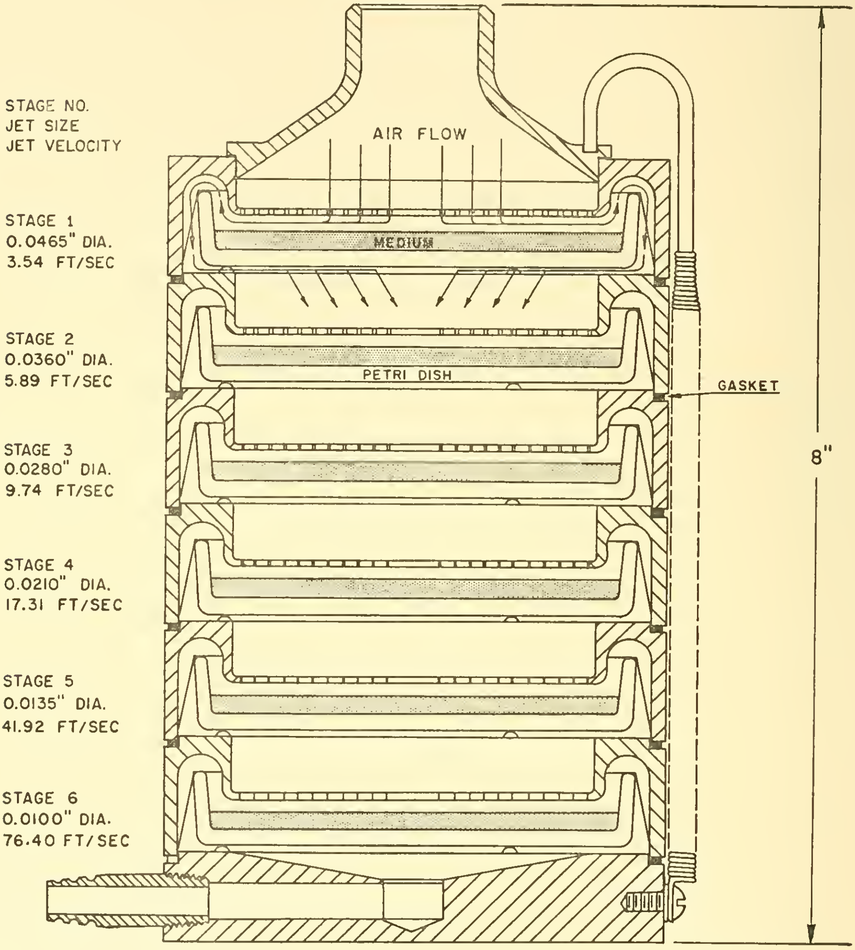
STAGE NO.
JET SIZE
JET VELOCITY
AIR FLOW
STAGE 1
0.0465" DIA.
3.54 FT/SEC
MEDIUM
STAGE 2
0.0360" DIA.
5.89 FT/SEC
PETRI DISH
GASKET
STAGE 3
0.0280" DIA.
9.74 FT/SEC
8"
STAGE 4
0.0210" DIA.
17.31 FT/SEC
STAGE 5
0.0135" DIA.
41.92 FT/SEC
STAGE 6
0.0100" DIA.
76.40 FT/SEC

FIG. 18.—Diagram of six-stage Andersen sampler. (Reproduced by permission of Dr. Ariel A. Andersen from the *Journal of Bacteriology*, 76, 1958.)

A desirable development of both the Hirst trap and the Portable trap would be versions which presented the catch in a form suitable for culture as an alternative to visual microscopic identification.

(xi) *The Andersen Sampler* can be regarded as a development of the so-called 'sieve device' of duBuy & Crisp (1944). In principle this sampler

(Andersen, 1958) resembles the Cascade Impactor; after entering a circular orifice, air is drawn in succession through a series of six circular plates, each perforated with 400 holes through which spores are impacted directly on to sterile medium in Petri dishes (Fig. 18). Succeeding plates in the series have progressively smaller holes; the largest particles are deposited in the first dish and the smallest in the last; different media can be used for the different size-fractions. Air is sampled at the rate of 28·3 litres per min.; wall losses are claimed to be negligible, and retention is said to be 100 per cent, even for single bacterial cells.

In our work the Andersen sampler has proved very convenient and has given good results with bacteria, actinomycetes and moulds, though for particles larger than about 8–10 μ the addition of some form of pre-impinger seems desirable for avoiding losses on the front of the first plate.

Reference should be made here to the use of the animal lung as a sampling device. Lurie & Way (1957) injected macerated lung tissue of various animals intraperitoneally into mice, from whose livers and spleens two dermatophytes (*Trichophyton mentagrophytes* and *Microsporon gypseum*) were subsequently isolated in culture.

(xii) *Whirling arm.* The principle of moving an object through air on a rotating arm has been developed in aerodynamics laboratories as an alternative to the wind-tunnel. As a device for air sampling it has been developed in the United States—beginning with the 'airwhip' of Durham (1947), who used a 36 in. aluminium rod to swing a forward-facing, sticky glass slide in a circle at 100 r.p.m. Near a stand of flowering ragweed (*Ambrosia* spp.), Durham recorded a maximum pollen concentration of about 10 million per cubic metre of air.

A high-speed whirling arm trap was developed by Perkins (1957) as the so-called 'Rotorod sampler'. It has been used in plant pathological studies by Asai (1960), and has been somewhat modified by Harrington *et al.* (1959). The Rotorod sampler consists of a length of 1/16th in.-square cross-section brass rod, bent to form a vertical U-shaped collector with arms 6 cm. high, 8 cm. apart, and fixed to the shaft of a miniature electric motor running at 2,520 r.p.m. over the range 9 to 15 volts from dry batteries. The sticky arms effectively sample air at 120 litres per min. Rotating at a peripheral speed of about 10 metres per sec., high collecting efficiency would be expected for pollens and spores down to about 12 μ diameter; for smaller spores, efficiency would fall below 50 per cent. This sampler has proved reliable in use, light in weight, and self-contained; the batteries are cheap, and will run continuously for two or three days.

ADHESIVES

The choice of adhesives for samplers is limited. Petroleum jelly and glycerine jelly have many advantages. Glycerine jelly has the best optical properties for visual examination, but it is hygroscopic and dissolves in damp weather. Petroleum jelly (e.g. 'Vaseline') is reliable for coating

Hirst trap slides, but addition of paraffin wax (12½ per cent) is often necessary to harden it. The coating must be kept as soft as possible, however, and for extremes of temperature Pady & Kelly (1949) introduced silicone grease for coating trap surfaces. When spores have to be picked off and transferred to culture media, pectin jelly is recommended by Prof. A. J. P. Oort (personal communication).

THERMAL PRECIPITATION

A hot body placed in a dust-laden atmosphere produces a dust-free space around itself (Watson, 1936). This well-known phenomenon has been used in the thermal precipitator, in which a dust-laden airstream flows slowly past a wire heated electrically to 100°C. above the ambient temperature, depositing dust particles on glass slips for examination. It has been little used for aerobiological work, but is highly efficient for sub-microscopic particles and larger ones up to 5 μ diameter. It is most suitable for use when the particles are in high concentrations, as the volume of air sampled is only about 7 cc. per min. (*see* Green & Lane, 1957).

ELECTROSTATIC PRECIPITATION

The movement of charged particles in an electrical field is widely used in industry to extract dust from air because the pressure drop imposed by the requisite apparatus is small, even with high rates of air-flow. Berry (1941) realized that an efficient sampling method could be developed on this principle, and the General Electric electrostatic air-sampler was devised by Luckiesh *et al.* (1946). Petri dishes of culture medium are placed on flat metal plates (electrodes) which are oppositely charged to 7,000 volts from a half-wave rectifier. Air enters through the apex of a fairly flat inverted metal cone extending to near the edge of each dish, and each cone carries a charge opposite to that of the electrode under its dish. A small pump draws air at 14 litres per min. over each dish, and particles move in the electrostatic field and are deposited on the agar surface.

When *Escherichia coli* in aqueous suspension was atomized into a room, the dish on the positive electrode collected nearly ten times as many cells as that on the negative. With naturally-occurring airborne bacteria, 30 per cent more were deposited over the *negative* electrode. Presumably each dish collects a proportion of the uncharged particles by gravity and impaction, as well as collecting the charged particles moving towards it. The positions and dimensions of the upper electrodes have been decided by empirical tests and may need modifying for mould spores and pollen. For naturally airborne bacteria the concentration, based on the sum of the counts on the two dishes, was from 2 to 3 per cent higher than simultaneous tests with the 'duplex radial-jet air sampler'. How far particles are charged by ions after entering the apparatus is not yet known. The apparatus was used in aerobiological studies by Kelly *et al.* (1951), and later by Pady and his colleagues in Kansas.

Other electrostatic sampling methods include those of Rack (1959), and O'Connell *et al.* (1960).

COMPARISON OF METHODS

Under simple conditions it is not difficult to define an absolute standard for air-sampling. With non-aggregated spores of one species liberated in a wind-tunnel, isokinetic sampling through a feathered orifice facing upwind (using a suitable membrane filter, a Cascade Impactor, or a liquid impinger, with precautions against overloading) should give a reliable visual estimate of the number of particles in a measured volume of air. The Cascade Impactor tends to reveal any spore clumps intact, and, if this feature is undesirable, the liquid inpinger should be used to break the aggregates. The more varied the population in species, size, and state of aggregation, the harder it becomes to devise equipment to measure microbial concentration in the air. Particles over 10 μ in diameter must be sampled directly and cannot be ducted around corners on the way to the apparatus without heavy wall-losses.

Air hygiene in bacteriology has been mainly a study of the air within buildings, and its equipment has therefore been developed for sampling still or slowly moving air. Aerodynamic effects have been neglected, despite the fact that bacteria are carried on 'rafts' or spray droplets of greatly varying size, so that efficiency of retention has been achieved but efficiency of collection has been neglected. Most devices, such as the slit sampler and the electrostatic sampler, avoid this difficulty by pointing the orifice upwards—but this makes them unsuitable for use in the open air.

In outdoor aerobiology the sizes of pollen grains and fungus spores (*see* Appendix I), and the variability of wind-speeds, has focused attention on collection efficiency. Results from the various 'surface' traps, depending on natural deposition processes, are usually difficult to translate into volumetric results. Over short periods while wind-velocity is constant out-of-doors, or in a wind-tunnel, a vertical strip or cylinder can be used to estimate concentration provided the wind-speed and the deposition efficiencies of the particles concerned are known. If the particle's terminal velocity is known, fairly close estimates can also be made by using theoretical formulae (e.g. of C. N. Davies & Peetz, 1956). Most data from surface traps, such as gravity slide and Petri dish counts, cannot be translated into concentration but merely measure surface deposition. Only the vast differences in natural concentrations, that occur at different times and places, make it possible to infer changes from deposition records. Nevertheless Hyde (1959*a*) shows that in general and over a long period, gravity slide sampling indicated the same quantitative composition and seasonal variation of the pollen cloud over South Wales as did the Hirst trap. As an exception, the Hirst trap revealed that the abundance of nettle (*Urtica*) pollen had been greatly underestimated by the gravity slide method.

Continuous records provided by the Hirst trap have proved highly illuminating in mycology, plant pathology, and allergy—even though the results are still limited to those obtainable by visual identification. Outdoor bacteriology awaits the development of convenient, continuous sampling equipment for cultures (*see* Miquel & Benoist, 1890), and this would lead also to further precision in knowledge of airborne fungi.

Air sampling, indoors and out, can have either of two aims: (1) to attain the broadest knowledge of the whole range of organisms in the air, which requires the most complete and undistorted sampling methods possible; or (2) to obtain detailed knowledge about a single species or group, which may require highly selective methods.

Air sampling has been successful in revealing the diversity of organisms forming the air-spora, in defining conditions for the outbreak of epidemics of some plant diseases, and in measuring dispersal gradients of spore concentration. So far it has proved less useful as a routine measure in forecasting outbreaks of crop disease, because existing methods are mostly insensitive to small concentrations of inoculum in the air (Table XVII).

TABLE XVII

ESTIMATED DETECTION THRESHOLDS OF CONCENTRATION (SPORES PER CU. METRE OF AIR) OF HIRST TRAP AND STICKY MICROSCOPE SLIDES INCLINED AT 45°, ASSUMING EXPOSURE FOR ONE HOUR AND COMPLETE COUNT OF 28 SQ. MM. OF SPORE DEPOSIT. (Hirst & Stedman, 1961.)

	Wind-speed (metres/sec.)					
	0·5	1·1	1·75	3·2	5·5	9·5
Microscope slide inclined at 45°						
Lycopodium	941	260	150	40	20	8
Erysiphe	2,000	1,500	860	340	70	10
Ustilago	28,000	13,000	20,000	1,400	640	490
Hirst trap						
Lycopodium	2	2	2	3	3	—
Ustilago	2	2	3	2	2	—

As pointed out by Hirst (1959): 'No trap is likely to detect spores as sensitively as an acre of a susceptible crop in weather favourable to infection. Thus epidemics may be started by spore concentrations which traps will not reveal, so we must define the value of "nil catches". With volumetric traps this can be done by calculating the "detection threshold", or concentration at which one spore should appear in the area scanned for each sample. In our routine scanning of hourly samples from the Hirst trap the detection theshold is less than 10 spores per cubic metre of air. This high value explains why spore traps are of little practical use in forecasting epidemics of potato blight which start from minute local sources, but are valuable for apple scab or black rust, with which initial spore concentrations may be high because of the sudden liberation of accumulated spores or the arrival of a spore-laden air-mass.'

Before using an air sampler, its performance should be explored experimentally. Consistency of performance alone is an unsatisfactory criterion, because a trap may be consistently misleading.

IX

THE AIR-SPORA NEAR THE EARTH'S SURFACE

ULTIMATELY we hope to attain an undistorted picture of the ambient outdoor air-spora. All air-sampling methods are more or less selective. This chapter deals with the concentrations of microbes in suspension in air near the ground—that is, within the laminar and turbulent boundary layers ordinarily inhabited by man, animals, and plants. The account is based on the limited amount of information obtained by volumetric air sampling with reasonably efficient apparatus. No attempt will be made to summarize the extensive results from gravity-slide and Petri dish traps, as these are already covered by excellent summaries by Feinberg *et al.* (1946), Maunsell (1954), Werff (1958), and others, though the results of long-term sampling with such surface traps will be drawn upon for supplementary information when required.

COMPOSITION OF THE AIR-SPORA

Some 1,200 species of bacteria and actinomycetes are recognized. Other spore-producing plants include perhaps 40,000 species of fungi, numerous mosses, liverworts, ferns and their 'allies', and more than 100,000 species of pollen-producing flowering plants of which about 10 per cent are wind-pollinated. (Of the Protozoa able to enter the air-spora, our information is very meagre and unsystematic.)

A taxonomist, having in mind the twenty-five volumes of Saccardo's *Sylloge Fungorum* or the many volumes and supplements of *Index Kewensis*, may wonder what useful statements can possibly be made about the air-spora where most of the fungus or other plant bodies whose characters could aid identification are lacking. Fortunately, as a cursory microscopic examination of the deposit from an impactor trap shows, the potentially airborne organisms are not all equally common in the air. One sample is normally dominated by one or two types of spore, with several other types in fair abundance and many more encountered in ones and twos only. The frequency distribution of individuals of different species in an air-spora resembles the series of the logarithmic and log-normal types discussed by Fisher *et al.* (1943), and by Williams (1947, 1960). Investigation will doubtless show that different air-sporas have different 'diversities'.

In practice the problem of recording an air-spora requires the recognition of a number of categories for the organisms most commonly present in the sample, including a miscellaneous group, which may ultimately contain from 10 to 15 per cent of the total. Pollens of flowering plants can often be identified to the species level, and so can a few fungal spores—especially of the Uredineae and some other plant pathogens (Appendix I, p. 207). In samples of the outdoor air, bacteria can seldom even be recognized visually as such, let alone identified, and the only sampling devices suitable for their study involve making cultures. In practice the categories adopted are of varying degrees of arbitrariness, and the names are applied to them for convenience of reference; but the different categories behave so differently that it would be intolerable to have no way of referring to them.

Taxonomic Groups Needing Study in the Air-Spora

We now have some knowledge of the occurrence of bacteria, fungi, and pollens as components of the outdoor air-spora, but there are some groups whose presence is obvious enough yet about which we have scarcely any quantitative information. Thus I know of no systematic records having been kept to assess the concentration of actinomycetes, and of moss and liverwort spores, in the atmosphere.

(i) *Protozoa.* For these we have the estimate by Miquel (1883) of an average of 0·1 to 0·2 airborne protozoan 'eggs' per cubic metre at the Observatoire Montsouris, Paris. Using a Pasteur-type filter, Puschkarew (1913) sampled air near ground-level on the right bank of the Neckar downstream from Heidelberg. In forty-nine tests, on different occasions and at different times of the day, his catch works out at an average of 2·5 protozoan cysts per cubic metre of air. His cultures included species of *Amoeba*, *Bodo*, *Monas*, *Calpoda*, etc. Curiously enough, he concluded that this concentration was too small to account for the observed almost world-wide uniformity of species of freshwater protozoa, and that other dispersal routes must be important (as no doubt they are). This study awaits convenient techniques.

(ii) *Algae.* Microscopic terrestrial and freshwater algae occur in the air, but have been little studied. A few samples were taken on the roof of buildings at Leiden by Overeem (1937), using the 'standard aeroscope' and Rettger bubbler. At least forty algae were obtained from a total of 20 cubic metres of air, including: *Chlorococcum*, *Chlorella*, *Pleurococcus*, *Stichococcus*, and *Navicula*.

The occurrence of blue-green algae resembling species of *Gloeocapsa* or other members of the Chroococcaceae was recorded by Gregory *et al.* (1955) from continuous sampling with a Hirst trap at Thorney Island in Chichester Harbour, England, from 30 June to 13 July, 1954. Concentrations averaged 110 colonies per cubic metre of air (averaging 8 cells per colony). Diurnal periodicity showed maximum numbers near midnight (210 colonies per cubic metre) and a minimum in the morning (30 colonies). Similar, but fewer, colonies were found regularly in London and Rothamsted. They showed no pronounced seasonal trend, according to Hamilton (1959), who also reported the rare occurrence of diatoms and desmids. Evidently microscopic algae are widely prevalent in the atmosphere in numbers varying from a few to a few hundred per cubic metre, and occasionally they may be heavily deposited on the ground (D.S.I.R., 1931).

(iii) *Ferns.* For ferns the reports are few. At Rothamsted—with no large areas of bracken within several kilometres, and only small quantities within 1 km.—spores of the *Pteridium* type occurred frequently in warm, dry weather from late July to mid September. They averaged 4 per cubic metre, with a maximum concentration of 36 per cubic metre (Gregory & Hirst, 1957; Hamilton, 1959).

Miquel's Work on Bacteria and Moulds

Recognizing the paucity of information on airborne microbes, Pierre Miquel made daily counts in Paris during the last quarter of the nineteenth century (cf. p. 9). Miquel's 'contribution to the microscopic flora of the air' is probably the most sustained series of volumetric measurements of the microbial population of the outdoor air ever attempted. Daily observations in the Parc Montsouris, about 5 km. south of the centre of Paris, served him as a standard for comparison with the polluted air in the densely populated city. The bacteria of the outdoor air were classified in the following percentages as: *Micrococcus* 66, *Bacillus* 25, *Bacterium* 6, *Vibrio* 1-2.

Miquel (1899) shows a seasonal variation in total bacterial and mould concentrations (Table XVIII). Most of the samples were taken with a form of the Pasteur trap (*see* p. 5), using a sterile plug of powdered anhydrous sodium sulphate as a filter. This was dissolved after exposure and inoculated to flasks of filtered saline beef extract. At the Parc Montsouris, bacteria were nearly three times as numerous in summer as in winter, but moulds fluctuated rather less. Near the Hôtel de Ville in the centre of Paris, bacteria showed a similar seasonal variation but were 2½ times as many as in the Parc; moulds were 10 times as numerous but showed little seasonal variation. At first Miquel argued that, as only one-tenth could have been blown in from the country to the centre of the city, the rest must have come from houses. But after the year 1881 he noted a steady annual decline and he attributed this to improved street cleaning and washing to lay dust which, we may suppose, consisted largely of soil enriched with horse droppings. Data are also given for a narrow, unhygienic street, and for one of the main sewers of Paris. The air of sewers was no more highly contaminated than the outside air, and was often surprisingly pure (Chapter XII).

TABLE XVIII

MEANS OF MONTHLY MEAN NUMBERS OF BACTERIA AND MOULDS PER CUBIC METRE OF OUTDOOR AIR IN PARIS (Miquel, 1899), IN CULTURE IN NEUTRAL BEEF BROTH

Month	Parc Montsouris (16- and 9-year means, respectively)		Near Hôtel de Ville, place Saint-Gervais (1888–1897)		Passage Saint-Pierre 1897–1898 (Mean)		Main sewer Blvd. Sebastopol (1891–1897)	
	Bacteria	Moulds	Bacteria	Moulds	Bacteria	Moulds	Bacteria	Moulds
January	198	160	3,840	1,555	6,610	1,665	2,670	4,535
February	148	110	3,475	1,375	3,265	1,790	3,095	1,965
March	209	155	4,995	1,290	2,790	1,630	2,555	2,485
April	362	140	8,260	2,445	11,710	1,885	3,875	6,290
May	295	230	8,725	1,560	4,910	1,650	3,845	1,865
June	355	222	10,830	1,835	5,015	2,630	2,705	2,360
July	464	205	12,040	2,590	5,930	4,235	4,460	3,490
August	450	270	10,300	2,450	4,265	2,770	4,645	3,195
September	395	215	9,920	2,435	5,545	1,735	3,630	1,845
October	260	228	7,160	2,445	7,900	2,165	3,965	4,135
November	195	240	5,845	2,175	4,735	2,270	3,800	5,210
December	167	166	4,365	2,005	4,015	1,390	6,750	2,560
Average	290	195	7,480	2,015	5,555	2,150	3,835	3,330

EFFECT OF RAIN

The numbers of bacteria in summer averaged several hundred per cubic metre, and were reduced in a few hours by rain to a mere 20–30 per cubic metre, but they increased again as the ground dried out. Surprisingly enough, bacterial numbers often increased after snowfall. The numbers of bacteria in the air increased with increasing wind-speed and remained high during a drought, unless it was prolonged. To Miquel it was clear that rain had a complex action: air that contained many bacteria after a fine, dry spell of weather was rapidly purified by rain, but often during a spell of humid weather the fall of rain would contaminate the air more than it purified it—possibly because raindrops collected bacteria in their fall towards the ground and, by evaporating before reaching the soil, added their collection to the air near ground-level. We may also suspect that bacteria were put into the air by rain-splash. The first rain after drought might contain 200,000 bacteria per litre instead of the average number of 3,380 per litre (*see* Chapter XI).

Slowly Miquel came to the conclusion that the source of most outdoor airborne bacteria is the surface of the ground, whence they are picked up with dry soil particles by wind—a conclusion still acceptable 80 years later.

Moulds reacted differently to the fall of rain. With the onset of rain, the air was at first purified; but when rainy periods lasted for some days, the numbers of mould spores in the air at Montsouris often increased remarkably, even reaching 95,000 to 120,000 per cubic metre. In dry weather coloured spores abounded. Re-invasion of the air after rain was mostly by colourless organisms, which Miquel diagnosed, probably incorrectly, as immature spores. Rain and warmth increased the atmospheric fungus spore content, though this might decrease during high winds because their extra lifting power did not compensate for their power of desiccation and, hence, killing.

DIURNAL PERIODICITY

(i) *Diurnal periodicity in numbers of bacteria* outdoors could be studied only on selected days of the year because, by Miquel's methods, for hourly studies from 600 to 700 culture flasks had to be handled in one day. The fullest data are probably those of 1884, which showed continual change from hour to hour of the day in relation to changes in meteorological factors that have not yet been unravelled.

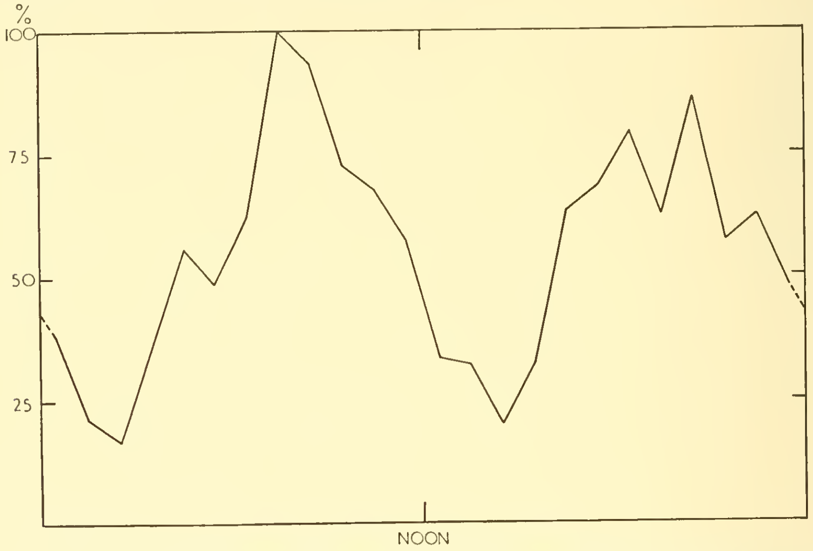

FIG. 19.—Diurnal periodicity of total numbers of bacteria in air at the Observatoire Montsouris, Paris, based on hourly readings between March 1882 and September 1884 (Miquel, 1886).

Bacterial numbers showed diurnal periodicities differing between Montsouris and the centre of Paris. At Montsouris there were two daily maxima at 08·00 hours and 20·00 hours, and two minima at 02·00 hours and 14·00 hours, respectively (Fig. 19). In the centre of Paris, however, there tended to be a single maximum at 14·00 hours and a minimum at 02·00 hours during most of the year, but in autumn the double peaks tended to occur in central Paris as at Montsouris.

This diurnal variation was shown to hold irrespective of wind direction—an effect that was possibly in part attributable to mechanical causes such as traffic and the sweeping of streets. Furthermore the peaks occurred also in rainy weather so long as not more than 2–3 mm. of rain fell in 24 hours. Miquel also showed that the outside changes soon penetrated into the rooms of buildings unless they were exceptionally well sealed.

(ii) *Diurnal periodicity of mould spore numbers* resembled that of bacteria. Trapping by impaction on a moving slide which gave him hourly readings, Miquel found that moulds had two maxima at 08·00 and 20·00 hours. These maxima were independent of wind velocity and fluctuated much more than did bacterial counts. Miquel then tried 15–minute sampling periods and discovered the important principle that hourly values are merely a smoothing of still more rapid fluctuations; he says (transl.) 'what I wish to establish by all these examples is the variability of the nature of the organisms living in the atmosphere'.

RELATIVE NUMBERS OF BACTERIA AND MOULDS

Miquel had started with the aim of describing the cryptogamic flora of the atmosphere, and in the earlier years of his work he reported much larger numbers of moulds than bacteria.

In 1879 Miquel was assessing mould spores visually by a continuously operated, aspirated aeroscope at 2 metres above ground-level at the centre of a lawn in the Parc. He caught microbes at 100 times the rate of the non-aspirated aeroscopes of Maddox and Cunningham, and he concluded that less than 10 per cent of the organism seen visually would grow in culture. The numbers of germs (principally mould spores as shown by his drawings) in the air at the Parc Montsouris during continuous sampling in 1878 averaged 28,500 per cubic metre. In rainy periods in June they rose to 100,000 or even 200,000 per cubic metre. In winter the numbers were as low as 1,000 per cubic metre during snow, though they might be 14,000 per cubic metre when the wind came from over the centre of Paris. Numbers increased again in spring; they remained high in summer and diminished again in autumn.

By the 1890's Miquel had lost interest in airborne moulds, and for sampling air he constantly recommends the use of sugar-free media which discourage moulds but enhance bacterial counts. Henceforth the mould counts which he reported fell to the level of the bacteria and, by deliberately using a selective medium, he could forget the rich fungus spora that had embarrassed him in the earlier years. The values already given (Table XVIII) are for media which favour bacteria but repress moulds, and are certainly underestimates for the latter.

Knowledge of the broad features of the bacterial flora of the outdoor air near the ground remains to this day substantially as Miquel left it at the beginning of this century. Further, comparable measurements in this century include those by: Forbes (1924), Wells & Wells (1936), Buchbinder *et al.* (1945), and Colebrook & Cawston (1948). On the whole the topic has been neglected and, significantly, the American Association for the Advancement of Science's book on '*Aerobiology*' (Moulton, 1942) has no chapter on bacteria in outdoor air over land.

Recent Study of Fungi and Pollen

The pollen and fungus components of the outdoor air-spora have attracted much attention in this century, and the development and extensive use of volumetric sampling equipment for the purpose has been highly illuminating. Quantitative visual counting of spores from 3 μ in diameter and upwards, confirms Miquel's impression of recurrent 'tides' of spore concentration; but different groups of organisms are now known to have separate 'tidal waves', and the concentration and composition of the air-spora varies enormously with place, season, time of day, weather, and human activity.

THE AIR-SPORA AT 2 METRES ABOVE GROUND-LEVEL

Continuous records in a mixed agricultural environment were obtained during the summer of 1952 by Gregory & Hirst (1957), using the Hirst automatic volumetric spore-trap. The mean spore concentration at 2 metres above the ground over the period 1 June to 25 October was 12,500 spores per cubic metre. These were grouped visually into twenty-five categories. The commonest spore-type was *Cladosporium* (probably mainly *C. herbarum*), which accounted for 47 per cent of the total. The second commonest were classified as hyaline basidiospores and made up 31 per cent of the season's catch; most of these were probably spores of species of *Sporobolomyces*, with *Tilletiopsis* adding another 0·56 per cent. Coloured basidiospores of mushrooms and toadstools (agarics, boleti, and bracket fungi) amounted to 3·3 per cent of the season's total. Pollen made up 1 per cent of the total. Conidia of powdery mildews (Erysiphaceae), 'brand spores' of *Ustilago* species, and conidia of *Alternaria*, amounted to between 1 and 2 per cent each. Ten other recognizable categories contributed between 0·03 and 0·5 per cent each. All other particles recognizable as spores of micro-organisms were put in the 'unclassified' category, totalling 8 per cent of the season's catch, and included many organisms which, although abundant in soils, form only an insignificant fraction of the summer outdoor air-spora (for example, *Penicillium*, *Aspergillus*, and various Mucoraceae). Bacteria and actinomycetes are not revealed by this trap method, which is efficient only for particles over 3 μ in diameter.

In Britain the attempts to get a relatively undistorted picture of the outdoor air-spora have demonstrated beyond doubt that *Cladosporium* and *Sporobolomyces* predominate, followed by the hyaline and coloured basidiospores of the mushrooms and toadstools. Fewer in number, but not necessarily less in total volume, are the pollens, *Alternaria*, ascospores, and the large-spored plant-pathogenic fungi. Under ordinary conditions, splash-borne types seem not to amount to more than a few per cent of the total air-spora. Many other types are also found, but they are infrequent, except in special localities or under special circumstances.

The importance of basidiospores from mushrooms, toadstools, bracket fungi, and especially mirror-yeasts, as components of the air-spora, is a recent discovery (Gregory & Hirst, 1952, 1957). It is remarkable that even the existence of the Sporobolomycetes was unrecognized until 1930. Basidiospores are not efficiently caught by surface traps, and confirmation of their numbers (which were doubted at first) has been slow in forthcoming. However, Hyde & Adams (1960) report that at Cardiff, over the whole year of 1958, the basidiospore types collectively amounted to 1,059 out of the average fungus spore content of 2,164 per cubic metre of air. Furthermore, estimating *volume* instead of number, they showed that basidiospores came second only to grass pollen. Daily estimates with a slit sampler for one year at Manhattan, Kansas, gave the numbers of basidiospores as 24·3 per cent of all spores caught—second only to *Cladosporium* (Kramer *et al.*, 1959*a*).

THE AIR-SPORA AT OTHER HEIGHTS NEAR THE GROUND

In general the spore concentration increases at positions nearer the ground than the standard sampling height of 2 metres, and decreases at greater heights. Using a Hirst trap at 24 metres in a lattice tower at Rothamsted, the average spore concentration was 81·5 per cent of that at 2 metres, though some spores characteristic of the night air-spora were actually commoner at the higher level (Gregory & Hirst, 1957).

Tests at heights below 2 metres with a portable suction trap in the New Forest, England, showed a general decrease with height (Table XIX). The difference was greatest at night, when the total spore concentrations were lowest. By way of exception, *Cladosporium* numbers were reversed at 13·00 hours: this is taken to mean that sources of *Cladosporium* were not present close to the trap and that the air nearest the ground was being depleted of this organism in passage over the Earth's surface.

TABLE XIX

TOTAL NUMBER OF POLLEN GRAINS AND SPORES PER CUBIC METRE IN OAK-BIRCH WOOD, NEW FOREST, ENGLAND, 23 JULY 1953 (Gregory, 1954).

	Height above ground-level		
	7 cm.	30 cm.	120 cm.
05·00 hours G.M.T.	20,600	19,000	7,250
13·00 hours G.M.T.	31,300	24,200	20,300

In his studies of the 'phyllosphere' of cereal leaves, Last (1955) sampled air among wheat plants at 11, 46, and 80 cm. above ground-level and found 237,000, 170,000, and 41,000 spores of *Sporobolomyces* per cubic metre, respectively.

The air-spora at greater heights than in these examples is dealt with in Chapter X.

