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- To promote standardization of meteorological and related observations and to ensure the uniform publication of observations and statistics;
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WEATHER AND AIRBORNE ORGANISMS

by
D. E. Pedgley
Rapporteur on
Meteorological aspects of aerobiology

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FOREWORD

Recognizing the important effects of meteorological factors on the introduction into the atmosphere of living organisms, (viruses, spores, insects, birds, etc.), on their subsequent survival, dispersal and transport through the air, and on their final deposition, the Commission for Agricultural Meteorology at its fifth session established a working group to study the meteorological aspects of aerobiology with a view to providing aerobiologists with appropriate meteorological information for use both in their research projects and in operational activities. At its sixth session, the Commission appointed a rapporteur to prepare a report on the subject, using the information compiled by the working group and further material if available.

The rapporteur's report is now published in this WMO Technical Note.

I am confident that this publication, which has been written with the aim of bringing aerobiologists and meteorologists closer together in their combat against harmful organisms in the air, will be of interest to workers in many disciplines such as agriculture, pollution, animal husbandry and human health.

I am happy to have this opportunity of expressing the gratitude of WMO to the rapporteur, D. E. Pedgley (U.K.) for the time and effort he has devoted to the preparation of this excellent report on a complex subject. I am also taking the opportunity to extend the appreciation of the World Meteorological Organization to the members of the working group - N. Gerbier (France) (Chairman), W. S. Benninghoff (U.S.A.), J. Bowden (U.K.), H. H. Krarup (Denmark) and A. A. Omara (Egypt) - for the diligent way in which they approached the subject and compiled the relevant information which has resulted in the publication of this useful Technical Note.

(A.C. Wiin-Nielsen)
Secretary-General
SUMMARY

Aerobiology is the study of living organisms in the air, ranging in size from viruses, through spores and seeds, to insects and birds. Some of these organisms cause heavy losses in crops and bring disease and even death to plants, animals and man.

Wind affects not only displacement of these organisms but also their take-off, landing and dispersion whilst airborne. Changes in temperature, humidity, cloudiness and rainfall are also influencing factors. Chapter 2 gives an outline of commonly observed weather changes which are important in aerobiology.

Chapter 3 contains the background information required to understand the take-off, displacement, dispersion and landing of airborne organisms, as well as their death in the air. Reviews from literature have been included to show the many kinds of organisms, scales of effect and kinds of observing and analysis techniques used.

Conclusions and recommendations for further work in the field are given in Chapter 4. A comprehensive bibliography is included at the end of the report.
RÉSUMÉ

L'aérobio logie est l'étude des organismes vivant dans l'air, de la taille des virus à celle des insectes et des oiseaux en passant par les spores et les semences. Certains de ces organismes causent d'importantes pertes de récoltes et sont responsables de la maladie et même de la mort de plantes, d'animaux et d'hommes.

Les vents influencent non seulement le déplacement de ces organismes, mais également leur envol, leur atterrissage et leur dispersion durant la phase aéroportée. Les modifications de la température, de l'humidité, de la nébulosité et des précipitations sont aussi des facteurs d'influence. Le chapitre 2 fournit un aperçu des changements météorologiques communs qui sont importants en aérobio logie.

Le chapitre 3 contient les connaissances fondamentales indispensables pour comprendre les phénomènes d'envol, de déplacement, de dispersion et d'atterrissage d'organismes aéroportés, ainsi que leur mort dans les airs. Il comprend des analyses de documents qui mettent en évidence les nombreux types d'organismes, les échelles des phénomènes et les types de techniques d'observation et d'analyses utilisées.

Les conclusions et les recommandations relatives à d'autres travaux à effectuer dans ce domaine figurent dans le chapitre 4 et le rapport se termine par une bibliographie très complète.
РЕЗЮМЕ

Аэробиология занимается исследованием живых организмов в воздухе размерами от вирусов, спор и семян до насекомых и птиц. Некоторые из этих организмов наносят тяжелый ущерб урожаю и вызывают болезни и даже смерть растений, животных и человека.

Ветры воздействуют не только на перемещение этих организмов, но также на их взлет, посадку на землю и рассредоточение, когда они находятся в воздухе. Изменения температуры, влажность, облачность и осадки также являются воздействующими на них факторами. В главе 2 содержится схема повсеместно наблюдающихся метеорологических изменений, которые являются важными для аэробиологии.

В главе 3 содержится справочная информация, необходимая для понимания взлета, перемещения, рассредоточения и посадки на землю живущих в воздухе организмов, а также их смерти во время пребывания в воздухе. Обзоры из литературы были включены с целью показать многообразие организмов, масштабы явлений и типы методов, используемых для проведения наблюдений и анализов.

Выводы и рекомендации для дальнейшей деятельности в данной области содержатся в главе 4. Полная библиография находится в конце отчета.
RESUMEN

La aerobiología es el estudio de los organismos vivos en el aire, desde la talla de los virus hasta los insectos y los pájaros, pasando por las esporas y las semillas. Algunos de estos organismos causan importantes pérdidas de cosechas y son responsables de enfermedades e incluso de la muerte de plantas, animales y hombres.

Los vientos influyen no sólo en el desplazamiento de estos organismos sino también en su vuelo, aterrizaje y dispersión durante la fase aerotransportada. Los cambios de temperatura, de humedad, de nubosidad y de lluvia son igualmente factores de influencia. En el Capítulo 2 se hace una reseña de los cambios meteorológicos comúnmente observados que son de importancia para la aerobiología.

El Capítulo 3 contiene los conocimientos fundamentales indispensables para comprender los fenómenos de vuelo, desplazamiento, dispersión y aterrizaje de organismos aerotransportados, así como su muerte en el aire. También contiene un análisis de trabajos que ponen de manifiesto los numerosos tipos de organismos, las escalas de los fenómenos y los tipos de técnicas de observación y de análisis utilizados.

Las conclusiones y recomendaciones relativas a los ulteriores trabajos que han de efectuarse en esta esfera figuran en el Capítulo 4. El informe termina con una bibliografía muy completa.
CHAPTER 1

INTRODUCTION

Aerobiology is the study of living things in the air. It deals with many kinds of organisms, ranging in size from viruses, through spores and seeds, to insects and birds. Some of these organisms cannot really be said to be airborne (for example, those that are merely thrown into the air or fall quickly through it), but there are many that fall so slowly (or that fly, like many insects, by means of flapping wings) that they stay airborne for hours or days. Among these organisms are those that cause crop loss or that bring sickness and even death to plants, animals and man. It is perhaps these harmful organisms that are the greatest concern of aerobiologists.

An ability to forecast the spread of harmful organisms could bring great advantages - more efficient control of numbers of organisms, more efficient use of fertilizers and cultivation techniques, less time and money wasted on surveys and applications of pesticides that are not needed, less resistance to pesticides, and less pollution of the environment. Unfortunately, even the causes of many diseases, let alone the means of their spread, are still unknown. Some harmful insects are better understood, yet little is known about the population dynamics of most plant pests - the mechanisms affecting numbers and their complex interactions with the environment.

The development of pest and disease control strategies that are practical, effective, efficient and economical must be based on a better understanding of the organisms themselves and their ecology, particularly in the less stable ecosystems like monoculture crops or city populations. Such understanding needs the work of teams of specialists. Amongst them are meteorologists, for they can help in finding out not only how the organisms thrive but also how they might spread on the wind. Such spread may be beyond the existing range of a species (particularly important if that range is determined by impermanent habitats, and the spread may lead to the formation of new colonies), or within that range. Although movements beyond the range of a species may often be of little value for the survival of the species, they can shed light on the kinds of movement that may be taking place within the range and that are difficult to find because there are so many possible sources for an individual organism. These internal movements can lead to an unstable state if numbers build up so that natural controls (such as resistance or enemies) are swamped, and there is an explosive and perhaps disastrous outbreak.

1.1 Aerobiology and meteorology

Once airborne, an organism tends to be carried downwind, although insect drift may be more or less offset by flapping flight. Winds affect not only displacement but also take-off, landing and dispersion whilst airborne. Moreover, changes in temperature, humidity, cloudiness and rain can also play a part. Aerobiology is therefore an interdisciplinary study.
Although many ways are known whereby organisms take off, spread and land, it has been found that studies of a given outbreak are seldom easy because of a lack of knowledge or understanding of those ways. Often it is not how the atmosphere behaves that is not understood, but knowing how many organisms there are, and how they are behaving - particularly, how far they are moving in numbers enough to be worrying. Almost always in studies of the spread of a cloud of airborne organisms there is far more known about the air than about the cloud.

1.2 Layout of the report

This report discusses only a little of what is known about the behaviour of airborne organisms. It is not a full review but a selection, hopefully representative, of already published facts and ideas. It has been written with the aim of bringing aerobiologists and meteorologists closer together.

Because the fate of an airborne organism hinges very much on the weather, an outline account of commonly observed weather changes is given in Chapter 2, and is mainly for the aerobiologist who wishes to have a brief introduction to atmospheric behaviour before discussing his problem with a meteorologist. More detail can be obtained from standard works on meteorology, some of the more recent ones being listed in the bibliography (Chapter 5). Chapter 3 aims at outlining the background needed to understand the take-off, displacement, dispersion and landing of airborne organisms, as well as their death in the air. Word-illustrations have been added to show the many kinds of organisms, scales of event, parts of the world, and kinds of observing and analysis techniques that have been used in published studies. Because Chapter 3 has been written for both aerobiologists and meteorologists, each likely to have only a partial understanding of each other's discipline, there are problems with presentation, so the reader is asked to excuse what may seem at times to be the labouring of obvious points. Much of Chapter 3 is based on those parts of the books Migration and dispersal of insects by flight (Johnson, 1969) and Microbiology of the atmosphere (Gregory, 1973) that deal with weather and airborne organisms, but note has also been taken of more recent works. The outlines given in Chapters 2 and 3 highlight some gaps in knowledge and understanding which are brought out in Chapter 4 together with some recommendations for further work that might help fill the gaps.

This report does not deal with the growth and death of organisms either before take-off or after landing, even though they can be strongly weather-sensitive, nor does it deal with the ways used to sample both clouds of organisms and the weather - they are discussed in many of the textbooks listed in the bibliography - or with the aerobiology of buildings or breathing.

1.3 Users of the report

Among aerobiologists who might find this report useful are entomologists, plant pathologists, plant breeders, palynologists and allergists. For meteorologists, the aim has been to throw light on problems of behaviour of airborne organisms that might be solved with their help, the more so by micrometeorologists and synoptic meteorologists.
It is hoped that this outline review will encourage further interdisciplinary studies by showing both what has been achieved and where the main gaps in knowledge and understanding lie.

1.4 Acknowledgements

This report has been based partly on contributions by members of the Commission for Agricultural Meteorology (CAGM) Working Group on Meteorological Aspects of Aerobiology, partly on replies to a questionnaire sent to many aerobiologists, seeking their views on the application of meteorology to aerobiology but largely on the work of countless researchers whose results and opinions have been consulted in the literature. Thanks are due to all who have helped in this way, whether named or not, but especially also to those who gave their useful advice during the preparation of the report: Dr. J. Bartlett, Dr. P. H. Gregory, Professor C. T. Ingold, Dr. C. G. Johnson and Professor R. P. Pearce, amongst others, as well as colleagues at the Centre for Overseas Pest Research, London. Thanks are also due to Dr. G. Iperti of INRA and Dr. M. Launois of GERDAT for their helpful comments and suggestions.
CHAPTER 2

WEATHER CHANGES

From the discussion in Chapter 3 on the effects of the atmosphere on the behaviour of airborne organisms, it will be seen that weather changes are particularly important. This chapter therefore attempts very briefly to describe and explain for aerobiologists some of the commonly observed weather changes that are most likely to affect an organism whilst in the atmosphere, and whilst entering and leaving it. For simplicity, each of the five parameters - temperature, humidity, wind, cloud and rain - is taken separately in the following sections, but in practice it should be remembered that two or more parameters can change simultaneously and their separate effects may be difficult to discern.

2.1 Temperature

2.1.1 Temperature changes

The temperature of greatest interest is that of the organism which may or may not be the same as that of the air. In sunshine, an airborne organism will be warmer than the air, whereas on a cloudless night it will be cooler. Temperature differences are least for small organisms, and in most cases will be less than 1°C. Moreover, insects which fly by flapping their wings, generate heat in their wing muscles and differences can exceed 5°C for large insects. An organism on the ground or on vegetation will have a temperature similar to that of its underlying surface, which in sunshine can be 10°C or more greater than that of the air only centimetres away. These differences tend to be less in windy weather, when conductive heat flow to the air is enhanced. Temperature can also vary markedly across the underlying surface, according to its inclination to the Sun's rays and exposure to the wind - for example, around a tree trunk, or across an apple, or around a stone lying on the ground, or from one side of a valley to another. Differences as great as several degrees Celsius can occur across a single leaf. Cloudy skies reduce these differences because clouds cut down the intensity of both incoming short-wave (visible) radiation from the Sun and outgoing long-wave (invisible) radiation from the ground, vegetation and air. In dull, windy weather there are only small spatial differences in the temperature of ground, vegetation and air.