TABLE XX

DIURNAL PERIODICITY IN THE AIR-SPORA ON LAND (APPROXIMATE TIME OF MAXIMUM CONCENTRATION IN THE LOWER ATMOSPHERE AS RECORDED BY VOLUMETRIC SAMPLERS)

Organism	Local time (hr.)	References
Bacteria	6 and 18	(1)
Fungi		
(Phycomycetes)		
Peronospora tabacina	6–10	(9)
Phytophthora infestans	11	(2)
(Ascomycetes)		
Filiform ascospores	19–3	(2), (3), (4)
Fusiform ascospores	1	(2), (4)
Erysiphe (conidial)	10, 13–15	(2), (3), (4), (5)
(Basidiomycetes)		
Sporobolomyces	3–5	(2), (3), (4)
Tilletiopsis	3–6	(3), (4)
Rusts		
'Uredospores'	12–16	(2), (3), (5)
Puccinia polysora	9 (dry season) 13 (wet season)	(6)
Smuts		
Tilletia	14 and 20	(5)
Ustilago	10, 12–16	(2), (3), (4), (5)
Hymenomycetes		
Coniophora	4	(5)
Ganoderma	22–3	(3), (5)
'coloured basidiospores'	1–3, 5	(2), (3), (4), (5)
'hyaline basidiospores'	23–3	(3), (4)
(Fungi Imperfecti)		
Alternaria and *Stemphylium*	10–12–15	(2) (3), (4), (5)
Botrytis	12–15	(3), (5)
Cladosporium	10, 11–15, 17	(2), (3), (4), (6)
Epicoccum	10–18	(3), (5)
Helminthosporium	14 (19 in London)	(3), (5)
Nigrospora spherica	11 (dry season) 13 (wet season)	(6)
Penicillium	14	(3)
Periconia	14	(5)
Piricularia oryzae	1–3	(10)
Polythrincium trifolii	10–12 (16 in London)	(2), (3), (5)
Pullularia	13–17	(3)
Torula herbarum	11–13	(3)
Algae		
'*Gloeocapsa*' type	22–23	(4), (8)

TABLE XX—*continued*

Higher Plants

Total grass and weed pollen	15–16	(2), (5)
Grass pollen	19	(3)
Betula (birch)	9–15	(3)
Corylus (hazel)	13	(3)
Fraxinus (ash)	11–13	(3)
Pinus (pine)	15–17	(3)
Platanus (plane)	13–15	(3)
Quercus (oak)	13, 15, 17	(3)
Tilia (lime)	11, 13, 17	(3)
Artemisia	9	(3)
other Compositae	13	(3)
Chenopodium	11, 13, 19	(3)
Plantago	13, 17, 23	(3)
Rumex	11, 15	(3)
Urtica	15, 17	(3)

Key to references

(1) Miquel (1886), (2) Hirst (1953), (3) Hamilton (1959), (4) Gregory & Sreeramulu (1958), (5) Sreeramulu (1959), (6) Cammack (1955), (7) Gregory & Stedman (1958), (8) Gregory *et al.* (1955), (9) Waggoner & Taylor (1958), (10) Panzer *et al.* (1957).

DIURNAL PERIODICITY OF THE FINE-WEATHER SPORA

Concentrations of spores of a single species or a group of related species often show diurnal rhythms comparable with those observed by Miquel (*see* above). This effect was studied in detail by Hirst (1953), whose mode of presenting the results has proved a convenient model for subsequent workers. Hourly or two-hourly concentrations are obtained on as many days as possible. At regular intervals throughout the day, the mean spore concentration is plotted as a percentage of the maximum. Geometric means are preferred to arithmetic means, and separate curves can be drawn for different weather types. Examples are shown in Fig. 20.

The time of day when various organisms reach maximum concentration in the Hirst trap and similar volumetric samplers is listed in Table XX. Ill-defined peaks or multiple peaks may perhaps be due to failure to discriminate in visual counts between two morphologically similar spore-types belonging to different organisms. Several patterns of diurnal periodicity are now obvious.

(i) *The bacterial pattern* found by Miquel at Montsouris, with two maxima and two minima, remains an unexplained phenomenon worthy of re-examination.

(ii) *The nocturnal pattern* contains a group of organisms appearing in highest concentration at some hour between sunset and dawn. This group comprises all of the ballistospore forms so far studied (notably *Sporobolomyces*, *Tilletiopsis*, basidiospores of hymenomycetes), and also certain fusiform ascospores. In cooler weather, however, coloured basidiospores may reach a maximum in the afternoon (Gregory & Stedman, 1958).

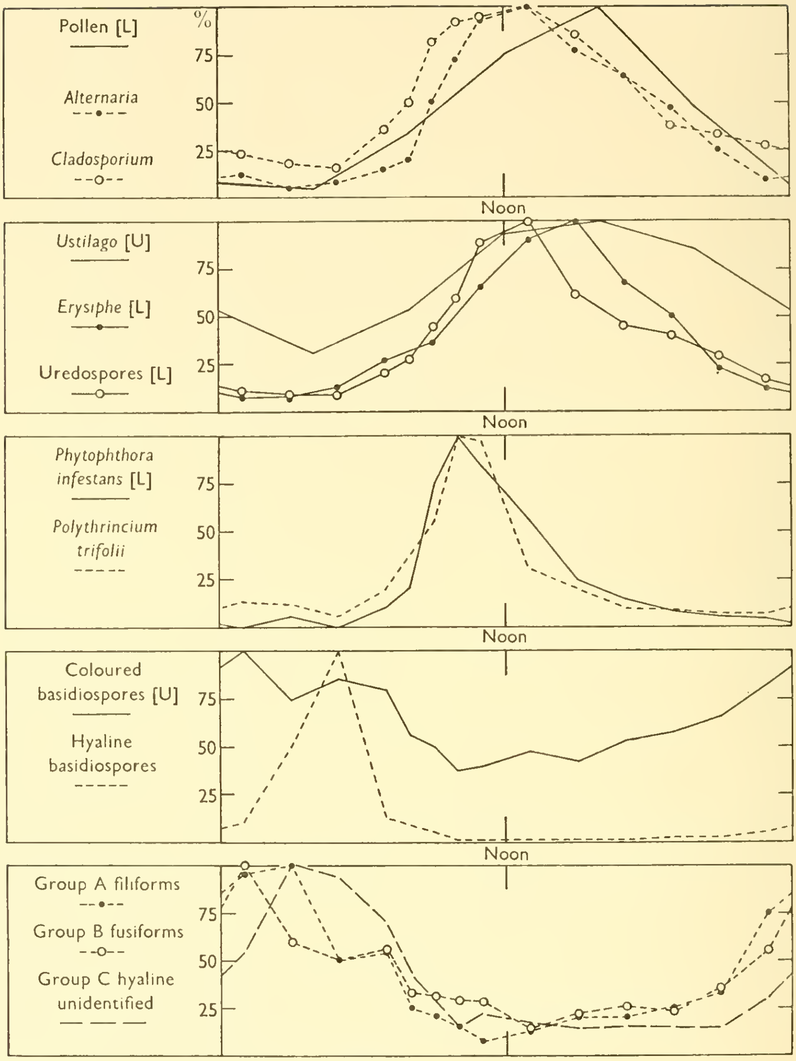

FIG. 20.—Mean diurnal periodicity curves of thirteen spore-groups expressed as percentage of the peak geometric mean concentration. (From Hirst trap records at Rothamsted Experimental Station, summer 1952.) (The symbols 'L' and 'U' refer to corrections applied to the data, based on wind-tunnel tests of the Hirst trap with *Lycopodium* and *Ustilago* spores, respectively.) (Reproduced by permission of J. M. Hirst from the *Transactions of the British Mycological Society*, 1953.)

(iii) *The forenoon pattern.* The hours after dawn, 06·00 to 10·00 hours, bring an interlude, but at about 10·00 or 11·00 hours the forenoon pattern is characterized by peak concentrations of a few crop-pathogenic fungi, e.g. *Polythrincium trifolii* and *Phytophthora infestans.*

(iv) *The afternoon pattern* develops from noon to 16·00 hours and contains the majority of the day-time spore forms, notably: *Cladosporium*, *Alternaria*, conidia of *Erysiphe*, many other Fungi Imperfecti, uredospores of rusts, and brand spores of smuts.

(v) *The evening pattern.* The early part of the evening, from 17·00 to 21·00 hours, forms another interlude with few well-defined maxima, until the nocturnal spora starts at about 22·00 hours, lasting until dawn.

All these diurnal periodicities are based on mean records for a number of days. Weather on a particular day may disturb the normal rhythm: for example, *Sporobolomyces* may persist to 10·00 hours or later; anthesis of grasses may be suppressed in dull weather, when pollen concentration may remain low. In the dry season in Nigeria, certain typically afternoon types may occur in the forenoon (Cammack, 1955). One other feature is shown by many organisms, namely, the rise from a low value to the maximum is often steep, whereas the fall is relatively slow; with others, such as *Sporobolomyces*, the reverse is often true.

Panzer *et al.* (1957) refer *Leptosphaeria*, *Epicoccum*, *Piricularia*, *Cladosporium*, *Diplodia*, and *Ophiobolus*, to the 'night spora' with maxima between 18·00 and 09·00 hours, and *Nigrospora*, *Penicillium*, *Alternaria*, *Curvularia*, and *Tricoconis* to the day spora, with maxima between 08·00 and 17·00 hours. Some discrepancies with findings in Britain, such as the occurrence of *Cladosporium* and *Epicoccum* at night, suggest that local conditions favouring a high concentration in air may be found by day in one climate and at night in another climate.

The causes of these diurnal fluctuations are complex. Hirst suggests that those spores which are commonest in the forenoon depend on hygroscopic changes during drying to liberate their spores; commonest in the afternoon are often those pollens and spores which are passively dispersed by shaking and wind erosion from dry surfaces, and conditions favour their liberation in the afternoon. Some nocturnal forms, such as *Sporobolomyces*, *Tilletiopsis*, and some ascospores, depend on dew. High night-concentrations need not always be interpreted as resulting from an increased number of spores being discharged at this time. We do not yet know whether the basidiospore diurnal rhythm (Fig. 20) reflects a diurnal spore-production rhythm, or whether spore emission is relatively constant during the 24 hours, being diluted through the considerable height of the turbulent boundary layer by day, but remaining concentrated near the ground during the night—when effects of frictional and thermal turbulence are usually small.

SEASONAL CHANGES

Seasons affect the air-spora profoundly. *Cladosporium* and *Alternaria* show pronounced seasonal periodicity, as of course do the pollens and spores of mosses, pteridophytes, and plant-pathogenic fungi. On the other hand *Penicillium* may show little seasonal change, whilst in cities it may even be more plentiful in winter than in summer (Maunsell, 1958; Hamilton, 1959). To the allergist the winter is a period of allergen-free outdoor air. Spring brings the deciduous tree-pollens, followed by those of conifers in early summer and, more important, by grass pollens characterizing the 'hay-fever' season. Late summer brings the moulds and what are known as the 'weed pollens' (including the notorious ragweeds, *Ambrosia* spp., in North America), extending into early autumn. Late autumn, like the winter, is relatively free from allergens.

Hamilton (1959) recorded the temperatures at which various spore types were in the air in maximum numbers (Table XXI).

TABLE XXI

TEMPERATURES AT WHICH HIGHEST CONCENTRATIONS WERE RECORDED.
(Hamilton, 1959.)

°F.	°C.	Spore Category
40–44	4·4–6·7	*Leptosphaeria.*
45–49	7·2–9·4	*Venturia.*
50–54	10·0–12·2	*Nolanea*, '*Penicillium*'.
55–59	12·8–15·0	Yellow basidiospores.
60–64	15·6–17·8	Fusiform (thin) ascospores, *Sporobolomyces*, *Tilletiopsis.*
65–69	15·6–17·8	*Coniophora*, *Entomophthora*, Fusiform (fat) ascospores, *Lactarius.*
70–74	21·1–23·3	*Cladosporium*, *Dicoccum*, *Erysiphe*, *Helicomyces*, *Periconia*, *Ustilago.*
75–79	23·9–26·1	*Alternaria*, *Chaetomium*, Filiform ascospores, *Ganoderma*, *Phytophthora*, *Polythrincium*, *Pullularia*, *Sordaria*, *Thelephora*, *Torula*, uredospores.
80–84	26·7–28·9	Brown basidiospores, Yellow basidiospores, *Botrytis*, *Epicoccum*, Fusiform (thin) ascospores, *Helminthosporium*, *Macrosporium*, *Psilocybe.*
85–89	29·4–31·7	Hyaline basidiospores.

EFFECT OF LOCALITY

The air-spora near the ground tends to be dominated by local sources, and these components of local origin are seen against a background of others from many distant sources. Volumetric sampling shows that some species are practically ubiquitous, whereas others are more or less confined to certain localities. Valuable surveys of airborne pollen are given by Hyde (1952, 1956, 1959), and of fungus spores by Werff (1958).

Species of *Cladosporium* belong to the ubiquitous group. They dominate the day-time spora in temperate regions and in the moist tropics (Hirst, 1953; Cammack, 1955; Gregory & Hirst, 1957; Pady, 1957; Hamilton, 1959; Kramer *et al.* 1959). This phenomenon agrees with surveys by gravity sampling methods in Britain and New Zealand (Dye & Vernon, 1952; Menna, 1955; Richards, 1954*b*). The dominance of various types of basidiospores (ballistospores) at night is probably also a widespread phenomenon whose magnitude is now becoming apparent.

At Rothamsted, Gregory & Hirst (1952) found that between early August and late September the concentration of coloured basidiospores seldom fell below 1,000 per cubic metre. From June to October, 1952, coloured basidiospores formed 3·3 per cent and hyaline basidiospores 46·5 per cent of the total air-spora in the size-range above about 4 μ, and their abundance at Rothamsted in 1954 was confirmed by Hamilton (1959).

It soon became clear that the hyaline basidiospores were mostly from colonies of *Sporobolomyces* occurring on leaves, and that their abundance varied greatly in different places. Last (1955), when sampling air within a stand of wheat, found large differences in concentration of *Sporobolomyces* between manured and unmanured plots in the same field (Broadbalk field, Rothamsted). The highest concentration of sporobolomycete spores so far reported (up to 1 million per cubic metre) was found near Chichester Harbour, England (Gregory & Sreeramulu, 1958).

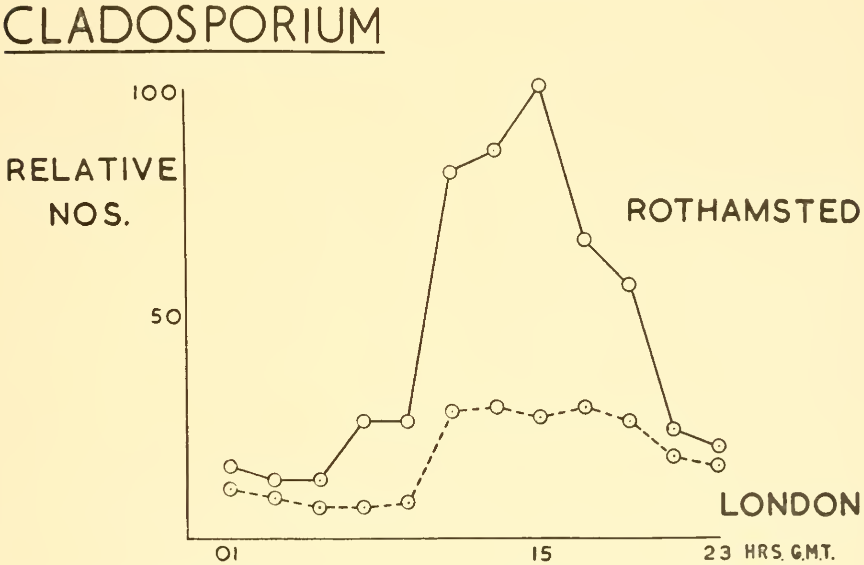

FIG. 21.—Diurnal periodicity of *Cladosporium* at London (South Kensington) and Harpenden (Rothamsted), based on Hirst trap catches from May to September, 1954. (Reproduced by permission of Elizabeth D. Hamilton from *Acta Allergologica*, 1959.)

In any one place it is difficult to disentangle the respective contributions of local and distant sources. It might be expected that spore concentrations would be lower in a city than in the near-by countryside. This was indeed found by Hamilton (1959), who compared continuous records from two Hirst traps, one at Rothamsted (2 metres above ground) and the other in London (16 metres above ground on a roof in South Kensington). The counts of total pollen were higher in London because of a large excess of *Platanus* (plane) pollen, but grass pollen grains were 50 per cent more numerous in the country. Fungus spores outnumbered pollen grains by

75 to 1, and although counts in London were less than half those at Rothamsted, they still averaged 6,500 per cubic metre during the 1954 season. With some species, diurnal changes in concentration tended to be less pronounced in London than in the country (Fig 21); this may perhaps have indicated that spores of the species trapped in London came mostly from distant sources.

Results of extensive surveys on a roof at Manhattan, Kansas, are based on daily sampling at approximately 09·00 local time. A Pady-Rittis slit sampler was used for visual identification and the G. E. Electrostatic sampler for making cultures on Rose-Bengal agar. The maximum numbers of fungus spores recorded at one time was 100,000 per cubic metre in visual traps and 20,000 per cubic metre in culture (Pady, 1957; Rogerson, 1958; Kramer *et al.* 1959). The main constituents were identified as follows:

	Visual per cent	In Culture per cent
Cladosporium	40·9	44·5
Basidiospores	24·3	—
Non-sporulating	—	17·6
Alternaria	3·4	12·6
Yeasts	7·3	8·4
Penicillium	—	6·1
Aspergillus	—	5·4
Smuts	5·9	—
2-celled hyaline	4·4	—
Fusarium	2·9	—
1-celled hyaline	1·4	—
Cercospora	1·0	—

EFFECT OF WEATHER

Atmospheric spore concentration fluctuates according to meteorological conditions. It also fluctuates for biological reasons such as growth and differentiation of the spore-producing organisms. Studies by Hirst (1953) show that the pollens, and spores of *Cladosporium*, *Erysiphe*, *Alternaria*, smuts, and rusts (which together form the main components of the daytime 'dry-air' spora), are mostly removed by prolonged rain which, however, soon puts into the air a characteristic damp-air spora.

Fluctuation is a property of the fine-weather air-spora, but some types depend on rain to get into the air, and occur in high concentration only after measurable rainfall. Keitt & Jones (1926) showed that liberation of ascospores of the apple scab fungus (*Venturia inaequalis*) is correlated with rain. Hirst *et al.* (1955) trapped no ascospores of this fungus during dry weather in orchards, and during the first hour after the onset of rain they found only a few ascospores; yet high concentrations occurred in the second and third hours. Rain at night led to lower concentrations than an equal amount of rain falling by day. In general, perithecia of most ascomycetes possessing them must be wetted before ascospores are ejected. Spores of *Ophiobolus graminis*, the wheat take-all pathogen, do not occur in the air during dry weather, but they reached a concentration of 3,700 per cubic metre in air over wheat stubble within 2 hours of the fall of 1·3 mm. of rain; a few ascospores were liberated by as little as 0·25 mm. of rain (Gregory & Stedman, 1958). Ascospores of some species are evidently discharged when the ground is wet with dew, and these types appear as part of the nocturnal air-spora.

Little is known yet about the composition of the damp-air spora, or about the occurrence of spores taking-off in rain-splash, and their study awaits improved technique.

Hamilton (1957) studied correlations at two centres (London and Rothamsted) between spore concentration of twenty-eight visual types and the weather. Her main positive findings are as follows. Rainfall had no effect on the atmospheric concentrations of hyaline basidiospores (including those of *Nolanea*, *Lactarius*, *Tilletiopsis*, and possibly *Sporobolomyces*). The concentrations of pollen and of most types of spore decreased with rain, but all ascospore types and *Helicomyces* increased with rain. In half of the types studied, concentrations were significantly increased by increases in temperature, dew-point, or relative humidity. The only significant decreases were in grass pollen (and possibly *Ustilago* spores) with increased relative humidity, and in *Nolanea* with increased dew-point. Sunshine had no significant effect except for positive correlation with *Ustilago* and algal groups ('*Gloeocapsa*'). Increased wind significantly decreased the concentration of *Alternaria*, some basidiospores (including *Ganoderma*, *Tilletiopsis*, and *Sporobolomyces*), *Botrytis*, *Cladosporium*, *Entomophthora*, *Pullularia*, uredospores, insect fragments, and *Urtica* pollen. By contrast, plant hairs and algal groups ('*Gloeocapsa*') were increased by increasing wind-speed—possibly because both are released by friction. Gustiness was associated with increases in *Alternaria*, filiform ascospores, and *Ustilago*.

Conidia of *Cladosporium*, one of the best studied of the spore types, show an interesting anomaly in relation to weather. Hamilton (1959) found an appreciable *decrease* in their number during the hours when rain was falling, but Ainsworth (1952), Hirst (1953), and Gregory (1954) demonstrated a transient *increase* in concentration of *Cladosporium* spores when rain started to fall. So far this phenomenon remains unexplained.

BIOTIC FACTORS

Human activity can also play a part in affecting atmospheric spore concentration. Mowing and tedding of grass can produce a great and immediate local increase in *Cladosporium* and *Epicoccum* spores, and (with an apparent delay of 2 hours) of grass pollen (Sreeramulu, 1958). Threshing of grain produces a local spore source (Heald & George, 1918). The role of overhead irrigation must not be overlooked, and spraying with insecticides and fungicides has been claimed to spread some fungal diseases.

MARINE AIR

The oceans, forming three-quarters of the Earth's surface, act as a vast source, putting a mainly bacterial microbial population into the atmosphere. Compared with air over land, the concentration in surface layers over sea is usually very small. Processes by which marine organisms become airborne include: spray droplets from the breaking of waves on shore or at sea; foam blown off white-caps; and bursting of bubbles produced by white-caps, rain or snow (Blanchard & Woodcock, 1957). These processes, however, also facilitate removal of suspended particles from sea-air by the large liquid surface whose relatively constant temperature determines continued up-and-down movement in the lower layers of air.

Much of the older work is reviewed, and new data added, by ZoBell (1946). A critical appraisal of the whole subject of aerobiology comes from Jacobs (1951), who calculated, on the basis of salt-concentration of the air and the bacterial concentration of sea water (which seldom exceeds 500 per cc.), that the number of marine bacteria in air near the sea surface averages about 5 per cubic metre.

The microbial exploration of marine air was pioneered by Miquel (1885, 1886) with the help of a sea captain, Mons. Moreau, during seven voyages. For visual examination of crytogamic spores, an aspirator was worked by suction provided by an engine condenser—an arrangement which sampled 700 litres per 24 hours. Bacteria were estimated by drawing air through glass-wool plugs in tubes at the rate 1,000 litres per 24 hours, washing the plugs, and inoculating aliquots into flasks of liquid beef extract. A total of 113 cubic metres sampled in the seven voyages averaged 1 bacterium per cubic metre, or 0·6 per cubic metre if samples taken within 100 km. of land were excluded.

Visual counts over the ocean usually showed a few hundred crytogamic spores and many pollen grains per cubic metre (1/30th of the number usual on land), but on one occasion a total of 3,700 per cubic metre were found at a distance of 30 km. from land in a wind off the coast of Senegambia; this comprised a spora very different from that found by Miquel in Paris. Near to continents the winds coming from land always brought impure air, but the sea rapidly purified it and so a broad stretch of water provides an effective obstacle to the spread of contagious epidemic diseases. In normal weather, bacteria from sea water were not put into the air, but in rough weather Miquel found that the sea air contained a few marine bacteria.

The air in a ship's saloon always contained incomparably more microbes than sea air, but its purity increased rapidly in the early days of the voyage until it reached an equilibrium between purification by ventilation and contamination by vital activity on board—at a level of perhaps 1 per cent of that in dwellings in Paris. Nevertheless, Miquel concluded, a ship travels in an atmosphere of self-contamination with bacteria, moulds, and starch grains.

On a voyage to the Caribbean, B. Fischer (1886) found very few terrestrial microbes in ocean air—except near major land-masses, where large numbers of bacteria appeared, apparently derived from the soil. Flemming (1908) sampled air on a voyage from Hamburg to Rio de Janeiro and Santos. Of his numerous 20-litre samples taken more than 200 km. from land, two-thirds were sterile—but even at this distance he averaged thirty-four viable spores per cubic metre. These were mostly of moulds and yeasts, though bacteria increased in proportion nearer to land.

Although over the sea the air is extremely pure in comparison with air over land, most investigators on board ship have found bacteria, yeasts and mould spores wherever tests have been made. Bisby (1935) exposed Petri dishes on a voyage from Montreal to England and isolated bacteria, *Botrytis cinerea*, and *Phoma hibernica*, all near the coast of Ireland.

The microbes of marine air have been studied at the Scripps Institution of Oceanography, California, by ZoBell & Mathews (1936) and ZoBell (1942). They claimed that less than 5 per cent of bacteria in sea water will grow in freshwater nutrient media, and a still smaller percentage of freshwater bacteria will grow on sea-water media. Petri dishes of nutrient media made up with distilled water (FW) or sea water (SW) were exposed horizontally at distances of up to 1,600 metres inland from a sea wall during a sea breeze of 5·8 m.p.h. (2·6 metres per sec.). The 'SW' count decreased and the 'FW' count increased with the distance inland, the 'SW'/'FW' ratio decreasing steadily from 10–20 at the sea wall, to 1·0 at 400 metres, and 0·5 at 1,600 metres inland. The number of mould spores usually increased with increasing distance from the sea.

In a land breeze, littoral spray puts into the air salt-water bacteria which can be detected at up to 8 km. out to sea, after which the ratio 'SW'/'FW' goes down to 1·0 owing to the predominance of terrestrial bacteria in the air for distances of 160 km. out to sea in fine weather. Exceptionally at 880 metres height on Mt. Woodson, 32 km. inland, plates exposed in a sea breeze following rain gave a ratio of 'SW'/'FW' = 2·06, which was interpreted as indicating a predominance of marine bacteria in the air in a region where soil bacteria normally predominate. It has been calculated that an average of 12·7 cubic miles of sea water is put into the Earth's atmosphere each year in the form of splash droplets, and this would provide an average of only about one marine bacterium per square centimetre of the Earth's surface per year—a small quantity compared with the deposition rate from the land air-spora (ZoBell, 1942).

Although all workers agree that marine air contains extremely few bacteria, ZoBell points out that the use of sea-water media might be expected to increase the counts of earlier workers by from 10 to 20 times. On these media gram-negative bacilli predominate, there are few cocci, no vibrio or spirilla forms, and fewer than half were spore-formers. A pink yeast has been reported from ocean air by several workers. This spora contrasts strongly with the gram-positive rods, spore-formers, cocci, Bacillaceae, and Micrococcaceae which, with mould spores, are normally abundant in air over land (ZoBell, 1942).

Rittenberg (1939) sampled in (presumably horizontal) Petri dishes at 21 metres above the deck of the vessel *E. W. Scripps* off the Pacific Coast of California. Contrasts between sea-water and fresh-water media were not so clear as in previous tests, and the numbers varied widely at different stations; but, on the average, moulds decreased in numbers with increasing distance from land (Table XXII).

TABLE XXII

NUMBERS OF MICROBES AND DISTANCE FROM LAND. SUMMARY OF 25 PETRI DISH EXPOSURES AT 21 METRES ABOVE DECK (Rittenberg, 1939).

Distance from land	Average number of colonies per hour of exposure (on 4 Petri dishes of each inoculum).			
km.	Sea-water Medium		Tap-water Medium	
	Bacteria (and yeasts)	Moulds	Bacteria (and yeasts)	Moulds
0–20	45	115	20	200
20–300	48	79	13	69
300–800	71	20	39	36

Detailed examination of 100 bacterial and yeast cultures taken at random by Rittenberg showed that 32 per cent were yeasts, 30 per cent cocci, 15 per cent gram-negative rods, and the remaining 23 per cent gram-positive spore-forming rods. They included: *Bacillus subtilis*, *B. flavus*, *B. megatherium*, *B. mycoides*, *B. tumescens*, *B. cohaerens*, *B. laterosporus*, *Flavobacterium aquatilis*, *Achromobacter liquifaciens*, *Staphylococcus aureus*, *S. albus*, *S. citreus*, *Micrococcus flavus*, *M. candidus*, and *Sarcina flava*.* One hundred mould cultures included: *Cladosporium* (*Hormodendrum*), 22 per cent; *Penicillium*, 18 per cent; *Alternaria—Macrosporium—Stemphylium*, 11 per cent; *Cephalosporium*, 7 per cent. Others identified included: *Plenozythia*, *Catenularia*, *Spicaria* or *Paecilomyces*, and *Trichoderma*. To avoid the usual embarrassment of the microbiologist, all sampling in free air seems to have been done with sugar-free media; otherwise, moulds might have been many times more abundant. Rittenberg points out that this marine airborne flora is unlike that of sea water itself, but resembles the air-spora over land.

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* But additional information by ZoBell (1942) indicates that these identifiable species were all from fresh-water plates.

Although the air-spora over the sea is clearly largely of land origin, Petri dish sedimentation tests are difficult to interpret and cultural and volumetric work is needed on the contribution from the ocean itself—both in the zone of littoral influence studied by ZoBell, and far from shore. The mode by which the ocean purifies the air flowing over it, and the fate of airborne spores trapped by the ocean, are still obscure.

Earlier workers, including Miquel and B. Fischer, found marine air almost free from pollen, but this freedom is now seen to be only relative. Erdtman (1937) operated a vacuum-cleaner filter trap at the masthead of the M.S. *Drottningholm* during a voyage from Gothenburg to New York extending from 29 May to 7 June, 1937. Compared with the average of 180 pollen grains per cubic metre recorded during spring at Västerås (110 km. west of Stockholm), he found only 0·18 per cubic metre in the North Sea, and 0·007 per cubic metre in mid-ocean, with an increase again on approaching North America. Temporary higher concentrations ('pollen rains') occurred three times: of *Pinus* (0·13 per cubic metre) in the North Sea; of *Alnus viridis* (0·045 per cubic metre) and Cyperaceae (0·006 per cubic metre) at a distance of 250 to 600 km. off Newfoundland; and of combined grasses, *Plantago*, and *Rumex* (totalling 0·1 per cubic metre) at 220 to 300 km. from Nova Scotia and Massachusetts. During strong western and north western winds, about mid way between Iceland and Ireland, Erdtman caught tree pollens (*Alnus*, *Betula*, *Corylus*, *Juniperus*, *Myrica*, *Picea*, *Pinus*, *Populus*, *Quercus*, *Salix*, *Tilia*, *Ulmus*) and herb pollens (Chenopodiaceae, Cruciferae, Cyperaceae, Ericaceae, Gramineae, *Plantago*, Umbelliferae, and *Urtica*), as well as spores of *Dryopteris* and *Lycopodium clavatum*.

Erdtman's volumetric sampling firmly establishes the occurrence of pollen in small but measurable concentration near the surface of the sea right across the Atlantic, and there is no reason to doubt that the land air-spora extends to all parts of the globe. Confirmatory evidence comes from Transatlantic sampling by Dyakowska (1947) and Polunin (cf. 1955).

Bishop Rock Lighthouse stands on a low rock at the southwestern extremity of the Scilly Isles, which are a group of small, rocky islands with few trees (mainly *Ulmus* and *Pinus*). Gravity slide sampling on the lighthouse platform 38 metres above sea-level (Hyde, 1956) showed mainly pollen of *Betula*, *Quercus*, and *Fraxinus*, with some *Pinus*. The total tree-pollen deposit was quite large (2,800 per sq. cm. per year, compared with 2,000 at Aberdeen and Brecknock Beacons, and 10,000 at Cambridge). The proportion of tree pollen of Bishop Rock was 27 per cent, and this is typical of country areas in Britain (in towns it may reach 50 per cent). It is remarkable that the greatest deposition of grass pollen recorded for any centre in Britain during Hyde's gravity slide survey was 1,679 grains per 5 sq. cm. at Bishop Rock on 29 June 1953. Whether this resulted from high concentration, or from high efficiency of turbulent deposition in strong winds, is not yet clear.

Sreeramulu (1958*a*) used a Hirst trap at 70 ft. above sea-level on a voyage in the Mediterranean in October and November, 1956. At 5 to 50 miles from land he found an average of 56·4 fungus spores and 1·6 pollen grains per cubic metre. In Malta Harbour the concentrations were 121 and 12 per cubic metre, respectively. At sea, *Cladosporium* predominated with 16 spores per cubic metre, followed by smuts with 5 per cubic metre, and coloured basidiospores with 7 per cubic metre. Also of interest was the occurrence of spores of *Helminthosporium*, *Alternaria*, *Torula herbarum*, *Nigrospora*, *Curvularia*, and *Epicoccum*, as well as hyphal fragments.

Pollen in marine air must come from land plants; the mould spora is more characteristic of above-ground sources than of the soil; the bacteria, however, may well come largely from sea water and soil.

THE AIR OF POLAR REGIONS

The air of polar regions seems to be still purer than that over the sea. Levin (1899), who aspirated air through powdered-sugar filters, obtained only three bacterial colonies and a few moulds in a total of 20 cubic metres of air sampled at various points in Spitsbergen (Svalbard).

During 2 years on an island near Graham Land, Antarctica, Ekelöf (1907) exposed Petri dishes at intervals; 40 per cent of them grew bacteria, which he thought came from the soil. On the average, one colony arose per 2-hours exposure.

Pirie (1912) exposed Petri dishes in the 'crow's nest' of the *Scotia* in the Weddell Sea, Antarctica, during the summer of 1903, for as long as 20 hours, and also on a glacier at Scotia Bay during winter; they all remained sterile. E. Hesse (1914) exposed Petri dishes while at sea south of Spitsbergen and also found the air to be almost sterile.

Darling & Siple (1941) exposed jars and dishes of media in remote places in Marie Byrd Land, Antarctica, and from their isolations identified: *Achromobacter delicatulum*, *A. liquidum*, *Bacillus albolactis*, *B. fusiformis*, *B. mesentericus*, *B. subtilis*, and *B. tumescens*. They concluded that, although some bacteria had been brought to Antarctica by man and migrating animals, the vast majority must have come as atmospheric dust in subsiding air.

Recent work in the Arctic has demonstrated a fair range but sparse 'population' of microbes to be present in the air in summer near ground- and sea-level in various parts of those vast regions. Polunin (1954, 1955) organized the exposure of sticky slides at several points ranging eastwards from Point Barrow, Alaska, to Spitsbergen, in 1950, and found a considerable variety of pollen grains and 'probable moss spores' at each station. Remarkably enough the pollen grains caught most plentifully through most of that summer in Spitsbergen were of *Pinus*—several hundreds of kilometres from their nearest possible source. In 1954 Polunin (1955*a*) was responsible for the exposure of sticky slides (cf. Polunin, 1960) off the north coast of Ellesmere Island and, in 1955, for the exposure of sticky slides (Barghoorn, 1960) and Petri dishes of nutrient media (Polunin *et al.* 1960; Prince & Bakanauskas, 1960) on Ice-Island T–3 when it was floating in the North Polar Basin at about 83°N. Here again the air-spora was found to be very sparse compared with middle latitudes, but it included pollen grains which, in some instances, were indicative of long-range transportation (cf. Barghoorn, 1960, p. 91, despite p. 88). From the T–3 exposures a small number of slow-growing fungus isolates (all identified as *Penicillium viridicatum*) and more of Actinomycetes were obtained, but none of bacteria.

THE ORIGIN OF THE AIR-SPORA

There is no reason to doubt the conclusion of Miquel and of Proctor (1935) that most bacteria of the air originate from the soil, or from the oceans (ZoBell, 1946). But it is doubtful whether the soil makes any substantial contribution to the fungus spore content of the atmosphere, as has been argued by some writers. It seems more likely that this air-spora is derived predominantly either from moulds, plant parasites, and other fungi growing on vegetation, or from surface-growing fungi equipped with explosive mechanisms which project their spores into the freely-moving turbulent air layer. In the soil, bacteria, Penicillia, and Aspergilli predominate; but *Cladosporium* predominates in the air, seconded by basidiospores. Similarity between the soil- and air-sporas results mainly from the soil being the ultimate 'sink' to which most of the spores of the air are destined.

Much of the air-spora comes from wild vegetation. Industry pollutes the atmosphere mainly with inorganic particles and gases. It is not generally appreciated, however, that agricultural practices may pollute the air with plant pathogens and with respiratory allergens on a large scale. Even such small operations as mowing grass may cause a local increase in the *Cladosporium* content of the air by a factor of 20 times, as I have found in recent tests (and cf. Sreeramulu, 1958).

For microbes to get into the air in the high concentrations observed at peak seasons, a take-off mechanism is necessary. However, the most unlikely organisms occasionally get into the air. Siang (1949) isolated one colony of the aquatic phycomycete, *Hypochytrium catenoides*, from air on a roof at McGill University, Montreal, Canada. Probably almost every kind of microbe would be found if sampling were continued long enough.

From recent work on the air-spora near the ground, we learn that its composition and concentration often fluctuate enormously—sometimes within quite short time-intervals. The significance of this for plant pathology and plant breeding is obvious. Some constituents, such as the grass pollens, are important in respiratory allergy (the volume of air inhaled by the human lung is of the order of 1 cubic metre per hour). In the course of 24 hours we inhale perhaps 50 micrograms of a mixture of microbes. Although some constituents of this mixture are harmful to allergic subjects, this dose might also bring in useful quantities of active organic compounds. Chauvin & Lavie (1956) found antibiotics in *Salix* and maize pollen, and their presence in fungus spores, too, would not be surprising (*see* Whinfield, 1947). We may wonder whether the reputed beneficial effects of country air for human health are attributable not only to its freedom from smoke and fumes, but also to positive gains from the air-spora.

Finally, to balance loss with gain, as the Earth's surface is the ultimate receptacle of almost all spores liberated, it can be estimated that the soil must receive a dose of fertilizer from the air-spora equivalent to perhaps 2 kg. of nitrogen per acre per annum—an amount that is negligible on fertile land, but enough to aid plants colonizing barren places.

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THE UPPER-AIR SPORA

The air-spora near the ground is dominated by fluctuations in its immediate local sources. In the upper air, however, the effects of local sources are smoothed out and attention can be focussed on organisms undergoing long-distance transport. Concentrations in the upper air are sparse, the necessity of keeping samples free from contamination is paramount, and sterile technique for enumerating the microscopically small particles becomes exacting when they are exceedingly dilute.

Vertical Diffusion

Whereas spores and pollen grains are heavier than air, and tend to fall under the influence of gravity, atmospheric turbulence and convection tend to work in the opposite direction. As a result, the atmosphere is in a sense a spore suspension that generally decreases in concentration from ground-level up to the base of the stratosphere. Eddy diffusion will bring spores to the top of the outer frictional turbulence layer: above this, convection will operate and, in the upper part of the troposphere, we would expect to find mostly components of the day-time spora. When it first became possible to explore the air overhead, it was a matter of surprise to find how far up microbes could go. As methods have been developed for exploring greater and greater heights, we can begin to form a picture of the changes in concentration with height and of the circulation of spores of micro-organisms over the surface of the globe.

Evidence that concentration decreases with increasing height comes from two distinct sources of information which have often been confused: (1) observations at a standard height above local ground-level at a chain of stations differing widely in altitude above sea-level; and (2) observations at widely different altitudes above local ground-level at a single station.

GROUND STATIONS AT DIFFERENT ALTITUDES ABOVE SEA-LEVEL

Observations in this category are extremely fragmentary and have the flavour of holiday tasks on fine days in summer. Samples at various altitudes are taken at successive times as the climber reaches a suitable station—as in Pasteur's visit to the Mer de Glace, where the relative purity of mountain air was convincingly demonstrated (*see* p. 4). Using a volumetric method, Miquel (1884, p. 524) confirmed this conclusion.

In July and August, while bacterial concentrations of 55,000 per cubic metre were current in the air of the Rue de Rivoli in Paris, and 7,600 per cubic metre in the Parc Montsouris, Miquel found only eight bacteria (and numerous moulds) per cubic metre at a height of 1 metre above the surface of a field at Lake Thun (570 m. above sea-level), and none at stations between 2,000 metres altitude and the summit of the Eiger at nearly 4,000 metres. Miquel attributed this purity to the effect of reduced atmospheric pressure doubling the volume of air and diluting its dust load, to the rarefied air less easily holding particles in suspension, and to the absence of local sources of contamination—especially in the regions of perpetual snow. In similar volumetric data from the Dauphine Alps recorded by Bonnier *et al.* (1911), bacteria decreased with height more rapidly than moulds.

No one has yet compared concentrations at different heights above ground-level over plateaux with those over mountains, or over flat and convex surfaces at the same altitude.

The purity of the air in regions of perpetual snow is understandable, but it is surprising that air at one or two metres above ground-level in mountain valleys should also contain so few microbes. Geiger (1950) envisages mountain slopes as covered with a skin of air having the usual characteristics of air near the ground but easily removed by wind and convection—except where protected by vegetation. Convex surfaces generally have a more extreme climate than flat surfaces, and concave surfaces are still more equable.

THE ROLE OF TURBULENCE

The role of turbulence in diffusing spore-clouds vertically was first emphasized by Schmidt (1918, 1925), although the theory was developed for heat transfer by Taylor (1915) with information derived from temperature records over the Great Banks of Newfoundland. Schmidt argued that, when a stable state of diffusion by eddies has been reached, the number of particles falling under the influence of gravity across any horizontal boundary is compensated for by the number of particles moved upwards by diffusion, and so the concentration of particles in the air should decrease exponentially with increasing height according to the equation

$$\chi = \chi_0 \exp. \left[-\frac{v_s z}{A} \right],$$

where χ_0 = concentration at height $z = 0$,
v_s = terminal velocity of fall,
A = Schmidt's 'Austausch' or intermixing coefficient which is assumed to be invariable with height.

The total spore content of the column of air standing above 1 sq. cm.

would be $\lambda = \chi_0 A/v_s$. Concentrations should give a straight line when plotted against the logarithm of the height.

The method of approach to the problem suffers from two defects in practice. The coefficient for diffusion (Schmidt's 'A' or Taylor's 'K') is not invariable with height, and it is doubtful whether a steady state is ever reached with the great diurnal changes occurring when the source consists of living organisms.

C. G. Johnson & Penman (1951) supposed that the vertical distribution of aphids at any one time is determined by the net effect of upward transport by turbulence and downward transport by the combined action of gravity and biological impulse—the mean clearance rate. If χ is the concentration at height z, and ω is the 'mean clearance rate', they deduced that a graph of log χ against log z should yield a straight line.

Attempts have been made to fit empirical curves to observational data on vertical gradients. Wolfenbarger (1946, 1959) used regression equations of the type: $Y = a + b \log x + c/x$. C. G. Johnson (1957) fitted records of insect-trap catches with: $f(z) = C(z + z_e)^{-\lambda}$, where f(z) is concentration at height z, C is a scale factor depending on population size, λ is an index of the diffusion process and the profile, and z_e is a parameter whose significance probably depends on the rate of exchange of insects between the air and the ground.

Particles entering the air near ground-level become mixed throughout the layer of frictional turbulence so long as the wind blows. Convection provides a local intermittent mechanism which distributes spores from the ground layer throughout the troposphere. Observed vertical concentration gradients sometimes fit theoretical lines quite adequately, and they may well describe long-term averages. But theoretical treatments of this problem are often unsatisfactory, especially in failing to predict concentrations in the first few hundred feet.

The ideal situation is seldom realized, because conditions change too rapidly for a stable state to be attained. Wind velocity increases with height, and layers of air at different heights in a vertical column at any one time will previously have been over different places at different times. The thickness of the turbulent layer of air is always changing. Biological factors in a diurnal cycle put vastly differing numbers of organisms into the air at different times, and vertical concentration is continually building-up or decaying. Temperature inversions will affect vertical diffusion; according to Jacobs (1951), 'The presence of a stable layer at the surface will prevent or retard the introduction of surface organisms into the upper atmosphere but will, at the same time, maintain higher concentrations of organisms in the surface layers; the presence of a discontinuity surface in the upper air will limit vertical transport in either direction, resulting in the concentration of organisms above or below such a surface'. Concentration will often start to decrease from the active surface of a crop and not from true ground-level.

Early Studies of the Upper Air

Measurements of microbial concentrations at heights above ground-level were first attempted from towers and tall buildings by Miquel (1883), Carnelley *et al.* (1887), and, more recently, by Kelly and others (cf. p. 143). Miquel found that the bacterial content of the air at the level of the Lanterne of the Panthéon in Paris was only 1/20th of that in the street below.

Probing upwards into the atmosphere for microscopic life started dramatically when the Manchester physician Blackley (1873) used two kites in series to lift sticky microscope slides to a height of 300 metres and caught from 15 to 20 times as much pollen as on slides similarly orientated at 1·4 metres above the ground. Kites were also successfully used in India by Mehta (1952) to catch spores of the cereal rusts, *Puccinia graminis*, *P. triticina*, and *P. glumarum*, and small balloons were used for the same purpose by Chatterjee (1931).

SAMPLING FROM BALLOONS

Cristiani (1893) obtained bacteria and a few moulds by volumetric sampling from a balloon at up to 1,300 metres above Geneva (at a total of 1,700 metres above sea-level). He was obviously puzzled by his results, which he regarded as inconclusive, and he attributed most of his catch to contamination from the surface of the balloon and its rigging—remaining convinced that the upper air is extremely pure.

The credit for first demonstrating the existence of a microbial population in the upper air should probably go to the mycologist Harz (1904), who sampled during a balloon ascent over southern Bavaria on a sunny morning in March. At altitudes of between 1,500 and 2,300 metres he aspirated air through a Miquel-type filter of powdered sodium sulphate by suction obtained with a horse's stomach-pump; culturing the catch in nutrient gelatine, he found a few moulds, and bacterial concentrations ranging from 179,000 to 2,870,000 per cubic metre. At 1,800 to 2,000 metres there was a zone with 16 times the concentration at 1,500 metres and 5 times that at 2,300 metres. These phenomenally large bacterial concentrations were associated with a large temperature lapse and strong convection from hot dry soil. Moulds were identified as: *Penicillium glaucum*, *P. cinereum*, *P. atro-viride*, *Sporidesmium* sp., *Acremonium alternans*, *Mucor racemosus*, *M. mucedo*, *Oospora ochracea*, *O. ferruginea*, *Periconia arta*, *Hormodendrum* (*Cladosporium*) *penicillioides*, *Arthrococcus lactis*, *Aspergillus niger*, and a sterile mycelium.

During ascents from Berlin with both captive and free balloons, Flemming (1908) used trapping methods similar to those of Harz. He found viable microbes up to 4,000 metres, averaging 370 per cubic metre above 500 metres, and 12,900 per cubic metre lower down. Sterile samples were rare. Concentrations were not uniform but increased strikingly at the level of the cloud base. Species identified included: *Micrococcus radicatus*, *M. albus*, *M. nubilus*, *M. aerogenes*, *Bacillus ubiquitus*, *B. aurescens*, *B. aureo-flavus*, *B. terrestris*, *B. aerophilus*, *B. submesenteroides*, *B. mycoides*, and *Penicillium crustaceum*—all spore-formers. Above 2,500 altitude he found *Bacillus terrestris*, *B. aerophilus*, and *Sarcina lutea*, and, at 4,000 metres, *Micrococcus citreus*, *M. luteus*, and *Penicillium crustaceum*. Flemming commented on the frequency of pigment-formers among the bacteria and yeasts of the upper air.

From catches made during balloon flights over southern Germany, Hahn (1909) concluded that, on the average, bacterial and dust counts run parallel with each other and decrease with height because of sedimentation. He claimed that the air above a certain height was germ-free, and that this zone was lower in winter than in summer.

THE STRATOSPHERE

We would expect the stratosphere to be almost devoid of organic particles, because of the apparent inadequacy of mechanisms able to carry them above the top of the troposphere. At great heights the intensity of radiation would be unfavourable to survival. However, well-documented evidence is worth more than theory and, for the present, we must admit that we know nothing of the possibilities of life in the stratosphere.

The only attempt to sample the stratosphere known to me was made with a balloon. Rogers & Meier (1936, 1936*a*) devised a sampler to be opened and closed by an aneroid between 21,000 and 11,000 metres during the descent of the Balloon 'Explorer II'. They obtained five bacterial cultures, all of which were different species of *Bacillus*, and five fungi (*Rhizopus* sp., *Aspergillus niger*, *A. fumigatus*, *Penicillium cyclopium*, and *Macrosporium tenuis*); in all, these were equivalent to approximately 0·14 viable organisms per cubic metre.

SAMPLING FROM AEROPLANES

Exploration for microbes in the upper air from aeroplanes was started in 1921 when Stakman *et al.*(1923) exposed Vaseline-coated slides over the Mississippi Valley to trap cereal rust spores. Flights from Texas as far north as Minnesota and at altitudes up to 3,300 metres yielded numerous pollen grains and fungus spores, among which *Alternaria* (often in chains) were most numerous, followed by *Puccinia*, *Helminthosporium*, *Cladosporium*, *Cephalothecium*, *Ustilago*, *Tilletia*, and *Scolecotrichum*. Among rust spores the uredo forms predominated, but some teleutospores and aecidiospores were also caught. Spores became relatively scarce at altitudes above 3,000 metres. At 5,400 metres (the highest altitude tested), two uredospores of *Puccinia triticina* were caught. *Alternaria* from altitudes of 1,000 to 3,000 metres germinated readily, as also did uredospores from 2,300 metres.

In the summer and autumn of 1923, Mischustin (1926) exposed Petri dishes of nutrient agar in flights from Moscow. On rather slender evidence obtained from tests in a wind-tunnel, he concluded that he was sampling 20 litres of air per minute—probably a large underestimate. The plane was first flown *above* the layer to be sampled to free it from ground dust, and then lowered to the required height. At 500 metres the numbers of bacteria increased in windy weather to 7,000 or 8,000 per cubic metre, from Mischustin's normal of 2,000 to 3,000 at this altitude. *Micrococcus* and *Sarcina* decreased greatly in calm weather, but the number of bacterial rods and of moulds increased. At 1,000–2,000 metres, numbers were small. The proportion of spore-forming bacteria, of moulds, and of actinomycetes, was greatest at the greater heights. The concentration of organisms over the city of Moscow at 2,000 metres included an average of 650 bacteria per cubic metre, and was from four to five times as great as that over the surrounding countryside.

Pollen was found at up to 5,800 metres over the Mississippi, with the greatest concentrations often at from 300 to 1,100 metres (Scheppegrell, 1924, 1925). Craigie & Popp (1928) caught wheat-rust spores at up to 3,000 metres over the Canadian prairies.

In flights from Cambridge, England, Weston (1929) found that fungi and bacteria were abundant up to 3,000 metres, but relatively scarce above this altitude. Air within clouds tended to contain more bacteria and fungi than did air above or below clouds—a phenomenon noted by other workers, including Heise & Heise (1948).

On flights up to 2,200 metres over the arid lands of southern Arizona, Browne (1930) isolated 'white and grey' bacterial colonies, *Aspergillus*, *Penicillium*, *Alternaria*, and yeasts; but no spores of wheat rusts were observed on slide spore-traps. Cotter (1931) studied dispersal of wheat rust in flights near Lake Michigan, trapping on oiled microscope slides. Uredospores were not more numerous during rain than in fine weather; fewer were caught over Lake Michigan than over near-by land, and more were caught over areas abounding in barberry (the alternate host of the parasite). MacQuiddy (1935) exposed Petri dishes and slides in flights up to 2,100 metres over Omaha, Nebraska. Pollen was abundant up to 900 metres, and bacteria and mould spores began to decrease between 1,200 and 1,500 metres. MacLachlan (1935) made flights in early May over Massachusetts, to trace spores of the juniper rust (*Gymnosporangium biseptatum*). Petri dishes exposed over the side of the 'plane for 1 minute gave viable spores up to 600 metres (the maximum height tested), although numbers and viability decreased steadily with height.

(i) *Aerobiological work of F. C. Meier*. Fred C. Meier of the United States Department of Agriculture planned an extensive investigation of the upper-air spora. Unfortunately, when only preliminary abstracts of his work had been published, he was lost on a flight over the Pacific Ocean (Haskell & Barss, 1939).

Sticky slides were exposed by Colonel Charles A. Lindbergh in special containers at about 1,000 metres altitude during a flight between Maine and Denmark. Material trapped over Davis Strait and East Greenland included algae, fragments of insects' wings, diatoms, and possibly sponge spicules, volcanic ash, and glass. Fungus spores were tentatively identified as belonging to: *Macrosporium*, *Cladosporium*, *Leptosphaeria*, *Mycosphaerella*, *Trichothecium*, *Helicosporium*, *Uromyces*, *Camarosporium*, and *Venturia*. Some of these were abundant over Maine and Labrador but diminished over Davis Strait, the ice-cap of Greenland, and Denmark Strait (Meier, 1935, 1935*a*).

Flights over the United States at from 150 metres to 5,500 metres showed a varied spore 'population' which usually decreased in both numbers and variety above 2,400 metres. Viable spores of *Pestalozzia* were caught above Washington at 5,500 metres on 22 March 1932. Other genera recognized included: *Acremoniella*, *Alternaria* (*Macrosporium*), *Aspergillus*, *Chaetomium*, *Cladosporium*, *Coniothyrium*, *Dematium*, *Epicoccum*, *Fumago*, *Fusarium*, *Helminthosporium*, *Penicillium*, *Sclerotinia*, *Stachybotrys*, *Stemphylium*, and *Trichoderma* (Meier *et al.*, 1933).

After flights over the Caribbean Sea, Meier (1936) came to feel that trade-winds might be important in disseminating microbes. Viable spores were found at 800 to 1,200 km. from land; but after rain squalls, Petri dishes sometimes remained sterile after exposure at 60–240 m. altitude a few kilometres to the leeward of islands—so demonstrating that showers remove spores from surface winds.

Sugar-beet pollen was trapped on agar plates during flights over a small sugar-beet seed-growing area of 900 acres in New Mexico. Viable beet pollen, mixed with pine pollen and fungus spores, occurred up to 1,500 metres, which was the greatest height tested and the level of the dust horizon (Meier & Artschwager, 1938).

(ii) *Vertical gradients.* During an epidemic of wheat rust in Manitoba in July and August 1930, Peturson (1931) trapped spores at different altitudes in eight aeroplane ascents. The average numbers of spores caught per square inch of trap surface (presumably with comparable exposure times) were: 305 metres, 10,050 spores; 1,520 metres, 1,180 spores; 3,050 metres, 28 spores; and 4,260 metres, 11 spores. By substitution in Schmidt's equation (*see* p. 132) we find $A = 5{\cdot}8 \times 10^4$, if $v_s = 1$ cm. per sec.

Hubert (1932) trapped spores during two flights at the time of an epidemic of yellow rust of wheat at Halle in Germany. During the second flight, for which data are more extensive, the numbers of spores trapped per square centimetre per minute of exposure at various heights were: 30 metres and less, 1,418 spores; 400 metres, 683 spores; 600 metres, 336 spores; and 800 metres, 82 spores. Substitution in Schmidt's equation gives $A = 1{\cdot}5 \times 10^4$.

Similar values for A were indicated when tree pollen was trapped over

German forests in spring during a series of aeroplane flights by day and by night (Rempe, 1937). In general, with light to moderate windy weather and with cumulus clouds at about 2,000 metres, the pollen concentration decreased only slightly up to 1,000 metres, and the maximum number of grains might occur as high as 200 or even 500 metres. This was regarded as a sign of a complete inversion of air masses. A similar distribution also occurred under high pressure conditions without clouds but with strong thermal turbulence. By way of contrast, conditions associated with a stratified cloud-layer and high wind velocities showed a marked decrease of pollen with height.

In night flights, the maximum number of grains was often reached at a height of about 200 metres, i.e. above the temperature inversion which often develops at night. At night the numbers trapped usually decreased with increasing height much more than by day. The total numbers trapped at all heights were also fewer by night than by day. From Rempe's data the mean numbers of pollen grains trapped per 1·275 sq. cm. of trap surface per 20 minutes for all flights which extended up to 1,500 metres were:

Altitude (metres):	10–40	200	500	1,000	1,500
Day flights	904	849	852	581	267
Night flights	577	560	283	85	45

These records include pollen grains of various species; but, taking $v_s = 3$ cm. per sec. as a moderate value for the speed of fall of pollen grains, it can be shown that, for altitudes above the zone affected by strong thermal turbulence and temperature inversions, Schmidt's interchange coefficient $A = 2{\cdot}6 \times 10^5$ for day flights, and $1{\cdot}6 \times 10^5$ for night flights. This provides further evidence of the appropriateness of considering the spore or pollen cloud as a suspension in air. Although at heights of about 1,000 metres and upwards the average distribution agreed well with that expected from terminal velocity balanced by eddy diffusion, near ground-level the suspension tended to become more uniform than predicted, owing to the intermittent stirring of the lower layers by strong mechanical and diurnal thermal turbulence.

(iii) *Sampling the upper air over the United States.* In the upper convective layer, Walker (1935) exposed Petri dishes of blood agar and, after sampling an estimated 2,400 cubic metres of air, he concluded that the atmosphere in that layer was sterile (two cultures of *Staphylococcus aureus* were reasonably enough ignored as contaminants). However, Proctor & Parker (1942) suggested that Walker's agar surfaces may have been frozen and non-adhesive, because their own researches at the Massachusetts Institute of Technology showed that the upper air over the United States was far from sterile.

In trapping from aeroplanes, Proctor & Parker used filters of lens paper supported on wire gauze in brass tubes connected with the free air and sampling about 28 litres per minute. The catches were examined both microscopically and by culturing. Bacteria averaged 12 per cubic metre on all flights, and 9 per cubic metre at 6,100 metres or higher. There was sometimes evidence of a zone of greater concentration at a height of several thousand metres. Moulds were usually less numerous than bacteria, but the nutrient agar on which filter washings were plated was recognized as unfavourable to mould growth. Bacteria were mostly spore-formers and those identified included species of *Bacillus*, *Achromobacter*, and *Micrococcus*. Among moulds, *Aspergillus* and *Penicillium* predominated, occurring with some other Fungi Imperfecti including *Cladosporium* (*Hormodendrum*) and *Fusarium*, as well as Mucoraceae, Actinomycetes and, occasionally, yeasts. Pollen was found on only three flights (Proctor, 1934, 1935).

The highest mould count obtained in the M.I.T. studies occurred at an altitude of 200 to 300 metres in May over a wooded area, where 22 bacteria and 260 moulds per cubic metre were recorded. Particularly large counts of bacteria and moulds occurred during a dust storm which apparently came from Nebraska and South Dakota—the same dust-storm during which Soule (1934) recorded mass invasion of his laboratories in Michigan by *Bacillus megatherium*. During this dust-storm, at an altitude of 1,500–3,300 metres over the Boston area, bacteria totalled 140, moulds 44, and dust particles 2,800, per cubic metre, respectively. However, during the whole survey, dust particles were over 100 times as numerous as viable microbes—suggesting that much of the dust came from industry and combustion rather than from the soil (Proctor & Parker, 1938).

Petri dishes of nutrient agar were exposed during flights at from 300 to 3,250 metres over Nashville, Tennessee, during winter by Wolf (1934). On this medium bacteria outnumbered moulds, the bacilli contributing 37·7 per cent, non-spore-forming rods 24·6 per cent, and cocci the remaining 37·7 per cent, of the total bacterial count. The bacteria were very similar to those found by Proctor (though with a smaller percentage of spore-formers) and further study supports the general conclusion that aerial bacteria are of types commonly found in soil and water, are generally unable to ferment common sugars with the production of gas, and are unable to produce indole.

From these flights by Wolf, *Actinomyces griseolus* was isolated twice, at 700 and 1,400 metres, and *A. phaeochromogenus* once, at 620 metres. A pink yeast was found at 1,750 and 3,050 metres. Fungi isolated, with their percentage frequencies, included: *Fusarium*, 29; *Alternaria*, 22; *Cladosporium* (*Hormodendrum*), 20; *Verticillium*, 5; *Aspergillus*, 3; *Penicillium*, 1·6; and among others were *Acladium*, *Brachysporium*, *Cephalothecium*, *Chaetomium*, *Helminthosporium*, *Macrosporium*, *Mucor*, *Oospora*, *Plenozythia*, and *Scopulariopsis*. The large numbers of *Fusarium* spores and small numbers of *Aspergillus* and *Penicillium* spores are remarkable.

The average of all samples gave a concentration of 7·5 cultivable organisms per cubic metre and varied from none at 850 metres altitude in December to a maximum of 42 per cubic metre at 460 metres in October. In general the concentration decreased with increasing height, but on 25 January there was a zone of high concentration at 900 to 1,200 metres altitude.

SPORES OF GREEN PLANTS IN THE LOWER TROPOSPHERE

Using a glass-wool filtration apparatus, Overeem (1936, 1937) sampled from aircraft over the Netherlands on six occasions extending from July to October at heights of 100, 500, 1,000 and 2,000 metres. Filter washings were inoculated to Pringsheim's culture solution for green plants and kept in the light. From a total of about 28 cubic metres of air she obtained the following cultures. Algae: *Chlorococcum* sp., 9; *Phormidium luridum* var. *nigrescens*, *Chlorella vulgaris*, *Pleurococcus vulgaris*, and *Stichococcus bacillaris*, 3 each; *Aphanocapsa* sp., 2; *Actinastrum* sp., *Stichococcus minor*, and *Hormidium flaccidum*, 1 each. Moss: *Funaria hygrometrica*, 2 (from 500 and 1,000 metres). Fern: 1 (unidentified, from 500 metres). Total numbers at the various altitudes were in the ratios 5 : 10 : 3 : 3 at 100, 500, 1,000 and 2,000 metres, respectively. This work is of particular interest as one of the few demonstrations that spores of green plants invade the troposphere in fair numbers and variety.

McGill University Studies

FLIGHTS OVER THE ARCTIC

Extensive exploration of the upper air by aeroplane was initiated by Polunin at McGill University, Montreal, in 1947, and continued until 1951 with the co-operation of the Royal Canadian Air Force and the United States Air Force. Flights during 1947–49 were primarily directed to the study of arctic conditions.

In the summer of 1947 flights were over the Northwest Territories northwards to Cape Bathurst, then north-east from Cambridge Bay to Victoria Island to beyond the region of the north magnetic pole and back, and finally south-west from Cambridge Bay to Yellowknife and to Edmonton, Alberta. Petri dishes with nutrient medium, and also sticky slides, were exposed from his planes by hand, mostly at about 1,500 metres altitude (Polunin *et al.*, 1947, 1948). There were small but measurable concentrations of fungus spores, and the composition of the air-spora appeared to depend on the origin and sometimes on the trajectory of the air mass rather than upon the locality of sampling (Polunin, 1951, 1951*a*, and cf. 1954). The bacteria were identified as: gram-positive rods, about 40 per cent (two thirds of which morphologically resembled *Corynebacterium*), *Micrococcus* (23 per cent), *Achromobacter* or *Flavobacterium* (17 per cent), spore-formers (4 per cent), and *Sarcina* (3 per cent). Fungi identified in culture included *Cladosporium* (over 40 per cent of the total), *Sporormia*, *Pullularia*, *Verticillium*, *Penicillium*, yeasts, *Phyllosticta*, *Leptosphaeria*, *Alternaria*, *Stemphylium*, *Chaetomium*, *Pestallozia*, and *Streptomyces* (Pady *et al.*, 1948; Pady, 1951; Polunin, 1951, 1951*a*).

The sticky slides exposed during flights over the Northwest Territories showed small concentrations of angiosperm and gymnosperm pollen, spores of pteridophytes and bryophytes, *Alternaria*, and *Helminthosporium sativum*, totalling about 1 per cubic metre. Uredospores of the cereal rusts *Puccinia graminis* and *P. glumarum* occurred in small numbers (except in the most northerly flight, though a few were found north of the Arctic Circle); their concentration rose to about 12 per cubic metre over northern Alberta, where there was also a smut concentration of about 6 per cubic metre (Pady *et al.*, 1950; Polunin, 1951*a*).

In further flights over the Arctic the McGill workers attempted more elaborate sampling methods to eliminate possible contamination from within the aircraft, which could have increased the counts in the first two or three exposures of the earlier flights. In September 1948, Polunin flew over the Geographical North Pole in a B–29 aircraft fitted with a breech loading tube to hold a Petri dish projecting 30 cm. forward of the nose. Before exposure the interior of the Petri dish was coated with a silicone grease; and after returning to base, the dish was poured with molten agar and incubated.

Immediately over the North Pole in late summer at 920 metres neither bacteria nor fungi were caught. However, at greater heights over the Pole and at other high latitudes, some Petri dishes caught nothing, while others, exposed at altitudes up to 6,770 metres, grew a few colonies of bacteria or moulds; no Actinomycetes were found (Polunin, 1951; Polunin & Kelly, 1952). Thus microbes appear to be present, though irregularly distributed, even over the Poles.

During a flight over the Geographical North Pole under winter conditions in March 1949, the McGill workers used three kinds of samplers: (1) siliconed slides exposed in the tube forward of the nose of the plane; (2) an electrostatic sampler installed in a box through which a slow stream of air was passed; and (3) a filter tube packed with glass-wool and lens-paper. The electrostatic sampler and filters indicated a viable concentration of 26 bacteria + yeasts and 1·6 fungi per cubic metre in some very high latitudes. The authors concluded that the air over the Pole and its environs is nearly sterile and that it is of very mixed origin. Here again there was evidence that the origin of an air-mass is more important than the locality of sampling (Polunin, 1951, 1951*a*, 1954; Polunin & Kelly, 1952).

The results of further arctic and sub-arctic flights are reported in detail by Pady & Kelly (1953) and Pady & Kapica (1953). On one from Winnipeg via Churchill to Baker Lake in the Northwest Territories at an altitude of about 1,000 metres, using the G.E. Electrostatic sampler, cultures averaged: bacteria 10, and fungi 25, per cubic metre. Bacteria were predominantly cocci and spore-formers (though in a local flight over Churchill gram-positive pleomorphic rods predominated). Fungi were mainly *Cladosporium* and *Alternaria*, but included *Penicillium*, *Papularia*, and *Stemphylium*.

In the summer of 1950, northern air was sampled daily by McGill workers for 21 days with the G.E. Electrostatic sampler and the slit sampler on a roof 17 metres above ground at Churchill near the tree-line on Hudson Bay. This survey formed the standard of reference for two flights to Resolute Bay, Cornwallis Island, some 1,600 km. to the north, on 1–3 August 1950, at an altitude of around 3,000 metres. At Churchill the catch consisted of: gram-positive pleomorphic rods (46 per cent), gram-negative rods (20 per cent), spore-forming rods (18 per cent), and cocci (15 per cent). In the two flights to Resolute Bay in the Arctic during this period, 51 per cent of the bacteria caught were spore-forming rods (Pady & Kelly, 1953). Fungi were assessed both in culture, and visually on silicone-coated slides: the numbers per cubic metre, with the visual counts in parenthesis, were: *Cladosporium*, 17 (132), with its maximum in an air mass of tropical origin; *Alternaria*, 0·7 (2·1); *Stemphylium*, 1·1 (1·8); rusts (9·2); smuts (*Ustilago*) (86); yeasts, 3·5 (304); and *Penicillium*, 2·1. Of the fungus cultures, 57 per cent were non-sporulating. In addition, *Fusarium* was reported as common on slides but rare in culture, and *Septoria* was sometimes abundant on slides. An interesting list of fungi which were caught only infrequently includes: *Pullularia*, Actinomycetes, *Botrytis*, *Aspergillus*, *Verticillium*, several ascomycetes, and a single culture of *Cunninghamella*—one of the rare isolations of a mucoraceous fungus from the upper air. In addition there were numerous moss spores and pollen grains, which together averaged 20 per cubic metre (Pady & Kapica, 1953).

On the flights to Resolute Bay at 3,000 metres, the fungi were essentially the same as at ground-level at Churchill; but they were in much lower concentrations averaging 12 per cubic metre (125 per cubic metre if determined visually) and were principally yeasts, *Cladosporium*, and *Ustilago*. Pollen grains averaged 16 per cubic metre; and in warm air on the southern part of the flight moss spores averaged 47 per cubic metre. It was thought that the southern parts of these flights lay through an old continental tropical air mass, which had moved into the Arctic where most of the spores had died; north of this was cold polar air containing very few spores. The general conclusion reached was that the air-spora over the Arctic comes mainly from the agricultural regions of the south (Pady & Kelly 1953; Pady & Kapica, 1953). However, the larger numbers caught at ground-level at Churchill, and the numerous moss spores, suggest that the tundra also made an important contribution.

MICROBIOLOGY OF AIR MASSES OVER NORTHERN CANADA

The earlier McGill studies suggested that, in the upper air above the level of pronounced concentration gradients, microbial concentration depends mainly on the history of the air mass. This was clearly shown in a series of ten flights over northern Canada (Kelly & Pady, 1953; Pady & Kapica, 1953) between September 1948 and August 1949. The history of air masses encountered during sampling and the positions of fronts were correlated with the results of sampling. The electrostatic sampler, loaded alternately with Petri dishes and siliconed slides, gave the most consistent results. (However, as sampling was non-isokinetic, pollen and large spores may have been underestimated.)

On these flights bacteria varied in concentration less than fungi. At the end of December many samples were blank and the air was almost sterile. Fungi were much more plentiful in June, July, and August, than in the rest of the year, but bacteria were most numerous in spring and autumn. Kelly and Pady suggest, reasonably enough, that the bacteria come mainly from soil which is exposed and cultivated in spring and autumn, giving the opportunity for wind erosion; but their suggestion that the fungi also come from soil seems to be contradicted by the predominance of fungi in summer, and all evidence points to the fungi coming mainly from vegetation and debris above ground-level. All the bacteria isolated and examined in detail were regarded as typical soil forms; they were classified as: aerobic spore-formers (37·9 per cent of the total recorded catch), gram-positive pleomorphic rods (23·8 per cent), *Micrococcus* (18·8 per cent), gram-negative rods (*Flavobacterium*, *Achromobacter*, or *Pseudomonas*, 4·8 per cent), and *Sarcina* (4·6 per cent).

Fungi obtained in culture were: *Cladosporium* (73 per cent), *Alternaria* (7 per cent), *Penicillium* (2·9 per cent), *Streptomyces* (2·9 per cent), *Stemphylium* (1·5 per cent), *Aspergillus* (0·7 per cent), yeasts (0·7 per cent), and other fungi (11 per cent). Many more fungi could be counted visually on silicone-coated slides than could be grown in culture—an effect which was exaggerated by the numerous smut spores that were obtained in one flight over the prairies in October 1948, which yielded: smut spores 52·4 per cent, *Cladosporium* 32·4 per cent, *Alternaria* 3·3 per cent, *Helminthosporium* 0·3 per cent, and rusts 0·1 per cent.