The atmosphere is largely transparent to sunshine; it is heated and cooled by contact with the ground and by exchange of long-wave radiation to ground and outer space. When the ground is warmer than the air, convective mixing carries heat upwards through a convective layer which is very variable in depth and can sometimes be several kilometres. Thorough mixing leads to a decrease of temperature upwards (lapse rate) at about 10°C km⁻¹ (the dry adiabatic lapse rate (DALR)). This decrease is due to (a) cooling inside the convective updraughts as they expand on rising into lower pressure aloft, and (b) mixing of the updraughts with their surroundings. The lapse rate is greater closer to the ground, where radiation and conduction dominate
convection in the upward exchange of heat, but for heights greater than a few metres the DALR can be used to obtain a good estimate of air temperature at any height within the convective layer. On a cloudless night, however, especially with light winds, the ground and vegetation tend to be cooler than the air, and heat flows downwards in the atmosphere. Air temperature then decreases downwards, and there is a temperature inversion, even as much as 10°C in 100 m. Such night-time inversions are weak or absent on cloudy or windy nights. Inside a vegetation canopy, highest daytime and lowest night-time temperatures are within the upper part of the canopy. Hence, there tends to be a temperature inversion in the lower canopy by day and in the upper canopy by night.

Temperature changes are due not only to changes in the local heat balance but also to arrival of warmer or cooler air from elsewhere. Such advection by the wind can be horizontal or vertical, and depends upon there being a wind blowing in the presence of a temperature gradient. Changes can be rapid with strong winds and a large gradient (section 2.1.2). Horizontal temperature gradients arise from differential heating and cooling of the Earth's surface by the Sun. This can happen on a wide range of scales - for example, between poles and Equator, between land and sea, between bare soil and vegetation, between air chilled by evaporation of falling rain and unchilled air. Vertical gradients (lapse rates) less than 10°C km⁻¹ arise where there is poor vertical mixing, as often happens above the daytime convective layer. Air sinking in the presence of such a lapse rate leads to warming at any given height, whereas upward motion leads to cooling. A greater sinking rate at greater heights can lead to a temperature inversion (subsidence inversion) based above the ground (unlike the night-time inversion that is based on the ground). Because both wind and horizontal temperature gradient can vary with height, temperature inversions can also form when warm air flows over cold (frontal inversion). At any one time, there can be several inversions above a given place and each may have one or more origins.

2.1.2 Diurnal* variation of temperature

Ground temperature varies from a maximum in the early afternoon to a minimum around dawn. At these times the upward and downward flows of heat just balance. The extent of the diurnal range of temperature and the shape of the temperature curve during the day vary greatly depending on season, latitude and cloudiness (affecting sunshine intensity and duration), nature of the ground (slope, aspect, density, porosity, composition - affecting reflectivity and the storage and downward flow of heat, and surface evaporation of water), and temperature, humidity and speed of the air (affecting upward flow of heat). Seas, lakes and large rivers have diurnal ranges less than 10°C, whereas bare, dry soil can exceed 50°C. Because the air is largely heated and cooled by contact with the ground, the diurnal range of air temperature decreases upwards, becoming only about 1-2°C above the convective layer. At the standard measuring height for 'surface' air temperature (about one metre above the ground), diurnal range is commonly 10-20°C in the warmer months over land, but almost nothing over the sea, and even over land in cloudy, windy weather during the

* Meteorologists use the word "diurnal" in reference to the whole 24-hour day, not just daylight hours.
cooler months in middle and high latitudes. Maximum air temperature tends to be
around mid-afternoon (when ground temperature is already falling) and the minimum is
about dawn. Depth of the convective layer also has a corresponding diurnal varia-
tion - from nil about dawn to a maximum about mid-afternoon. These diurnal changes
are often more or less modified by advective changes.

2.1.3 Sudden changes of temperature

Small but rapid fluctuations of air temperature are typical of sunny days -
changes of 1-2°C can take place within a minute. These fluctuations are caused by
wind gusts (section 2.3.3) in the presence of a lapse rate slightly greater than
10°C km⁻¹ in the lower part of the convective layer, where rising air is warm and
sinking air is cool. When the lapse rate is less than about 10°C km⁻¹, temperature
changes are reversed, but then gustiness tends to be damped. A sudden increase in
wind speed at night enhances mixing, increases the lapse rate and raises the air
temperature near the ground.

Over country having a patchwork of vegetation, soil types and topography,
and perhaps on a variety of space scales, a complex pattern of temperature can be
set up - day or night - when there is little wind. Fluctuations of up to a few
degrees and lasting a fraction of an hour, can then occur. Strong winds tend to
smooth out such irregularities.

Near coasts, strong temperature gradients can develop due to differences
in the diurnal range of land and sea temperatures. By mid-afternoon, differences of
10°C or more can occur, with comparable air-temperature differences over a few kilo-
metres, sometimes much less. A change of wind direction from offshore to onshore can
lead to a temperature fall of several degrees in as many minutes, the change then
perhaps being kept for the rest of the day. This arrival of cool sea air need not
be confined to the immediate coast - it can spread tens of kilometres inland, and
sometimes exceed 100 km by dusk or even later. A comparable temperature rise can
occur when cool sea air is replaced by a hot wind from inland. Coastal fronts,
marking the edge of cool sea air, are best developed along desert coasts.

Rain partly evaporates as it falls, and so cools the air. Some heavy
rainstorms in dry air can lead to a cooling of 10°C or more, with very strong
horizontal temperature gradients at the edge of the chilled air (10°C km⁻¹ or
greater). Outward spreading of cool air at up to 50 km h⁻¹ can lead to temperature
drops of several degrees in as many minutes.

Part of the global-scale temperature increase from pole to Equator can
become concentrated into fronts - zones tens of kilometres wide, and hundreds or
thousands long, across which the temperature may change by 10°C or more. Fronts of
this size are large enough to be depicted on weather maps shown in newspapers and on
television. They are of two main kinds, according to their movement: warm fronts,
where warm air replaces cold, and cold fronts, where cold air replaces warm. Tem-
perature changes can be as large and rapid as those at coastal fronts and rainstorm
outflows, but they are often smaller and slower and masked by effects of differences
in diurnal variation of cloudiness and rainfall from one side to another.
2.2 Humidity

2.2.1 Humidity changes

Atmospheric humidity is a measure of the water-vapour content of the air. It is expressed in two main ways: (a) absolute humidity, the amount of water vapour in the air (for example, the humidity mixing ratio, or mass of water vapour in unit mass of air), and (b) relative humidity, the degree of saturation of the air. Air is saturated when its absolute humidity cannot be increased by evaporation at constant temperature. Saturated humidity mixing ratio increases with temperature; at 0°C it is about 4 g kg⁻¹, and at 30°C about 27 g kg⁻¹. Hence, cooling of saturated air tends to give a humidity mixing ratio greater than the saturated value at the new, lower, temperature, and condensation results. For example, at 15°C, a cooling of saturated air by 1°C leads to condensation of about 0.7 g kg⁻¹. Conversely, heating of saturated air makes it unsaturated, and evaporation can occur. Relative humidity is the ratio of actual humidity mixing ratio to the saturated value at the same temperature (usually expressed as a percentage); the difference is the saturation deficit. Sufficient cooling of unsaturated air will lead to saturation; the temperature at which this happens is the dew point, which is another expression for absolute humidity.

Water vapour enters the atmosphere by evaporation from oceans and other open water surfaces, from vegetation, from soil and from falling rain. It is mixed upwards by wind gusts and then taken to greater heights in the gentle broad-scale, and usually cloudy updraughts in fronts and cyclones, as well as by the more localized but vigorous updraughts in deep convective clouds. In the presence of a temperature inversion near the ground much vapour can remain trapped in the lowest few hundred metres of the atmosphere. Thoroughly mixed air has a uniform humidity mixing ratio, but usually there is a hydro lapse - a decrease upwards. When the ground is colder than the dew point of the air, and water vapour is being condensed out of the air, the mixing ratio increases upwards near the ground. Within a plant canopy, the hydro lapse is more complex because there can be evaporation from, and condensation on, both soil and vegetation.

Absolute humidity changes are due not only to local evaporation and condensation but also to advection of moister or drier air from elsewhere - by wind in the presence of a humidity gradient. Horizontal gradients of absolute humidity arise from differential evaporation over the Earth's surface, and the dependence on temperature of saturated absolute humidity. As with temperature, horizontal gradients occur on a wide range of scales. Vertical gradients arise when mixing is not thorough and they are common. Absolute humidity can increase or decrease upwards (negative or positive hydro lapse) the variation being strongly affected by differential horizontal advection (due to variation of wind and horizontal humidity gradient with height) and to differential vertical advection. For example, the air above a subsidence inversion often has small absolute humidity because it has sunk from heights where temperatures were so low that even saturated absolute humidities were small. Relative humidity changes are more complex because they depend upon changes in both temperature and absolute humidity. For example, in thoroughly mixed air, where the absolute humidity is constant with height, the relative humidity increases upwards, because temperature decreases upwards.
2.2.2 Diurnal variation of humidity

In the absence of horizontal advection, absolute humidity can change only by evaporation or condensation, or by vertical advection. It is these processes that cause the diurnal variation of absolute humidity. Evaporation is possible if the air is unsaturated, but even then it will happen only if the soil is moist or the vegetation is transpiring. Where there is such a source of water vapour, evaporation rate grows during the morning as temperature rises and saturation deficit increases. At the same time, mixing takes place through a deepening convective layer. As a result, there tends to be a weak humidity maximum during the morning and a minimum in the afternoon, after which continued evaporation but a rapid decline in convection lead to a rise of humidity into the evening. If later the temperature of the ground or vegetation falls below dew point then dew (or fog) will form, the condensation leading to a drop in absolute humidity. Thus, there tend to be two weak maxima (mid-morning and during the night) and two weak minima (mid-afternoon and about dawn). The size of the diurnal range will depend on the availability of water and heat for evaporation, the depth of atmospheric mixing and the hydrological before mixing starts.

Diurnal variation of relative humidity is simpler because it is dominated by the diurnal variation of temperature (and hence of saturated absolute humidity) rather than actual absolute humidity. There is a maximum about the time of minimum temperature, and a minimum about the time of maximum temperature.

These diurnal changes are often more or less modified by advective changes.

2.2.3 Sudden changes of humidity

As with temperature, small but rapid fluctuations of humidity are typical of sunny days. Changes of dew point by 1-2°C can take place within a minute and are caused by wind gusts in the presence of a hydrological. With the usual upward decrease of absolute humidity, minor jumps in humidity occur with upward-moving gusts, and dips with downward-moving gusts. In contrast, when humidity increases upwards, a sudden increase in wind can bring down to the ground air with higher humidity.

Near coasts there can be strong contrasts in the diurnal variation of absolute humidity. Over the sea it is negligible, but moist sea air spreading inland is mixed by convection with drier air aloft so that surface humidity decreases and a humidity gradient forms along the coast by day. A sudden onshore wind can bring the moist sea air inland, so that at a given place the dew point increases by several degrees in as many minutes. With a more or less simultaneous fall of air temperature, there is a sudden rise of relative humidity - as much as 50 per cent in an hour where cool, moist sea air replaces hot, dry land air.

Evaporation of falling rain does not always cause a rise in absolute humidity. Where a downdraught develops, it can bring down dry air from heights of several kilometres. If the fall in humidity due to this downward advection is not compensated by evaporation, absolute humidity can fall, if only temporarily, after onset of the downdraught. Relative humidity usually rises suddenly, however, because it is dominated by the temperature fall.
WEATHER CHANGES

Absolute humidity usually changes as a front passes overhead, although not necessarily in the same sense as temperature. Hence, relative humidity may change rapidly or remain more or less unaltered, depending on the occasion. Some fronts are marked by big changes in both absolute and relative humidity, but little change in temperature; these are dry lines. Humidity changes at fronts are sometimes more complex due to evaporation of falling rain and differences in diurnal variation from one side to the other.

2.3 Wind

2.3.1 Wind changes

Wind is air moving over the ground. It has both speed and direction, the latter being that from which it is blowing. Although the wind is in general three-dimensional, its vertical component is about two orders of magnitude smaller than the horizontal component (except on certain occasions mentioned later in this section), and is therefore less than the fall speed of most airborne organisms.

Winds are caused by differential heating or cooling of the Earth's surface (although often modified by barrier effects due to the Earth's topography). Density differences develop on the various space scales mentioned in section 2.1, and these in turn lead to pressure differences that may be depicted on weather maps by patterns of isobars (lines joining places with the same pressure - corrected to some standard height, such as mean sea-level). Air tends to flow from high to low pressure, but the Earth's spin deflects the flow along the isobars, not across them. Time is needed to bring about this deflection. Hence, a wind newly set up due to differential heating or cooling will at first blow from high to low pressure (such as coastal and rainstorm outflow winds - see section 2.3.3), but after some five to ten hours (longer nearer the Equator) it will be blowing about parallel to the isobars. (This is not necessarily true when the isobar pattern itself is moving or changing shape.) Steady flow along straight isobars parallel to the Equator is said to be geostrophic. Wind systems seen on weather maps, usually lasting up to a few days, are more or less geostrophic (not quite - the difference being essential to their development, and to the formation of updraughts, clouds and rains - see sections 2.4 and 2.5). Hence, isobar patterns are a good guide to wind patterns, except close to the Equator, where the Earth's spin about the local vertical is small. These wind patterns often take the form of vortices and waves with dimensions of hundreds or thousands of kilometres (synoptic scale). Vortices spin either in the same sense as that of the Earth (cyclones) or in the opposite sense (anticyclones). A wave may be considered as a cyclone or anticyclone embedded in a broad, straight wind flow. Global-scale wind systems, such as the middle-latitude westerlies, the tropical easterlies (trade winds) and the monsoons, are also more or less geostrophic. In contrast, wind systems associated with coasts, mountains and rainstorms are shorter-lived and smaller (mesoscale), and are not geostrophic, unless the air takes about ten hours to pass through them (as may happen with winds blowing across a highland area hundreds of kilometres wide).