AIR MASSES OVER MONTREAL

In a further survey of microbes associated with different air masses, the McGill workers used the electrostatic sampler and the slit sampler between 10·00 and 13·00 hours on 113 days between September 1950 and December 1951, at the top of a building high in Montreal (Kelly & Pady, 1954; Pady & Kapica, 1956). Ten types of air mass were recognized, classified on the basis of exposure to agricultural land; but as most examples of any one type occurred at one time of the year, the effects of differences in origin of the air mass may be confounded with seasonal effects. Further, at the altitude of 130 metres, sampling at midday is likely to be done in the frictional turbulence layer and to be dominated by local ground sources which are themselves affected by the temperature and humidity of the air mass.

This survey is therefore perhaps best regarded as a valuable contribution to knowledge of the local air-spora near the ground; judging from knowledge about the upper-air, the amount contributed by the air mass is likely to have been small. *Cladosporium* and yeasts were the chief constituents of all the air masses (even of fresh polar air), and on our interpretation the abundance of *Penicillium* is not surprising for samples taken in a large city. *Alternaria* and *Fusarium* were commoner in tropical air. Smut spores occurred in all air masses and at all seasons. Basidiospores of agarics were suspected but not positively identified. Fungi were most numerous in July and August, when 625 cultivable (8,610 visible) spores were recorded per cubic metre, and least numerous from December to February, when 36 (28) were recorded per cubic metre. Bacteria were present in greatest numbers in polar air during spring and autumn, rising from fewer than 70 per cubic metre during March to 710 per cubic metre in June, then decreasing to the end of August and rising to a second maximum during November. In air of maritime origin the trend was irregular.

AIR MASSES OVER THE NORTH ATLANTIC OCEAN

In two flights from Montreal to London, England, at altitudes ranging between 2,700 and 3,000 metres, the McGill workers were able to study the relation between microbial concentration and air mass (Pady & Kelly, 1954; Pady & Kapica, 1955). Over the ocean polar air had generally fewer bacteria and fungi than tropical air (Table XXIII).

Over Quebec Province, in one air mass which was classified by meteorologists as of polar origin, and which gave few bacteria or fungi in culture, very many fungus spores were caught on a silicone-coated slide in the slit sampler. The authors interpreted this as evidence of a load of non-viable organisms which could only have originated in the tropics, and suggested that the air had been carried into the Arctic, thence eastwards, and finally southwards, during which passage most of the suspended micro-organisms lost their viability. However, another explanation seems possible on careful examination of the data. The visible total on the silicone-coated slides, amounting to 18,700 per cubic metre, was made up largely of yeasts (9,900 per cubic metre) and yellow-brown spores (7,500 per cubic metre). As 'about 50 per cent of the latter had an apiculus and were considered to be basidiospores', the other 50 per cent were probably also basidiospores lying in the alternative position (in which the apiculus would be invisible). The flight may well have been through one or more thermals arising from coniferous forests of Labrador and Quebec Province, by which a polar air mass was becoming charged with the air-spora of the ground layer.

TABLE XXIII

ANALYSIS OF PADY & KELLY'S (1954) DATA ON TWO RETURN FLIGHTS OVER THE NORTH ATLANTIC, SHOWING CONCENTRATIONS PER CUBIC METRE OVER LAND, AND MEAN CONCENTRATION OF BACTERIA AND FUNGI IN AIR-MASSES OVER OCEAN

			Bacteria		Fungi		
						S	
Air mass	Month	Position	E	S	E	Culture	Visual
Polar	June	Over Quebec Province	—	—	—	—	240
Polar	Aug.	Over Quebec Province	14·0	7·0	53·0	92·0	—
Tropical	Aug.	Over Quebec Province	28·0	11·0	57·0	160·0	940
Polar	Aug.	Over Quebec Province	6·4	3·9	18·0	32·0	12,700
Polar	Aug.	Over Labrador	3·5	7·0	21·0	70·0	—
Polar	June	Over Ocean	5·9	7·5	3·9	19·0	26·0
	Aug.	Over Ocean	8·2	4·6	2·8	16·0	56·0
Tropical	June	Over Ocean	6·8	6·9	35·0	140·0	208·0
	Aug.	Over Ocean	5·2	15·0	23·0	194·0	67·0
Tropical	June	Over England	1·3	2·0	170·0	317·0	—
Tropical	Aug.	Over England	13·7	53·0	52·0	215·0	580·0

E = electrostatic sampler S = slit sampler — = not investigated

The bacteria obtained on these flights were classified as:

	June per cent	August per cent
Micrococcus & *Sarcina*	41·4	13·2
Gram-negative rods	4·3	20·7
Gram-positive pleomorphic rods	20·4	37·0
Aerobic spore-formers	33·2	29·0

The fungi identified occurred in the following percentages (mean of the two flights): *Cladosporium*, 82·3; *Alternaria*, 2·6; *Pullularia*, 2·3; yeasts, 2·1; *Penicillium*, 1·6; *Botrytis*, 1·5; *Stemphylium*, 1·1; non-sporulating colonies, 3·2 per cent. Of these, *Alternaria*, yeasts, *Botrytis*, and *Penicillium* were noted as more abundant in tropical air, whereas *Stemphylium*, *Pullularia*, *Fusarium*, and *Papularia* were more abundant in polar air. *Sporormia* was found several times, always in polar air. Many other fungi occurred in small numbers.

Among the many interesting results that stand out clearly from these flights is the discovery that viable bacteria and fungi occur at an altitude of 3,000 metres in air masses all the way across the North Atlantic, though the bacteria were so few that some samples of about 2 cubic metres appeared to be entirely devoid of them. There was, however, no gradual diminution with the distance from land. *Cladosporium* is the dominant fungus over the oceans, as it is also over land, but it probably loses viability as the air mass travels.

VERTICAL GRADIENT OVER THE OCEAN

The McGill workers showed conclusively that the upper air contains an appreciable spore-load in all the places which they examined. Even in the high-arctic winter, the evidence proves that samples of a few cubic metres of air may or may not be sterile. *Cladosporium* appears to dominate the upper-air spora, often together with many yeasts and bacteria. Possibly the purest air is to be found near sea-level in mid-ocean. The few observations suggest that samples taken on board ship are collected in a purified layer of the atmosphere, and that higher up over the ocean surface the spore concentration is greater than at sea-level. The troposphere is always more or less contaminated with micro-organisms. From Erdtman's (1937) results a ship in the North Atlantic in spring would be in a region of about one pollen grain per 100 cubic metres, whereas Pady & Kapica (1955), at 3,000 metres over the same ocean, recorded up to 25 pollen grains (with moss spores) per single cubic metre.

On a flight from New Zealand to Australia, at about 1,000 metres above the Tasman Sea, Newman (1948) exposed sticky slides behind a leading wire in the hope of improving the trapping efficiency by breaking the stagnant layer. At a position 1,100 km. off Australia, he estimated pollen grains at 0·73 per cubic metre, and fungus spores at 0·70 per cubic metre; at 340 km. from Australia he found pollen to be 8·75 and fungus spores 16·8 per cubic metre—which is about 100 times as numerous as the concentration of pollen grains and fern spores at ship's mast-level on the North Atlantic crossing recorded by Erdtman (cf. p. 127). Newman's values for fungus spores are somewhat similar to those of the McGill University workers for the upper air over the Atlantic. It seems likely that Erdtman's samples, taken on board ship, were from a zone of surface air which had been largely cleaned by rain-wash, sedimentation, and contact with the ocean, and only partially replenished from the stock in the air mass overhead, where aircraft samples were taken.

Summary

Knowledge of upper-air microbiology is based on occasional samples and is affected by place, season, weather, air mass, and so on. There are no continuous records; but there are some hints that a 'biological zone' occurs at middle height, which can probably be explained in terms of temperature inversions, air masses, and precipitation.

Molisch (1920) introduced the concept of *aeroplankton* to denote the microbial complex referred to in this book as the air-spora. It has been argued that the word 'plankton' suggests organisms based on the air during at least a vigorous phase of growth, whereas the air-spora is only airborne temporarily, even though adapted to wind transport as a means of dissemination. Clearly this argument is valid for pollens and plant spores;

but is there, in addition, a vegetative air-inhabiting plankton? We cannot yet give this apparently improbable hypothesis a decisively negative answer. Evidence in favour of it has been stated by R. C. McLean (1935, 1943), who wrote : ' "Dust to dust" seems to be the only cycle envisaged. Yet the experiments of Trillat and others show at least the possibility that the air may be a vegetative habitat and the large proportion of non-spore-formers present . . . needs more than a conventional explanation.' Proctor & Parker (1942) noted that one third of the bacteria collected from the upper air could grow at 0°C., and survive 48 hours exposure at − 26°C.

If there is a truly indigenous aeroplankton, its habitat must be exacting in the extreme, and tolerable only by specialized bacteria, yeasts, or actinomycetes. Frequent drying must reduce the population to inactivity, though metabolism could be resumed in a cloud of water droplets when gaseous nitrogen and carbon compounds could be absorbed and used. In constant danger of being removed from the air by rain or snow or by contact with the ground, the risk of removal would be increased by any attempt to parasitize organic particles brought up by convection from below. However, radioactive dust can persist for several weeks in the troposphere, and this is a long period on a microbial time-scale. The aerial environment is not obviously beyond the range of exploitation by micro-organisms, for the rate of loss by death or deposition might not be greater than for bacteria in the sea, and there would be freedom from predators. If anywhere, such an aeroplankton might be expected to ride clouds on the ascending side of a tropical convection 'cell' over the Equator.

Although the origin of the upper-air spora from the soil has been assumed by most investigators, the circumstantial evidence suggests a wider range of sources. The bacteria are probably mainly soil forms with a small proportion from sea water. But hyphal fragments, especially conidiophores of *Alternaria* and *Cladosporium*, which are commonly reported from the upper-air (Pady & Kapica, 1953, p. 321), evidently come from the ground vegetation-layer rather than from the soil. The numerous yeasts, coloured basidiospores of toadstools, and smut spores, evidently originate above the soil surface. It is hard to believe that wind could burrow into soil, picking out the few spores of *Cladosporium* and *Alternaria*, yet leaving behind most of the far more numerous *Penicillium*, *Trichoderma*, *Aspergillus* and Mucoraceae spores—not to mention clay particles!

XI

DEPOSITION IN RAIN, SNOW, AND HAIL

Airborne microbes can be deposited direct or they may be washed out of the air in raindrops, hailstones, or snow-flakes. Trillat & Fouassier (1914), from their laboratory experiments with artificial fogs condensing on a suspension of pathogenic bacteria in small vessels, thought that airborne microbes act as condensation nuclei. Condensation nuclei are now thought to be small hygroscopic particles, and it seems more likely that droplets already formed collect spores by impaction (*see* Chapter VII). McCully *et al.* (1956) estimate that, over all land areas of the globe, from 35 to 50 per cent of the total atmospheric dust load is washed out each day. Here we will consider the results of rainwash in nature and the spore content of precipitation water.

Over the last 300 years about a score of people are known to have sought microbes in precipitation water. Collecting the sample has some pitfalls, however; the vessel must obviously be clean, but the danger of contamination by rain-splashed soil has not always been anticipated though, with current knowledge of the magnitude of splash and its part in soil erosion, the danger is now clear (Laws, 1940). Much of the early work summarized below, however, is clearly trustworthy.

Animalcules in rain-water delighted Leeuwenhoek (1676, *in* Dobell, 1932). Rain was collected in a clean porcelain dish set on a wooden tub to avoid earth being splashed by rain. Minute organisms were searched for in vain until after the rain-water had stood for some days, by which time it would also have been contaminated by dry deposition—so we do not know whether or not Leeuwenhoek found microbes of precipitation water.

RAIN

The only systematic study of precipitation micribiology comes from Miquel (1884, p. 597; 1886, p. 530) at the Parc Montsouris, Paris. Miquel caught his rain in a metal funnel fixed at 1.7 metres above ground-level on a pillar, well away from trees and buildings. Rain falling into the funnel was collected in a platinum crucible with a cover, both funnel and crucible having been heated to redness just before sampling. The sample was then sown, drop by drop, in 50 to 100 flasks of beef broth. Miquel also designed apparatus which placed raindrops on a moving band of nutritive paper. After 6 days' incubation, the paper was dried and kept as a record of bacterial and mould colonies. The largest catches of bacteria occurred in the warmer months, when numbers varied from 0·0008 to 8·3 per ml., with a general mean of 4·3 per ml., but these figures excluded the first rain after several dry days when 200 bacteria per ml. might be recorded.

During prolonged rainfall the numbers fluctuated instead of continuing to diminish, suggesting to Miquel that the rain clouds themselves had a characteristic bacterial content, with the percentage composition of: *Micrococcus* (60), *Bacillus* (25), and *Bacterium* (15). Moulds fluctuated in the same manner as bacteria and averaged 4 per ml. Miquel estimated the annual precipitation of bacteria and moulds at Montsouris at over 4 million per square metre—a figure that was obviously too low as he excluded the contribution of the first rain after dry days.

The pharmaceutical use of rain-water induced Lindner (1899), in Germany, to collect 28 samples of rain in a clean porcelain dish on a bleaching ground near his house. Samples were then added to sterile hay-infusions, albumen, milk, or blood serum. His liquid cultures gave a regular succession of bacteria, flagellates, and monads, in the first day or two and, later on, stalked *Vorticella*-like ciliates, *Paramaecium*, *Stylonychia*, and *Volvox*. Once he got two amoeboid forms, but never gregarines or coccidiens. Lack of precautions against splash-contamination appears to leave the interpretation of his data in doubt.

In this century various workers have cultured microbes from rain. Minervini (1900) collected numerous rain samples on board ship in the North Atlantic. Bacteria were abundant, half the samples yielded pink yeasts, and a quarter of them *Penicillium*. He also obtained *Aspergillus glaucus*, *A. niger*, *Monilia candida*, and many other moulds. Busse (1926) recorded pine pollen in rain.

Rain-water collected over the ocean at considerable distances off shore by ZoBell (1946, p. 179) averaged 1 to 10 bacteria per ml., with few or no mould fungi. Rain-water collected on land at the Scripps Institution of Oceanography, California, contained from 10 to 150 microbes per ml. As usual, the highest counts were obtained during the first rain and were associated with a predominance of mould spores.

Protozoa in rain were studied at Heidelberg by Puschkarew (1913), who collected ten samples of rain-water in a sterile funnel, and added nutrient solutions. At the start of rain he found large numbers of fungi and bacteria, and the numerous protozoa included a new species, *Amoeba polyphagus*, with species of *Bodo*, *Monas*, *Calpoda*, and other genera.

Twice in the month of November, rain was collected in sterile flasks on a roof at Leiden by Overeem (1937) and inoculated into flasks of a nutrient medium favourable to growth of green plants in light. In a total of 221 cc. of rain-water she obtained the following cultures. Algae: *Stichococcus minor* (8), *S. bacillaris* (5), *Chlorococcum* sp. (7), *Pleurococcus vulgaris* (4), *Chlorella vulgaris* (2), *Hormidium flaccidum* (2), and *Navicula* *minuscula* (1). Myxomycete: *Physarum nutans* (1). Moss: *Brachythecium rutabulum* (1).

Another worker who made a rewarding study of autotrophic plants in rain-water was Pettersson (1940), working at the Zoological Station at Tvärminne, Finland, in the summer of 1936. Glass funnels (176 sq. cm. in area) were lined with filter-paper, sterilized and taken, covered, to the trapping site. After exposure, the filter-paper was sprayed with a nutrient solution, and the funnel was covered with a glass lid and left to stand in a light place for a few days. Developing organisms were picked off and transferred to new culture vessels to continue their growth.

The originality of the method lies in the medium being unfavourable for the development of bacteria and fungi because the cellulose of the filter-paper was the only carbon source provided. Pettersson, like Overeem, was therefore able to explore a novel part of the air-spora. Snow-traps were also used, consisting of shallow glass dishes 15–20 cm. in diameter, with a thick bed of blotting paper and an upper layer of filter-paper. These two methods gave an unexpectedly rich harvest. A sample of snow taken at Pikis (Piikio) from the start of snowfall on 1 March 1936, gave thirty-six lichen thallus fragments and a moss gemma. On the next day, 2 hours after the start of another snowfall, a sample corresponding to 625 ml. of water yielded nineteen lichens and two *Chlorococcum* colonies. A third sample of 805 ml. of water, taken 4½ hours later, yielded six lichens, and three mosses which were identified after 6 months' growth as *Brachythecium velutinum*, *Hypnum cupressiforme*, and *Pylaisia polyantha* (*see also* Pettersson, 1936).

Pettersson's rain-trap yielded a wealth of information from the fourteen samples investigated, for details of which the original paper must be consulted. The interest was taxonomic and qualitative rather than quantitative. For the early samples the funnel was placed on a low rock, 2·5 metres above sea-level, on open grassy soil. Some of the organisms caught may possibly have come by splash from the ground, but not many can have done so because the largest catch of mosses belonged to a genus hitherto unrecorded in Finland (*see* Chapter XIV). The precaution of raising the funnel on a wooden base 1 metre high was adopted in later tests.

In a total of 1,373 ml. of rain collected, Pettersson obtained 1,200 conifer pollen grains, 300 liverwort spores (all of *Marchantia polymorpha* except for one of *Metzgeria*), Myxomycete spores (*Stemonitis fusca* three times and *Arcyria denudata*), and numerous algae. Blue-green algae were scarce, being represented only by *Nostoc commune* and *Gloeocapsa* sp. in separate samples. Green algae were abundant in almost every sample, those identified including: *Chlamydomonas nivalis*, *Chlorella vulgaris*, *Chlorococcum humicolum*, *Cystococcus pseudostichococcus*, *Prasiola stipitata*, *Roya* sp., and *Tetraedron punctulatum*. Some of these, the author suggests, may have originated from lichen soredia. Lichen spores and soredia were not the main source of lichens in the traps, for the lichens mostly originated as thallus fragments and were evidently of fairly local origin.

The 2,000 moss plants cultured from the spores caught in Pettersson's traps included specimens of: *Aloina brevirostris*, *A. rigida*, *Amblystegium serpens*, *Brachythecium velutinum*, *Bryum* spp., *B. argenteum*, *B. pallens*, *Ceratodon purpureus*, *Funaria hygrometrica*, *Leptobryum pyriforme*, *Mniobryum carneum*, *Pohlia cruda*, *P. nutans*, and *Pylaisia polyantha*.

Observations on micro-organisms in rain were made at Rothamsted Experimental Station in 1951 by Gregory, Hirst, and Last (*see* Hirst, 1959) while they were comparing various spore-trapping techniques. Two conical glass funnels 20 cm. in diameter were exposed on a wooden structure at a height of 2 metres above ground-level. One funnel was open to rain (rain-trap), while the other (dry-trap) was protected by a flat asbestos-cement disk held 25 cm. above the mouth of the funnel—to keep off rain but still allow dry deposition. Washings from both funnels were collected daily and the fungus spores separated by sedimentation onto a glass cover-slip. On dry days the fully exposed rain-trap consistently caught fewer microbes than the dry-trap; but, as might be expected, this was reversed during rain—especially in the first rain after dry weather (Table XXIV).

TABLE XXIV

GEOMETRIC MEANS OF RATIOS OF CATCHES BY RAIN-TRAP TO DRY-TRAP, 2 METRES ABOVE GROUND, ROTHAMSTED, JUNE-SEPTEMBER 1951 (Hirst, 1959).

	Ratio for dry days	Ratio for all rainy days	Ratio of single rainy days to the first of a succession
Smuts (mainly *Ustilago*)	0·6	3·8	6·0
Cladosporium	0·8	1·3	1·8
Alternaria	0·8	3·7	6·9
Pollens $< 20\,\mu$	0·8	1·4	2·3
Pollens $> 20\,\mu$	0·8	1·5	2·4

Rain falling during one thunderstorm was studied in detail (Gregory, 1952; Hirst, 1959), and a detailed account of changes in the air-spora during this period, observed with the aid of the Hirst automatic volumetric spore-trap, has already been published (Hirst, 1953, pp. 382–5). A 7-day spell of warm, dry weather ended in a thunderstorm at 13·25 hours on 22 July 1951. The rain-trap was cleaned immediately before the rain started, and the first 1 mm. of rain which fell in the first half-hour of the storm was collected separately from the succeeding 3·75 mm., which contained many fewer spores (Table XXV).

As Hirst (1959) remarks in discussing this series of observations: 'Spores released during rain are presumably removed from the air as readily as spores already there when rain starts to fall, so that concentrations of airborne spores measured during rain represent, not the total released, but the excess of those released over those removed. Rain-scrubbing seems an ideal method of deposition for air-dispersed soil fungi. For foliage pathogens its biological significance is far from clear. Many spores may be lost in "run-off" unless they can attach themselves to the leaf surface or penetrate into crevices they would be unlikely to reach when deposited from dry air.'

TABLE XXV

SPORES BROUGHT DOWN BY THUNDER RAIN TERMINATING 7–DAY DRY SPELL, ROTHAMSTED, 22 JULY 1951 (Gregory, Hirst & Last, *unpublished*).

	Number of spores per ml. of rain	
	in 1st 0·95 mm. of rain falling 13·25–13·55 hr.	in succeeding 3·75 mm. of rain falling 13·55–08·25 (23 July)
Smuts (mainly *Ustilago*)	455	55
Cladosporium	1770	205
Alternaria	370	20
Erysiphe	280	10
Small pollen grains	270	10
Large pollen grains (over 20 μ diameter)	120	5

In contrast Asai (1960), who introduced the useful method of filtering rain through membrane filters under reduced pressure, failed to obtain uredospores of *Puccinia graminis*, although they were known to be in suspension in the air at the time the rain samples were collected.

Spores in raindrops appear to play a part in some processes of plant infection. Dry wind-blown spores of barley loose-smut (*Ustilago nuda*) rarely infect the ears of susceptible barley varieties but, when drops containing spores in suspension fall on flowers, the spores are brought into direct contact with the ovary, and infection follows (Malik & Batts, 1960).

Snow

Janowsky (1888), Pettersson (1940), and others have found a few organisms in falling snow. Only Gazert (1912) gave a negative report from the Antarctic on the microbial content of fresh-fallen snow in Kaiser Wilhelm II Land. A. L. McLean (1918), on the other hand, reported numerous organisms in snow and ice in Adelie Land; but it is not certain whether they were brought down with the snow or deposited dry in fine weather from the atmospheric dust which settles over the Antarctic. However, on three occasions McLean caught falling snow in a sterile basin: 'elaborate precautions having been taken to prevent contamination, the thawed-out samples showed under a cover-slip cocci, motile bacilli, and, invariably, zoogloea masses of bacteria in moderate numbers. Diplococci, and occasionally cocci, were observed to be invested by a pale capsule. . . . A glucose agar slope culture of falling snow showed a few small greyish colonies.'

Atkinson isolated a motile bacterium believed to have been carried to the Antarctic by upper-air currents and brought down by the snow (Scott, 1913). Most of the arctic and antarctic snow samples were taken from fallen snow, and organisms could therefore possibly have reached the snow by a process of dry deposition (e.g. Salimovskaja-Rodina, 1936; Darling & Siple, 1941) and are considered in Chapter IX.

HAIL

Large numbers of microbes were recorded by Bujwid (1888), who collected hailstones in Warsaw in the month of May, washed them in sterile water, and, plating out the melt-water, found 21,000 bacteria per ml. They included *Bacillus fluorescens liquefaciens*, *B.f. putridus*, and *B. janthinus*. From these numbers Bujwid concluded that surface waters must have been carried aloft and frozen.

During a hailstorm in St. Petersburg, windows were broken by hailstones the size of walnuts. Foutin (1889) washed some of these and, on plating-out the melt-water, obtained 628–729 bacteria per ml., but no fungi or yeasts.

In July storms at Guelph, Ontario, Harrison (1898) collected hailstones, washed them in 1 in 500 mercuric chloride solution and, after rinsing, plated-out the melt-water. One storm gave 955 colonies per stone, of mixed bacteria and moulds, including '*Penicillium glaucum*', *Mucor* sp., *Aspergillus* sp., *Bacillus fluorescens liquefaciens*, *B.f. non-liquefaciens*, and *Proteus vulgaris*. A later storm averaged 1,125 colonies per ml. but these included fewer moulds than the first. Harrison concluded that the bacteria must have come from surface water, but that the moulds were picked up from the air. Belli (1901) obtained 140 organisms per ml. of hail melt-water, of which eight were *Aspergillus* or *Penicillium* and the remainder bacteria. Hail has also been sampled by Dubois (1918).

The organisms in precipitation water remain almost unstudied. The little we know from existing records is tantalizing. Precipitation water is non-sterile, whether on land, over the oceans, or about the poles. A wide variety of organisms has been recovered from such waters—including bacteria, fungi (moulds, yeasts, and plant pathogens), algae, liverworts, mosses, pollens, and protozoa. Microbes are found in rain, hail, and snow, when collected as it falls—before the possibility of ground contamination.

The highest counts are recorded from hail and, at present, these are perhaps the most reliable records—because hailstones can be surface-sterilized. The first rain after a dry spell is heavily contaminated and, even during prolonged wet weather, the spore numbers in rain remain substantial.

A spore liberated near ground-level has a high probability of being deposited dry; but wash-out by rain, hail, or snow, probably most often terminates the journey of spores reaching the tail-end of the dispersal gradient. Microbial sampling of precipitation is still in the naïve stage. Methods have not been tested, and we still do not know how a collecting vessel should be placed to avoid contamination from soil and vegetation.

Conceivably, spores may undergo re-concentration within a cloud. Rising convection bubbles may bring new spores to the top of the cloud, where they can be collected and washed down in raindrops to the base of the cloud. Here the drops might evaporate, allowing the spores to be carried up again—perhaps eventually to be brought down to earth in hailstones. The abundance of microbes in hail, and the reports of a 'biological zone' at several thousand metres, supports the suggestion that convective clouds may be spore-concentrators.

Exploration of organisms in precipitation needs an experimental study of methods of sampling from ground, ships, and aircraft. Systematic sampling could then be attempted with some prospect of learning what part such precipitation plays in terrestrial microbial circulation.

XII

THE AIR-SPORA OF ENCLOSED SPACES

A SMALL but important fraction of the atmosphere is walled-in and provides microbes with an environment different from the outdoor world. Indoor air-hygiene is an aspect of medical science with a voluminous literature which can be approached through such works as: *Aerobiology* (Moulton, 1942), *Studies in Air Hygiene* (Bourdillon *et al.*, 1948), *Airborne Contagion and Air Hygiene* (Wells, 1955), and *Mould Fungi and Bronchial Asthma* (Werff, 1958). The brief treatment given here of 'intra-mural aerobiology' presents an ecological instead of a medical viewpoint.

Outdoor air moves as wind flowing bodily over surfaces, and a point near the ground is immersed in a continually flowing stream of fresh air. Rooms, on the other hand, are *ventilated*, and fresh air is assumed to mix thoroughly with the existing air instead of displacing it bodily. By one 'air-change' ('ventilation turn-over') is meant the introduction of a volume of fresh air equal to the volume of the room; an equal volume of mixed stale and fresh air is displaced during the process, leaving a mixture of stale and fresh air in the room. Unless continually renewed, any microbial concentration in the air of an enclosed space will tend to diminish with time as a result of ventilation and deposition. Concentration of viable organisms will also decrease with time—following the natural death-rate, or because of any disinfection that may have been applied.

DIE-AWAY OF CONCENTRATION

Die-away of concentration is a phenomenon seen most clearly under intra-mural conditions, because out-of-doors a concentration is carried away bodily by wind. So far it has not been feasible to trace concentration changes out-of-doors in one air mass during its travels.

Decrease of concentration with time is caused by: (1) exchange with outside air (i.e. ventilation); (2) deposition on walls, ceiling, and floor, by various processes including sedimentation; and (3) reduction in the viable count through death. Ventilation does not immediately sweep away the whole microbial load, but progressively dilutes it exponentially. Then 'n' air changes will reduce concentration in the ratio: $1/e^n$. Decreases in concentration due to deposition, death, or disinfection, may also follow a logarithmic law, and these can then be expressed in units of equivalent ventilation turn-overs for ease of comparison.

Ways of expressing rates of removal or death of bacteria are discussed by Bourdillon *et al.* (1948), and are based on the constant, 'K', in the equation: $N = N_0 e^{-KT}$, where N_0 is the number present at time $T = 0$ (e = base of Naperian logarithms); K, the 'die-away', is the rate of removal of bacteria by all processes during the period, and may be subdivided. Thus K_D is the death-rate, K_R is rate of removal by ventilation only and is identical with the ventilation rate in air changes per hour, and K_S is the rate of removal by sedimentation. In an example of die-away rates of bacteria from all causes in a bedroom with open windows during fine weather at midsummer K, was equivalent to 6·1 air changes per hour after the occupants settled down to sleep at 23·00 hours; K = 4·9 after they went down to breakfast at 07·55 hours; and K = 6·8 after the making of the beds at 08·50 hours (Lidwell, 1948, p. 253). Another example is shown in Fig. 22. The case of die-away with stirred settlement has been discussed by C. N. Davies (1947).

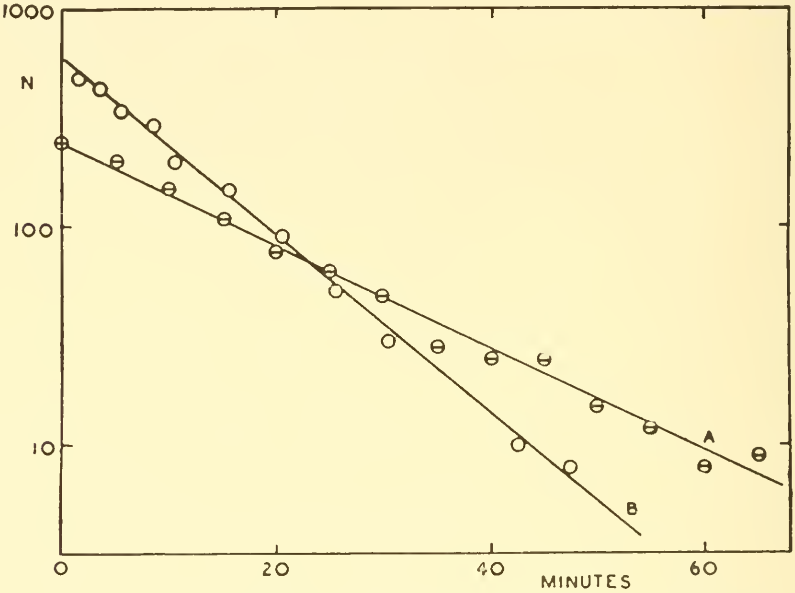

Fig. 22.—Exponential form of the die-away of bacteria-carrying particles from the air of a room. Line A: In an observation military canteen after the occupants had left suddenly. Line B: Observations on the die-away following a group of sneezes in a small room. (*From* Lidwell (1948), reproduced from *M.R.C. Special Report* No. 262, *Studies in Air Hygiene*, by permission of the Controller of H.M. Stationery Office.)

Spore Movement in Convection Currents

Convection currents alone, in an enclosed space without access of outside air, are often sufficiently active to diffuse fungus spores evenly through the whole volume of air. With fruit-bodies of basidiomycetes enclosed in chambers, Falck (1904) found that vertical tiers of horizontal paper shelves became covered with spore deposit in a remarkably uniform manner. By contrast, suspending the pileus of an agaric in a small glass vessel often resulted in 'curious and fantastically' irregular spore deposits on a piece of paper placed underneath. These were interpreted by Buller (1909) as due to the convection currents in the vessel being of a velocity comparable with the terminal velocity of the spores. The heat from a lamp was sufficient to alter a previously established convection system.

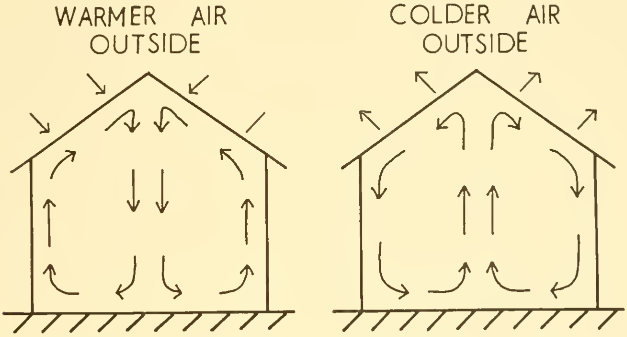

FIG. 23.—Diagram showing changes of circulation in a room according to relative temperature of walls and of inside air.

Even without any ventilation, air *circulates* in a room because of thermal convection. Heating of air by rock surfaces in a mine may result in a flow along an adit and up a shaft. Heating of glasshouses in sunlight also leads to strong convection currents.

Within a building the temperature of the air may be less changeable than that outside, and this may lead to characteristic air-movement patterns. Warmer walls will generate an up draught, colder walls a down draught—each being balanced by opposite currents in the centre of the room (Fig. 23) and often moving fast enough to counteract sedimentation under the influence of gravity. Circulation of air within a house is complex, but there is evidence of a fairly rapid exchange of air and of its suspended spores throughout a house. C. M. Christensen (1950) experimented with spores of *Hormodendrum resinae*, a mould that is peculiar for its ability to grow on a coal-tar creosote medium, and therefore suitable for use as a 'marker' spore in dispersal experiments. Spores were liberated in a room on the lowest floor of a house while all doors to the central hall-way were left open. Within a few minutes, spores were found deposited on Petri dishes in rooms communicating with the hall-way, but situated one, two and three storeys higher.

INTRA-MURAL SOURCES

Microbes in indoor air may come from the outdoor air-spora by ventilation, or they may originate within the enclosure—in which case they are probably limited in variety but may occur in high concentration.

Defective timber attacked by fungi may be an important source of spores in dwelling houses. A. W. Frankland & Hay (1951) showed that some asthmatics are sensitive to the spores of the dry-rot fungus (*Merulius lacrymans*), and spore concentrations ranging from 1,630 to 360,000 spores per cubic metre have been recorded in buildings with active fructifications of this fungus (Gregory *et al.*, 1953). Timber in mines is particularly liable to fungal decay and may also have superficial moulds growing on it. Extensive growth of *Sporotrichum beurmanni* (the pathogen of human sporotrichosis) was found on fresh timber of mines in Transvaal by Brown *et al.* (1947). The fungus was isolated from the air, and ventilating currents of 1 metre per sec. could detach spores from wood provided its moisture content was less than 80 per cent.

Processes by which infectious diseases are transmitted through the air have been matters of vigorous controversy in medicine, and the answers given have influenced social habits and prophylactic measures. Cornet (1889) held that pulmonary tuberculosis is normally acquired by inhaling dust of dried sputum, but Flügge (1897) believed that infection was from germs expelled from the mouth and nose when coughing. G. S. Wilson & Miles (1955) conclude that both processes occur, dust infection being commoner in drier countries whereas droplet infection is the rule in moister climates and in crowded places.

Air exhaled from the lungs in normal breathing is optically clean and almost sterile; but in coughing and sneezing, large numbers of droplets of mucus and saliva are propelled with explosive violence into the atmosphere.