Winds are always accelerating or decelerating on various time and space scales; as a result, they always either converge or diverge. Because the resulting air density changes are small, convergence and divergence lead to up-and-down motions.
Convergence near the ground goes with upward motion, and divergence with downward. These motions can lead not only to formation and dispersal of clouds and rain (sections 2.4 and 2.5), but also to dispersion or concentration of airborne organisms (section 3.3). Convergence near the ground can be markedly strong near fronts (sections 2.1.3 and 2.3.3), and markedly long-lived in the intertropical convergence zone (ITCZ - a world-girdling zone near the Equator where tropical easterly winds meet from the northern and southern hemispheres, or where the easterlies meet monsoon west winds).

Both speed and direction of the wind change with height; hence surface wind need not be representative of the wind in which an organism is airborne. There are two main causes for this vertical wind shear - friction due to ground roughness, and horizontal temperature gradients. Because the effect of ground roughness decreases upwards, the depth of the layer is limited within which the wind is frictionally slowed. This planetary boundary layer is often 500-1 000 m deep; within it, wind speed varies with height more or less logarithmically, varying with roughness and lapse rate. Mixing is inhibited by a small lapse rate, and the boundary layer is then shallow. With temperature inversion, large vertical wind shears are possible. For example, on a clear, quiet night, almost stagnant air at the ground can be overlain by a smooth wind of several metres per second above heights of only a few metres. Wind direction also changes upwards through the boundary layer - clockwise in the northern hemisphere and anti-clockwise in the southern (the difference being due to the opposite spins about the local vertical). The change is about 30° but can be more with small lapse rates or inversions. When the wind blows across a change in ground roughness, a new planetary boundary layer starts to grow upwards from the ground, thus leading to the possibility of a complex wind profile.

A plant canopy bends somewhat in the wind, and its roughness is therefore less than might be expected. Within the canopy, the profile is affected by leaf density (leaf area per unit ground area) and its variation with height. For example, in a forest, where crowns are much denser than trunk space, winds are much lighter than above the canopy but there tends to be a weak maximum in the lower trunk space. Wind entering the edge of a crop is slowed by friction, and on leaving the downwind edge it is speeded up. Wind passing through a porous windbreak, such as a row of trees or an open fence, is also slowed by friction, particularly on the leeward side, thereby affecting not only the take-off and landing of organisms but also the heat and water balances of soil and vegetation.

Where winds are not geostrophic, vertical shears can be complex - as in coastal and rainstorm winds. In contrast, where winds are more or less geostrophic, the wind shear between the top and bottom of any layer in the atmosphere is parallel to the isotherms (lines joining places with equal temperature, in this case averaged through the depth of the layer). For example, with east-west isotherms and cold air on the poleward side (as occurs over most of the world for much of the time), there is a westerly wind shear. Hence, the surface westerly winds typical of middle latitudes increase with height. Shears up to 5 m s⁻¹ km⁻¹ are common, but can be as much as 10 m s⁻¹ km⁻¹, leading at times to very strong winds aloft - greater than 50 m s⁻¹ at heights of 5-10 km. These jet streams are mostly associated with fronts, where horizontal temperature gradients are strong. Westerly shear can change surface tropical east winds to west above heights of a few kilometres. Ground roughness then leads to a speed maximum in the top of the boundary layer (a low-level jet stream);
below the maximum, frictional shear is great enough to outbalance the shear due to the poleward decrease in temperature. In monsoon winds, where temperature decreases towards the Equator, there is easterly wind shear, which can reverse surface west winds at heights above a few kilometres.

Within a few millimetres of the ground or vegetation, mixing is very strongly damped by air viscosity. In this viscous boundary layer, winds are weak but not gusty, and airborne organisms have little chance of getting into gusty air unless they can fall out of the layer.

2.3.2 Diurnal variation of wind

In open country away from coasts, the wind varies diurnally because of the effect of vertical mixing on frictional drag at the ground also varies diurnally. Where wind speed increases upwards, vertical mixing brings down faster-moving air. This mixing is most effective in strong winds and when the ground is warmer than the air. Diurnal variation of wind therefore tends to be greatest in quiet weather with little cloud. Winds are lightest at night (when mixing is weakest), and they strengthen during the day as the convective layer deepens until a maximum is reached in mid-afternoon and mixing brings down air from the greatest heights. Then winds weaken as the lapse rate near the ground decreases. Such a mid-afternoon maximum is characteristic of the middle latitudes, where the westerlies often increase with height. By contrast, in the tropical easterlies and the monsoons, where speed usually decreases upwards above the planetary boundary layer, the maximum tends to be in mid-morning, for deepening of the convective layer later brings down slower air from aloft. In cloudy or windy weather, with small diurnal variations of temperature and lapse rate, the diurnal variation of wind is also small. As with temperature and humidity, these diurnal changes are often more or less modified by advective changes.

2.3.3 Sudden changes of wind

Gusts and lulls in the wind, lasting minutes or seconds, are well known. Their presence may be indicated by the fitful stirring of vegetation or the flapping of a flag. They are due to countless atmospheric eddies passing by, with dimensions less than one kilometre. There are three main sources of these eddies: instability of vertical wind shear, obstacles in the path of the wind, and convection. Vertical wind shear is unstable because the kinetic energy of a sheared flow lessens after mixing. The energy released can raise or lower eddies when such movement is resisted by the presence of a lapse rate less than adiabatic. The smaller the lapse rate, the stronger the shear that can persist without breaking down into eddies. Such eddies are probably forward-tumbling, i.e., their axes are horizontal and they lie across the wind, giving updraughts of about one metre per second. Their presence can be seen in the top of a cloud of dust or smoke blowing in the wind. A wind blowing around an obstacle sets up eddies, often breaking away either in more or less regular trains or as a jumble in a wake. Complex obstacles, such as cities, hilly country or patchy forest, can make winds very gusty.

When the atmosphere is heated from below, buoyant convective eddies appear, rising at speeds of about one metre per second to the top of the convective layer.
These are of three kinds: (a) thermals, more or less hemispherical masses of warm air, turning inside out and mixing with their surroundings as they rise; (b) plumes, more or less columnar, topped by thermals at a few hundred metres; and (c) dust devils, or spinning plumes, with winds sometimes greater than 15 m s$^{-1}$ and able to pick up dust and other loose things from the ground. Similar but more vigorous convective eddies occur over fires and in explosions. Sometimes, convective eddies are arranged in rows along the wind shear direction, or in a cellular pattern consisting of polygonal rings with either sinking air at the middle and rising air at the edges, or the other way around. Row spacing and cell width are several times the depth of the convective layer. The kinds of eddies present at any given time will depend on ground roughness, topography, vertical shear and lapse rate.

Near a coast where a strong horizontal temperature gradient has formed, a characteristic onshore wind, or sea breeze, can develop. It is a cool wind flowing beneath and taking the place of warm, land air. It starts a few hours after dawn, strengthens to 5-10 m s$^{-1}$ by mid-afternoon, and dies away during the evening. The wind at first blows onshore, from high to low pressure, but then turns clockwise (in the northern hemisphere) so that by evening it may be blowing along the coast. If at night the land becomes cooler than the sea, the wind turns further to become a land breeze, blowing from land to sea, but usually at less than 5 m s$^{-1}$. With further turning, by dawn, the wind can again be blowing along the coast. Thus, the wind turns clockwise around the compass each day (anti-clockwise in the southern hemisphere). Larger-scale advective changes, however, can greatly modify this cycle. During the day the sea breeze spreads inland and its leading edge is a windshift line, or sea breeze front. Passage of the front overhead marks the sudden onset of a wind from the sea, but the air may not have been long over the sea if it had been taken there on the previous night’s land breeze. Sea breezes are usually 500-1 000 m deep, with decreasing speed upwards above a maximum at about 200 m (due to ground roughness). Because the front moves slower than the breeze until late afternoon, it has a narrow band of updrafts of about one to two metres per second feeding a seaward return flow aloft.

A similar kind of breeze can develop over a city warmer than its surrounding countryside. City warmth (urban heat island) can be due to differences in heat and moisture balances between city and country, or to the presence in the city of an artificial heat source.

Over sloping country, the convective layer is also sloping and tends to flow upslope because it is warmer, height for height, than the air over nearby plains. In this way, an upslope or anabatic wind starts to blow during the morning, its strength depending on slope inclination, aspect, length and vegetation cover, but seldom blowing more than five metres per second. Where a valley is closed at one end, upslope winds are fed by an up-valley wind. At night, when air over sloping ground is cooled, a downslope or katabatic wind tends to blow. Downslope winds often start an hour or two after sunset, but sometimes earlier on slopes shaded from the later afternoon sun. They are weak, as shown by smoke drift, and can feed a down-valley wind, which in favoured valleys can reach five metres per second, with a sudden onset. Coastal mountains have complex wind systems with sea and land breezes interacting with slope winds.
WEATHER CHANGES

Partial evaporation of falling rain leads to a cooling of the air, which then sinks, strikes the ground, and spreads outwards. Heavy rainstorms can produce strong downdraughts, aided by frictional drag by the drops, and a strong, squally outflow. Where squalls combine from a line of rainstorms, a line squall, sometimes hundreds of kilometres long, can cross country at speeds of 50 km h\(^{-1}\) or more. Downdraught squalls arrive suddenly, often with heavy rain and changes in temperature and humidity.

Large-scale fronts, as shown on weather maps, are also often windshift lines - where there is a more or less sudden change of wind speed, or direction, or both (i.e. there is horizontal wind shear, as well as vertical). The windshift that takes place as a front passes overhead may be modified by the presence of downdraught squalls, or by barrier eddies in hilly country.

2.4 Cloud

2.4.1 Cloud changes

Clouds consist of minute water droplets or ice crystals or both, about 10 \(\mu\)m in size with densities of about 100 cm\(^{-3}\). These sizes and densities are determined by the water content (seldom more than 1 g m\(^{-3}\)), and the number density of specks (nuclei) on which water vapour condenses. Cloud particles fall through the air at speeds less than 1 cm s\(^{-1}\) - much less than most updraughts in the atmosphere. Hence, clouds appear to float in the air.

Clouds are formed by the cooling of moist air to below its dew point, either as a result of rising and expanding, or by contact with cold ground (when some or all of the condensation may be fog or dew rather than cloud). From their shapes, there are two main kinds of cloud, heaped (cumulus) and layered (stratus), depending upon the methods of formation. Convective updraughts tend to be localized and vigorous (up to about 10 m s\(^{-1}\)) and they lead to more or less detached cumulus clouds which each change quickly. Other kinds of updraughts are often widespread and gentle (about 10 cm s\(^{-1}\)), and lead to extensive stratus clouds which change slowly. Sometimes convection develops only after layered cloud has formed, resulting in the sprouting of convective towers from a layer (castellanus clouds). Gravity waves in the atmosphere enhance cloud formation in their crests and can lead to a complex patchiness within stratus clouds. Lifting of the wind over mountains can produce clouds that move or less reflect the underlying topography.

It is common to have several kinds of clouds together, and for one kind to change into another. For example, cumulus tops can spread and combine into a layer; boundary layer stratus clouds can break up and change into cumulus as a result of surface heating.

Satellite pictures show great detail about the spatial distribution of clouds, especially in relation to topography and the nature of the underlying surface. Pictures at frequent intervals allow monitoring of the growth and decline of cloud systems. Many clouds, however, are related to fronts and cyclones, and their patchiness reflects not only the updraught patterns but also the distribution of humidity that has come about due to the varied histories of different parts of the cloud systems.
2.4.2 Diurnal variation of clouds

Cumulus clouds over land, formed by sunshine heating the ground, have a characteristic daily cycle of development. They appear when the convective layer has deepened enough to allow condensation to occur in the rising thermals. Because cloud-base height increases with surface-air dryness, cumulus clouds first appear late in the morning, or not until the afternoon (or even not at all) if the air is very dry. Large clouds may last an hour or more, smaller ones much less, so although the sky may not appear to change as a whole, individual clouds constantly come and go. Latent heat released by condensation adds to the buoyancy of cloudy thermals, so that some clouds may tower up well above the top of the convective layer. Thus, both base and top rise from first formation to late afternoon, when convection begins to die away. Over the sea there is little diurnal variation of cumulus clouds - surface temperature and humidity, and hence cloud base, change little. Depth of convection may oscillate somewhat due to the westward passage of two thermal tides in the atmosphere each day.

Stratus clouds in the planetary boundary layer over land also have a characteristic daily cycle. Daytime heating is usually enough to set up weak convection, and cloud base rises as surface relative humidity falls. When the base rises to the same height as the top, cloud may disperse, usually through a broken phase and aided by mixing with dry air from aloft, or it may change to cumulus. Higher stratus clouds (such as occur at fronts or in cyclones) show little diurnal variation of amount or height. Stronger variations occur in stratus clouds formed by the spreading of cumulus tops, and in those formed by windflow over mountains.

2.4.3 Sudden changes of clouds

Sudden changes of clouds can be due to cloud formation (in ways already mentioned) and to cloud movement. Some clouds move with the wind; others grow through the atmosphere because the updraught pattern propagates through the atmosphere like waves through water. Cumulus clouds are of the former kind; large stratus layers associated with fronts and cyclones are of the latter kind - cloud forms on one edge and disperses on another, so that a layer as a whole does not move with the wind, whereas its constituent parts do. Cumulus lines and clusters related to topography can be almost stationary but, by contrast, cumulus clouds accompanying line squalls can cross country faster than the wind in which they are embedded because new clouds continually form on the downwind side.