Jennison (1942) obtained photographic evidence of 20,000 droplets being put into the air from a single sneeze. The largest number observed was 40,000, and a weak, stifled sneeze gave only 4,600 droplets. A cough produced a few hundred droplets and the enunciation of consonants was also productive. Sneeze droplets, ranging in diameter from a lower limit of 5–10 μ, and with 20–40 per cent smaller than 50 μ, could evaporate instantaneously to 'droplet nuclei'.

The concept of droplet nuclei, developed by Wells (e.g. 1955), has proved fruitful. 'Droplet nuclei' are the particles formed from the smallest droplets, which evaporate before falling to the ground and so remain suspended in air. They consist of the solid residue of the evaporated droplet, together with any bacteria or virus particles, and may be coated with semi-dried-up mucus which tends to preserve activity and viability. Few droplets are actually propelled more than 2 or 3 ft.; but, when evaporated, the resulting droplet nuclei, with any bacterial cells or virus particles, would remain in suspension almost indefinitely. The droplet nuclei have no trajectory but move with the slightest air currents, and are emitted in large numbers. Thus although most airborne bacteria seem to be carried on rafts of dust particles which settle rapidly, they appear to be relatively innocuous saprophytes; the pathogens are present only in special environments, being carried in much smaller and more insidious droplet nuclei which are small enough to be capable of entering, and being retained by, the alveoli of the lungs.

The Air of Different Environments

DWELLING HOUSES

In spite of ventilation, *Penicillium* dominates the air inside most houses, in contrast to *Cladosporium* outside, and bacteria tend to be more abundant indoors in winter than in summer.

Microbial concentration indoors varies greatly with mechanical and human activity. Carnelley *et al.* (1887), using Hesse's tubes in schools and mills in Dundee, Scotland, observed that, in densely-populated rooms, stirring up dust increased the total air-load and increased the ratio of bacteria to moulds. When air in rooms is left undisturbed the bacteria (or particles to which they are attached) settle out rapidly, but the moulds do so much more slowly.

Maunsell (1954, 1954*a*) used the slit sampler in bedrooms and found that shaking beds, brushing carpets, and any building repairs, increased the mould-spore content of the air up to 17 times, but that it rapidly returned to normal when activity ceased.

Other studies of the air of dwelling houses are discussed by Miquel (1879, 1883), Rostrup (1909), Winslow & Browne (1914), Flensborg & Samsoe-Jensen (1948), Nilsby (1949), Wallace *et al.* (1950), and Swaebly & Christensen (1952), among others.

Tests with the portable volumetric spore-trap (Gregory, *unpublished*) show that the airborne dust in inhabited rooms is commonly dominated by what appear to be fragments of human skin in the form of minute, flattened scales from the stratum corneum of the epidermis. Concentrations of several thousand of these potential bacterial 'rafts' per cubic metre are common indoors, and 390,000 per cubic metre have been noted after bed-making. These epidermal scales probably carry a large proportion of the airborne bacteria of indoor air.

HOSPITALS

In studies of hospital air over a period of 15 months, Miquel (1883) found a mean value of 11,100 bacteria per cubic metre in the crowded wards of the Hôpital La Pitie, Paris, the counts varying from 5,100 in June to 23,100 in December. The general improvement in hospital hygiene since that time is illustrated for example by Colebrook & Cawston

(1948) for a Birmingham hospital, where they found from 210 bacteria and moulds per cubic metre under quiet conditions, to 2,800 per cubic metre with bed-making in progress (one very high count of 22,000 per cubic metre, including many moulds, was obtained with the ward windows closed).

Recommendations for the maximum tolerable number of particles carrying bacteria in operating theatres are 700 per cubic metre for minor operations, and down to 70 or even 15 per cubic metre for dressing burns and for operations on the central nervous system (Bourdillon *et al.*, 1948*b*; *and see* Bourdillon & Colebrook, 1946).

FACTORIES AND WORKSHOPS, SCHOOLS, PUBLIC BUILDINGS

Anthrax is one of the few bacterial diseases which is clearly spread by airborne dust to workers who handle wool and hair contaminated by infected animals. Inhalation of airborne spores of *Bacillus anthracis* sometimes produces fatal infection of the lung.

Bacterial counts in a variety of English factories and offices were reported on by Bourdillon *et al.* (1948*a*).

SUBWAYS, MINES, AND CAVES

London's underground railways have been investigated by Andrewes (1902) and by Forbes (1924), and the New York Subway by Soper (1908).

Studies in caves are few, but include those by Lurie & Way (1957) and by Mason-Williams & Benson-Evans (1958).

SEWERS

Miquel (1880), in Paris, gave special attention to the sewer in the Rue de Rivoli near its junction with the large collector of the Boulevard Sebastopol. He found a steady load of from 800 to 900 bacteria per cubic metre. Pollens were absent, and cryptogamic spores were only $\frac{1}{3}$ to $\frac{1}{4}$ as numerous as in outdoor air at the same time. The contamination of the air in the near-by Rue de Rivoli was lower in winter but higher in summer than it was in the sewer.

Comparable results were reported from London in sewers under the Palace of Westminster (Carnelley & Haldane, 1887).

AIR-SPORA OF FARM BUILDINGS

High microbial concentrations often occur in farm buildings, such as cowsheds, where hay is being fed to animals, or in barns where thrashing or cleaning is in progress. Inhalation may produce symptoms of the still-little-understood farmer's lung and thrasher's lung, as well as various diseases of farm animals. Milk also needs protection from contamination by barn air (*see* Ruehle, 1915; Ruehle & Kulp, 1915).

AIR-SPORA OF GLASSHOUSES

The air of glasshouses has received little attention, in spite of the fact that workers and crop plants in it may be exposed to high concentrations of micro-organisms. Glasshouses may act as important spore emitters by means of convection through open ventilators (Hirst, 1959).

SHIPS

Air in holds and living quarters on board ship was studied early by Miquel (1886). A modern study of air in ships—including submarines, which are relatively clean—is reported on by Ellis & Raymond (1948).

XIII

DEPOSITION GRADIENTS AND ISOLATION

Chapter V described efforts to formulate changes in concentration of the spore-cloud while it diffuses and travels downwind. We must now discuss the more complex phenomenon of deposition gradients—the decrease in number of spores deposited with increasing distance from the source.

The infection of a plant by an airborne spore is itself a complex process of which physical transport is an important part. Infection may fail at any one of a chain of stages; and, for a deeper understanding of the whole process, it is necessary to understand the parts. Spore diffusion and deposition are stages selected for special attention in this chapter.

It is impossible to predict, from knowledge of the characteristics of spore deposition gradients, how many infections will be acquired by a plant at a given distance from a source of known strength, because conditions may be unsuitable for infection; but there is a possibility of being able to predict an upper limit, and to use this knowledge in choosing safe isolation distances. This chapter deals with gradients measured up to distances ranging from a few metres to a few kilometres from the source; long-distance dispersal is discussed in Chapter XIV. The discussion assumes the simplified conditions described on page 47; but, even so, deposition and infection gradients have complications.

Factors Complicating Infection Gradients

(i) *Deposition coefficient.* With sources at or near ground-level, the diffusing cloud of spores, unlike a gas or smoke, is robbed by heavy deposition close to the source. Concentration and area-dose at a point downwind therefore depend on two factors—the diffusion history and the deposition history which the relevant part of the cloud has experienced.

In view of the evidence given in Chapter VII, velocity of deposition can provisionally be taken as proportional to terminal velocity, and the importance of deposition will increase with spore size.

(ii) *Viability.* It is assumed, in the absence of experimental evidence to the contrary, that viability is not affecting gradients over the short distances discussed here, though the future may show this assumption to be an over-simplification (p. 190).

(iii) *Available sites.* Deposition gradients do not necessarily give rise to observable infection gradients. For instance, a fruit-body of *Ganoderma* *applanatum* will emit spores continuously and copiously for months, and the spores will be diffused and deposited; yet the occurrence of *Ganoderma* fruit-bodies remains erratic throughout a forest, their occurrence being limited by what may be expressed in the ignorance-blanketing phrase—'availability of sites'. An infection gradient can only develop when sites such as trap surfaces, nutrient medium, susceptible host-plants, ripe stigmas, or burnt soil, are freely available. The deposition gradient is a regular phenomenon: an infection gradient follows when the deposition gradient is superimposed on unoccupied sites. Ecologically, an infection gradient is a stage in succession, not a characteristic of a balanced state.

(iv) *Multiple infections.* As long as the number of available sites is large, the slope of the infection gradient will be parallel to that of the deposition gradient. But as soon as available sites begin to be used up, the infection gradient will be flattened, the flattening beginning nearest the source, and the relation between the two gradients under simple conditions is given by the multiple-infection transformation (Gregory, 1948).

When disease incidence is recorded as the number or percentage of plants attacked, irrespective of whether the plant has one or many lesions, aphid punctures, etc., the percentage will have to be suitably transformed before the formula for deposition can be applied.

The need for the transformation may be illustrated by considering a hypothetical example of 100 potato plants, uniformly susceptible and exposed to infection by *Phytophthora infestans* from a distant source. The first spore that causes an infection must obviously infect 1 per cent of the plants. A second infecting spore, so long as it falls *at random* among the 100 plants, will have one chance in 100 of alighting on the one plant already infected, instead of infecting a second plant. As the percentage of infected plants increases, the probability that each additional infection falls on a plant already infected (thus producing no increase in the percentage of plants infected) increases greatly. When 99 per cent of the plants are infected, another infection will have only one chance in 100 of falling on the single remaining healthy plant. Different parts of the percentage range, therefore, correspond to very different spore densities per unit area, and the transformation can be neglected only in the lower-percentage categories.

Thompson (1924) applied the Poisson distribution to the problem of multiple infection and showed that if N = number of hosts available, and y = average number of hosts infected after the deposition at random among the hosts of x parasites, then

$$y = N\,(1 - e^{-x/N}),$$

Table XXVI gives x calculated for values of y varying from 1 to 99·9 per cent; it shows that whereas only one infection is required to bring about an increase from 1 to 2 per cent, the increase from 98 to 99 per cent requires sixty-nine infections (that is, 460 minus 391 according to the table).

TABLE XXVI

MULTIPLE-INFECTION TRANSFORMATION: PERCENTAGES TO INFECTIONS (CALCULATED FROM 5-FIGURE LOG TABLES)

y %	x	y%	x	y%	x	y %	x	y %	x	y %	x
1	1·00	23	26·14	44	57·98	65	105·0	83	177·2	93·5	273·3
2	2·02	24	27·44	45	59·78	66	107·9	83·5	180·2	94	281·3
3	3·05	25	28·77	46	61·62	67	110·9	84	183·3	94·5	290·0
4	4·08	26	30·11	47	63·49	68	113·9	84·5	186·4	95	299·6
5	5·13	27	31·47	48	65·39	69	117·1	85	189·7	95·5	310·1
6	6·19	28	32·85	49	67·33	70	120·4	85·5	193·1	96	321·9
7	7·26	29	34·25	50	69·31	71	123·8	86	196·6	96·5	335·2
8	8·34	30	35·67	51	71·33	72	127·3	86·5	200·2	97	350·7
9	9·43	31	37·11	52	73·40	73	130·9	87	204·0	97·5	368·9
10	10·54	32	38·57	53	75·50	74	134·7	87·5	207·9	98	391·2
11	11·65	33	40·05	54	77·65	75	138·6	88	212·0	98·5	420·0
12	12·78	34	41·55	55	79·85	76	142·7	88·5	216·3	99	460·5
13	13·93	35	43·08	56	82·10	77	147·0	89	220·7	99·1	471·0
14	15·08	36	44·63	57	84·40	78	151·4	89·5	225·4	99·2	482·8
15	16·25	37	46·20	58	86·75	79	156·1	90	230·3	99·3	496·2
16	17·44	38	47·80	59	89·16	80	160·9	90·5	235·4	99·4	511·6
17	18·63	39	49·43	60	91·63	80·5	163·5	91	240·8	99·5	529·8
18	19·85	40	51·08	61	94·16	81	166·1	91·5	246·5	99·6	552·1
19	21·07	41	52·76	62	96·76	81·5	168·7	92	252·6	99·7	580·9
20	22·31	42	54·47	63	99·43	82	171·5	92·5	259·0	99·8	621·5
21	23·57	43	56·21	64	102·2	82·5	174·3	93	265·9	99·9	690·8
22	24·85										

With acknowledgements to Drs. S. B. Fracker and H. A. Brischle of the United States Department of Agriculture.

If the distribution of infections is at random among the hosts, a straight line will be obtained when the logarithm of the percentage that remain uninfected (100 minus the percentage infected) is plotted against the number of infections. The slope of the line is given by 'b' = − 0·00434. Blackman (1942), in ecological studies of flowering-plant communities, found that the occurrence of plants on quadrats may depart from the expected random distribution and yet still give a reasonably straight line when plotted as before. The slope of the observed line, however, differs from that of the expected line. Blackman's 'correction factor', the ratio of the slope of the expected line to the slope of the observed line ($K = b_{\text{expected}}/b_{\text{observed}}$), then gives a useful measure of the departure from the random arrangement.

Various other mathematically plausible formulations of this deviation have been attempted and are reviewed by Fracker & Brischle (1944). Non-random distribution may result from various factors such as repulsion between individuals ('under-dispersion' as understood by ecologists), and K will then be less than unity. Aggregation ('over-dispersion'), on the other hand, leads to K being greater than unity. Aggregation may be due to such causes as local spread of infection, progeny remaining near parent, or to local differences in susceptibility. Plank (1946) has given a useful test for detecting aggregation in the field.

(v) *Infection efficiency.* Gradients may be observed either by directly counting the numbers of spores deposited on equal areas at different distances, or by counting some consequent effect such as colonies, leaf-spots, or diseased plants. Usually these gradients will be the same when numbers are plotted against distance, but the infection gradient will be much lower than the deposition gradient. Even with a nearly 100-per-cent viable spore suspension, the general experience in inoculation tests with plant pathogens is that only a small proportion of the spores deposited will give rise to a lesion—even when conditions for infection are as favourable as possible; in unfavourable conditions the formation of lesions falls to zero. The proportion of spores successfully infecting is termed 'infection efficiency' by Gäumann (1950, p. 157), and values recorded by various workers under highly favourable experimental conditions include: *Phytophthora infestans* 6·5 per cent, *Alternaria solani* 1·7 per cent, and *Septoria lycopersici* 0·2 per cent (all on tomato leaves, cf. McCallan & Wellman, 1943); *Botrytis* sp. on *Vicia faba* 5 per cent (F. T. Last, unpublished); *Peronospora tabacina* approximately 1 per cent (Waggoner & Taylor, 1958).

Rust fungi show relatively higher efficiencies. Thus Petersen (1959) observed penetration by 30 per cent of uredospores of *Puccinia graminis tritici* on wheat leaves; but, at the high concentrations tested, over 100 uredospores were required to produce one sporulating uredosorus (*see* Durrell & Parker, 1920). With the same fungus, Rowell & Olien (1957) obtained as many as eleven uredosori per 100 spores applied. McCallan (1944) evidently obtained about 10 per cent efficiency from uredospores of *Puccinia antirrhini*. R. H. Cammack (personal communication) obtained 15 to 23 per cent efficiency when inoculating *Puccinia polysora* to susceptible maize.

Considering its importance in plant pathology, it is remarkable how little attention has been given to infection efficiency. Its value must vary with dispersal conditions, but commonly the height of the infection-gradient curve above the x-axis will be only about one-hundredth that of the deposition curve, though the slopes of the two curves would be similar.

(vi) *Secondary spread.* From turbulence theory we can predict only primary dispersal gradients. As Waggoner (1952) points out: 'Because proximity of a source is relatively more important than strength of the source, spatial distribution of diseased plants becomes more uniform as secondary infection progresses.' The infection gradient will therefore be flattened if observed long enough after deposition for secondary spread to occur around the primary lesions. Examples of this effect are found in Pape & Rademacher (1934), Zogg (1949, Figs. 10 and 11), Waggoner (1952, Fig. 2), and Cammack (1958).

(vii) *Sampling.* At low levels of infection, the size of samples must be increased, as otherwise the sampling error becomes large (*see* Finney, 1947).

EMPIRICAL METHODS

As noted in Chapter V, gradients can be represented by either an empirical or a theoretical model. In the empirical method we make the curve to fit the data, but in the theoretical method we test the fit of the data to the curve.

Frampton *et al.* (1942) concluded that incidence of some insect-transmitted virus diseases decreased logarithmically with distance. Zentmeyer *et al.* (1944) studied the spread of the Dutch elm-disease pathogen, *Ceratostomella ulmi*, which is transmitted from tree to tree by the elm-bark beetle, *Scolytus multistriatus*. Their data, to distances of about 84 metres, indicated that the probability of infection decreased with the logarithm of the distance. Most subsequent curve-fitters agree that such decrease is logarithmic.

Wolfenbarger (1946, 1959; *see also* Wadley & Wolfenbarger, 1944), in valuable surveys of literature on the dispersal of bacteria, spores, seeds, pollen, and insects, concluded that the observed data could be fitted by one of the two following equations:

$$E = a + b\,(\log x), \text{ or}$$
$$E = a + b\,(\log x) + c\,(1/x),$$

where $E =$ the expected value, $x =$ distance from source, and a, b, and c are parameters derived from the observed data. Values of the parameters a, b, and c, obtained by Wolfenbarger, showed enormous variation between the numerous sets of published results, and it is not possible to make any kind of generalization using this method, or to use the parameters, as given, to predict gradients.

E. E. Wilson & Baker (1946, 1946*a*) made field observations in California on the dispersion pattern of apricot brown-rot (*Sclerotinia laxa* on *Prunus armeniaca*), and they also liberated *Lycopodium* spores experimentally. They fitted the following equations to their data:

(1) $y = 100/x^2$ for the gradient of aerial spore concentration (concentration at distance x_2 and at subsequent distances being expressed as a percentage of the concentration at x_1).

(2) $y = 100\,(1 + a)^2 / (x + a)^2$, for the gradient of infection by airborne spores, where a is a parameter for the experiment.

Dispersal by insect vectors is usually fitted by a logarithmic expression. Bateman (1947*b*) found that the proportion (F) of contamination of seed crops by insect cross-pollination at distance (D) was fitted by the expressions:

$$F = ye^{-kD^{\frac{1}{2}}}, \text{ or}$$

$$F = \frac{ye^{-kD}}{D},$$

where y = contamination at zero distance, and k expresses the rate of decrease of contamination with distance.

Gregory & Read (1949) concluded that data for insect-borne viruses could be fitted well by the empirical expression:

$$\log I = a + bx,$$

where I = number of infective punctures at a distance x from the source after a given time, and a and b are constants for any one given set of field conditions.

With the empirical method an equation can usually be obtained, containing at most three parameters, which gives a good fit to any particular set of data. However, it is not easy to compare the results obtained by different workers. The empirical method is difficult to use because point, strip, and area sources are not distinguished, the multiple-infection transformation has not been applied even when appropriate, and the parameters as calculated from the data correspond to no obvious natural phenomena; they may even conceal different units of measurement varying from centimetres to nautical miles! Progress with the empirical method requires attention to these matters and, especially, the adoption of a standard metric unit of distance.

Diffusion and Deposition Theories

The more difficult, but potentially more useful, theoretical approach is derived from the diffusion phenomena described in Chapter V.

W. SCHMIDT'S THEORY

Schmidt (1918, 1919) used his diffusion theory to calculate Q_x/Q_0, the fraction of the eddy-diffusing spore-cloud which remained in the air at distance x. To do this he assumed that any part of the cloud whose diffusion path would have brought it down to ground-level, would have been removed from the cloud by deposition. He represented the terminal velocity of the particle as equivalent in effect to tilting the ground, and he gives a table from which the 'dispersal limit' under average conditions of wind-speed and turbulence could be read for particles with different terminal velocities. Dispersal limit (V) was defined as the distance exceeded by only 1 per cent of the particles liberated.

Schmidt's theory was developed further by Rombakis (1947), who brought the fall velocity of the particles into the differential equation and replaced the arbitrary 99 per cent of Schmidt's dispersal limit by the concept of 'probable line of flight'. Rombakis postulated that a point P at height z and time t will be a point on the probable line of flight when it is statistically equally probable for a particle to occur above or below P. At the 'probable flight range' (a distance about one-tenth of Schmidt's 'V'), 50 per cent of the particles liberated will have been deposited; 'probable flight height', and 'flight duration', are similarly defined. Rombakis also reached the interesting conclusion that the 'probable final velocity' of a particle is half its terminal velocity in still air. These concepts were applied to the dispersal of fungus spores by Schrödter (1954), who used Falck's (1927) calculations of terminal velocities to predict probable flight ranges, altitudes, and durations for various spore-sizes, wind-speeds, and values of the turbulence coefficient. Examples from Schrödter's extensive calculations are given in Table XXVII. In his later, valuable review of the topic Schrödter (1960) uses Rombakis's method for estimating distance of dispersal, and Sutton's equations for the concentration of the spore-cloud.

TABLE XXVII

'PROBABLE FLIGHT RANGE' (Schrödter, 1954) BASED ON ROMBAKIS'S MODIFICATION OF SCHMIDT'S THEORY

	Interchange coefficient, *A* (gm./cm. sec.)	Probable maximum flight altitude (metres)	Probable flight duration	Probable flight range (km.) in winds of velocity (metres/sec.)		
				2	6	10
small spores						
(5 × 3 μ)	0·1	5·41	17 hr.	124 km.	371 km.	618 km
T.V.* 0·035	10·0	541	72 days	12,400	37,100	61,800
cm./sec.	50·0	2,705	1 year	62,000	185,500	309,000
large spores						
(22 × 16 μ)	0·1	0·19	1 min.	0·2 km.	0·5 km.	0·8 km
T.V.* 0·975	10·0	19	2·2 hr.	16	48	80
cm./sec.	50·0	95	11 hr.	80	240	400

* T.V. = terminal velocity.

DEVELOPMENT OF SUTTON'S THEORY

Sutton's equations predict concentration when there is no loss by deposition. To adapt them for particles which deposit appreciably during travel, it is necessary to calculate Q_x, the number of spores remaining in suspension after the cloud has travelled a distance x, from the equation:

$$Q_x = Q_o \exp.\left[\frac{-2px^{(1-\frac{1}{2}m)}}{\sqrt{(\pi)}\,C\,(1-\frac{1}{2}m)}\right], \text{ (p. 77).}$$

Expected depositions at various distances from point, line, strip and area sources can then be calculated (Gregory, 1945, and *unpublished*).

(i) *Point source.* D, the *total* number of spores deposited on an annulus 1 cm. wide at a distance x from a point source, is given by:

$$D = \frac{p2Q_x}{\sqrt{(\pi)}\,Cx^{\frac{1}{2}m}}.$$

(ii) And d, the *mean* number of spores deposited per square centimetre on an annulus 1 cm. wide at a distance x from a point source, is given by:

$$d = \frac{p2Q_x}{2\pi^{\frac{3}{2}}Cx^{\frac{1}{2}(m+2}}.$$

(iii) And d_w, the number of spores deposited per square centimetre at a distance x downwind from a point source, is given by:

$$d_w = \frac{p2Q_x}{\pi C^2 x^m}.$$

(iv) *Line source.* d_{lw}, the number of spores deposited per square centimetre at a distance x downwind from a line source, is given by:

$$d_{lw} = \frac{p2Q_x}{\sqrt{(\pi)}Cx^{\frac{1}{2}m}}.$$

d_{lw} is thus numerically equal to D.

(v) *Strip source.* d_{aw}, the number of spores deposited per square centimetre at a distance x downwind from a strip source of width w, is given by integration as:

$$d_{aw} = \frac{p4Q_x}{\sqrt{(\pi)}C(2-m)}x^{1-m/2}\left[\left(1+\frac{w}{x}\right)^{-m/2} - 1\right].$$

Gregory (1945, p. 69) gave a set of calculated values for D, d, d_w and d_{lw}, assuming $Q_0 = 10^{10}$, $p = 0{\cdot}05$, $C = 0{\cdot}6$ (cm.)$^{\frac{1}{8}}$, $m = 1{\cdot}75$ and $1{\cdot}24$. With further knowledge of these parameters, revised calculations are now given (pp. 171–6).

Meanwhile, in a series of papers on pollen contamination of seed crops, Bateman (1947, 1947*a*, 1947*b*) gave many examples of dispersal gradients, adopting and simplifying the Gregory formulae and using a regression method for testing the adequacy of the diffusion theories of W. Schmidt and of Bosanquet & Pearson (1936). Bateman's method also makes it possible to estimate p/C and Q_0, provided all measurements are expressed in the same units. Regression tests showed that pollen dispersal was best fitted by the 1945 formulae of Gregory, but the data were inadequate for choosing between the values 1·76 and 1·24 for the parameter *m* of Sutton's equations.

Combining field inoculation studies with eddy-diffusion models, Waggoner (1952) made an important contribution by adapting the formulae: (1) to allow for non-isotropic turbulence; and (2) to incorporate the ratio of spores deposited to percentage leaves (or leaflets) diseased. Waggoner used the findings of E. E. Wilson & Baker (1946) and of Scrase (1930), to put the variance of concentration of vertical distribution (σ_x^2) as equal to 4/9 of the variances in the x and y planes. This led to the formula (in our symbols):

$$\chi = \frac{3\,Q_x}{2\pi^{\frac{1}{2}}\,x^{3m/2}}\,\text{exp.}[-x^{-m}\,(r^2 + 9z^2/4)],$$

where $r^2 = x^2 + y^2$.

From observed gradients of late-blight (*Phytophthora infestans*) around artificially inoculated potato plants in the field, Waggoner took k as the ratio of spores deposited per square centimetre to the proportion of leaflets diseased, and estimated the parameters p (deposition rate) and Q_0/k from the equation

$$D = \frac{0{\cdot}135p(Q_0/k)}{x^{15/8}}\,\text{exp.}\,(-\,6{\cdot}78px^{\frac{1}{8}}),$$

where D = proportion of leaflets diseased. (In Waggoner's tests, D was comparatively small and did not need the multiple-infection transformation.)

In his experimental potato plots in Iowa in 1949 and 1950, respectively, Waggoner found $p = 0{\cdot}12$ and $0{\cdot}15$, and $Q_0/k = 18 \times 10^4$ and $7{\cdot}8 \times 10^4$. Subsequently for *Peronospora tabacina* Q_0 was estimated at approximately 10^3 spores per sq. cm. of lesion per day (Waggoner & Taylor, 1958).

For assessing concentrations of radioactive clouds, Chamberlain (1956, pp. 20–27) at Harwell developed expressions combining the eddy-diffusion equations (of Sutton, 1947) and the allowance for loss by deposition (of Gregory, 1945). Chamberlain also modified the equations to allow for elevation of the source above ground-level, illustrating the fact that elevating the source greatly reduces the loss by deposition.

Re-calculation of the Deposition Gradient

With new information and further development of the statistical theory, deposition gradients can now be calculated for a wider range of conditions than was possible earlier. The values worked out here are offered as giving a useful indication of trends, but much further work still remains to be done.

Chamberlain's modifications have been adopted, in preference to Waggoner's, because the latter uses the parameter k, which can vary over a wide range down to zero—depending as it does on leaflet size in a particular crop, and on how favourable conditions were for infection.

Two sets of graphs are provided. Fig. 24 gives Q_x for $m = 1{\cdot}75$, $C = 0{\cdot}6$ (metres)$^{\frac{1}{8}}$, and a variety of heights and distances from the source.*

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* The parameter 'C' is now given in units of (metres)$^{\frac{1}{8}}$, in place of (cm.)$^{\frac{1}{8}}$ used in Gregory, 1945.

Another set, Figs. 25–27, gives values of D, d, d_w, d_{lw}, and d_{aw} on a logarithmic scale for sources of various geometrical form, assuming no loss from the cloud by deposition. To predict a gradient, the deposition values are first read-off for various distances from the appropriate line on Figs. 25 to 27, and allowance can then be made for loss from the cloud at each distance by reading-off Q_x as a fraction of Q_o in Fig. 24.

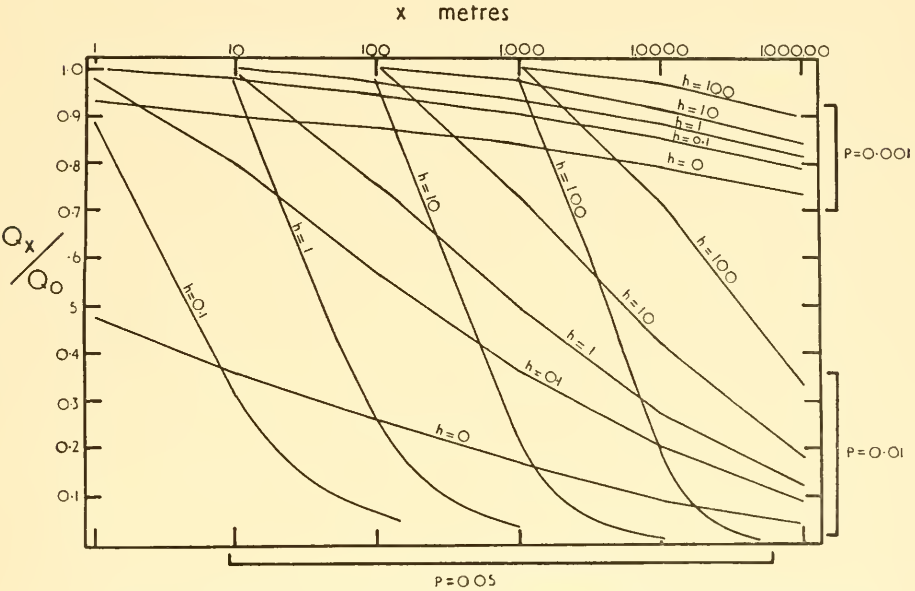

FIG. 24.—Fraction of spore-cloud remaining airborne (allowing for loss of spores from spore-cloud by deposition to ground), expressed as Q_x/Q_o. Calculated from Chamberlain (1956): for $m = 1{\cdot}75$; $C_z = 0{\cdot}21$ (metres)$^{1/8}$; height of source above ground, h = 0·0, 0·1, 1, 10, and 100 metres; distances from source, x = 1 metre to 100 km.

CALCULATION OF Q_x

Except in experimental spore-liberation tests, the quantity liberated, Q_o, is usually unknown. However, cloud concentration and deposition are proportional to Q_0 so, although the *height* of the gradient line will depend on the source-strength, its *slope* will be unaffected by the value of Q_0.

Elevation of source has been allowed for by using the equation number 52 of Chamberlain (1956), to calculate values of Q_x for heights h = 0, 0·1, 1, 10 and 100 metres.

Fig. 24 shows that elevating the source decreases deposition on ground near the source, and in using Figs. 25–27 for elevated sources it is important to neglect those parts of the curves before deposition starts. This decreased deposition near an elevated source was confirmed experimentally by Colwell (1951), who liberated P-32 radioactive *Pinus* pollen at 3·5 metres above ground-level into a wind averaging 8·1 metres per sec. Colwell sampled simultaneously with vacuum cleaners and Petri dishes on the ground, and estimated the number of pollen grains with the help of a Geiger-Müller counter. Maximum deposition in this experiment was obtained at 5·8 metres horizontal distance from the source.

For Sutton's parameters, the values adopted here are:

$$C_x = C_y = 0{\cdot}21 \text{ (metres)}^{\frac{1}{8}},\ C_z = 0{\cdot}12 \text{ (metres)}^{\frac{1}{8}}, \text{ and } m = 1{\cdot}75.$$

As a measure of deposition, p has been chosen in preference to Chamberlain's v_g/u, because the wind-speed under which deposition occurred is usually not known in the open air. However, the curves, which are calculated for p = 0·05, 0·01, and 0·001 in Figs. 25, 26, and 27, respectively, can be used with Chamberlain's velocity of deposition if the wind-speed is known, because provisionally it is taken that $p = v_g/u$.

More field experiments are needed before we can decide whether deposition over rough ground depends on time or on distance—a contrast analagous to the rival diffusion theories of W. Schmidt and Sutton. From Chapter VII it seems that p depends on the terminal velocity of the particle, and numerically it has a value of about one-fiftieth to one-hundredth of the terminal velocity expressed in centimetres per second. No allowance has been made in these calculations for the hitherto unexplained larger values of p which have been observed within a few metres of a source near ground-level.

Some plant pathogens have large, readily-impacting spores. When liberated at, or near, ground-level, although a small proportion may travel vast distances, most of these spores probably do not move very far from the source. Fig. 24 suggests that for 'impactor' spores with a deposition coefficient of p = 0·05, and liberated at 10 cm. above ground-level, 94 per cent would be deposited within 100 metres of the source.* But 'penetrators', with p = 0·001, would be deposited only to the extent of 6 per cent within 100 metres under similar conditions.

In spite of neglecting terminal velocity during the diffusion process—a feature criticized by Schrödter (1960)—this method predicts a much more rapid loss of material from the cloud than does Rombakis's method: perhaps because the ground-level concentration of the cloud is restored by downward diffusion much more efficiently than by sedimentation. On our theory, 50 per cent of large spores liberated at 10 cm. above ground would be deposited within 10 metres, but, according to Schrödter's calculations, this fraction would travel at least 200 metres (Table XXVII). Such rapid decrease in the value of Q_x near a ground source emitting large spores is supported by experimental evidence which has already been summarized in Table XIV (Chapter VII). Yet some

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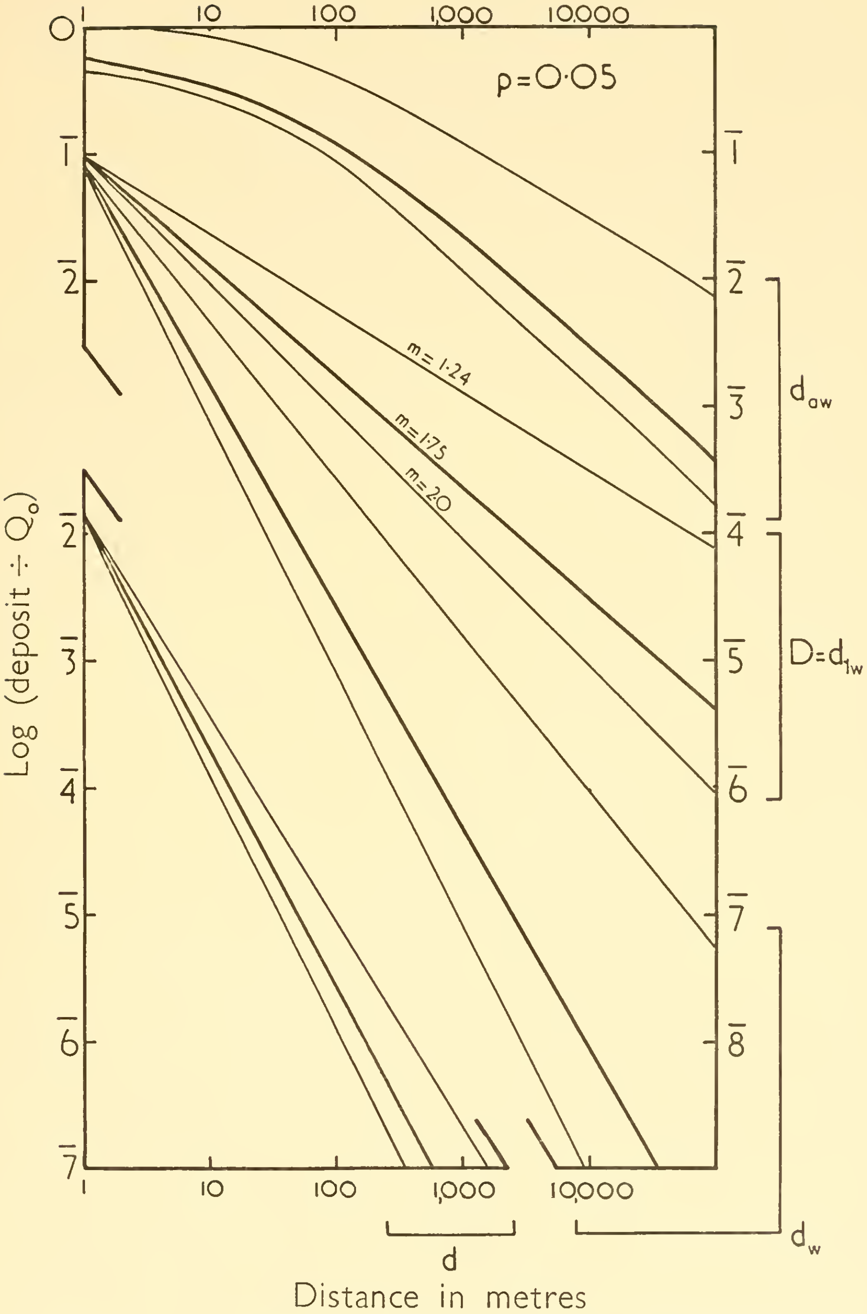
* My mistake (Gregory, 1952; *see correction*, 1958) in stating that 99·9 per cent of those liberated at ground-level would be deposited within 100 metres, was due to misreading $Q_0 = 10^{12}$ as 10^{10} in my own table (Gregory, 1945, Table 21)—not to the misunderstanding suggested by Schrödter (1960, p. 178).



FIGS. 25 to 27.—Dilution of spore-cloud by eddy diffusion. Calculated for $m = 1{\cdot}75$ (also $m = 1{\cdot}24$ and $2{\cdot}0$), expressed as logarithms of: d, d_w, d_{1w}, D (and also for d_{aw} with width of 100 metres).

FIG. 25.—Deposition coefficient, p = 0·05.

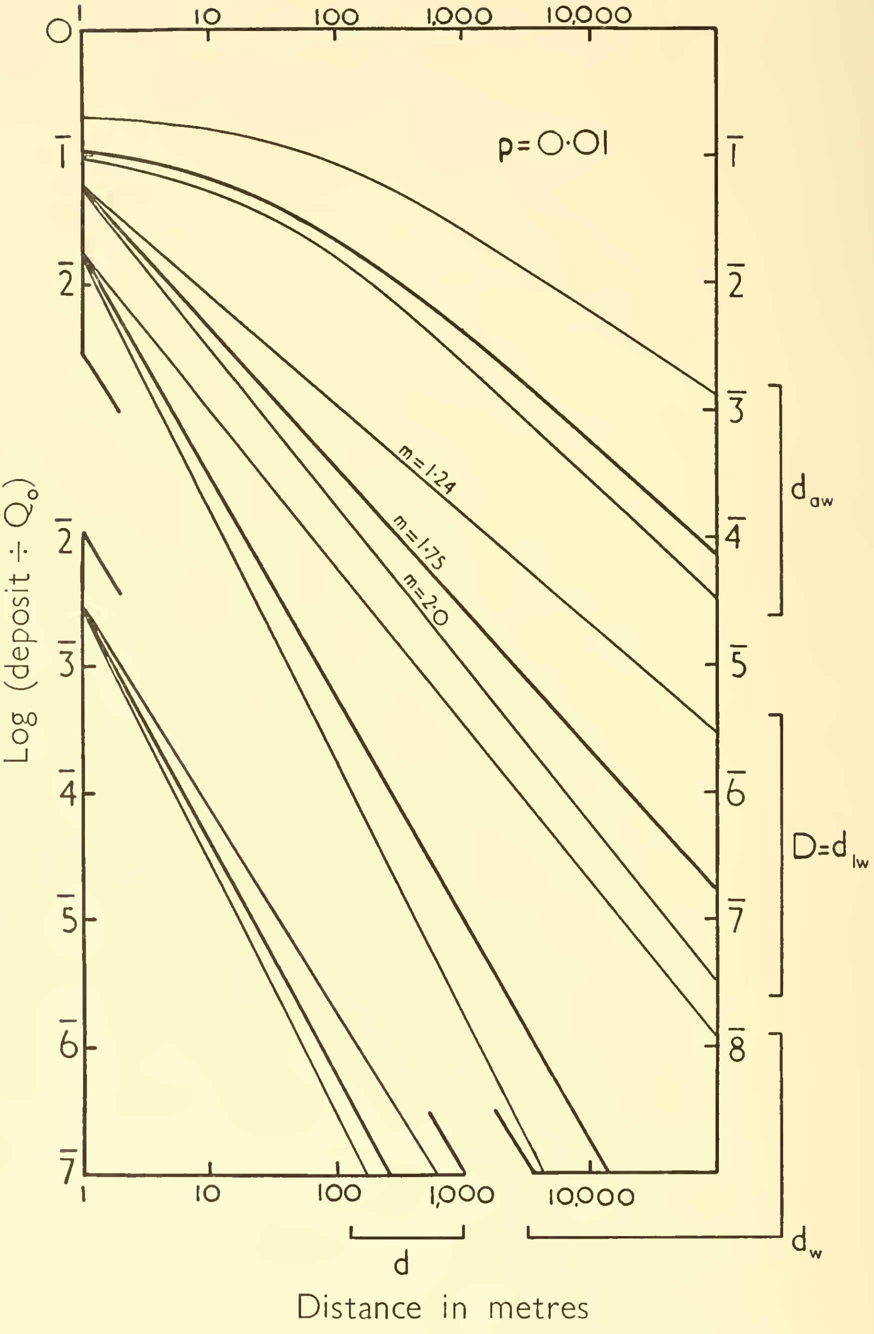


FIG. 26.—Deposition coefficient, p = 0·01.

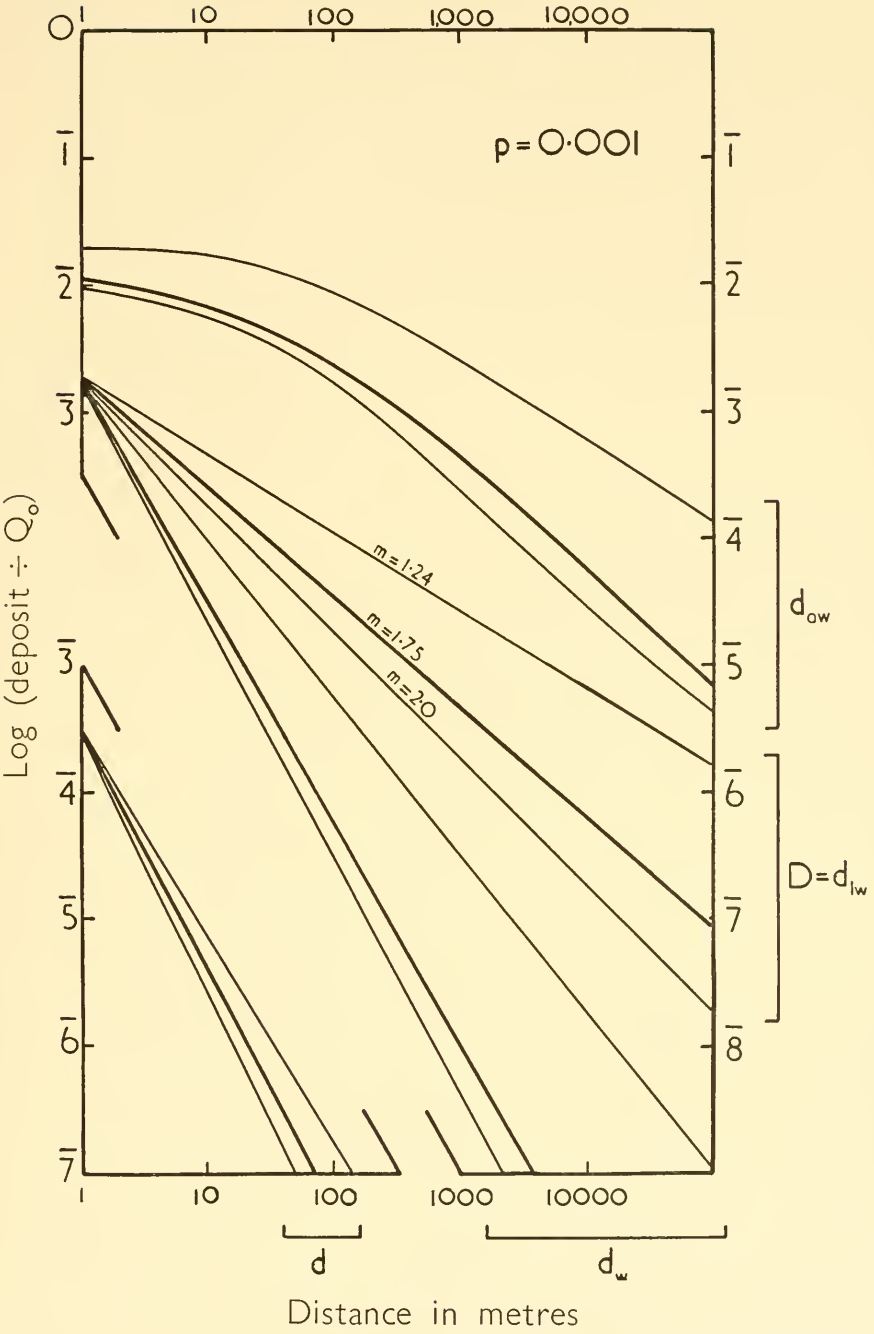


Fig. 27.—Deposition coefficient, p = 0·001.

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workers have considered that these large estimates for deposition near the source are incompatible with the facts about dispersal in the upper-air, and over long distances, which are discussed in Chapters X and XIV. This dilemma is considered further below (pp. 180 and 197).

The effect of values of m lower than $1{\cdot}75$ is to increase deposition near the source and to decrease it at greater distances. With liberation at ground-level, the distance at which deposition per unit area is equal with either $m = 1{\cdot}75$ or $1{\cdot}24$, lies between $x = 10$ and $x = 100$ metres. For other heights of liberation above ground-level, calculations are not yet complete.

APPLICATION OF GRADIENTS

The results given graphically in Figs. 24 to 27 can be used in various ways, some of which are illustrated in the following examples.

(i) *Deposition at a point downwind.* Assuming that a million uredospores are liberated at a point one metre above ground-level under standard atmospheric conditions, what number would be deposited per square centimetre of ground at a point 100 metres downwind? Choose Fig. 25, because $p = 0{\cdot}05$ is the relevant coefficient of deposition for uredospores (rather than Figs. 26 and 27, which refer to smaller spores). Choose the group of three lines marked 'd_w' (deposition per square centimetre downwind of a point source). Choose the middle of these three lines, as $m = 1{\cdot}75$ under standard conditions. Read-off the value of 'logarithm (deposit $\div$ Q_0)' for the distance of 100 metres. This value is approximately $= \bar{5}{\cdot}4$. As in this example $Q_0 = 10^6$, $\log Q_0 = 6{\cdot}0$, so we now have $\log d_w = 6{\cdot}0 + \bar{5}{\cdot}2$, therefore $\log d_w = 1{\cdot}4$, and $d_w = 25$ spores per square centimetre.

But this calculation assumes no depletion of the cloud, and deposition must now be allowed for by replacing Q_0 by Q_x. From Fig. 24, choose the group of curves marked $p = 0{\cdot}05$ and, as the height of liberation is 1 metre, choose the line for $h = 1$, and read off the value for Q_x/Q_0 at 100 metres. This value is approximately $0{\cdot}25$, indicating that only about a quarter of the spores liberated are still in suspension at the distance of 100 metres from the source. We therefore have the value of the corrected $d_w = 0{\cdot}25 \times 25 = 6$. The answer to the problem is that we predict a deposit of six uredospores per square centimetre under the conditions postulated.

(ii) *Fitting theoretical curve to observed data* can best be illustrated by a published example that gives actual distances and percentages of leaves infected. Relative distances are useless because the slope of the gradient-line is characteristic of an absolute distance, and also with relative percentages we cannot apply the multiple-infection transformation if the data require it.

Waggoner (1952) gives two sets of data on the spread of potato late-blight (*Phytophthora infestans*) at Clear Lake, Iowa. 'Point source' foci were established in field plots by artificial inoculation. Hollow curves were plotted, showing the proportion of leaflets diseased at various distances from the source on the ninth day after inoculation in 1949 and the eighteenth day in 1950. Reading-off observed values from Waggoner's graphs gives the values for 1949 and 1950 as plotted in Fig. 28; these agree well with the *slope* of the predicted gradient (d) for dispersal from a point source. (The highest incidence was between 7 and 8 per cent, so the multiple-infection transformation is unnecessary.)

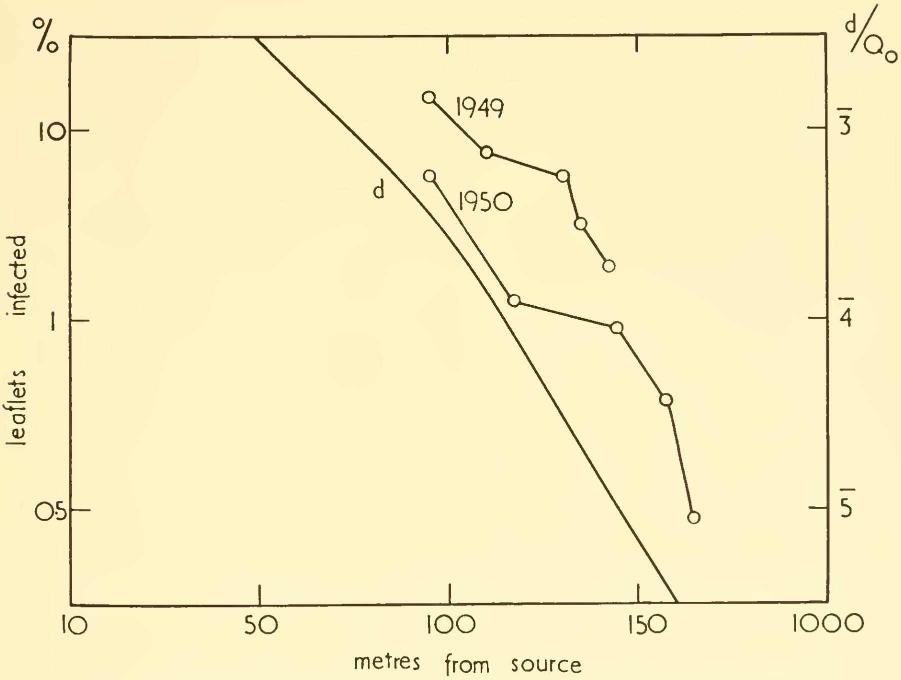

FIG. 28.—Infection gradients of potato late-blight (*Phytophthora infestans*) observed by Waggoner (1952) at Clear Lake, Iowa, in 1949 and 1950; compared with d = theoretical line for deposition downwind from a point source, assuming $m = 1{\cdot}75$, $C_y = 0{\cdot}6\ (\text{metres})^{\frac{1}{8}}$, $p = 0{\cdot}05$, and allowing for Q_x.

(iii) *Fixing limits for isolation.* The formula for d (average deposition at distance x in all directions around a point source) may be chosen when spread of a disease within a field, or gene dispersal, is being considered. For safe decision on isolating a healthy crop from contamination, the use of d_w may be preferable as it predicts maximum concentration downwind.

Suppose we wish to estimate the upper limit of the percentage of those plants infected with *Ustilago tritici* to be expected at 50 metres distance from a 10-metre-square plot of smutted wheat acting as a source—knowing from past local experience that seed saved from the source plot itself is likely to produce only 5 per cent of diseased plants. We choose the curve for deposition downwind of an area source, with liberation height $h = 1$ metre, under standard conditions ($m = 1{\cdot}75$), and $p = 0{\cdot}1$. Assume that infection at 1 metre distant is also 5 per cent. From Fig. 24 we find that Q_x is $0{\cdot}88\ Q_0$ at 50 metres distance, and from Fig. 26, d_w at 50 metres is only about 28 per cent. of the value at 1 metre. The expected maximum level of infection at 50 metres is therefore $28/100 \times 0{\cdot}88 \times 5$ per cent $= 0{\cdot}12$ per cent. Under similar conditions, Oort (1940) recorded about half this decrease at 50 metres. At 1 km. downwind of a 10×10 metre plot, it would be more appropriate to adopt the curve for a point source and estimate the level at $1{\cdot}5 \times 10^{-5}$ per cent.

(iv) *Relative contributions of near and distant sources.* A susceptible plant in a field is often exposed simultaneously to infection from near-by and distant sources. The problem arises as to the relative importance of a few diseased plants within the crop as compared with possible massive sources of infection in neighbouring fields. Quantitative answers have to be guessed to set limits of tolerance for issue of health certificates, and the data from gradients can be used to improve such guesses.

A simple case would be to inquire how many diseased plants at 1,000 metres distance would give the same amount of deposition as that on a plot of 100 metres radius with a single diseased plant at its centre, assuming that distribution by wind is uniform in all directions. From Fig. 25, over the range $x = 0$ to $x = 1{,}000$ metres (for $m = 1{\cdot}75$, $p = 0{\cdot}05$, and $h = 0{\cdot}1$ metre), the total deposition is $Q_0 - Q_x$ (for $x = 100$ metres) $= 1{\cdot}0\ Q_0 - 0{\cdot}06\ Q_0 = 0{\cdot}94\ Q_0$. From Fig. 27, the average deposition from one plant at a distance $x = 1{,}000$ metres is $4 \times 10^{-13}\ Q_0$ spores per sq. cm. The circle of radius 100 metres around the single plant contains $3{\cdot}14 \times 10^8$ sq. cm., so a plant at 1,000 metres contributes: $(4 \times 10^{13}\ Q_0) \times (3{\cdot}14 \times 10^8) = 12{\cdot}5 \times 10^5\ Q_0$ spores. The number of plants 1 km. away required to equal the contribution of one plant within the 100 metre radius circular plot is therefore approximately:

$$0{\cdot}94\ Q_0/12{\cdot}5 \times 10^5\ Q_0 = 7{,}500 \text{ plants.}$$

Characteristics of Gradients*

Some observed gradients fall off much more steeply than the line calculated for $m = 1{\cdot}75$. For example, the only gradients recorded for aecidiospores of *Puccinia graminis* (A. G. Johnson & Dickson, 1919; and Lambert, 1929) follow closely the expected gradient for a strip source with $m = 1{\cdot}24$, suggesting that these spores are dispersed when turbulence is small. Data on potato late-blight (*Phytophthora infestans*) contributed by Limasset (1939) and Bonde & Schultz (1943), and for *Peronospora destructor* on onions by Newhall (1938), also suggest dispersal under low-turbulence conditions.

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* Other properties of gradients are discussed by Plank (1960).

Further study will show whether certain groups of fungi are usually dispersed only under low-turbulence conditions. If it is confirmed that they are, a much smaller isolation distance could safely be permitted between disease sources and healthy crops than is permissible with pathogens that are dispersed in normally turbulent air, because with a small degree of turbulence the contaminated area is narrower and more intense. Meanwhile it is safer for isolation purposes to choose for prediction the line from the appropriate set which has been calculated for normal turbulence, $m = 1{\cdot}75$.

The rapid decrease in deposition with increasing distance from the source helps to explain the observations of Schmitt *et al.* (1959), who showed that many small rust infection foci distributed over a wheat field are more destructive to the crop than the same number gathered together at a single focus.

The fact that the slope of the curve is a characteristic of a particular distance can be used in the field to locate an unknown source. If lesions (or spores) are uniformly scattered over an area, we can assume that the source is so distant that the place of observation is on the tail of one (or many) dispersal gradients. Where counts increase rapidly, there is evidence that a source is being approached. Stakman & Hamilton (1939) located a large rust-infected barberry bush in western Minnesota, by first identifying unusual rust races in the vicinity and then tracing the telial stage of the rust on grasses leading up to the bush.

TOPOGRAPHICAL MODIFICATION OF GRADIENTS

Diffusion has been treated so far under nearly ideal conditions, but the literature contains information on the effects of topographical features which modify the gradient.

Pollen of wind-pollinated plants is distributed in typical gradients, as shown, for example, by Roemer (1932), Jensen & Bøgh (1942), Jones & Newell (1946), and Bateman (1947*a*). During strong winds in open fields, Jensen & Bøgh's catches of pollens of rye, ryegrass, cocksfoot, timothy, sugar-beet and mangold, on sticky microscope slides, showed a steady decrease with distance up to 1,200 metres from the source field. But they found that hedgerows and plantations protected ryegrass, cocksfoot, and mangolds, in proportion to the height of the obstacle. In tests near to the source, a protection corresponding to an isolation distance of about 200 metres of open ground was obtained behind hedges, even so far downwind as 5 to 10 times their height (cf. Rider, 1952; Schrödter, 1952; U.S. Weather Bureau, 1955; Caborn, 1957).

GENE DISPERSION

The physical mechanisms of wind dispersal have a bearing on population genetics. Theories of gene dispersion in populations at first assumed that there is a random scatter around the source. In such a distribution the gradient in any direction would have the form of one-half of the normal frequency curve. S. Wright (1943, 1946) studied genetic effects of isolation distance, and his methods were applied by J. W. Wright (1953) to compare dispersion distances of pollens of various forest trees with a view to delimiting a 'neighbourhood' for race formation. Simple sticky-slide traps were exposed at various distances around isolated trees, and pollen counts were used to find the standard deviation of the scatter. Observed values for the standard deviation were as follows: ash, 17–46 metres; Douglas-fir, 18 metres; poplar and elm, 300 metres or more; spruce, 40 metres; Atlas cedar, 73 metres; Lebanon cedar, 43 metres; and pinyon (pine), 17 metres. Dispersal data were well fitted by the Gregory formulae, but not by theories which assume that the trajectory of each grain can be calculated from the rate and distance of fall, and the wind velocity.

Bateman (1950) questioned whether gene dispersal is statistically 'normal', and showed by his regression method that many observed distributions—including those of fungus spores, passively borne insects, pollen, and wind-dispersed seeds—were highly leptokurtic, i.e. the peak and tails of the distribution are exaggerated at the expense of the shoulders. Compared with a normal frequency distribution having the same standard deviation ('same over-all degree of inbreeding'), the leptokurtosis characteristic of passive airborne dispersal produces more breeding between close relatives and simultaneously more breeding between distant relatives (*see also* Parker-Rhodes, 1951).

XIV

LONG-DISTANCE DISPERSAL

Dispersal of microbes over long distances is an ever-present, world-wide phenomenon. Its experimental study is almost non-existent; but there is circumstantial and observational evidence of its magnitude, some of which has been reviewed by J. J. Christensen (1942).

CONTROVERSY ON THE IMPORTANCE OF THE AIR-SPORA

The discovery of air dispersal in any group of plants has usually been followed by controversy between opposing specialists, some maximizing and some minimizing the significance of the phenomenon. Exaggeration is dangerous, and the object of this book is to present evidence from which balanced conclusions can be derived.

Views current on air hygiene affect the design and planning of hospitals. The air dispersal of human pathogens was confidently accepted in the golden age of bacteriology, but was gradually discounted after the experiments of Flügge which focused attention on the limited scatter of droplets from the mouth and nose (cf. Chapter XII). The balance has now been restored by Wells (1955) and others who have stressed the floatability of 'droplet nuclei'.

In plant pathology the two schools of thought have been prominent simultaneously. Butler (1917) held that spores of plant pathogens could be transported for short distances by air or by rain-splash, but claimed that 'the distance to which spores may be carried in the air has often been exaggerated in the past, and is much less than might be expected'. The discontinuous spread of plant pathogens, he considered, was likely to occur on seeds, plants, and horticultural produce; but 'infection by spores carried through the air from remote centres is not a contingency which needs to be taken seriously into account'. Naumov (1934) held that human activity accounted for most long-distance transport of fungus pathogens and that, in the absence of host plants, fungi were dispersed with extreme slowness. *Endothia parasitica* in North America could not cross, in a period of 10 years, a 45–60 km.-wide tract that was free from chestnut trees; the spread of a disease of palm trees was estimated at only 4–5 km. per annum.

The literature contains many instances of fungus pathogens failing to infect hosts at distances of a few metres (e.g. H. W. Long, 1914), or to colonize apparently favourable environments. Not all of these necessarily represent the failure of transport: genetic differences in host populations, or the pre-establishment of competitors, may explain many puzzling failures.

Diverse views have also been held about Bryophytes and Pteridophytes; however, most authors accept the possibility of their dispersal over great distances, although the minimizing view has been held by some (*see* Pettersson, 1940, p. 22).

Probably these differences in viewpoint will be resolved by quantitative studies. The maximizing view, if held too strongly, may lead to fatalism and to the neglect of local hygiene and of reasonable precautions when transporting plants from place to place. However, evidence presented in earlier chapters stresses the overriding importance of local sources. The minimizing view, if applied to certain diseases, may lead to overreliance on local hygiene and neglect of protection by chemical and genetic measures. It may also increase the danger of introduction of a vigorous organism by neglect of quarantine precautions.

Long-distance dispersal will be discussed under two headings: (1) diffusion theories extrapolating from short-range experiments; and (2) observations on distant dispersal of inorganic and radioactive particles, of rust fungi, and of other micro-organisms. The problem is complicated by the curvature of air-mass trajectories, by the possibility that spores are re-concentrated within cumulus and other clouds, by unpredictable removal in precipitation, and by loss of viability.

Theoretical Discussion

Presumably the tropopause limits the vertical expansion of the spore-cloud, and an extensive temperature inversion at a lower level may have the same effect. After the spore-cloud has travelled perhaps 20 km. or less, diffusion will become two-dimensional, and concentration may be expected to decrease more slowly with increasing distance than it would when the spore-cloud was nearer the source, where its diffusion was three-dimensional. In the limiting case of a land-mass acting as a long strip or area source, the decrease of concentration at 20 km. or more out to sea can be expected to depend only on depletion of Q_x (the fraction of the cloud remaining in suspension).

Sutton's theory appears satisfactorily to describe dispersal of microbes in air up to the limit of distance studied experimentally, but there is some doubt about its use for distances greater than 1 km. or heights above 30 metres. This is emphasized by Pasquill (1956), who dispersed fluorescent dusts and sampled, both on the ground and by aeroplanes, at distances of up to 64 km. and at heights of up to 1220 metres. In these tests the height of the cloud was much less than the width: the width did not increase uniformly with distance and the angle subtended at the release point by the cloud at the greatest distance was only about half that subtended by the cloud at 1 or 2 km. (Charnock, 1956). At distances greater than those considered in Chapter XIII, the difference between turbulence in a vertical and horizontal direction evidently becomes important. Further diffusion is limited by the tropopause, if not by the top of the turbulent layers of the atmosphere.

Samples taken after the accidental emission of about 20,000 curies of iodine-131 from a stack 122 metres high at Windscale atomic pile on 10 October 1957, have provided detailed records of ground contamination by the main plume over distances up to 290 km. (Booker, 1958). These records provide some evidence over longer distances for which microbial data are lacking. Plotted on a log.-log. scale, the radioactivity deposition curves, whether measured on herbage or in milk, are relatively flat up to 15 km.—a fact that is consonant with the height of emission. From about 28 km. onwards the slope is similar to that of d_w for $m = 1{\cdot}75$. There seems no reason, therefore, why we should not use our formulae for distances of several hundreds of kilometres—bearing in mind that, as in the Windscale accident, the trajectory of the cloud is not likely to be in a straight line over the Earth's surface.

Another view of long-distance dispersal of 'crowd diseases' of crop plants comes from Plank (1948, 1949, 1949*a*, 1960), who used gradients to define the novel concept of a 'horizon of infection' around a field, from beyond which the amount of infection received is negligible. Crowd diseases are defined as: 'diseases which neither spread far in considerable amount nor persist long in the soil'. They can be controlled by mixed cropping and by isolation. Plank put forward the generalization that 'if disease entering fields can easily be controlled by isolation, it can also be controlled by making the fields larger and proportionally fewer'; this is thought to be true, whether infection enters from uncultivated plants outside the field or moves from field to field.

For airborne spores travelling over distances between fields, Plank empirically estimates the probability that a spore will settle at a distance 'x' from its source as $p = k/x^n$, where 'k' and 'n' are constants. From published data n is 2 or more for distances over 30 metres, and approaches 4 as the distance from the source increases. With a number of uniform fields scattered evenly over a large area, Plank shows that, if Q is the number of spores received by one field from immediately neighbouring fields, the total number of spores received from all other fields, however distant, would be:

$$Q\left(1 + \frac{1}{2^{n-1}} + \frac{1}{3^{n-1}} + \cdots\right).$$

If $n = 2$ or less, the series is divergent and there is no horizon. If n is more than 2, the series is convergent and, if $n = 3$ or more, a useful horizon exists (Table XXVIII). The data suggest that, for potato late-blight

(*Phytophthora infestans*) and onion downy mildew (*Peronospora destructor*), n approaches 4. If n is small, local hygiene will soon be defeated by the flow of infection from outside; but if n = 3 or more, 'a considerable reduction of infection should be possible by a group of neighbours without it being neutralized almost immediately from elsewhere'.

TABLE XXVIII

EFFECT OF GRADIENT ON DISTANCE OF HORIZON OF INFECTION (Plank, 1949).

	Percentage coming from:			
	Neighbouring fields	More than 3 fields away	More than 5 fields away	Distance of horizon (No. of fields away)
$n = 2{\cdot}5$	38	40	32	> 50
$n = 3$	61	17	11	5
$n = 4$	83	3	1	2

OBSERVATIONS

RE-COLONIZATION OF KRAKATOA

The volcanic island of Krakatoa lies between Java and Sumatra and is almost encircled by land. The eruption of August 1883 blew away the mountainous two-thirds of the island, leaving a hole in the sea-bed 300 metres deep and covering the remainder of the island with lava and ashes. A column of fine dust rose to a height estimated at 27 km., and was carried westwards by the prevailing wind. Eventually this dust circled the Earth repeatedly, spreading over the whole tropical and temperate zones (Symons, 1888). Although this world circulation of dust is relevant to long-distance dispersal of microbes, the story of re-colonization of the island after the destruction of living things, which is usually considered to have been complete, is of even greater significance.

Three years after the eruption, the only flowering plants found by Treub (1888) were two species of Compositae and two grasses. There were also eleven species of ferns, and the volcanic deposit was colonized by a film of blue-green algae (Cyanophyceae). All these were thought to have been carried in by wind—the nearest land being 40 km. away.

Records of subsequent visits are summarized by Ridley (1930), who concluded that, of the 144 species of flowering plants then reported, 24 per cent were wind-distributed, 42 per cent were sea-borne on floating tree-trunks, and most of the remainder had probably been carried by birds. In addition there were forty-eight species of Pteridophytes and nineteen of Bryophytes—all potentially wind-borne. Boedijn (1940, *and see* Leeuwen, 1936), who believed that most of the fungi present had been carried to Krakatoa by wind, was impressed also by the paucity of lichens, of which he found only thirteen species (0·1 per cent of the world's list), compared with sixty-one species of Pteridophytes and 263 of flowering plants. Moreover, none of these lichens inhabited rocks: all were epiphytes which probably arrived on driftwood. Evidently lichens are poorly equipped for wind transport in comparison with Myxomycetes, which were represented by twenty-eight species (7 per cent of the world's list). Only two rusts were recorded (0·02 per cent of those known), but these obligate parasites must needs wait for their flowering-plant hosts.

QUANTITATIVE STUDIES

Ample qualitative evidence exists of mass transport of microbes by wind over large distances, but there are few quantitative data. The work of Zogg (1949) on one of the maize rusts in the Upper Rhine Valley is of exceptional interest, both for the distance studied and for the complex topography of the area.

In that part of Switzerland, *Puccinia sorghi* overwinters in its aecidial stage on the wild *Oxalis stricta*, which grows in the level area where the Rhine flows into Lake Constance. In early summer, near-by maize becomes infected and a uredospore focus is established from which the fungus is spread by wind up the narrow Rhine Valley. At various dates in the 1945 and 1947 seasons, Zogg measured the incidence of infection for 66 km. (up as far as Chur). Three striking facts about the gradients observed are: (1) the general decrease in the number of uredosori per plant with increasing distance from the source; (2) the flattening of the gradient as a result of secondary spread later in the season; and (3) the great irregularity of the gradient, because the incidence of the rust decreased locally wherever the valley widens, and increased again where it narrows: a feature which Zogg attributes, no doubt rightly, to the nozzle effect of the valley increasing spore concentration, though other ecoclimatic factors may play a part. In the terminology adopted in the present book, both area dose (A.D.) and efficiency of deposition (E) would be increased where the valley narrows.

The diffusion theory developed in Chapter XIII referred to dispersal over a level plain, and these modifications, imposed on a spore-cloud by dispersal up an alpine valley, are therefore particularly interesting. In comparison with the distance travelled, the focus of infection near Lake Constance would appear as a point source, though some flattening of the gradient would be expected near the source. As the winds blow characteristically up or down the valley, it seems appropriate to consider d_w (deposition downwind of source). Plotting Zogg's data on a log.-log. scale, we find that the linear regression (calculated as $\log. y = 5{\cdot}356 - 1{\cdot}818 \log. x$) is compatible for the slope of d_w as predicted by our theory (Chapter XIII). We take this to indicate that in the valley *diffusion* by atmospheric turbulence proceeds much as elsewhere, but that *deposition* is subject to pronounced fluctuations associated with the width of the valley.

Observations over similar distances above the sea come from Hesselman (1919), who traced the transport of tree pollens from the Scandinavian forests across the Gulf of Bothnia. Pollen was trapped in open Petri dishes on two lightships, 'Västra Banken' and 'Finngrundet', situated respectively 30 and 55 km. from land, from 16 May to 25 June 1918 (Table XXIX).