The spread of boundary-layer stratus clouds depends not only on wind but also on space and time changes in the rates of heating or cooling. For example, such cloud in an onshore wind from a cool sea may disperse by day near the coast due to surface heating, but at night can spread far inland, arriving suddenly.

Fronts can mark a junction between airstreams with different cloud types - for example, a cover of stratus on one side and scattered cumulus on the other.
2.5 Rain

2.5.1 Rain changes

Few clouds give rain. In those that do some cloud particles grow large enough to fall out and perhaps reach the ground. Growth is either by collision, or by distillation of vapour from supercooled droplets to crystals. Collision of droplets with each other leads to rain and drizzle drops; collision of supercooled droplets with ice particles leads to hailstones; collision of ice crystals with each other leads to snow flakes. Distillation enables a few crystals to grow at the expense of many supercooled droplets. Snow and hail can melt to rain before reaching the ground. Growth takes about one hour - less in clouds with a large water content. Thus, for a cloud to give rain it must persist for at least an hour; it must also be deep enough so that the growing particles do not fall out too quickly - about 0.5 km for stratus and 2 km for cumulus.

Cumulus and castellanus clouds give local, intense and short-lived rains (showers): local because the convective updrafts have widths comparable with their depth; intense because the condensed water is at first stored in the rapidly growing and dense cloud, then released (at rates commonly 10-100 mm h\(^{-1}\)) when the drops have grown large enough to fall against the updraft; short-lived because rain-induced downdraughts tend to replace the updraughts. Stratus clouds give more widespread, lighter, but persistent rains: more widespread because the cloud layers are extensive; lighter because the water falls out at about the same rate as it condenses from the vapour (around one millimetre per hour); persistent because the cloud-forming updraughts last hours and sometimes days, and the rain-cloud sheets may take hours to pass overhead. Deep cumulus rains are typical of low latitudes, and deep stratus rains of high latitudes.

2.5.2 Diurnal variation of rain

Diurnal variation of rainfall incidence and amount depends upon the diurnal variation of cloud depth and persistence. Cumulus clouds over land tend to be largest and most persistent in late afternoon, so this is the time of day when showers are heaviest and most frequent. Showers also tend to form earlier over mountains than over valleys and plains. Showers propagating through the atmosphere, having started at some preferred site, may lead to peak frequency later in the day than expected. Large castellanus clouds can be triggered after dusk by sea-breeze fronts and by upslope winds, the latter probably accounting for night-time rainfall maxima over large tropical highlands. Sea breezes can lead to a morning maximum at the coast.

Boundary-layer stratus clouds are seldom deep enough to give more than drizzle. Places where such clouds are frequent (for example, desert coasts with onshore winds that have blown across cold, upwelled water) can have a well-marked diurnal variation of drizzle, with a maximum in the early morning. Rain from higher stratus clouds has little diurnal variation, except for weak effects of thermal tides, and over mountains where there can be diurnal variations of both relative humidity and the pattern of windflow.
All these diurnal changes are often modified by advective changes.

2.5.3 Sudden changes in rain

Unlike temperature, humidity and wind, which are with us all the time, rain is rare and its onset and cessation are often more or less sudden. They are determined by the growth and movement of rain clouds. Showers form quickly and they have more or less clearly defined edges; hence they start and often stop very suddenly, even without much movement. In contrast, rain from stratus clouds often starts and stops more gradually. Fronts can mark a junction between airstreams with different rain types, e.g. more or less continuous rain from stratus clouds on one side and scattered showers from cumulus clouds on the other.
CHAPTER 3

LIVING THINGS IN THE AIR

We turn now from the brief look in Chapter 2 at the behaviour of the atmosphere to the behaviour of things in the air. We try to do this by discussing the mechanisms involved and by giving shortened case studies that have been written at length elsewhere. The aim has been to pick out some cases to help show the many kinds of organisms and scales of happenings that have been studied, as well as ways of working, all of which might be used as guides when planning new studies. Further cases are given in the bibliography (Chapter 5).

The five sections in this chapter deal with how living things move into, with, through and out of the air, and how they are killed whilst airborne.

3.1 Take-off

Many organisms become airborne in vast numbers, but the chance is often very small that any one organism will reach a place where it can thrive. Aphids, fungal spores and pollen grains are clear examples. A tiny organism, smaller than the depth (around one millimetre) of the laminar boundary layer around the body on which it has formed or has been resting, must take off through that layer into gusty winds before it stands any chance of being carried away. There are many ways of doing this but they can be grouped into two:

(a) Active take-off, due to work done by the organism itself (such as the leap before flapping flight of an insect) or by the body of which it once formed a part (such as the throwing off of a fungal spore from its place of growth);

(b) Passive take-off, when the organism is propelled into the air by an outside force such as a gusty wind, a raindrop, or an electrostatic effect.

3.1.1 Active take-off

Active take-off may well be triggered from outside, but only when the organism is ready - as when an insect becomes able to fly, or when the part fixing a seed to a plant changes in such a way that the seed is thrown into the air. Readiness for take-off varies with the state of growth, which itself varies with past weather. Study of the growth-rate of readiness is not touched upon here because it is more a part of agrometeorology or biometeorology.

Bacteria and viruses do not take off actively; we will therefore take note only of spores, seeds and insects.
3.1.1.1 Spores

Many fungi, mosses, liverworts and ferns throw spores into the air, sometimes up to several centimetres. Thus, many species of the fungi Ascomycetes have fruit bodies in the form of tiny bags (asci) filled with sap in which spores (ascospores) are lying, and when inside pressure becomes great enough the bag opens suddenly, squirting out the spores. The fungi Basidiomycetes, however, grow their spores not within bags but at the tips of fine threads (basidia). A spore is shot off just after a drop, or a bubble, grows at the base where it was fixed. There are countless basidia beneath the well-known cap-shaped fruiting bodies of mushrooms and toadstools (raised from the ground on stiff stalks) and of bracket fungi (growing from the sides of trees, for instance), from which spores can fall into the gusty wind and be carried away. A mushroom can give off $10^6$ spores in one minute. Both groups of fungi put forth their spores into moist air, perhaps because a high relative humidity is needed for the build-up of inside pressure to bend or even break the plant cells and so shoot off the spores.

*Colonectria crotalariae*, (Loos) Bell & Sobers.
*(See Rove & Beute, 1975)*

This fungus causes a black rot disease in the peanut, *Arachis hypogaea* L. Its ascospores are sometimes shot off into the air. Cultures were grown in a chamber where relative humidity could be switched between 100 and 65 per cent. Lowering the humidity, in about 15 minutes, led to a massive discharge of spores, tailing away to nothing after about an hour, but a rise in humidity did not result in a shedding of spores.

In the small cup-shaped fruiting bodies (aecia) of rusts, the walls of strained and mis-shaped cells next to the spores are suddenly rounded off, thereby pushing the spores into the air. Some of the fungi Phycomycetes throw off their spores when the relative humidity is falling, as on most mornings after sunrise, and the branched threads on which they have grown dry out and in so doing make sudden twists. Yet other fungi have a kind of sling in which the straining cell next to a spore suddenly changes shape as a bubble forms with falling relative humidity.

Mosses grow spores in capsules; in most species the capsule simply opens with falling relative humidity, but in the bog-moss, *Sphagnum*, an air space below the spore mass is squeezed until the capsule suddenly breaks and spores are shot out.

Most ferns throw off their spores from minute capsules that split open in dry air. As the wall cells of the split capsule dry out further they become greatly strained until there is a sudden return to their former shape, due to bubble formation in the cell water, and spores are flung out as the capsule snaps shut. Leafy liverworts throw off their spores in much the same way - from the outside of a capsule that shrinks in dry air and then suddenly regains its shape as a bubble forms inside.

Only a few flowering plants - such as the nettle, *Urtica* - throw their pollen into the air.
3.1.1.2 Seeds

Many flowering plants have their seeds blown away by wind gusts (section 3.1.2.4) but some throw their seeds into the air as do fungi. A strain can build up in the seed coat, or in the fruit as a whole, due to the cells either swelling or drying out. Some leguminous plants are well-known for the sudden splitting and twisting of their pods in warm, dry weather, and similar ways of throwing off their seeds are used by other plants, among which are some Geraniaceae, Euphorbiaceae, Cruciferae and Acanthaceae. Throwing may be triggered by knocks from wind gusts or passing animals, and also rain.

**Blepharis ciliaris** (L.) Burtt, (formerly *B. persico* (Burm.) Kuntze)
*(See Gutterman et al., 1967)*

This plant, a member of the family Acanthaceae, is able to live in the dry parts of north-east Africa and south-west Asia where rains are fitful. It sheds its seeds after wetting by rain. On wetting, the four tightly fitting sepals curl back from the seed capsule, which then explodes noisily. Studies have shown that wetting the tip of the capsule releases a strain that has been built up by the varied drying of parts of the capsule. Some plants shed their seeds upon the first light rains, whereas other do so only on heavier and longer rains later in the season. Hence shedding is spread over a time when there is enough water for growth of new plants.

3.1.1.3 Insects

Most species take off soon after the winged stage comes out of its pupal or nymphaal stage (often at fixed times of day, as when flight is triggered by high or low light intensity), or after over-wintering or over-summering. It can take place only when the insect is able to fly - after growth of flight muscles, storing of food, and commencement of biochemical systems that release energy from the food. Even then, take-off may not occur until there is the right trigger from outside. Flight muscles must be warm enough to give the power needed for wing beating that will lift the insect. There is a temperature threshold below which there is no flight, and this threshold varies not only with individuals and species but also with bodily state at the time due, for example, to eating, earlier flight and sexual growth, each of which varies more or less with past weather. For small insects like aphids and thrips this muscle temperature is likely to be much the same as air temperature, but for larger insects like locusts and hawk-moths the muscles can be warmer than the air because the insect sits in the sun or beats its wings.

Sometimes many insects take off together. Such mass take-off has been attributed to several causes:

(a) After coming out of a nymphaal or pupal stage, growth goes on at temperatures below the threshold for flight so that more and more insects become able to fly although they do not take off until the weather becomes warm enough;
(b) The rate of coming-out itself varies with temperature;
(c) A few insects taking off from a crowd bring about the take-off of others;
(d) Crowding heightens the readiness for flight.

Take-off rate has been well-studied for the bean aphid, *Aphis fabae*, in summer, but many other insects may well take off in much the same way. On fine, warm days, flying density above a settled crowd of this species has two peaks: early morning and late afternoon. Newly emerged winged insects need a certain amount of heat (measured as degree-hours above a threshold) before they fly and before flight is triggered. Because temperature varies with time of day, the time needed to achieve this heat also varies with time of day. Those that become able to fly during the night do not do so because of cold and darkness, so mass take-off is held back until the temperature threshold for flight is passed, thereby giving the early morning peak. During the day, because temperatures rise, the rate at which aphids become ready to fly quickly grows so the volume density of insects flying just above the source reaches another peak, after which the density falls away as darkness comes on. A smaller density around midday can be due to too few aphids being ready to take off, not because the weather is against flight or because insects are carried aloft. If the night is cold, two few aphids are ready by the time the flight threshold is reached and so the morning peak is lost. If the day is too warm, the rate at which aphids become ready to fly is also slowed down and so the afternoon peak may be lost. With *Aphis fabae*, the range of temperatures for take-off is 9 to 28°C; it will not be the same for other species.

Many kinds of insects fly more or less straight upwards after take-off (aphids, moths, beetles, dragonflies, mosquitoes, flies and ants, amongst others), maybe because they are drawn towards a bright part of the sky (such as a white cloud) or because light is polarized differently from different parts of the sky. Once airborne, insects can be taken higher in updraughts.

Apart from temperature changes, other outside triggers cause insects to take off: changes in light strength, or things seen to be moving; smells from a host or mate; sudden noise, or the wing-beating of others of the same species. Weather acts in other ways too. For some species, take-off becomes more likely as relative humidity falls; for others the relative humidity must rise. Winds stronger than an insect's air speed often stop take-off, but short-lived lulls in the almost always gusty winds (section 2.3.3) may allow it. Moreover, a wind that is too strong at the height of measurement may not be so where the insect is positioned. A light wind, rather than a calm, helps take-off, perhaps because it is felt by organs that cause a standing insect to turn into wind before take-off. Too much or too little rain, may also trigger take-off.

Ladybird, *Semioctena undecimnotata* Schinz
(See Iperti, 1978)

This aphid-feeding species, along with others, regularly migrates during hot weather from lowlands to nearby mountain tops. Field studies at Digne (44°N 6°E), in south-east France, where ladybird movements have been
traced by using iridium-191 as a marker, have shown that take-off for migratory flight (rapid and steep climb to heights above 10 m) is favoured by temperatures above 27°C, relative humidity below 45 per cent, and wind speed (at 1.25 m) 5 m s⁻¹ or less. Males prefer lighter winds, presumably because they are lighter and have smaller wings than females.

Red Locust, Nomadacris septemfasciata (Serville)  
(See Chapman, 1959)

Like all locusts, the Red Locust is a grasshopper that sometimes gathers into swarms able to move a long way across country (see also the Desert Locust and African Migratory Locust, section 3.2.3). It is often found scattered across some of the grassy plains in eastern Africa which are susceptible to seasonal flooding. Swarms sometimes get away from these 'outbreak areas'. In a study of take-off during fitful winds, the numbers of locusts flying across fixed lines in the Rukwa Valley of Tanzania were noted. Take-off was found to be thwarted by strong winds but helped by lulls. Numbers flying were greatest about two minutes after the first dropping of the wind below 1.5 m s⁻¹, a lag that hints at take-off being helped by a temperature rise during the lull. The inside body temperature of a locust, pinned above a windvane so that it always lay broadside to the wind, went up by about one degree Celsius in the first two minutes of a lull and then more slowly. It is likely that surface-temperature changes were larger.