TABLE XXIX

POLLEN TRAPPED ON LIGHTSHIPS IN GULF OF BOTHNIA, 16 MAY TO 25 JUNE 1918 (Hesselman, 1919)

Pollen type	Terminal velocity cm./sec.	No. of grains per sq. cm. Västra Banken (30 km. from land)	Finngrundet (55 km. from land)	F/VB × 100 per cent
Spruce	8.7	696,100	408,900	58.6
Pine	2·5	239,000	106,900	44·4
Birch	2·4	681,100	364,900	53·5
Others	—	4,300	1,200	27·9

Pollen can be carried over much greater distances than this. In the month of June, Dyakowska (1948) found pine and spruce pollen falling on the coasts of Greenland, 600 to 1,000 km. from the nearest pine and spruce trees. Still further north, in Spitsbergen, Polunin (1955) noted a deposition of pine and spruce pollen which must have been equivalent to about 200 grains per square metre per day in July and August (Chapter IX). The long-distance record is probably that noted by Hafsten (1951), who reported *Nothofagus* pollen in peat on the island of Tristan da Cunha, 4,500 km. from the nearest source in South America.

An instance of long-distance transport of moss spores is reported by Pettersson (1940), whose investigations of plant spores in rain-water were described in Chapter XI. At Tvärminne, Finland, during 22–23 July 1936 (when there were persistent rains and light, mainly easterly winds), 104 cc. of rain-water were collected during 15 hours. This sample proved particularly rich in the spores of bryophytes, yielding 300 plants of *Marchantia polymorpha* and *Metzgeria* sp. Most remarkable, however, was the occurrence of spores which yielded 278 plants of *Aloina brevirostris* and 2 which were identified as *A. rigida*. These are small, annual or biennial mosses of dry calcareous soils, and belong to a genus hitherto unrecorded in Finland. There are a few records of *A. brevirostris* in Eastern Europe, but their presence in such large numbers in rain over Finland suggested that the spores must have come from a rich and extensive source area. This, Pettersson suggested, must lie in Siberia, in the region of the River Yenisei—a distance of at least 2,000 kilometres east of Tvärminne. It is true that this conclusion has been questioned by Persson (1944), who thinks that they must have come from a nearer source such as European Russia or possibly Sweden; and by Bergeron (1944), who examined air-mass trajectories for the day in question and reached a similar conclusion to that of Persson. Yet Pettersson found that *Aloina* spores were being deposited in rain to the number of ten thousand per square metre and, although their origin is unknown, they must clearly have travelled a very long way.

As an example of the diffusion of components of the air-spora over long distances, we have quantitative information about the deposition of uredospores of stem rust of wheat (*Puccinia graminis tritici*) contributed by Stakman & Hamilton (1939). In the early summer of 1938 they studied the deposition of uredospores of this pathogen at various points to the north of ripening winter-wheat fields in the southern United States, which were acting as a vast source of uredospores. At this time of year it could be assumed that spores were not being produced locally in the spring-wheat area in the northern United States, but that infection would follow the arrival of the spore-cloud borne on southerly winds. Table XXX, compiled from Stakman & Hamilton's data, indicates the amount of deposition first in the source area and then at various points farther north.

TABLE XXX

STAKMAN & HAMILTON'S (1939) DATA FOR LONG-DISTANCE DISSEMINATION OF *Puccinia graminis* (deposition on ground, 24–25 May 1938)

Place	Approx. distance from source	Uredospores per sq. ft. per 48 hours
Dallas, Texas	(source area)	129,216
Oklahoma	300 km.	6,288
Falls City, Nebraska	560 km.	7,680
Beatrice, Nebraska	840 km.	1,968
Madison, Wisconsin	970 km.	192

Another series, taken during 13–14 June, gave the following numbers of uredospores deposited per square foot in 48 hours: Kansas, 336,000; Nebraska, 54,336; Iowa, 21,360; South Dakota, 12,624; Minnesota, 32,256; and North Dakota, 1,344.

This long-distance transport of cereal rusts is not merely an occasional risk. On the contrary, it is clear from work done over a vast area that an annual double transcontinental migration through the atmosphere is an essential condition for the development of the rust epidemics which regularly attack cereal crops in North America. Moreover, wind dispersal is relatively unselective, and what happens to rust fungi no doubt happens also to countless other organisms whose spores travel on a global scale.

It has been possible to demonstrate this phenomenon for cereal rusts because of the concerted study of a disease of a major food-crop (wheat) by a generation of scientists in plant pathology laboratories scattered over North America, and also because of the strange life-cycle of these rusts, which makes it possible to obtain clear evidence. The evidence derived from spore-trapping, field records of outbreaks, geographical distribution of the physiological races, and meteorological data, has recently been summarized by Stakman & Harrar (1957, pp. 221–32). To simplify a complex story, *Puccinia graminis* and *P. rubigo-vera* (= *P. triticina*), for various reasons, do not survive the cold winters of the northern part of the continent or the hot and dry summers of the southern parts. Spring-sown wheat in the northern United States and Canada receives rust-spore showers annually from rusted autumn-sown wheat in Mexico and Texas. In some years it comes by a succession of short jumps, with intervening stops for local multiplication, whereas in other years infection spreads suddenly from the south—for distances of a thousand or more kilometres when atmospheric pressure distribution produces suitable winds. Similarly, winter-wheat in the south becomes infected during the autumn by spore-showers from the north. Large-scale movement east and west across the North American Continent is relatively infrequent. Yellow rust of wheat (*Puccinia glumarum*) seems to be spread only much more locally than *P. graminis* or *P. rubigo-vera*—perhaps because its uredospores are more easily killed by exposure.

A somewhat similar annual flow of airborne cereal-rust spores has been demonstrated in other parts of the world. For example, India has an annual flow from the hills to the plains: Mehta (1940, 1952) found that no local sources of rust infection survived the long hot summers of the Indian plains, yet rusts on wheat and barley caused heavy annual loss there. The explanation lies in the over-summering of rusts on cereal crops and self-sown plants at 2,000 or more metres in the hills, whence inoculum is carried by winds to start infection foci here and there on the plains in early winter. Upper-air currents and katabatic winds both play a part in the dissemination. The early dissemination of rust from inoculum coming from central Nepal and the Nilgiris and Palni Hills to the Indo-Gangetic plain, is the cause of annual devestating outbreaks.

Russian work, mainly by L. F. Rusakov and A. A. Shitikova-Russakova (summarized by Chester, 1946), suggested transport of rust uredospores over hundreds of kilometres from the west across the Sea of Azov, and also from Manchuria up the Amur Valley in Eastern Siberia. On the other hand, the Irkutsk wheat-growing area west of Lake Baikal seems, for practical purposes, to be isolated from the rest of the world by deserts, mountains, and tundra. *Puccinia graminis* does not occur in the Irkutsk region, and *P. rubigo-vera* survives because it can form aecidia on *Isopyrum fumarioides*, a common weed of arable land which serves as an alternate host. The wheat-growing areas of Australia and the Argentine also seem to be autonomous to the extent that airborne spores from outside do not affect either the annual rust epidemic cycles or the population of rust races present. Chester (1946, p. 164) concludes: ‘In Australia and Argentina, as in the Lake Baikal region of Siberia, we evidently have regions which are so separated from other wheat areas by natural barriers, mountains, oceans, deserts, and vast distances, that for all practical purposes they can be considered as totally isolated from the rest of the world, insofar as the introduction of wind-borne rust is concerned.'

For the cereal rusts we thus have a picture of free interchange of uredospores over long distances, sometimes in the form of an annual immigration or even a return trip each year; but isolation of several thousand kilometres limits this dispersal process. No other kind of microbe has been so fully traced in its atmospheric dispersal as have the cereal rusts. Rust uredospores are relatively large, and we would expect some smaller-spored organisms to be at least as well equipped for long-distance dispersal—e.g. the coloured spores of agarics and myxomycetes.

The width of the Atlantic Ocean, combined with the prevailing wind pattern in tropical latitudes, has formed a natural barrier to one of the maize rusts. From 1879 onwards (Cummins, 1941), *Puccinia polysora* has been collected on *Zea mays* and *Tripsacum* in the eastern and southern United States, in Central America, and in the Caribbean Islands; in 1940 Stakman found it on maize in Peru. In 1949 the fungus suddenly appeared in Africa, causing a widespread and severe disease on maize in Sierre Leone, spreading rapidly, and reaching most other parts of West Africa by 1951; Congo, and East Africa from the Sudan to Tanganyika, were invaded in 1952; Southern Rhodesia, Portuguese South Africa, Madagascar, Mauritius, and Réunion all in 1953; and then the islands of Agalega and Rodriguez in 1955. Simultaneously another focus developed in Malaya in 1950, reaching Siam, the Phillipines, and Christmas Island in the Indian Ocean in 1956 (Wood & Lipscomb, 1956; Cammack, 1958). Evidently, until about 1949, the fungus lived quietly on tolerant American varieties of maize, isolated from vast areas of highly susceptible maize in Africa by the 5,600 km. of the Atlantic Ocean which, with its trade-winds, formed an impassable barrier.

Cammack (1959) considered possible modes of immigration of *Puccinia polysora* into Africa and rejected wind transport in favour of introduction by aircraft on seed-corn or corn-on-the-cob, much of which was flown to West Africa from America during the last world war and post-war years. Once the parasite was established in Africa, the natural barriers there were evidently insufficient to stop its spread by wind over the whole continent, so that it reached Madagascar in only four years.

Airborne pathogens present serious disease-control problems which are quite unlike those of such soil-borne diseases as potato wart. Other examples where a plant pathogen has spread rapidly after introduction by man into an isolated area include: potato late-blight (*Phytophthora infestans*), which was introduced into Europe in the 1840's, and to Australia and South Africa in 1909; hollyhock rust (*Puccinia malvacearum*), which spread over western and central Europe between 1869 and 1874 (Gäumann, 1950, p. 141); and antirrhinum rust (*P. antirrhini*), which recently spread over New Zealand (Close, 1958).

For the extreme limit of dispersal we have as yet no direct quantitative microbial evidence, but recent nuclear test explosions throw light on the problem (Libby, 1956; Stewart & Crooks, 1958). Clouds of radioactive dust, thrown up from bombs of less than one megaton, rise to 10–12 km., but tend to stay in the troposphere without penetrating to the stratosphere. In the troposphere the dust-cloud, consisting of particles mostly less than 1 μ in equivalent diameter, diffuses vertically and horizontally as it travels eastwards on the prevailing winds of temperate latitudes. The cloud circles the Earth every 4 or 5 weeks, but most of the particles are removed from the atmosphere in a month or two. A region of stable air over the tropics acts as a barrier to its spread between the northern and southern hemispheres.

A thermonuclear bomb of the megaton range, exploded near the ground, puts a large proportion of its sub-microscopic dust into the stratosphere, where it behaves quite differently from the radioactive dust in the troposphere. The cloud spreads uniformly over all latitudes and is removed much more slowly, depletion to 50 per cent of the original quantity being variously estimated as taking from 5 to 10 years. Dust from successive tests thus accumulates in the stratosphere. As no natural mechanism has been suggested which would convey micro-organisms into the stratosphere on a similar scale, the results of thermonuclear tests are of less immediate interest to aerobiology than are tests of lower power or so-called 'normal bombs'.

Possibly a hint at the ultimate horizontal dispersal-limit of micro-organisms in air is to be found in a study of the geographical distribution of species. In a world survey of the fungus, *Schizophyllum commune*, the numerous incompatibility factors appeared to be randomly distributed (Raper *et al.*, 1958), though the same may not be true of *Coprinus*. On the whole, fungi are believed to show a wider natural geographical distribution than flowering plants. Europe and North America share more species of Hymenomycetes (mushrooms, toadstools, and their allies) than of flowering plants. The species of fungi in the tropics and the south-temperate regions differ considerably from those of the north-temperate regions (Bisby, 1943). Many saprophytic species of fungi, especially soil moulds, tend to be cosmopolitan. How far wind has operated in their transport, and how far other means, especially man, are responsible for the world-distribution of these micro-organisms, is unknown; but the limits of the rust fungi give us some evidence.

VIABILITY

Although, under ideal conditions, dispersal of airborne microbes is a limitless process, phenomena discussed in this chapter indicate that practical limits exist. One factor or another may reduce to negligible proportions the amount of inoculum transmitted between distant places.

The source of supply at the place of origin may be too weak or, because of dilution and deposition, the spore-cloud may arrive at a concentration below the threshold for detection. Or again, when the spore-cloud arrives, few of the spores may be viable, or perhaps all may be dead.

The dispersion equations given in Chapter XIII ignored the death-rate of spores in transit, and treated merely their diffusion as particles—regardless of whether they were living or dead. The justification for this is that the physical processes controlling dispersal likewise fail to discriminate between living and dead spores. Further, although a plant pathologist or plant breeder is concerned only with living cells, to an allergist a spore or pollen grain is equally significant whether alive or dead. None of the gradients measured so far contains any hint that loss of viability is affecting the dispersal process: it may very well do so, but the distances covered in any quantitative study are still too short, and our methods too coarse, to allow us to detect a decrease in viability along a gradient. Yet, over longer distances, loss of viability may well dominate the gradient. Some organisms may lose viability while travelling quite short distances in air; but this effect has apparently not yet been disentangled from effects of changes in concentration caused by diffusion and deposition.

Uredospores of some cereal rusts as, for example, *Puccinia graminis* and *P. rubigo-vera*, can evidently remain viable after travelling many hundreds of kilometres and reaching the top of the troposphere, though we suspect that others, such as those of *P. glumarum* and *P. polysora*, are less robust. Aecidiospores of rusts in general are believed to travel shorter distances in the viable state, and the basidiospores (sporidia) of the white-pine blister-rust (*Cronartium ribicola*) may well have their viable range restricted to a few hundred metres. Intensive study of this phenomenon in the open air is needed before we can know the quantitative significance of death for the dispersal gradient.

PHYSIOLOGICAL STUDIES OF VIABILITY

The immense literature on microbial survival and death-rates throws much light on factors influencing percentage viability in a population, under almost all imaginable conditions—except during suspension in air. Of changes in the viability of organisms during air-dispersal we have only circumstantial evidence, except for bacteria which are small enough to allow their longevity to be studied while suspended as aerosols in the rotating steel drum devised by Goldberg *et al.* (1958). Using this method, Webb (1959, 1959*a*) concluded that bacterial cells suspended in air die as a direct result of loss of bonded water from their protein. Loss of viability takes place in two stages: a rapid killing in the first second of time, followed by a slow death-rate which might be delayed by some bacteriostatic substances whose presence might actually increase survival.

The death-rate of a microbial pure culture normally proceeds exponentially with time, the same fraction of surviving individuals dying in each successive equal time-interval—a process analogous to radioactive decay. But natural populations are often heterogeneous, and these mixtures of individuals or species with different propensities for life may deviate from the exponential die-away curve. Measurements of survival-time are often expressed as the time taken for most or all of the organisms to die under a particular set of conditions. Yarwood & Sylvester (1959) rightly point out that this limit is difficult to measure accurately, and that a more useful concept is the half-life of a population (as already used for decay of radioactivity). Apart from being easier to measure accurately than the end-point, the half-life is more logical than an arbitrarily selected value such as 90 per cent or 99 per cent death of the population, because it is the time at which all the individuals in a population which were alive at the start have an equal chance of being alive or dead. As an example, Yarwood & Sylvester give the half-life of basidiospores of *Cronartium ribicola* as 5 hours. It is not always easy to determine the status of a particular spore or cell. If it can be grown it is clearly viable, but failure to grow may merely reflect failure to provide suitable conditions.

Standard texts on microbial physiology deal with the effects of external conditions on the longevity of micro-organisms. Most of the experimental work is in the laboratory, with organisms in a liquid or at a solid/gas interface, and it is evident that the main factors of the aerial environment which affect survival (not always in the direction expected) are: humidity, temperature, and the visible or ultra-violet radiation. For instance, in laboratory tests, Whisler (1940) found the common airborne *Sarcina lutea* to be one hundred times more resistant to ultra-violet radiation than was the intestinal *Escherichia coli.*

At first sight, conditions in the atmosphere might appear to be very unfavourable for the survival of isolated microbial cells (or even of resting spores) which, because of their minute size, have a high surface/volume ratio giving great exposure to external conditions. Endospores of bacteria are highly resistant to unfavourable environments; but this is not true of all plant spores, many of which are more delicate structures than the parent.

Desiccation is a hazard already mentioned; it is greatest in day-time and in air-layers near the ground. At higher altitudes, and throughout the atmosphere at night, conditions are less favourable for evaporation, and spores may even be found germinating in clouds—a phenomenon occasionally reported for the uredospores of rust fungi. We are still not clear how to relate meteorological observations to conditions for viability. Evaporation in still air is a function of the absolute dryness of the air, but in moving air evaporation may be more nearly related to relative humidity. Possibly it is best to regard an airborne spore as 'still' in relation to the air in which it is suspended. A complicating factor is that, because of heat radiation, a spore is seldom at the same temperature as the air in which it is suspended; though, because of its small heat-capacity, the difference is not likely to be great. Improvements in the technique of freeze-drying show that damage to organisms is greatly affected by the temperature and speed at which they are desiccated. Repeated wetting and drying often lowers viability.

As physiological experiments show, many of the regular components of the air-spora are resistant to desiccation. Less hardy organisms are probably better able to survive when they are high above the Earth's surface. Most micro-organisms will survive in a resting condition longer at the temperatures found in the upper air than they will at ground-level; temperatures in the atmosphere are preservative rather than lethal for most of the air-spora (*see* Meier, 1936*a*).

Radiation is a much more serious hazard, and on this there is a rapidly increasing literature. The most quickly lethal radiations in the atmosphere are in the ultra-violet region, and these are largely absorbed by the air before they reach the ground. Ascent to the upper air therefore brings the risk of greatly increased dosage of ultra-violet radiation—except in the shelter of clouds. Pigmented spores, and bacteria carried on larger rafts, may also be effectively screened from radiation. The interactions of humidity, temperature, and radiation are not well known, and it may be that low temperature and desiccation partly protect a spore against radiation damage. In addition, when a spore returns to ground-level, the recently studied phenomenon of photo-reactivation by visible light of organisms which have been exposed to ultra-violet, may perhaps reduce the damaging effects of radiation received at high altitudes. Photo-reactivation is defined by Jagger (1958) as: 'the reversal with near-ultraviolet or visible light of ultraviolet radiation damage to a biological structure.' Visible light reverses lethal effects of ultra-violet radiation in many microbes—including bacteria and actinomycetes, fungi and yeasts, and also protozoa—but the survivors of high-altitude passage may be expected to show an increased mutation rate on their return to Earth.

The suitability of the atmosphere for the survival of 'aerial-plankton' is summed up by Gislén (1948) as follows: 'While the lower cloudy air-strata—let us say under 3,000 to 4,000 metres—form a suitable medium for the transport of micro-organisms, the higher layers are very inhospitable to them, not so much because of the low temperature, drought and barometric pressure, as because of destructive radiation.'

XV

AEROBIOLOGY

THE literature of aerobiology is scattered, but extensive reference lists are given in the following works: Cunningham (1873), Heald (1913), Gardner (1918), Sernander (1927), Stepanov (1935), Rempe (1937), Pettersson (1940), Craigie (1941), Moulton (1942), duBuy *et al.* (1945), Gregory (1945), Stakman & Christensen (1946), Wolfenbarger (1946, 1959), Jacobs (1951), Maunsell (1954), Wells (1955), Werff (1958), and Hirst (1959).

It now remains to review the conclusions of each of the preceding chapters in the light of the whole, to consider their implications, and to attempt a synthesis.

THE PHENOMENA

Airborne microbes, whether carried singly, in groups, or on 'rafts', are heavier than air. In still air they fall under the influence of gravity, with constant terminal velocities ranging from 0·05 to 150 cm. per sec. according to their size and density. This falling would lead to their sedimentation out of the air if other forces did not oppose gravity. Two atmospheric processes tend to prevent sedimentation through the quiet boundary layer: turbulent diffusion in wind carries the spore-cloud horizontally, at the same time diffusing it both horizontally and vertically; and thermal convection can carry a spore-cloud to great heights in the troposphere. Modes by which spores cross the boundary layer of air near the Earth's surface and reach the turbulent wind layer, are therefore of prime importance in the dispersal of microbes. Energy for 'take-off' may be supplied by the organism itself or may come from external sources supported by a wide variety of mechanisms, such as wind or rain-splash, and factors controlling the take-off mechanism also control the occurrence of spores in the air. The more an organism is specialized towards one dispersal route, the more unfit it becomes for dispersal by another route. For many purposes, knowledge of the 'take-off' mechanism is important.

Rain-splash dispersal results in a local scatter because the larger splash droplets, which are less easily carried by the wind, pick up more spores than do smaller droplets.

Frictional turbulence will diffuse the spore-cloud to the top of the dust horizon—convection will take it higher. The concentration of spore-clouds approximates to the expected logarithmic decrease with height, but equilibrium is never reached in the atmosphere. Often there is a zone of increased concentration at an altitude of two or three thousand metres.

Dilution of the spore-cloud as it travels horizontally downwind is the result of eddy diffusion. Of the various meteorologists and physicists who have formulated eddy diffusion, O. G. Sutton has provided the most useful method. Experimental values obtained in microbiological work for the parameters in Sutton's diffusion equations are useful in predicting spore concentrations at various distances from the source. We await still better methods; but they may be long in coming, for the problem appears to be particularly intractable.

Concentration of the spore-cloud decreases not only by diffusion but also because particles are lost by various deposition processes—of which impaction, turbulent deposition, and sedimentation under the influence of gravity, are the most important. Wind speed, the area and orientation of the surface, and the size of the particle, all have great effects on impaction efficiency, both in the wind-tunnel and out-of-doors.

Deposition from the atmosphere under natural conditions outdoors has been studied experimentally. Under uniform conditions, particle size has an important effect on the amount deposited from a spore-cloud of given concentration at ground-level. When liberation is near ground-level, loss by deposition is great. We cannot yet choose between two theories of deposition to the ground, one of which depends on the wind-speed and the other on the distance traversed by the cloud. Near the source, unexplained high deposition values have been observed. Elevating the point of liberation reduces the amount of deposition near the source. Topographical features which affect wind-speed also affect the number of spores deposited, and may play a part in development of a plant disease epidemic—complicated by the fact that they may simultaneously modify the ecoclimate in a direction favouring or inhibiting infection.

Estimation of the microbial content of the air is particularly difficult because, although microscopic, the particles are often large enough to demand attention to the aerodynamic design of the sampling equipment. Choice of the correct sampling equipment must be determined by the range of organisms to be sampled. Throughout this book emphasis has been placed on methods, because methods commonly determine results. Single bacterial cells in aerosols are small enough to be handled in the manner of a gas, without regard to their inertia; but larger organisms (and bacteria on 'rafts') impact on surfaces, stick on corners, slip out of streamlines, and settle under the influence of gravity. These aerodynamic effects must be allowed for in the design of apparatus for reasonably accurate sampling.

The basic study of the air-spora must be by visual methods under the microscope. Crude as visual identification is, it is based on the only common property shared by all airborne microbes—visibility—and no other method can reveal the whole range of the air-spora and disclose what numbers and kinds are in the air awaiting identification. More precise methods can then be applied to the study of smaller groups.

The air-spora is very imperfectly explored, but sampling has already shown that bacteria, algae, yeasts, spores of fungi, mosses and ferns, pollens, and protozoa, commonly occur in the air. The air-spora near the ground is extremely variable, both from time to time and from place to place. It changes with season, and with weather—the concentration of constituent types often changing several thousand-fold in the course of an hour or two. It changes regularly in composition and concentration throughout the day and night. Visual methods indicate that fungus spores are normally in the majority over other components of the air-spora—probably outnumbering bacteria. However, we lack methods for the complete enumeration of the bacteria in outdoor air, and improved techniques may reveal the presence of far more bacteria than we can recognize at present.

We now know that basidiospores (ballistospores) form an important part of the air-spora, often carrying electrical charges, and probably outnumbering even *Cladosporium* (which is the dominant mould almost everywhere). The tardy recognition of the abundance of basidiospores is partly explained by their inefficient collection by standard sampling methods, and partly by the unfamiliarity of many microbiologists with the spores of the higher fungi (cf. Plate 6). Damp night air has its characteristic spora, but at dawn the night-spora disappears suddenly; where it goes we do not know. Rain removes the dry-air spora and substitutes a different one.

Vegetation is the main source of the air-spora, but most bacteria come from blown soil or splashed water. The source of the yeasts, which are sometimes recorded in large numbers, is still obscure—unless they prove to be Sporobolomycetes. Air near the ground at times contains from tens of thousands to hundreds of thousands of micro-organisms per cubic metre. The air-spora near the ground is commonly dominated by contributions from local and intermediate sources; but local effects are smoothed out at high altitudes, over the oceans, and in polar regions.

Spore concentration over the land usually decreases with altitude, though not always regularly. Often a large proportion of the air-spora must occur at altitudes higher than 10 metres. Far out at sea, a few metres above sea-level, the microbial content of the air is usually small; but, at an altitude of a few thousand metres over the ocean, the air often contains a few bacteria and from tens to hundreds of fungus spores per cubic metre. Current information suggests that, over the oceans, concentrations are greater in the upper air than near sea-level. Clearing the lowest zone of the atmosphere from microbes is most evident over the ocean. For above land the spore-cloud near the ground is not only fed from above by diffusion and, to a minor extent, by gravity, but it may also be fed from below, from new sources of soil and vegetation. Even over the Arctic in winter, the air is only relatively sterile; samples of a few cubic metres may or may not contain viable spores. Wind transport of microbes is a process that is evidently going on continuously on a world-wide scale.

Many unsolved problems remain. Is there a biotic zone at the height of a few thousand metres? Or is the lower air cleared by rain, with microbes re-concentrating transiently at the base of a cloud? Is there a true aerial plankton in the sense of a population permanently living and reproducing at great heights, as suggested by R. C. McLean (1935, 1943)? This would seem improbable—unless a microbial population is permanently balanced over tropical regions by rising air-currents and descending cloud droplets. Do air masses retain a characteristic polar or tropical spora, or do they rapidly receive and give up the spora of the land over which they pass?

Sooner or later, if they have not been already deposited by other means, airborne microbes are removed from the atmosphere by collection in rain, snow, or hail. If the carrying droplet later evaporates below the cloud base, there could possibly be an actual local increase in concentration high above ground. Rain, hail, and snow bring down a large microbial flora and are factors making for non-uniform deposition, in contrast with the more uniform diffusion which results from turbulence.

Spores deposited on the ground, or on vegetation near to a source, show a pronounced gradient (following the concentration gradient of the wind-blown spore-cloud). This can be estimated by making assumptions based on observed data, and can be used in predicting the danger of contamination by foreign pollens, plant pathogens, and so on. In practice the ideal gradient is often modified by topography—sometimes a decreased wind velocity decreases spore deposition.

In the past it may have been too easily assumed that the dispersion of an organism around its origin is like a normal frequency distribution. This may be true when dispersion is due to motile surface animals, actively flying insects, and possibly even rain-splash. But wind-dispersal is not 'normal' (in a statistical sense) around the point of origin; by contrast, it is a hollow curve. This throws light on a paradoxical situation: in the wind-dispersal of microbes liberated near ground-level, the gradient near the source is very steep, and relatively short isolation-distances give good protection. Pollens and plant pathogens with large dry spores liberated at ground-level may have 90 per cent of their spores deposited within about 100 metres—or perhaps more than 90 per cent if allowance is made for the unexplained large values of p observed within a metre or two of a ground source. Yet spores can travel immense distances, and spores found over the ocean clearly represent the tails of the distributions of all the sources on the up-wind continent. The equation for Q_x has the curious property that the farther a spore has travelled, and the longer it has survived deposition, the farther it is likely to travel.

Although most spores are deposited near their source, some are readily transported to great distances. Transport over long distances plays a regular role in some crop disease epidemics, and presumably in the movement of many other organisms. Mountain ranges, oceans, and deserts, may all be effective barriers to dispersal. Although conditions in the upper air, especially in cloud, may not be unfavourable for survival, loss of viability rather than failure of the transport mechanism limits the colonization range of many organisms. Enhanced variability may be expected among microbes that survive exposure to ultra-violet radiation. Because of the overwhelming importance of unsuspected near-by sources, it is often difficult to be sure that an organism observed has come from a great distance.

Implications of Aerobiology

BIOLOGICAL WARFARE

It seems that microbiological weapons have not been used on any large scale by man against man. The example of myxomatosis in rabbits should convince sceptics of what might happen when all conditions are suitable for epidemic spread. The topic is shrouded in official secrecy, but the little information already released suggests that, if deliberate dissemination of pathogens (or toxins) were ever attempted, contamination of the air might be one of the dangers to be anticipated. Rosebury *et al.* (1947), from their comprehensive analysis of the principles of bacterial warfare, consider that the airborne group of pathogens contains the most important infective agents for war use (*see also* Rosebury, 1947, 1949). The published studies on air-sampling equipment and epidemiology that come from official defence laboratories are small compensation for this threat by man to his own health and agriculture.

ISOLATION, QUARANTINE, AND GEOGRAPHICAL DISTRIBUTION

The prodigious reproductive powers of microbes always excites comment and is particularly remarkable in the matter of the number of spores produced by fungi. The wastage of spores must be enormous. The world is more or less fully populated with fungi and, within reasonable geographic and climatic bounds, a fresh substratum will rapidly select its normal flora from the ample supply of suitable spores brought to it. In crop pathology we study a system that is temporarily unbalanced by human activities—large, reasonably pure stands of susceptible, 'artificial' crop-plants which are renewed at regular intervals, are especially subject to attacks by parasites. Dispersal gradients become obvious under these conditions, and our isolation and quarantine methods can play a major role in limiting the development of a fungus flora on a crop.

Willis (1940) claims that 'nothing in the distribution of plants would lead anyone to suppose that the "mechanisms for dispersal" have produced for the plants that possess them any wider dispersal than usual'.

In the unbalanced condition necessary to agriculture, this claim obviously fails; it is comparatively easy to limit the dispersal of *Sclerotium cepivorum* and *Synchytrium endobioticum* which have poor dispersal mechanisms, difficult with *Phytophthora infestans*, and impossible with *Puccinia triticina* whose dispersal mechanism is excellent. Willis's claim refers to floras which man has not greatly disturbed, and, it seems, mainly to higher plants.

The rules of M. W. Beijerinck and L. G. M. Baas Becking, as given by Overeem (1937), state that 'as far as microbes are concerned; "*Everything is everywhere*" and, from this "everything", "*the milieu selects*" '. This is an exaggeration, a microbiological half-truth that is useful as a corrective to narrow parochialism; but, if it were universally true, aerobiology would not be interesting. For example the rubber-tree is attacked by two serious pathogens, *Oidium heveae* and *Dothidella ulei*, which fortunately are at present limited in their distribution, the former to Asia and the latter to the Americas.

Many saprophytic microbes have a world-wide distribution, and the soil bacteria and moulds tend to be similar on all continents. Floras of different areas are remarkably uniform in their coprophilous fungi, and in their green and blue-green algae—a testimony to the effectiveness of various dispersal processes where similar environments, existing over long periods, have given time for equilibrium to be established. With local disturbances from time to time, sites become available in the midst of a population of organisms in apparent equilibrium. Man is the most active disturber of this equilibrium, and human activity therefore frequently operates in the border-line region of a microbial concentration gradient. In this region we can attempt to interfere with the dispersal process.

Normally in a field-population, multiplication and elimination are going on simultaneously. Altering the balance between these two processes may sometimes lead to the disappearance of an organism or a disease. Isolation is one of the methods of doing this. Isolation of allergic patients from allergens out-of-doors may need greater distances, because the threshold may be so low that one pollen grain is enough to provoke an attack. Isolation and quarantine in medicine scarcely falls within the province of this book; intra-mural aerobiology is mainly the concern of hygiene and public-health workers. But the use of distance to control cross-pollination and plant diseases out-of-doors is obviously relevant.

Where the geographical distribution of a pathogen is more restricted than that of its host crop, the existence of natural barriers, for practical purposes uncrossable by airborne plant pathogens, makes control of some crop diseases by official action a feasible procedure.

Where natural wind-transport fails, other methods may dominate dispersal. With freshwater and soil micro-organisms, transport by birds may be important. But of all animals, man is the most dangerous, because his opportunities for carrying exotic microbes are greatest. The major portion of the load carried across international boundaries by the world's highly organized transport system consists of unprocessed plant material. There are two dangers to be guarded against in this connection. An important crop disease may be excluded from a country where the pathogen does not occur by: (1) prohibiting imports of possible host plants; (2) inspection in the country of origin or on arrival; and (3) disinfection (supplemented by local eradication measures should the pathogen gain a temporary hold). The more insidious danger, however, is in an organism which has settled down in its original home as an insignificant parasite on a host with which it is in balanced relationship, suddenly being transported to a new country and finding a highly susceptible host-crop where it can cause devastating losses—e.g. *Puccinia polysora* on African maize (cf. p. 189), and *Endothia parasitica*, a trivial parasite on oriental chestnuts, but devastating when introduced into the United States of America from Asia (McCubbin, 1944*a*, 1954).

MEDICAL MYCOLOGY AND ALLERGY

The winds, which had been suspected from antiquity of bearing epidemic diseases, have been gradually exonerated so far as the major human and animal epidemics are concerned. Malaria and yellow fever come through the air, but only by the activity of their insect vectors. The old scourges of cities are now known to be spread by vectors, water, milk, or contact, and are no longer attributed to the winds. Air is not entirely blameless, however. Droplets expelled from the mouth and nose spread disease in confined places; wind carries pollens and other allergens; and some of the less well-known fungus diseases of man, such as coccidioidomycosis and histoplasmosis, are clearly airborne (Rooks, 1954; Hoggan *et al.* 1956; Furcolow & Horr, 1956; and Fiese, 1958). Air emerges as one of the major routes for transport of micro-organisms, pollens, and many crop pathogens.

Outdoor airborne allergens appear to originate from vegetation above ground, but not significantly from the soil (though the allergenic possibilities of various soils themselves would be well worth testing). To a large extent, therefore, their origin is an agricultural problem, aggravated by our need to cultivate plants in pure stands. Fortunately, the interests of farmers and allergic patients are to some extent identical. The farmer, unless he is a seed grower, does not require his grass to scatter protein-rich pollens uselessly, and the development of non-flowering strains of grasses (from seed raised in other countries where conditions such as length of day permit flowering) is beginning to attract the attention of farmers and seed-merchants alike (Peterson *et al.*, 1958); nor does the farmer want his wheat-straw weakened by *Alternaria* or *Cladosporium*.

Improved methods of measuring the spore concentrations of the air are enabling us to bring many organisms forward for test as potential allergens, and may throw light on the causes of some of the seasonal asthmas—especially those of late summer whose etiology is unknown (Maunsell, 1958). The purest air appears to be just above the ocean, though life on board ship has its own allergic hazards.

PALYNOLOGY

Pollen statistics, pollen analysis and, more recently, palynology, are various names given to a group of studies including investigation on the ecology, vegetation, and pre-history of the Quaternary Period by examination of the pollens preserved in peat and other deposits. Palynologists have contributed considerably to the development of aerobiology, and are well aware of the complications of wind-borne pollens from distant sources (e.g. Buell, 1947). The problem is one of sampling in a given locality, so as to eliminate uneven distribution from the dominating influence of one near-by source.

We still need to know how the total deposit at one point is made up of the few local distributions plus the tails of the distributions of many distant sources. Furthermore, we must expect that sometimes an active re-concentration in a cloud may reverse the diffusion process, and may lead to the kind of incident which Pettersson recorded with a heavy shower of *Aloina* spores. How far re-concentration in the air needs to be taken into account, and how far surface obstacles may lead to local deposition, is a matter for study.

Spores and pollen preserved in glacial ice in mountainous and polar regions offer scope for investigation that is still almost unexplored (cf. Vareschi, 1942).

EVOLUTION

It seems that in each locality or habitat, mutation and recombination are apt to act, through selection, to evolve special local divergent populations. But, simultaneously, dispersal mechanisms tend to counteract this process by encouraging outbreeding and so increasing uniformity. How the two processes balance is a genetical problem depending on external factors and on the breeding systems involved. Aerobiology contributes quantitative information on the size of the breeding group, which must be determined partly by the characteristics of the dispersal gradient. Wind-borne genes are not distributed 'normally' (in a statistical sense) around their point of origin but in a characteristic hollow curve, which has the interesting property of involving greater frequencies near the source and at great distances (at the expense of intermediate distances) than if the genes followed the normal frequency distribution.

Over the greater part of the Earth's land surface the ecologically dominant flowering plants and conifers belong to wind-pollinated (anemophilous) species. Temperate and tropical grasslands, coniferous forests and deciduous forests, and some semi-desert lands, are dominated by species which reach up to shed pollen into the turbulent boundary layer. Tropical rain forest, on the other hand, is dominated by insect-pollinated plants. Probably the number of anemophilous *individuals* is many times greater than the number of entomophilous *individuals* in the world, yet only about one-tenth of the *species* of flowering plants are anemophilous. By contrast, tropical rain forest is noted for its extraordinary number and diversity of species of flowering plants. Perhaps it is because of meteorological factors such as rain or the difficulty of access for turbulent wind that these plants are mostly insect-pollinated, and clearly the two phenomena are inextricably linked. The wider possibilities of gene dissemination in wind-pollinated plants has tended towards relative uniformity over wide areas, while the statistically more 'normal' and localized character of insect pollination has favoured specialization and speciation.

The role of air-dispersal is evidently two-fold. Its role in leading to colonization is clear enough with seed plants and many micro-organisms, and the establishment of infection is an example of this process in pathogens.

A second important role, obvious enough in wind-pollinated flowering plants but curiously overlooked in microbes, is that of gene transmission. In the fungi this process is probably a major function of spore dispersal (Gregory, 1952). So far as well-established fungi are concerned, the immense output of spores probably does little to promote the extension of the range. When some accidental or cyclic effect offers a suitable environment within the range, the area involved rapidly becomes colonized and the average number of mycelia of the species is at least maintained. From this we need not necessarily deduce, as has been usual hitherto, that all the rest of the spores are functionless. The higher fungi possess one characteristic that is unmatched in other organisms—their ability to form vegetative hyphal fusions which lead to a mixing of cytoplasm and nuclei from spores of different origin—and it is tempting to speculate, as Transeau (1949) did with *Coprinus variegatus*, that far more spores germinate and fuse with an already-established mycelium than ever themselves succeed in establishing a new mycelium.

The work of H. M. Hansen & Smith (1932), on heterocaryosis, shows that wild mycelia may contain genetically different nuclei. Some of these may be due to mutations in mycelia derived from a single nucleus, but experimental evidence shows that heterocaryons can also be produced by artificial mixing of suitable, genetically different mycelia, and it seems highly probable that this mixing process also occurs in nature. The value to a species of storing an adequate supply of mutant genes to be drawn upon in future, and so giving plasticity under varying conditions, has been stressed by workers on fungus genetics, including Craigie (1942) and Whitehouse (1949).

Our speculation would suggest that spore dispersal of the higher fungi has one other function besides those of increasing the range and colonizing new substrata within the range—that of dispersing genes and transmitting novelties, arising from mutation and recombination, between one established mycelium and another. The shift of sexual reproduction from the sedentary spores of the Phycomycetes, which lack hyphal fusions, to the dispersal-spore form in the Ascomycetes and Basidiomycetes, may be a phase in the evolution of this habit. On this hypothesis, a perennial mycelium would be the locus of activity and multiplication of individual nuclei—some perhaps descended from the original spore-colonizer, others descended from outside immigrant sources. The mycelium would remain, whereas nuclei would come and go. The established mycelium would resemble a city rather than an individual. Thus, besides their function as colonizers, spores may perhaps act as a sort of unreliable air-mail service, transmitting genes between established mycelia.

Dispersal spores of some fungi such as the Gasteromycetes are difficult to germinate. If we reject, as first choice, the hypothesis that they are functionless, we must suppose that there exist special conditions under which germination occurs naturally. The experiments of Ferguson (1902), who discovered that mushroom spores would germinate readily when in contact with living hyphae of the same species, are suggestive in this connection. Other examples are known of spores that are stimulated to germinate by hyphae of the same species, an instance being the spermatia (pycniospores) of *Puccinia helianthi* (Craigie, 1933). Experiment may show that this phenomenon of gene interchange plays a bigger part than we have hitherto considered possible. If this speculation is justified, the production and dissemination of novelty must be a major activity of the fungi.

Ascospores and basidiospores are the spore forms most likely to contain genetic novelty, and they are most commonly dispersed by wind to potentially new environments. The conidia, which are ordinarily dispersed by wind, splash, or insects, were well named 'repeating spores' in the older literature, functioning as they did for exploitation of the same environment as the parent. However, G. Pontecorvo's discovery of parasexual re-combination shows that genetic novelty can also arise from conidial forms in several ways.

BEYOND THE ATMOSPHERE

Aerobiological technique has much to contribute to research beyond the Earth's atmosphere.

To counter the idea that living organisms evolved from non-living matter on this planet, Arrhenius (1908) put forward the hypothesis that space is permeated by spores. On this hypothesis, spores might be carried to great heights—for example in the Earth's stratosphere by volcanic activity—and then driven off into space by electrical repulsion. If this were so, a planet might leave a trail of dust in space, and large particles might move in the sun's gravitational field; but the smallest bacterial spores (0·2 μ) would move away from the sun with high velocities under radiation pressure, even crossing interstellar space and entering planetary atmospheres. Arrhenius's hypothesis now appears improbable. Conditions in space seem inimical to the survival of a spore (Oparin, 1957); and our increasing knowledge, as we probe beyond the confines of our atmosphere, of the intense radiation to which a nucleo-protein would there be exposed, raises serious doubts about this speculation. However, this negative conclusion should not prevent us from making attempts to sample Space for microbes in the wake of this planet—an experiment which seems already within reach of an artificial satellite. Knowledge so gained could be used for sampling in outer space near other planets, to discover whether there is a microbiology of Space.

The techniques of aerobiology would probably not solve the novel problems that would arise in sampling in Space, but present knowledge will need thorough exploitation when we begin to probe the *atmospheres* of other planets. Many problems will arise, such as: (1) the necessity of studying any atmospheric spore-flora of another planet; (2) the moral obligation to avoid contaminating its atmosphere; and (3) the practical necessity to avoid contaminating our own atmosphere with completely unknown organisms which might be carried on a returning space-vehicle. We must explore any atmospheric spora of other planets less inefficiently than we have done our own, and for this much developmental work remains to be done.

FUTURE STUDY OF OUR ATMOSPHERE

Our knowledge of the terrestrial air-spora is fragmentary in the extreme. The air has never been systematically explored simultaneously in different parts of the world by comparable methods. There is a heap of accumulated data, from which Chapters IX to XII attempt to sort out a few principles. Here and there are intriguing suggestions of phenomena; but many of the data are uninterpretable, and we need a fresh study of aerobiology as part of a vast terrestrial process.

Before starting, aims must be clearly defined, and the needs of three separate analyses formulated—concentration in air, concentration in precipitation, and surface deposition. Methods must then be worked out, based on visual examination of the whole air-spora, and supplemented by cultural and other methods for the taxonomically diverse components. Equipment must be tested and calibrated in wind-tunnels and in the open air, including sampling during flight at high altitudes.

When methods have been developed, international co-operation will be necessary to organize a chain of routine sampling stations and to co-ordinate programmes. Routine sampling stations should cover a wide variety of climates, of topographic, altitudinal, and ecological environments, and also the special interests of cities, agriculture, and medicine. An international aerobiological research institute is needed, with laboratories in temperate and arctic regions and, above all, in the tropics and on remote oceanic islands, about which we know least.

After exploring the stratosphere, we shall then be better able to tackle outer Space. Time is short; before we know where we are, we shall have the Moon at our doorstep and Mars and Venus on our hands.

APPENDIX I

VISUAL IDENTIFICATION

Pollen identification and description can be carried to considerable detail, and the beginner who is faced with the problem of visual identification of the catch on a series of trap slides can get help from books, including the two volumes by Erdtman (1952, 1957) and the one by Hyde & Adams (1958), as well as from the journal, *Pollen et Spores*, published in Paris. For many other groups of organisms little help can be had from books, and in any laboratory doing visual scanning of slides it is essential to get together a reference collection of slides in the standard mountant adopted, and prepared from reliably identified specimens from the field. (Fungus spores from cultures are often abnormal and unlike the forms which occur on spore-traps.)

Plates 5, 6, and 7 illustrate some typical plant spores etc. at the uniform magnification of 1,000 diameters to help the beginner, who may have been confused by many published illustrations which tend to portray plant spores at various and often widely different magnifications. These paintings, by Maureen E. Bunce, attempt to depict the object as it appears under the microscope—with a minimum of interpretation. As far as possible they are from collected specimens and are mounted unstained in glycerine jelly. Protozoa have been omitted.

Key to Source

c. from culture	*h.* from hay
s. from field specimen	*t.* from Hirst-trap slide

PLATE 5

Spores of Phycomycetes, Ascomycetes, and Fungi Imperfecti.

1. *Entomophthora muscae*, conidium, *s.*
2. *Peronospora parasitica*, sporangium, *s.*
3. *Mucor spinosus*, sporangiospores, *c.*
4. *Absidia corymbifera*, sporangiospores, *c.*
5. *Absidia ramosa*, sporangiospores, *c.*
6. Unknown ascospore, *t.*
7. *Tubercularia vulgaris* (= conidium of *Nectria cinnabarina*), *s.*
8. *Nectria cinnabarina*, ascospore, *s.*
9. Unknown ascospore, *t.*
10. Unknown ascospore, *t.*
11. *Claviceps purpurea*, ascospore, *s.*
12. *Ophiobolus graminis*, ascospore, *s.*
13. *Helvella crispa*, ascospore, *s.*
14. *Humaria granulata*, ascospore, *s.*
15. *Pyronema confluens*, ascospore, *s.*
16. *Bulgaria inquinans*, ascospore, *s.*
17. *Xylaria polymorpha*, ascospore, *s.*
18. *Hypoxylon coccineum*, ascospore, *s.*
19. *Hypoxylon multiforme*, ascospore, *s.*
20. *Chaetomium indicum*, ascospore, *c.*
21. *Chaetomium globosum*, ascospore, *c.*
22. *Venturia inaequalis:* (*a*) conidium; (*b*) ascospore, *s.*
23. *Rosellinia aquila*, ascospore, *s.*
24. *Sordaria fimicola*, ascospore, *c.*
25. *Daldinia concentrica*, ascospore, *s.*
26. *Pleospora herbarum*, ascospore, *s.*
27. *Melanospora zamiae*, ascospore, *s.*
28. 'Hyaline rods', *t.*
29. *Polythrincium trifolii*, conidia: (*a*) *t*; (*b*) *s.*
30. *Botrytis* sp., conidium, *c.*
31. *Trichothecium roseum*, conidium, *c.*
32. *Aspergillus fumigatus*, conidia, *c.*
33. *Aspergillus glaucus* (series), conidia, *c.*
34. *Aspergillus niger*, conidia, *c.*
35. *Aspergillus nidulans:* (*a*) ascospore, *c.*; (*b*) 'Hülle' cell, *c.*
36. *Penicillium chrysogenum*, conidia, *c.*
37. *Penicillium digitatum*, conidia, *c.*
38. *Penicillium cyclopium*, conidia, *c.*
39. *Erysiphe* (*graminis*?), conidium, *t.*
40. *Helicomyces* sp., conidium, *t.*
41. *Diatrype stigma*, conidia, *s.*
42. *Epicoccum* sp., conidium, *t.*
43. *Papularia arundinis*, conidia: (*a*) face view, *c.*; (*b*) edge view, *c.*
44. *Monotospora lanuginosa*, conidium, *h.*
45. *Torula herbarum*, conidium, *t.*
46. *Bispora monilioides*, conidium, *s.*
47. *Stemphylium* sp., conidium, *c.*
48. *Alternaria* sp., conidium, *t.*
49. *Sporidesmium bakeri* (*Pithomyces chartarum*), conidium, *c.*
50. *Helminthosporium* sp., conidium, *t.*
51. *Cladosporium* sp., conidia, *t.*
52. *Streptomyces* sp., spores, *h.*
53. *Tetraploa aristata*, conidium, *s.*

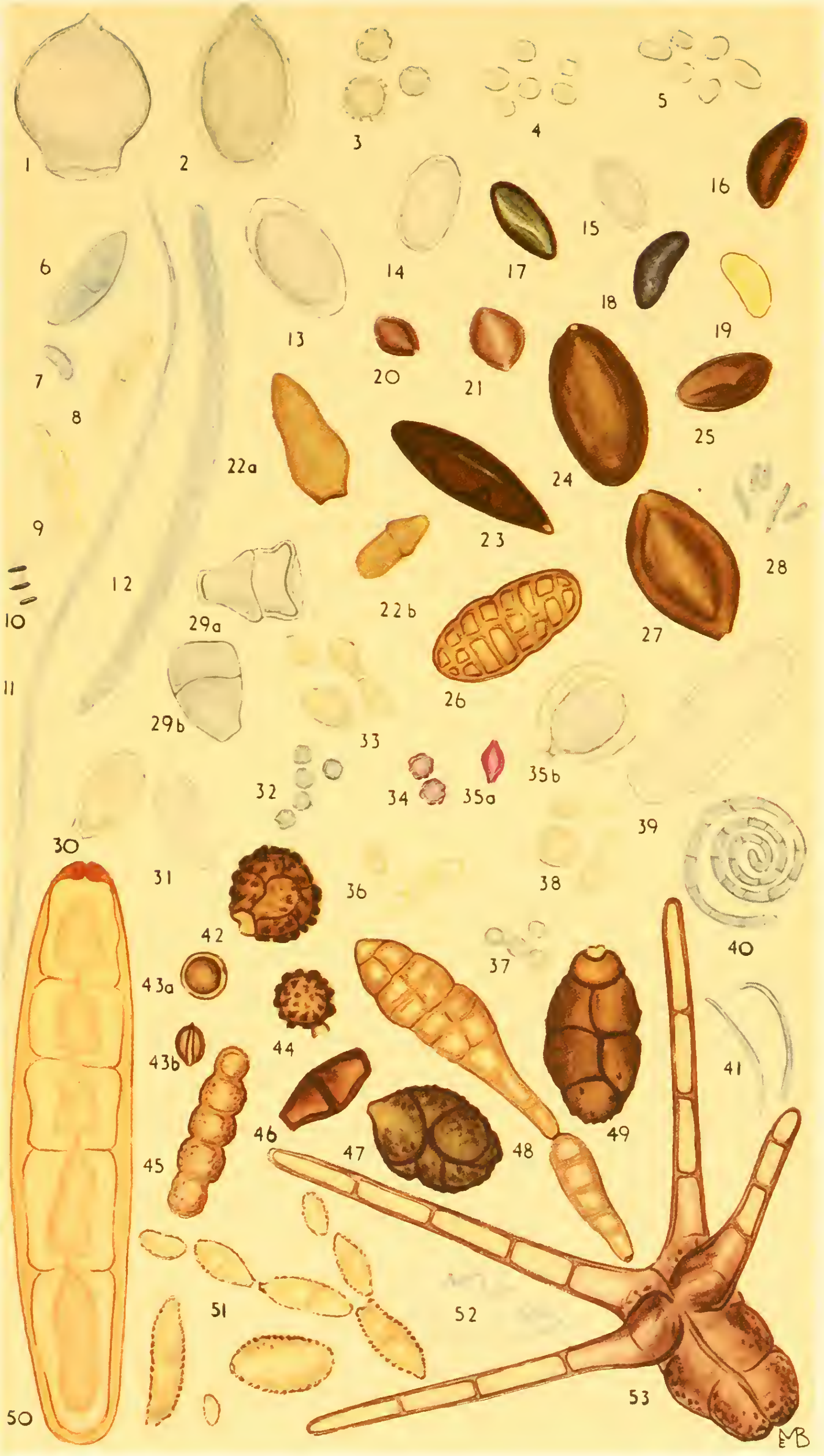
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PLATE 5
Spores of Phycomycetes, Ascomycetes and Fungi Imperfecti.

Plate 6

Spores of Basidiomycetes, Myxomycetes, Pteridophytes, Bryophytes, etc.

1. *Panus torulosus*, basidiospore, *s.*
2. *Collybia maculata*, basidiospore, *s.*
3. *Tricholomopsis* (*Tricholoma*) *rutilans*, basidiospore, *s.*
4. *Russula nigricans*, basidiospore, *s.*
5. *Russula vesca*, basidiospore, *s.*
6. *Lactarius blennius*, basidiospore, *s.*
7. *Lactarius rufus*, basidiospore, *s.*
8. *Amanita* (*Amanitopsis*) *fulva*, basidiospore, *s.*
9. *Pholiota* (*Naucoria*) *myosotis*, basidiospore, *s.*
10. *Bolbitius vitellinus*, basidiospore, *s.*
11. *Hygrophorus niveus*, basidiospore, *s.*
12. *Armillaria mellea*, basidiospore, *s.*
13. *Amanita rubescens*, basidiospore, *s.*
14. *Inocybe geophylla*, basidiospore, *s.*
15. *Nolanea staurospora*, basidiospore, *s.*
16. *Cortinarius elatior*, basidiospore, *s.*
17. *Lacrymaria* (*Hypholoma*) *velutina*, basidiospore, *s.*
18. *Coprinus atramentarius*, basidiospores: (*a*) profile; (*b*) face view, *s.*
19. *Hypholoma fasciculare*, basidiospore, *s.*
20. *Psathyrella* (*Hypholoma*) *hydrophila*, basidiospore, *s.*
21. *Entoloma rhodopolium*, basidiospore, *s.*
22. *Fistulina hepatica*, basidiospore, *s.*
23. *Tilletiopsis* sp., basidiospores, *t.*
24. *Sporobolomyces* sp., basidiospores, *c.*
25. *Panaeolina* (*Psilocybe*) *foenisecii*, basidiospore, *s.*
26. *Panaeolus sphinctrinus*, basidiospore, *s.*
27. *Phaeolepiota* (*Pholiota*) *spectabilis*, basidiospore, *s.*
28. *Pholiota squarrosa*, basidiospore, *s.*
29. *Merulius lacrymans*, basidiospore, *s.* (small form)
30. *Stropharia aeruginosa*, basidiospore, *s.*
31. *Crepidotus mollis*, basidiospore, *s.*
32. *Fomes annosus*, basidiospore, *s.*
33. *Stereum purpureum*, basidiospores, *s.*
34. *Thelephora terrestris*, basidiospore, *s.*
35. *Ganoderma applanatum*, basidiospore, *s.*
36. *Boletus chrysenteron*, basidiospore, *s.*
37. *Boletus elegans*, basidiospore, *s.*
38. *Boletus scaber*, basidiospore, *s.*
39. *Ustilago avenae*, smut spore, *s.*
40. *Triphragmium ulmariae*, uredospore, *s.*
41. *Melampsoridium betulinum*, uredospore, *s.*
42. *Tilletia caries*, smut spore, *s.*
43. *Tilletia holci*, smut spore, *s.*
44. *Puccinia graminis:* (*a*) teleutospore, *s*; (*b*) uredospore, *s.*
45. *Badhamia utricularis*, myxomycete spore, *s.*
46. *Fuligo septica*, myxomycete spore, *s.*
47. *Leocarpus fragilis*, myxomycete spore, *s.*
48. *Reticularia lycoperdon*, myxomycete spore, *s.*
49. *Urocystis agropyri*, smut spore, *s.*
50. *Dryopteris filix-mas*, fern spore, *s.*
51. *Pteridium aquilinum*, fern spore, *s.*
52. *Phyllitis scolopendrium*, fern spore, *s.*
53. *Selaginella pulcherrima*, spore, *s.*
54. *Funaria hygrometrica*, moss spore, *s.*
55. *Barbula fallax*, moss spore, *s.*
56. *Lycopodium*, club-moss spore, *s.*
57. *Gloeocapsa* sp., algal group, *t.*
58. *Cladonia* sp., lichen soredium, *s.*

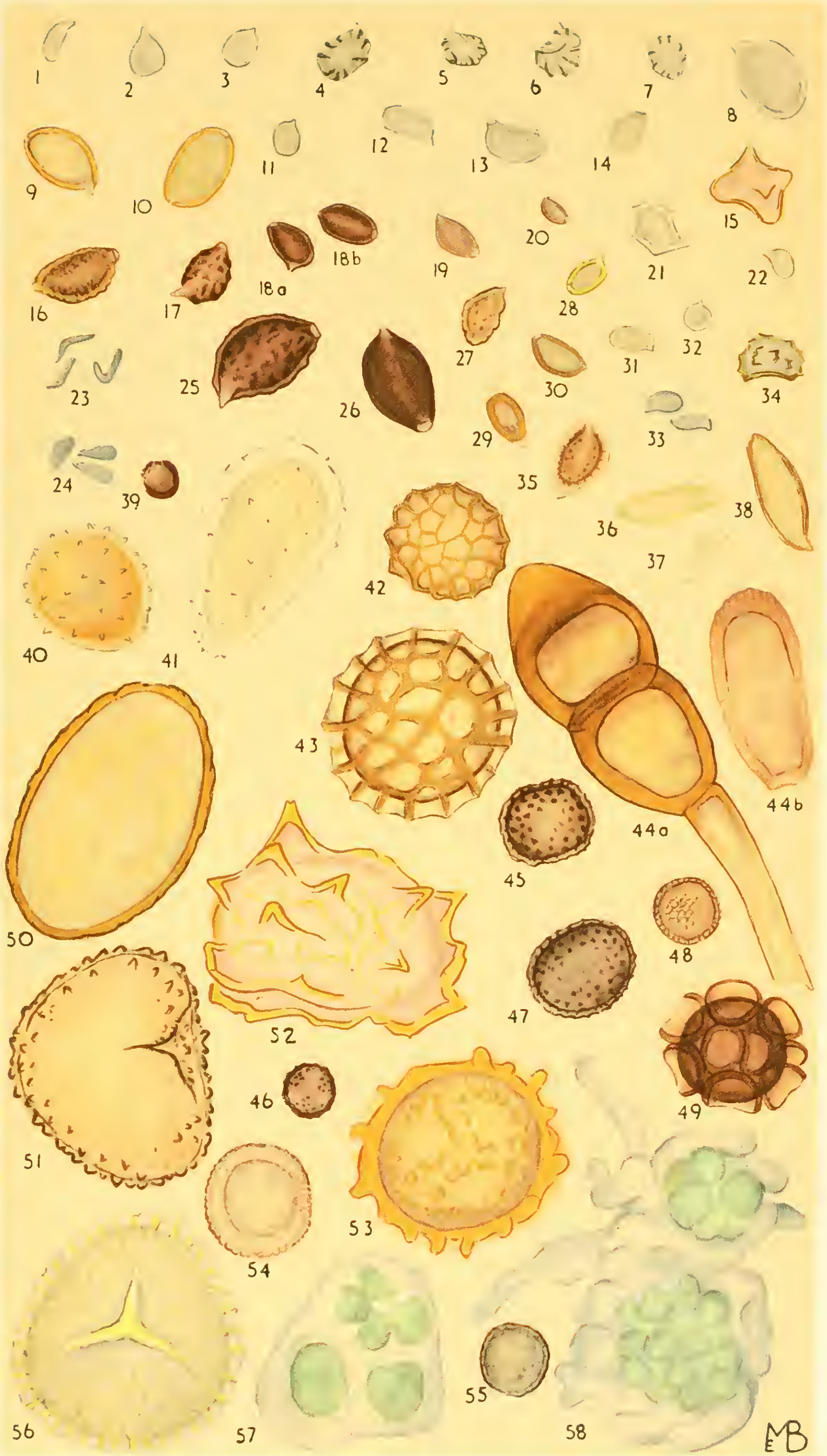
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PLATE 6
Spores of Basidiomycetes, Myxomycetes, Pteridophytes, Bryophytes, etc.

Plate 7

Pollen grains and miscellaneous particles.

1. *Phleum pratense*, grass pollen, *s*.
2. 'Fly-ash' spheres, *t*.
3. *Taxus baccata*, yew pollen, *s*.
4. 'Cenosphere', *t*.
5. Insect scale, *t*.
6. *Betula verrucosa*, birch pollen, *s*.
7. *Corylus avellana*, hazel pollen, *s*.
8. *Pinus sylvestris*, pine pollen, *s*.
9. *Acer pseudoplatanus*, sycamore pollen, *s*.
10. *Quercus robur*, oak pollen, *s*.
11. *Fagus sylvatica*, beech pollen, *s*.
12. *Castanea sativa*, sweet chestnut pollen, *s*.
13. *Ulmus* sp., elm pollen, *s*.
14. *Salix caprea*, willow pollen, *s*.
15. *Platanus* sp., plane pollen, *s*.
16. *Tilia* sp., lime pollen, *s*.
17. *Urtica dioica*, nettle pollen, *s*.
18. *Chenopodium album*, fat-hen pollen, *s*.
19. *Artemisia vulgaris*, mugwort pollen, *s*.
20. *Solidago* sp., golden-rod pollen, *s*.
21. *Anthriscus sylvestris*, cow-parsley pollen, *s*.
22. *Calluna vulgaris*, ling (heather) pollen, *s*.
23. *Rumex acetosa*, sorrel pollen, *s*.
24. *Thalictrum* sp., rue pollen, *s*.
25. *Plantago* sp., plantain pollen, *s*.

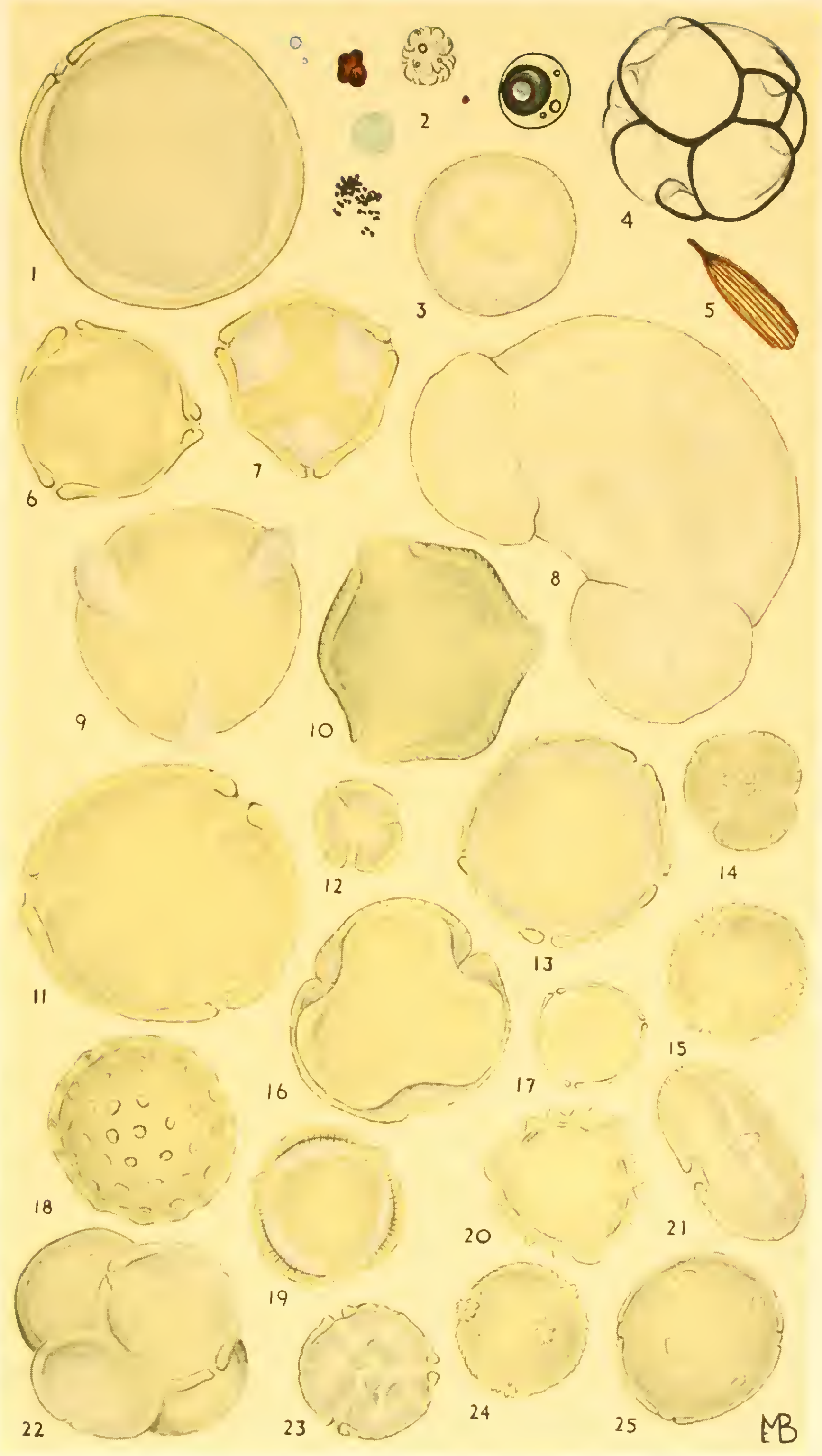
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PLATE 7
Pollen grains and miscellaneous particles.

W. H. O. I.
WOODS HOLE, MASS.

APPENDIX II

CONVERSION FACTORS

MEASURES OF WEIGHT—*Avoirdupois to Metric*

1 dram (dr.)	27·343 grains	1·772 grams
1 ounce (oz.)	16 drams	28·3 grams
1 pound (lb.)	16 ounces	0·454 kilogram
1 stone (st.)	14 pounds	6·350 kilograms
1 quarter (qr.)	2 stones	12·701 kilograms
1 hundredweight (cwt.)	4 quarters	50·802 kilograms
1 (long) ton	20 hundredweight	1·106 tonnes

Metric to Avoirdupois

1 milligram (mg.)		0·015 grain
1 gram (gm.)		0·564 dram
1 kilogram (kg.)	1,000 grams	2·205 pounds
1 tonne	1,000 kilograms	0·984 ton

American Weights to Metric

1 pound		453·592 grams
1 cental	100 pounds	45·359 kilograms
1 (short) ton	20 centals	0·907 tonne

Metric to American Weights

100 kilograms (kg.)	1 quintal	2·205 centals
1 tonne	1,000 kilograms	1·102 (short) tons

MEASURES OF LENGTH—*British to Metric*

1 inch (in.)		25·400 millimetres
1 foot (ft.)	12 inches	30·480 centimetres
1 yard (yd.)	3 feet	0·914 metre
1 mile	1,760 yards	1·609 kilometres

Metric to British

1 micron (μ)	1/1,000 mm. (1/1,000,000 m.)	1/25,400 inch
1 millimetre (mm.)		0·039 inch
1 centimetre (cm.)	10 mm.	0·394 inch
1 decimetre (dm.)	10 cm.	3·937 inches
1 metre (m.)	10 dm.	1·094 yards 3·281 feet 39·370 inches
1 kilometre (km.)	1,000 m.	0·621 mile

MEASURES OF AREA (*Based on* 1 *metre* = 39·370 *inches*)

British to Metric

1 square inch (sq. in.)		6·452 sq. centimetres
1 square foot (sq. ft.)	144 sq. in.	0·093 sq. metre
1 square yard (sq. yd.	9 sq. ft.	0·836 sq. metre
1 acre	4840 sq. yds.	0·405 hectare
1 square mile	640 acres	2·590 sq. kilometres 258·998 hectares

Metric to British

1 square millimetre (sq. mm.)		0·00155 sq. inch
1 square centimetre (sq. cm.)	100 sq. mm.	0·155 sq. inch
1 square metre (sq. m.)	100 sq. dm.	1·196 sq. yards
1 hectare (ha.)	10,000 sq. m.	2·471 acres
1 square kilometre (sq. km.)	100 ha.	0·386 sq. mile

MEASURES OF VOLUME—*British to Metric*

1 cubic inch (cu. in.)		16·387 cu. centimetres
1 cubic foot (cu. ft.)	1,728 cu. in.	28·317 cu. decimetres
1 cubic yard (cu. yd.)	27 cu. ft.	0·765 cu. metre

Metric to British

1 cubic centimetre (cc. = ml.)		0·061 cu. inch
1 cubic decimetre (cu. dm.)	1,000 cu. cm.	0·035 cu. foot
1 cubic metre (cu. m.)	1,000 cu. dm.	1·308 cu. yards

MEASURES OF CAPACITY—(*based on* 1 *Imperial gallon* = 4·546 *litres*)

1 American gallon—3·785 litres
1 litre—1,000 cc.

British to Metric

1 pint (pt.)—0·368 litre
1 quart (qt.)—2 pints—1·13 litres
1 gallon (gal.)—4 quarts—4·546 litres

Metric to British

1 millimetre (ml. = cc.)—0·061 cu. in
1 centilitre (cl.)—10 ml.—0·610 cu. in.
1 litre (l.)—100 cl.—1·760 pints

TEMPERATURE

0° Centigrade (= Celsius) = 32° Fahrenheit

The following formulae connect the two major thermometric scales :

Fahrenheit to Centigrade : °C = 5/9 (°F − 32)
Centigrade to Fahrenheit : °F = (9/5 °C) + 32

ADDITIONAL CONVERSION FACTORS FOR THIS BOOK

Volumes

1 cubic metre = 1000 litres = 1 million cu. centimetres
= 35·3 cubic feet
1 cubic foot = 28·32 litres

Velocity

1 metre per second = 2·24 miles per hour
= 197 feet per minute
1 foot per second = 0·305 metres per second
= 0·68 miles per hour
1 mile per hour = 0·447 metres per second
= 1·1465 feet per second

Calculation of area dose

velocity of wind	*volume through* 1 *cm.*^{2}	*wind run*
1 metre/sec.	8·64 cu. m.	86·4 km./day
0·116 metres/sec.	1·0 cu. m.	10·0 km./day

Altitude above ground

1000 metres = 3281 feet
1000 feet = 304·8 metres

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