Blow-fly, Calliphora erythrocephala Mg.  
(See Digby, 1958)

Laboratory studies with groups of about 40 flies standing in a small wind tunnel have shown how take-off rate ('flight activity' - the number of flights by a fly in one minute) varies when wind speed suddenly changes from 0.5 m s⁻¹. Changes to both stronger and weaker winds led suddenly to slower take-off rates, whereas changes back to 0.5 m s⁻¹ suddenly gave faster take-off rates. Changes to or from a stronger wind were followed by a slow return to the rate for 0.5 m s⁻¹ winds (over 10-20 minutes - greater for longer spells at the strong wind), whereas changes to or from a weaker wind were followed by almost no trend to go back to the rate for 0.5 m s⁻¹ winds. Take-off was most rapid for 0.7 m s⁻¹ winds. These studies hint at two conflicting ways in which flies behave in a suddenly stronger wind: the first leads to a greater take-off whenever the wind strengthens, no matter what its speed is; the second cuts down take-off rate when a strong wind suddenly strengthens even more. Lulls therefore, lead to an increased take-off rate during fitful winds in the field.

Small insects on leaves heavily bathed in morning dew may be unable to take off until the leaves have dried. Rain may hinder take-off by evaporative cooling of wetted insects, but in showery weather this hindering may be compounded by changing light strength. Indeed, it is seldom easy to see which triggers help or hinders take-off when several occur simultaneously - e.g. the greater cloudiness,
stronger wind or lower temperature as the downdraught from a convective storm approaches (sections 2.3.3 and 2.5.3). This mixing of triggers may be a reason why changes in take-off rate have sometimes been put down to changes in air pressure, for pressure changes often go with changes in wind, temperature and such like, but laboratory work has shown a real link with pressure for some species.

Blow-fly, Calliphora vicina R.D.
(See Edwards, 1961.)

When a fly takes off it receives a small electric charge and therefore an electric potential. The take-off rate of flies in an earthed cage can therefore be measured by means of an electrometer. Small groups of flies were put in a cage which itself was put in a pressure chamber. The pressure was kept constant for a day, and was then made to fall steadily. Take-off rate grew as the pressure fell, but not when the pressure was steady. Sudden pressure drops (one millibar in 15 minutes) caused noteworthy jumps in the take-off rate.

3.1.2 Passive take-off

Some organisms that enter the air actively can also be knocked into it before they are ready, and are then likely to die. Others, of which there are many kinds, enter the air only by being knocked there.

3.1.2.1 Viruses and bacteria

Viruses and bacteria lying in a wet film on the outside of a body are seldom made airborne by the wind. On the other hand, water films can sometimes be broken into airborne droplets. Infected spray droplets can be formed by splashing (such as of rain or drip drops), and by the bursting of bubbles in foaming rivers and breaking waves. When a falling drop hits, say, a plant, any water film on it is suddenly swept outwards in the shape of a disc, the edges quickly splitting into jets and then droplets. In still air, such splash droplets can be thrown more than one metre the smallest fall mostly near the point of strike, but in a wind they are carried further.

When a bubble bursts at a water surface, the tiny pit it had formed falls inwards to give a jet that rises from the middle and breaks into droplets. Laboratory work has shown that bursting bubbles can set free countless microbe-laden droplets into the air. The smallest droplets from splashing or bursting bubbles can dry out quickly, leaving single or clumped microbes in the air.

Bacterium, Serratia marcescens
(See Blanchard and Syzdek, 1970)

This rod-shaped bacterium, about one micrometre long, conveniently forms easily visible red colonies. Bubbles passed through a water suspension of the bacterium and the droplets made by their bursting were collected on culture plates to give the number of bacteria in a droplet. Bacteria
density was found to vary with droplet size (radii 10-70 μm) being greatest at 30-40 μm, where it was about a thousand times the bulk density in the suspension, probably because the bacteria had been crowded into the skin of the droplet.

Infected droplets can also be formed by the sudden breaking up of films of mucus when animals breathe or, more obviously sneeze, cough or empty their guts, especially if there is much watery mucus, as when animals have illnesses of the breathing tubes or gut.

Foot-and-mouth Disease Virus
(See Sellers and Parker, 1969)

When cattle, sheep and pigs with this disease were kept in loose-boxes, and samples were taken of the air around them (once or twice a day for an hour at a rate of 1 000 l min⁻¹), the pigs were found to give off about 30 times as much airborne virus as the cattle and sheep. Most was in particles more than 6 μm across, but 10 per cent were less than 3 μm. The source was unlikely to have been blisters on tongue or feet because they had not broken when the greatest airborne density was found. It is also unlikely to have been droppings as cattle would then have been considered the main source, which is not the case; moreover, pigs gave off much virus before defecating or urinating. The most likely source was the upper breathing tubes. It is not known why pigs give off so much virus, but in any outbreak it seems they can spread disease faster than cattle or sheep.

Man adds to these sources by talking, hosing down floors, flushing water closets, bubbling air through sewage, spreading sewage and farm slurry onto fields, transporting infected milk, and the overhead watering of crops. Organisms can also take off in specks from unhealthy plants or animals, as seems to be the case with the virus causing swine vesicular disease (Sellers et al., 1974). Mucus droplets carrying microbes can land on the skin and dry out. The microbes may then be shed on rafts of skin scales or rubbed onto clothing or bedding from where they can be reshed on rafts of fibres or skin, and perhaps be caught up in buoyant air warmed by the skin (Clark and Cox, 1973). Microbe-carrying dusts like these are common in places where many people or animals live, and they encourage the spread of disease in hospitals. After settling they can be made airborne again by, for example, the movement of animals or the sweeping of floors.

Viruses can also be carried in spores, seeds and, more often, insects. Some insects that have been killed by virus diseases let off vast numbers of specks that are rafts on which the virus is carried.

Tilling the soil, particularly when it is dry, gives off many specks with bacteria, protozoa and fungal spores, some of which cause disease. Strong winds can create clouds of dust carrying these microbes.
3.1.2.2 Spores

Some simpler organisms, like Actinomycetes and Myxomycetes (slime moulds), as well as certain fungi (especially moulds such as Cladosporium, Penicillium, Aspergillus and Trichothecium), lichens, mosses, liverworts and ferns have their spores at the ends of stalks tall enough to pass through the laminar boundary layer around the body on or in which the plant is growing. The spores are knocked off and blown away by wind gusts, which can be very sharp-edged and briefly remove the viscous boundary layer so that spores are exposed to a sudden wind. Gusts also cause leaf flutter and rubbing, both of which seem to aid spore take-off. Likewise, parts of dried plants such as lichens can be removed. Various farming methods also release fungal spores, such as the very small ones that can be breathed in deeply and lead to an illness known as 'farmer's lung'.

Cereal Powdery Mildew, Erysiphe graminis D.C.f.sp. tritici
(See Hammett & Manners, 1974)

Two-to-five-week old seedling wheat plants infected with mildew were put into a wind tunnel where temperature, humidity and wind speed could be varied. Increasing the wind over a period of about one second was shown to be the way by which spores were released, whereas changes in temperature and humidity did not result in the shedding of spores, thus demonstrating the need for gusts in shedding spores from field crops.

Lead (1976) has suggested that electrostatic repulsion between a spore and the place where it is fixed may also cause sudden take-off, the charge build-up being put down to water-vapour exchange between atmosphere and plant surface.

Fungal spores are also shed into the air when knocked by falling raindrops or drips from plants, as in the following four ways:

(a) **Blowing** - a bellows-like fruit body is pushed out of shape by the falling drop, and a spore-laden puff of air blows out of a hole;

(b) **Tapping** - knocking causes leaf flutter and the shedding of spores from parts of the leaf which are still dry;

(c) **Puffing** - the spreading of a drop as it strikes a dry leaf, for instance, causes very short-lived puffs of wind in the laminar boundary layer strong enough to carry away spores from the unwetted part of the leaf;

(d) **Splashing** - breaking up of a film of spore-laden water, or even of dry spores, and carrying away on the wind of spray droplets, or the spores themselves, if the droplets are small and can evaporate quickly in dry air.

The following examples show some of the laboratory work that has been carried out on take-off of spores in rain.
(See Gregory, 1949.)

Water drops about five millimetres across were made to fall on large, spore-filled fruit bodies of this fungus, and the bellows way of throwing out spores was filmed by very high speed Schlieren cinematography. A puff of spores was found to leave 3 ms after a drop struck, and had almost come to a stop at about 2 cm after 30 ms. The smallest kinetic energy needed to form a puff was about 50 ergs - that of a freely falling rain-drop one millimetre across. In the steady rain of temperate lands, about a quarter of the drops have this kinetic energy, and for a rainfall of one millimetre there are about 200 puff-making hits on each square centimetre. Since a large puff-ball has a level area of about 10 cm², there are therefore about 2 000 hits on it for each millimetre of rain.

(See Hirst and Stedman, 1963.)

The ways whereby the spores of this fungus can be set free by rain were studied by letting water drops and glass beads fall on rusted wheat straws. When straws were stapled to cards, tapping caused spore take-off but when straws were half embedded in wax, fewer spores took off. Drops set free more spores than did beads, thereby suggesting that drops help take-off in some way other than by tapping. This idea was upheld by straws fixed to bendable plastic strips, for fewer spores took off when a straw was on the underside of a strip rather than the upper. Tests with *Lycopodium* spores on an unbendable iron block showed little take-off when struck by beads, but many spores took off when struck by drops and some of those left were spread into rings in a way that would follow from a sudden, powerful, outward-spreading puff of air from where a drop strikes.

Coral Spot Fungus, *Nectria cinnabarina* (Tode ex Fr.) Fr.  
(See Gregory et al., 1959.)

A wetted sycamore twig (*Acer pseudoplatanus*) was held at 45° to the horizontal, 10 cm above a network of sampling slides in rows and columns out to 50 cm. Five water drops five millimetres across fell on to the twig from a height of 7.4 m and each gave about 2 600 droplets by splashing. The droplets fell onto the slides, leaving clear spots in the coating of gelatin dyed with naphthal green B. Less than one droplet per square centimetre fell beyond 15 cm. All the droplets carried spores.

Fog droplets, despite their minuteness, can knock some small spores from their growing places by means of the so-called 'mist pick-up'.

Bluestain Fungus, *Ceratocystis*  
(See Dowding, 1969.)

Some species invade pine trees that have been weakened by attacks from bark beetles. Cultures were put in a wind tunnel and blown by a wind
charged with 2–60 \( \mu \)m droplets from a spinning disc. Spores were easily made airborne, even though they were knocked into the air with great difficulty by a 25 m s\(^{-1}\) wind having no droplets.

Work in the field with the mould Botrytis showed that more than 30 m\(^2\) could be infected with spores from one source during a 45-minute shower. Splashing is also the most forceful way of launching microbes from wet places. Moreover, it may well spread them upwards between the leaves of plants better than a gusty wind – after all, rainfall of one centimetre has about \(10^8\) splashing drops for each square metre of ground.

The spores of many fungi are carried by insects, for example flies, beetles and moths. Some of these fungi are parasitic; others cause fruit rots, smuts and stains. One of the most damaging in the last few years has been the fungus which causes Dutch elm disease, Ceratocystis ulmi, carried by a beetle (Scalytus) that breeds between the bark and wood of dead or dying tree trunks. The fungus grows on the walls of tunnels eaten by the grubs, and the slimy spores are carried by the new beetles as they bore their way out and fly away to feed on the new wood of healthy trees and thereby spread the disease.

3.1.2.3 Pollen

The oldest way of spreading plant spores is probably the wind. It is used for example, by fungi and ferns, as well as by conifers – the greatest bearers of pollen. Among flowering plants, however, there may be ten times as many species whose pollen is carried by insects (entomophilous plants) rather than by the wind (anemophilous plants). Grasses form the largest group of wind-pollinated plants. Grass pollen is also the most common cause of ailments such as hay fever and skin allergies, especially at the peak of flowering in early summer. As little as one grain per cubic metre of air can induce hay fever. Rushes (Juncaceae) and sedges (Cyperaceae) also give off much pollen but they do not cause hay fever. Wind-pollination is also found in many other plants but most shed too little pollen, or the plants are too sparse, to cause much hay fever, but many are known or are thought to do so. These include herbs, often summer- and autumn-flowering, among them the Compositae (especially the ragweed Ambrosia, false ragweed Franseria, and mugwort Artemisia), Chenopodiaceae (especially beet Beta vulgaris L., where it is grown for seed, and some weeds like Russian thistle Salsola, burning bush Kochia, and saltbush Atriplex), and others such as Plantago, Rumex and Artiga. Others are trees or shrubs, often spring-flowering, especially Betula, Alnus, Corylus, Platanus, Fagus, Quercus, Ulmus, Morus, Broussonetia, Juglans, Corya, Populus, Acer, Fraxinus and Ligustrum.

Flowers of wind-pollinated plants tend to be small and easily overlooked; they are well placed at the ends of branches, and often open before the leaves (as in the catkins of many temperate-latitude trees); the two sexes are not in the same flowers and even if they are in the same plants, do not open at the same time and they have anthers that stand out on slender stalks. These flowers help pollen to take off by moving in gusty winds in dry, warm weather, generally in the afternoon. Wetting by rain slows down take-off, but soon after a shower is often quickly followed by faster take-off. Hence the passing of a front (section 2.1.3) can cause great changes in the rate of pollen shedding.
Airborne pollen grains seldom have a radius larger than 20 μm and they fall with speeds of, at most, only a few centimetres per second. They are small, dry and powdery, and are therefore easily kept apart, unlike the sticky pollen carried by insects.

3.1.2.4 Seeds

Flowering plants have various ways of aiding the dispersion of their seeds by the wind (anemochorous plants). Apart from those with dust-like seeds small enough to be carried like spores or pollen (particularly those of Orchidaceae), most seeds would not be light enough to go further than a few tens of metres through the air, were it not for several methods that greatly enlarge their surface area without overly changing their weight. Three such methods are well-known:

(a) Balloons: The seed or fruit has air-filled spaces (e.g. the pods of Colutea that do not open but break away from the plant) or parts of the flower grow and then dry to give a loose, light bundle that blows away;

(b) Plumes: The seed may have long hairs - singly, in tufts, or in masses (such as cotton, Gossypium) - or the fruit may be hairy or have feathery outgrowths (pappus), so that they behave like parachutes (some Compositae). Plumed seeds or fruits are rare on forest plants, but are often found among species from open country;

(c) Wings: Seeds and fruits with two wings tend to glide as they fall; those with one wing tend to spin. Most species are trees or high climbers.

Fruits of the Ash Tree, Fraxinus
(See McCutchen, 1977.)

High-speed ciné photography of the one-winged fruits (samaras) of this tree show that they not only spin whilst falling but also turn about their long axes. The leading edge of the wing rises and moves back endlessly, with the underside moving through the air faster than the top, thereby generating lift that lessens the fall speed.

Some fruits are like pepper-shakers on long stalks, with holes through which seeds are shed when the fruit is knocked by a gust of wind. Sometimes a part, or the whole, of a dead plant breaks away and rolls along the ground, like a tumbleweed, shedding its seeds as it goes. This is particularly common in species from windswept, open places.

Some seeds are thrown into the air by falling raindrops - there may be splash cups like those in some fungi; or the fruits are horizontal pods which, when open, have their seeds knocked out; or there may be a spring-board as in Salvia.
Salvia lyrata, L.
(See Brodie, 1955)

The fruits of this plant are nutlets. They become ready for take-off at the base of a tube-like calyx that lies more or less level and is fixed to the main stem by a springy stalk. Raindrops hitting the upper side of the tube bend it down. On springing back, the nutlets are shot out to 0.5-2.0 m, guided by a groove in the lip of the lower part of the calyx. Shaking or brushing the plant knocks out only a few nutlets.

3.1.2.5 Insects and spiders

The knocking of insects and spiders into the air has been little studied. Some are pushed off plants by gusty winds or even by falling raindrops, but many wingless insects such as certain insect caterpillars and spiders, have not been knocked into the air - they launch themselves either by falling from a high place to which they have crawled, or by spinning silk threads and letting go their hold.

Gipsy Moth, Lymantria dispar (L.)
(See Leonard, 1971)

First-stage caterpillars of this moth can be carried easily by the wind; they weigh less than one milligram at hatching, have long hairs that lessen the fall speed and let out silk threads when airborne. At night, or in cool or rainy weather, caterpillars stay on the underside of leaves; otherwise they move about and feed, but when crowded some arch their bodies to the wind and let go of the leaf. Field studies using nets among oakwoods in Connecticut, U.S.A., showed that the first caterpillars were airborne the day after hatching started, and that the biggest catches occurred in the late morning.

Wolf Spider, Pardosa purbeckensis
(See Richter, 1970)

Five-to-ten day old hatchlings, about two millimetres long, were put on a wooden rack in a cage where temperature, humidity and wind speed could be varied. Spiders climbed upwards and then crawled, letting out silk threads up to 70 cm long before releasing their hold. Crawling increased in frequency with temperature, saturation deficit and wind speed (range 0.35-1.7 m s⁻¹), suggesting that, in the field, take-off would be most likely on warm, dry days with light winds. A sudden onset of the wind greatly stimulated take-off.

Another kind of passive take-off by an insect is by the plant bug Nysius groenlandicus, whose eggs are laid on the ripe fruits of the plant Dryas integriflora, which have feathery plumes and are carried away by the wind (Böcher, 1975).
3.2 Displacement

Any airborne organism tends to be carried downwind, whereas a cloud tends to be not only carried downwind but also spread out, like a puff of smoke. Dispersion is considered in section 3.3; here we treat lone organisms and those clouds, such as locust swarms, which stay together in such a way that, for displacement studies, they can be treated as lone organisms.

Before looking at some of the many cases of displacement that have been studied on various time and space scales and for a growing number of species (sections 3.2.3 to 3.2.6), it is useful to take note of how the likely trajectory, or path, of an airborne organism can be built up (sections 3.2.1 and 3.2.2). Such paths are used in studies as of the windborne spread of harmful pests and of organisms causing illnesses. We first take organisms that are not flying by means of flapping wings, for insect flight through the air may partly or wholly offset the trend to be carried downwind. The path of a flying insect may be quite unlike that taken by the wind itself.

3.2.1 Paths of airborne organisms not flying

Many kinds of organisms that are unable to fly have been found in the air; not only spores, pollen and bacteria, but also large organisms like mites, spiders and insect larvae. When airborne, these organisms are taken downwind. Their paths are often hard to follow for more than a few metres but much longer paths can be built up from maps of wind fields on the strong likelihood that an organism moves, like a balloon, with the speed and bearing of any wind in which it lies.

On scales of hundreds or thousands of kilometres, paths can often be built up from a run of weather maps. Some studies are to be found among the cases in this chapter and others are listed in the bibliography. Because weather maps can be drawn from observations made every three hours (and sometimes hourly) by national Meteorological Services, paths of airborne organisms can be built up more or less clearly for many parts of the world. But path-finding is awkward wherever there are few weather observations, such as over deserts and oceans, or in well-marked meso-scale wind patterns on scales of tens of kilometres. Further doubts often arise from not enough being known about the organism itself:

(a) The place or time of beginning and ending of a patch may be unknown. Thus, the time when fungus spores settled on a plant may have to be judged from the known or believed growth of the disease it caused, or the day when an insect pest first arrived may have to be judged from counts made, for example, every few days;

(b) Movement on the wind may not go unbroken – there can be spells spent on the ground or on plants, particularly in the case of feeding insects;

(c) The height of flight may be unknown. Because wind speed and direction often vary with height, it may be helpful to build up paths for several heights. The most likely flight height might then be obtained by noting which path crosses, or comes closest to, a known or believed source of the organism.
On the mesoscale, paths can seldom be built up from weather maps because the network of observing stations is too open to provide all that is needed for analysis of wind fields every hour or less. The likely wind field must be judged from the ways that synoptic- and smaller-scale wind patterns are thought to change each other. If mesoscale patterns are strong they can lead to crooked paths quite unlike those built up from larger-scale wind fields alone. Often, however, mesoscale patterns are weak and may be thought of as a kind of gustiness embedded in the synoptic-scale patterns.

A horizontal wind does not keep an organism airborne by itself. To arrest fall, its weight must be overcome either by drag in an updraught or by lift brought about by flapping flight. In a cloud of organisms moving on a gusty wind some will meet more updraughts than downdraughts and will therefore stay airborne longer than they would if they had been falling freely. Others will meet more downdraughts and reach the ground quickly.

### 3.2.2 Paths of flying insects

An insect's flapping flight enables it to move through the air, so its path will not in general be the same as that of the wind. We need here to note clearly the following terms:

(a) **Heading and track**: Heading, or orientation, is the bearing towards which a flying insect is pointing; track is the bearing towards which it moves. The two will not be the same wherever the wind blows at least partly across the heading, the difference being the drift angle;

(b) **Air speed and ground speed**: Air speed is that of the insect through the air - along its heading (the upshot of which is a flow of air felt by the insect); ground speed is that of the insect over the ground - along its track (the insect can perhaps sense this from the way the ground seems to move).

The air speeds of most insect species are unknown, although some are known from laboratory work, and a few from the field. By and large, air speed is greater for larger insects, varying up to about 10 m s⁻¹. Heading and ground speed are seldom noted at times of insect sightings, although tracks may be. Wind speed and bearing are also seldom noted, in the sometimes doubtful belief that the wind noted somewhere nearby can be used instead of that where the insect is flying. Schaefer (1976) has shown how powerful a tool radar can be in finding the track and ground speed of an insect (through multiple exposure photography), as well as heading (because radar sees an insect more easily sideways on than head on) and air speed (when the wind speed is known).

Two simple cases show how heading can change track and ground speed:

(a) When the heading is more or less towards some fixed compass point (like some butterflies on migration), the track is to the left or the right of the wind bearing. In the case of heading downwind, the track is also downwind and ground speed is the sum of air and wind speeds;
When heading changes occasionally to all bearings (as with locusts in some swarms) the track is very crooked, but over spells of hours or days it is downwind and the mean ground speed is the same as the mean wind speed.

If an insect flies faster than the wind it has the chance to go upwind across country, otherwise its track is more or less downwind, even if it is heading upwind.

When building up the path of a flying insect we need to know not only the wind field and its changes with time but also the way the insect flies, especially its heading and duration of flight. Some butterfly species take on a new heading when they meet a changed wind such that a track is kept more or less on the same bearing. Among cases that have been studied are: Vanessa cardui in California (Abbott, 1951), Ascia monuste in Florida (Nielsen, 1961) and Pieris brassicae in Europe (Williams et al., 1942). Because such tracks can be kept up day after day as countless numbers pass by, it was widely thought that these tracks were fixed mainly by the insects. Where heading is unknown, the most likely track may still be built up afterwards by using maps of the wind field, if heading is taken as, for example, upwind, downwind, towards a compass point, or even on all bearings. But it is known that heading can change from day to night in the same species (Taylor et al., 1973).

Insect flight is often fitful. Moreover, the time spent on flying is set not only by the amount and type of fuel carried (although flight usually ends before all fuel is used) but also by temperature, and maybe most of all by readiness to fly. Each species has a threshold temperature below which there is no flight. This temperature is of the wing muscles, which are warmer than the air during flapping flight or in sunshine. At night, if there is a temperature inversion, insects may be flying aloft even when there is little flying near the ground. The longest non-stop flight in the field is unknown for many species, but many tethered flights in the laboratory show that it can be as much as 20 hours.

Where many flying insects are in a cloud, and each changes its heading more or less to all bearings, the cloud moves downwind as a whole. A drawing together by the insects themselves may stop any dispersion that might otherwise be brought on by gustiness of the wind. Downwind movement by insect clouds is perhaps most clearly shown by the dreaded swarms of the Desert Locust (Rainey, 1963). Photographic studies of dense swarms of this locust species (Waloff, 1972) have shown that insects do not head on all bearings throughout a swarm, but mostly downwind in the upper parts. It is likely, however, that these high fliers turn and come down on reaching the front of a swarm, where they make up the locusts that are often seen near the ground heading into wind, and then settling and feeding while the front of the swarm passes overhead. This turning and settling seem to be needed to stop the shearing away of the faster-moving upper parts of the swarm; they also show why swarms move more slowly than the wind.

There are grounds for believing that low-flying insects of at least some species, when they fly into a changed wind, can quickly change their heading and air speed to keep to a chosen ground speed (Kennedy & Thomas, 1974). This is perhaps most clearly shown by insects that hover, or clouds (such as of midges) that stay almost fixed, near a marker such as a flower or twig. If an insect is heading upwind
and the wind strengthens such that the chosen ground speed cannot be reached, even by flying faster, then it may land or turn and head downwind. Because wind speeds often strengthen upwards through a layer at least some hundreds of metres deep (section 2.3.1), there may, at a given time, be a height above which heading turns downwind. The air layer up to this height is known as the insect boundary layer (Taylor 1958, 1960, 1974) which is not the same as the planetary boundary layer (section 2.3.1).

We look next at flight within this layer, and then above it.

3.2.2.1 Flight within an insect's boundary layer

Insect flight is almost always seen close to the ground, and is therefore often likely to be within the insect's boundary layer, where such flight may be quite unlike that higher up. Many insect species may well have more or less clear-cut times in their life when flight is either mostly within or mostly above the boundary layer. Thus, the so-called 'appetitive' flights, when an insect seeks a goal such as food, a mate or an egg-laying site, are likely to be within the boundary layer because an insect could then fly to any given point on or near the ground, wherever that goal may be. In some species such flights are known to be made with the help of smell plumes flowing downwind from a source, such as a settled female giving off a sex pheromone that lures flying males towards her. How an insect uses such a smell is still poorly understood (Farkos & Shorey, 1974). Flight may be thought of as being, for instance, downwind or crosswind until a sought-after plume is found and the smell strength passes a threshold that turns flight upwind. For sex pheromones at least, the threshold may be as little as a single molecule. Once flight turns upwind along the plume it may be thought of as taking place in three stages:

(a) Farthest from the source, where the plume is wide and weak, flight is fairly fast and more or less straight upwind;

(b) Nearer the source, where the plume is stronger but narrower and more easily lost, flight is slower and in a zig-zag path, still overall upwind but with turning at the edges of the plume (sensed maybe by changing smell strength);

(c) Close to the source, where the plume is very narrow and strong, flight is slower still, the path is zig-zag, and changes in flight become triggered by what the insect sees or hears, rather than smells.

If the plume is lost, flight turns crosswind or downwind until the same plume or another is found again (Kennedy & Marsh, 1974).

Two suggestions have been put forward to explain how a flying insect finds the bearing of a source, although the latter seems unlikely (Kennedy, 1977).

(a) Anemotaxis, whereby the insect lies along or at some fixed angle to the wind. The insect needs to know that there is a wind, presumably by seeing how the ground seems to move. If the wind is light, so that drift is small and goes unseen, then anemotaxis cannot be used. Nor can it be used in darkness or over featureless ground;
Chemotaxis, using the smell threads of which a plume is very likely made. These threads, in the mean, would be further apart and weaker farther from the plume axis as well as downwind or the source. A flying insect would then pass through a series of smell strengths above the threshold, the timing becoming more rapid towards either the source or the axis.

Cotton Leafworm Moth, *Spodoptera littoralis* (Boisd.)
(See Murlis & Bettany, 1977.)

Caterpillars of this moth are a pest of many crops. Ciné films of male moths flying at night to a sex-pheromone source in Crete were made with the aid of infra-red light and a night-viewing device, and showed that about 90 per cent of moths had a consistent flight pattern upwind towards the source. Moths approached with a straight and level flight and a ground speed of about 3 m s⁻¹, turned to undulating flight in a vertical plane within 2-4 m of the source and at a ground speed of about 0.5 m s⁻¹, and finally undertook vertical movements only within 0.2-0.5 m of the source and whilst still heading upwind.

Plume length will vary with source strength and time, wind speed and gustiness, and the insect's air speed and ability to smell; it is usually some tens or hundreds of metres, but in some species may be a few kilometres. Campion et al. (1974), using a pheromone trap in Cyprus to catch moths of the Cotton Leafworm, *Spodoptera littoralis* (Boisd.), found that more were caught in stronger winds over the range 1-5 m s⁻¹, suggesting that females call longer in stronger winds.

Flight can be fitful and on a changing heading, leading to small displacements, the more so in light winds with fast fliers like house-flies, blow-flies, hover-flies, screw-worm flies and tsetse flies (see the mark and recapture experiments of Cilmour et al. (1946), Lindquist et al. (1951), Schoof et al. (1952) and Quarterman et al. (1954)) or it can be steady, even against or across the wind, as with some moths and butterflies. Migration can also take place upwind. A fast-flying insect in weak winds may move 100 km a day in this manner. For example, wasps and bumblebees migrate upwind in spring over southern Finland in spells of warm, south-easterly winds and gather at the coast (Mikkola, 1978).

Coconut Leafroller Moth, *Hedylepta blackburni* (Butler)
(See Bess, 1974.)

Caterpillars of this moth are a pest of coco palm, *Cocos nucifera* L. On the windward side of the Hawaii Islands, the persistent north-easterly winds do not prevent moths from reaching trees nearest the shore, whereas their main larval parasite, an ichneumen wasp, *Trathala flavoovibalis* (Cameron), which acts as a natural control on the caterpillars in the more sheltered trees, is apparently unable to fly against the wind to the most distant trees in sufficient numbers.

Radar studies in Mali (Riley, 1975) of an unknown insect (but very probably a species of grasshopper), flying with an air speed of five metres per second at night at heights of up to a few hundred metres against a wind of two metres per second,
showed that a common heading could be kept despite their flying about 50 m apart. Such a common heading may be put down more to the way each insect keeps its own track rather than trying to fly like its neighbours, as is believed to be the case in the streams of commonly headed and closely flying locusts within some swarms of the Desert Locust. Similar common downwind headings among day-flying insects have been found using Doppler radar in the U.S.A. (Gray et al., 1975), and among night-flying moths in Kenya (Brown, 1970), where the upward beam of light from a lamp showed that 90 per cent of moths, flying mostly at four to eight metres above the ground, were heading within 22.5° of downwind.

3.2.2.2 Flight above an insect's boundary layer

By using traps on aircraft (e.g. Glick, 1939 and 1960; Berry & Taylor, 1968; Rainey, 1973) and balloons (e.g. Johnson, 1957), many insect species have been found flying at heights of up to several kilometres above the ground, often well above their boundary layers. Among these insects are strong and weak fliers, both those thought to shun strong winds (such as butterflies) and others (such as aphids) known to climb through their boundary layers. Some may reach these heights by being carried in updraughts faster than their fall speeds, as in convective cells (section 2.3.3) and at fronts (sections 2.1.3). Many insects have fall speeds of about one to two metres per second.

Volume densities (insects m⁻³) at heights above the boundary layer may be small and therefore hard to find, but the rate of flow of insects through unit area lying across the wind (insects m⁻² s⁻¹) can still be large if there are strong winds through deep layers. How far an insect goes on a wind stronger than its air speed varies more with wind speed and flight time than with air speed. The time that can be spent flying is strongly set by the readily usable fuel, as well as by age and the need to seek food, a mate, an egg-laying site or a resting site.

Strong winds, usually found far from the ground, (section 2.3.1) can lead to large displacements. Thus, unbroken flight in a wind of 20 m s⁻¹ would give a displacement of about 2 000 km in one day. Such strong winds are common in cyclones of middle latitudes, and in squall lines; they probably carry insects far and fast. Fitful flight and lighter winds can take insects just as far but over many days or weeks. Many species, even some widely thought not to move far, have now been found to be carried far away (see section 3.2.3).

No single insect has been followed along its path for more than some tens of metres. However, by marking, setting free and re-catching it is possible to find the beginning and end of a path. Moreover, back-tracking from sightings at known places and times can give truer paths if flight is taken to be downwind. Because flight paths can be far from straight, it is unwise to infer them from winds noted only at the time and place of sighting. Moreover, when studying displacements of a whole species over a spell of, for example, weeks or months, it is unwise to use mean wind fields for that spell (or even for other spells at the same time of year). This is because insects are likely to fly on some days during the spell and not on others (e.g. in strong or cold winds). Thus, long downwind displacement on a day of, let us say, warm winds from low latitudes may be followed by little or no displacement on several days with cool winds from high latitudes. The mean wind for all days could be equatorward although displacement would be poleward.
Migratory flight, where an insect has a chance to flee from a deteriorating habitat and thrive in a new one, is likely in many species to be above the insect's boundary layer, because downwind displacement will often be the swiftest way of reaching the new habitat. Many, if not most, insect species migrate as soon as the flight muscles have finished growing after the adult has emerged from the nymphal or pupal stage. Migratory flight can last from minutes to weeks, varying with the species and probably ends when physiological changes within the insect induce a change to goal-seeking flight (for example, to find food, a mate or an egg-laying site). It is harder to lure migrating insects into a trap than goal-seeking insects.

Migration may well have come about as a way of outliving fitful habitats, even though many individuals may die before reaching a place where they can thrive. A particular migration is not necessarily triggered off by a deteriorating habitat. Seasonal rains can lead to fitful habitats. Where there are seasonal rains there is seasonal low-level wind convergence in the mean, whereas in the following dry season there is mean wind divergence. Because winds tend to blow from places with divergence to places with convergence, it follows that downwind displacement will be, on average, towards and even into places where there is still likely to be rain. Two outstanding cases of this kind of migration are those of the Desert Locust and the African Army-worm Moth (section 3.2.3). Both species move into the ITCZ (section 2.3.1), perhaps the largest and longest-lived of wind convergence zones.

In crop protection, those who plan how insect pests can be killed seldom look into the likelihood of pest migration (Joyce, 1973). A knowledge that some known kinds of wind pattern lead to migration, however, makes forecasting possible some days before an insect pest is brought to crops that had been wholly or largely unin- fested thereby providing the opportunity to set the already agreed survey and control tactics into motion (Hurst, 1971).

3.2.3 Displacements on the global scale

Taking spores first, there are grounds, although not all straightforward, for thinking they can be carried over thousands of kilometres, even tens of thousands. The following points uphold this claim:

(a) Spores are found over oceans (e.g. Erdmtman, 1937; Polunin, 1955) and high latitudes (e.g. Pady et al., 1953; Polunin, 1954; Ritchie et al., 1967) far from their sources on plants and in the soil;

(b) Spores are found at heights even above three to five kilometres (e.g. Meier et al., 1938). Because approximately one day is needed for a spore to fall one kilometre at one centimetre per second (a fall speed that is large for most spores but small for most pollen grains), drift during fall would be about 1 000 km in a wind of, say, ten metres per second, a speed that is not great for heights above the planetary boundary layer over much of the world (see section 2.3.1). For a spore falling more slowly and from a height of, for example, five kilometres, a drift of 10 000 km is not unusual. Moreover, the drift of some of the spores can be lengthened if there is an updraught. (Because the time spent airborne
by at least some kinds of spores seems to be much the same as that of water vapour, which is about 10 days, spore clouds might be used to trace the path of moving air;

(c) The kinds of spores reaching a given place seem to change with path on the synoptic and global scales (e.g. Kelly et al., 1953).

It is likely that many kinds of spores can be carried on the wind to all parts of the world. There are grounds, too, for thinking that much the same kind of displacements are made by pollen and bacteria, but the seeds of only a few flowering plants seem likely to be carried so far. Species of Orchidaceae and Compositae have seeds the most easily carried on the wind - the former because they are so small and dust-like, the latter because they have plumes acting as parachutes. These species can be found on distant islands which gives some idea of how far their seeds can be airborne (although, by continental drift, the islands are not necessarily so far away, and, moreover, the seeds might have been imported, for example, by man or birds). Among Atlantic islands, the Orchidaceae of the Azores are like those of Portugal (1 500 km to the east), whereas the Compositae on Tristan da Cunha (37°S, and often in the middle-latitude west winds) are found in South America (3 000 km to the west), unlike those of St. Helena (16°S, and in the easterly trade winds), which are mostly found in Africa (1 500 km to the east).

Human epidemic diseases do not seem to be caused by organisms that are themselves carried by the wind on this scale. On the other hand, windborne displacement of infected insects may well encourage epidemics. Moreover, some plant pathogens seem to be carried a long way on the wind; among these are rusts of cereals, and maybe of coffee. The following two cases show how fungal diseases can be spread on a continental scale:

Maize Rust, *Puccinia polysora* Underw.
(See Cammack, 1958)

This fungus seems to belong to the Americas, where American maize is only slightly harmed. In 1949 the fungus suddenly arrived in Sierra Leone and laid waste to the African maize which was more susceptible to an outbreak of rust. Once there, the fungus spread eastwards, crossing the whole of west Africa by 1951, east Africa by 1952, and Madagascar by 1953. Its spread suggests that spores were carried on the wind during the maize-growing season, when monsoon winds were blowing south of the ITCZ over west and central Africa, and northerlies over east Africa reached as far south as the ITCZ over Madagascar.

Coffee Leaf Rust, *Hemileia vastatrix* Berk. & Br.
(See Bowden et al., 1971)

This fungus has long been widespread in Asia and Africa, where it can decimate the crops of *Coffea arabica*. The Americas seemed free until 1970 when the fungus was found within a few weeks scattered over an area of about 1 000 by 500 km in Bahia, Brazil. Later, the fungus was found to have been spreading in Bahia over a period of four to five years prior
to 1970. Spores could have been carried on the south-east trade winds from Africa south of the Equator. Grounds for thinking this are:

(a) The disease occurred in Angola in 1966;

(b) Spores have fall speeds of about one centimetre per second and can be airborne for about a week if first carried up to a height of one kilometre;

(c) Mean wind speeds in the lowest three kilometres of the atmosphere can carry spores across the Atlantic Ocean in about a week.

Insects may not be displaced on a global scale as often as spores, pollen and bacteria, but there are still insufficient grounds to be sure. Many species have been seen or caught in flight 1 000 km or more out over the ocean. Some locusts, butterflies and moths are known or thought to migrate seasonally over thousands of kilometres. The following cases show displacements on a continental scale; further studies may well show that other species move just as far.

Locusts are rather large grasshoppers that can change their ways when they become crowded - rather than be alone, they gather into swarms (of flying adults) or bands (of flightless nymphs, or 'hoppers'). Swarms of several species can go far on the wind. Here we look at two species from Africa and the Middle East:

African Migratory Locust, Locusta migratoria migratorioides (R. & F.)
(See Batten, 1967 and 1972)

Scattered locusts of this species can be found widely throughout Africa south of the Sahara, and small outbreaks have been observed from time to time in several countries. They feed mainly on grasses and can greatly harm cereal crops, particularly bulrush millet, Pennisetum typhoideum when huge numbers build up and lead to a plague of swarms. The last plague began in west Africa in 1928 and ended in 1941. It started on the southern part of the flood plains of the middle Niger River in Mali but reached, at one time or another, most countries south of the Sahara. Mapping the first few years of spread showed that swarms moved seasonally, reaching ever-wider areas. Swarms moved north-eastwards from about March to September, and south-westwards from about October to February, and bred during the rainy season when the monsoon winds were blowing. This to-and-fro movement indicates a link with the moving ITCZ and the seasonal turn-about of winds over west Africa. It seems that swarms moved downwind, but few were watched long enough to uphold such an idea.

It is widely believed that plagues of Locusta start from a few 'outbreak areas', with swamps lying near dry, sandy places where eggs can be laid. There may be several such areas, but only the one on the middle Niger River in Mali seems large enough for breeding of the countless, crowded locusts needed to join into swarms. On the other hand, the Desert Locust does not have such outbreak areas:
Desert Locust, *Schistocerca gregaria* (Forsk.)
(See Rainey, 1963)

This species also feeds mainly on grasses, and it is a worrying pest of cereals, sugar cane and grazing land. It also feeds on cotton plants and fruit trees, as well as other crops. In times of plague it has been found at places within an area of some 30,000,000 km² in northern and eastern Africa and in south-western Asia. Between plagues it is hemmed into a smaller 'recession area', where there may be few or no swarms. Plagues do not come at fixed times and although the causes are not fully understood, plague onset might be linked with the timing, amount and spread of the fitful rains within its often-dry 'invasion area', whereas a plague decline seems to be set biologically (Waloff & Green, 1975).

Swarms are displaced downward between seasonal breeding sites. Eggs are laid in rain-wetted soil from which they need to take up water before they can hatch. There is often only one generation for each seasonal rainfall. Migrations between about May and July (from spring breeding at the southern edge of middle latitude rains) are down the trade winds – blowing from north or north-east over north Africa, and north or north-west over the Middle East, Pakistan and India. Over east Africa, migrations at this time of year are on southerly winds south of the ITCZ. Migrations between about September and November are mostly away from the monsoon breeding areas - westwards from India and Pakistan to the Near East, and from the Sahel to north-west Africa. These are on the easterly trade winds, but on some days there is migration northwards on warm, southerly winds in the leading parts of synoptic-scale waves moving eastwards across north Africa and the Middle East. Over east Africa, migrations at this time of year are on north-easterly winds north of the ITCZ. Migrations between about December and April are away from the winter breeding areas - northwards from around the Red Sea, and south-westwards across east Africa. All these migrations have been well borne out by the mapping of numerous sightings over more than forty years. No two years are the same, because rains can fail and locusts can breed in different places each year. For a much fuller look at, and many case studies of, this species - the most studied of all migratory insects - see Rainey, 1963 and Waloff, 1966.

From the links between weather and the habits of the Desert Locust, forecasts of likely breeding and displacement have been made for many years, based on knowledge of day-to-day changes in both weather patterns and locust groupings (Betts, 1976). These forecasts have been made mostly for spells of several weeks ahead (when they have been used in many countries to help plan strategies of survey and control), but forecasts have also been made for:

(a) A few days ahead, if foreseeable weather changes seem likely to lead to a sudden movement of locusts;

(b) A few months ahead (when they can be used for long-term planning).
African Armyworm, *Spodoptera exempta* (Walk.)
(See Brown et al., 1969.)

The African Armyworm is the caterpillar of a night-flying moth, and is so called because it tends to crawl in huge numbers, sometimes at densities greater than 1 000 m\(^{-2}\). It feeds on wild grasses as well as cereals and pasture, in eastern and southern Africa, and can cause as much harm as the locust. Outbreaks vary in size from year to year. At a given place there are large seasonal changes in the numbers of caterpillars, and outbreaks have a strong tendency to follow one another in place and time. Thus, the first outbreaks in east Africa are often in Tanzania at the end of the year, and later outbreaks are farther and farther north, reaching Ethiopia by the middle of the year. The suddenness of these seasonal outbreaks, after months with none in the vicinity, takes farmers unawares and gives grounds for thinking they came from a sudden inrush of parent moths. This view is supported by the fact that there seem to be no differences in enzyme systems from 17 specimens caught up to 2 000 km apart in east Africa (Den Boer, 1978). As yet, moths have not been tracked downwind, but such a movement seems very likely. Downwind displacement would take moths towards and into the ITCZ, so that most of the insects, whether caterpillars or moths, would be near the ITCZ, where rains fall and grasses grow. Moreover, the following generations would move with the ITCZ as shown by catches from a network of moth traps over east Africa. Huge numbers of moths carried downwind can lead to eggs being laid in very close proximity. The subsequent dense masses of caterpillars pupate in the soil after about two weeks and the moths emerge and leave at night, often unseen. As the part played by weather in the timing of outbreaks became better understood, a forecasting service was initiated in 1970 (Betts, 1976) utilizing: (a) weekly news by telegram of numbers of moths caught nightly at each of the traps in the network; (b) links between changes in moth numbers and outbreaks of caterpillars (based on catches and outbreaks from earlier years); (c) wind fields at the time, and (d) a study of the changing spread of moths and caterpillars in earlier years.

A case for long flights over the ocean lasting a few days has been fairly well made out for several species of moths. The following two studies were for the Atlantic Ocean.

Small Mottled Willow Moth, *Spodoptera exigua* (Höbner)
(See French, 1969.)

Caterpillars of this moth, known as the Lesser Armyworm (Beet Armyworm in the U.S.A.; Pigweed Armyworm in South Africa), are a pest of much of central and northern Africa, feeding on the leaves of most plants. It is unlikely that this species over-winters, as pupae, in Europe north of about 44°N, yet this moth comes to Britain almost every year. On 6 May 1962, it came to southern England in such numbers as had not been seen for many years. Sightings and catches of the moth by many amateur
entomologists showed that the time was around mid-evening and that most crossed the coast about 50°50'N 01°35'W. Such careful timing and placing enabled a back-track to be built up, starting at 1800 GMT on 6 May and going back to 1200 GMT on 4 May, beyond which time back-tracking was difficult because winds were light near the middle of an anticyclone. An air speed of one metre per second was taken, as well as a northward heading (as there might be for a spring migration). Wind fields and temperatures from 1 to 3 May over the coasts of Portugal, southern Spain and Morocco showed that the most likely place and date for the source of the moths was Morocco on 2 May. Thus, there seems to have been an unbroken spell of flying over the sea lasting about four days. This is a long time, and landing on the sea would surely have led to drowning, so it is possible that many were killed that way and only a few reached England. Winds could have brought moths from north-west Spain on 5 May, or north-west France on 6 May, but the numbers seen or caught in England must have come from a source far greater than any likely to have been in Spain or France during May. Moreover, the moths were more widely spread along the south coast of England than if they had come from nearby sources. Mild south-south-west winds such as were blowing on 6 May 1962 were found on all other notable moves by this moth to England between 1947 and 1963, with sources early in the year in Morocco or Madeira, but from May onwards in north-west Spain.

Diamond-back Moth, *Plutella xylostella* (L.)
(See French & White, 1960)

Caterpillars of this moth are a pest of cruciferous plants over most middle and tropical latitudes. At 1200 GMT on 4 July 1958 many moths were seen on an Ocean Weather Ship at 59°N 20°W. These moths were part of a great westward flight that had reached north-east Britain on 28 June, later crossing mainland Scotland and the Shetland Islands to the ship, as well as to the Faroe Islands and Iceland. Back-tracks from the ship, and from two other sightings, taking errors of about one metre per second in the winds used, gave paths coming from western U.S.S.R. at 1200 GMT on 29 June. Weather there in the ten days before would have let moths come from their pupae in large numbers, and they were seen at the end of June in Finland, Sweden, Estonia, Norway and Denmark. Caterpillars later ate cruciferous crops throughout Britain, but the harm done was much less than it might have been, partly because of the control undertaken following widespread warning of the sudden arrival of great swarms of moths.

Perhaps the greatest fetch so far known for displacements of moths and butterflies is across the Atlantic Ocean, for which fair cases can be made out for two species:

Stephens Gem, *Autographa biloba* (Steph.)
(See Hurst, 1969)

This moth, formerly *Phytometra biloba*, belongs to North America and is seldom seen in Europe or Africa. Nevertheless, lone moths have come to
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Britain. The first known sighting was on 19 July 1954 near 52°25'N 4°05'W. If this moth is assumed to have come two days earlier (a lone moth is unlikely to have been seen only hours after coming), a back-track gives a source over West Virginia, with a flight lasting about three to five days in strong, warm, west-south-westerly winds. The second sighting was on 1 October 1958 near 50°30'N 3°30'W, for which a four-day path from near Boston can be built up if the moth is assumed to have come to Britain the day before.

Monarch Butterfly, Danaus plexippus (L.).
(See Burton & French, 1969.)

This well-known migrant of North America (Urquhart, 1960) does not breed in Europe, yet more than 60 were seen in Britain in 1968. The first to come in any number were on 3 October, but by the middle of the month they were seen at several places in southern and western Britain. Back-tracks for the period mid-September to 7 October showed only one chance to cross the Atlantic, taking three days ending late on 28 September, in gale-force warm-sector winds. Of course, as with the two likely crossings by Stephens Gen, the insects may have come at least part of the way by ship. The coming of American birds along with the Monarchs, however, and in numbers unheard of before, upholds the idea of an Atlantic crossing.

Crossing the Atlantic at low latitudes, if it happens, would most likely be only from east to west, because west winds there are fitful and do not go far from land. Although such crossings have not been proven, several species of insects have nevertheless been seen in mid-ocean (Johnson & Bowden, 1973).

Viruses that cause illnesses in animals also seem able to be taken across continents by infected flies carried on the wind.

Ephemerol Fever of Cattle
(See Murray, 1970.)

This viral disease has been found widely in the tropics. It is marked by a sudden fever lasting a few days, often with lameness, shaking, and watering from nose and eyes. It seldom kills, but milk yields may fall, and there can be a troublesome break in the breeding plan as well as in the moving and marketing of stock.

In 1967-68 there was a big outbreak in Australia. It was first discovered near Darwin on 25 September 1967, after which it spread east and then south-east to reach north-western New South Wales and north-eastern South Australia by early February, and the east coast of Victoria by the end of February. It did not reach southern South Australia, southern Victoria nor Tasmania. Such a wide and swift spread of the disease could not be put down to the moving of stock. Moreover, in the later stages there were enough data to show that lone animals, in herds well apart from each other, were becoming ill along a front 500 km broad and moving at about 300 km a week. The most likely cause of this spread was the wind, for it could be linked with the onset of monsoon west winds over northern Australia, and
particularly with north-west winds on the eastern side of the slow-moving summer cyclones common over inland Queensland. Moreover, subtropical anticyclones moving slowly eastwards over the Tasman Sea let northerly winds flow at times from Queensland into south-eastern Australia. Two such anticyclones gave spells of strong, hot northerlies from 26 January to 2 February, and from 12 to 20 February. As about a week is needed for the virus to grow in cattle before they became ill, these spells coincided with the spread. The virus is probably carried by the midge Culicoides, so it is not surprising that the disease can spread downwind on such a small, weak flier.

3.2.4 Displacement on the synoptic scale

There have been only a few studies that link the displacement of spores to wind fields on this scale, despite their undoubted bearing on the spread of pathogens and allergens. The role of wind in spreading plant diseases is difficult to ascertain as so little is known about the way these diseases actually do spread. Hence, the part played by synoptic-scale wind patterns in fixing the times and sizes of peaks on spore and pollen cloud densities at a given place cannot yet be measured. There is much scope for work linking changes in wind fields to the day-to-day and hour-to-hour changes in cloud density. The following three causes show the kinds of studies that have been made:

Structure of a spore cloud
(See Hirst, Stedman & Hurst, 1967)

On 15 June 1962, south-west winds covered Britain and the North Sea. An aircraft fitted out to sample spores was flown over the southern North Sea. To obtain profiles of cloud density and spore type, but also to save the time needed for spiral climbs, a 'saw-tooth' plan was used with up-and-down flight on a fixed bearing. In this way the spore cloud was looked at up to a height of 1.8 km and along a downwind track of 350 km. There were three kinds of spores: world-wide Cladosporium, pollens and 'damp-air' spores. (The first two take off mostly by day, and the last by night.) Each kind had smallest density about 100 km offshore, and largest about 300 km offshore. Back-tracking gave the following most likely sources: at the north-eastern end of the flight - south-west England on the day before; at the south-western end - north-west France on the day before, or the south-east England on the morning of 15 June. Densities tally with this and show that clouds of spores set free by day can be found far downwind. The cause of fewer spores being set free by night than might have been expected along the middle of the flight-track is unknown. Smaller densities near sea-level rather than aloft may have been due to settling onto the sea. Largest pollen densities were at a height of 500 m, and of Cladosporium at 1000 m, the lower height for pollens perhaps being caused by their falling faster than Cladosporium.
Tree Pollen in the Shetland Islands
(See Tyldesley, 1973)

The Shetland Islands are situated at 60°N 1°W with the nearest land being 250 km to the south-west and 400 km to the east. It is mostly moorland and there are almost no trees. Pollen caught in traps comes from rushes, sedges and grasses (in spring) and from heather (in summer); tree pollen can come from only faraway sources. During 1970, when 25 m³ of air were sampled each day, tree pollen came in two main spells: 5–19 May (mostly birch, *Betula*) and 2–10 June (mostly pine, *Pinus*). Daily back-tracks for the latter spell ending at 00 GMT, based on six-hourly surface weather maps, showed that the peak catch on 9 June fitted with a short, swift displacement on east winds from Scandinavia, whereas the much smaller catches on other days came with longer paths over the sea. There was no tree pollen on 11 June which tallied with a sudden change to northerly winds behind a cold front.

Pollen over the North Atlantic
(See Erdtman, 1937)

From 29 May to 7 June 1927, pollen in the air over the North Atlantic Ocean was sampled daily during a westward passage of the M.S. *Drattningholm*. Vacuum cleaners were used to draw air through filter papers at about one cubic metre per minute. There were three peak catches:

(a) Sample I, when southerly winds were blowing across the North Sea, and most pollen was *Pinus* (most likely from a source over north-west Europe);

(b) Sample V, when north-westerlies were blowing from Newfoundland behind a cold front that had passed the ship late on 3 June, and most pollen was of *Alnus* and *Cyperaceae*;

(c) Sample VII, when south-westerlies were blowing offshore from northeastern U.S.A., and most pollen was of grasses (*Gramineae*), *Plantago* and *Rumex*.

Elsewhere, cloud densities were smaller, but in a sample taken between Ireland and Iceland there was a noteworthy mingling of pollens from trees, shrubs and herbs. North-west winds were blowing around a depression moving slowly east from Iceland to Scandinavia, most likely bringing European pollen that had been airborne for at least a few days on a long curved path over the open ocean.

Poplar Rust, *Melampsora*
(See Wilkinson & Spiers, 1976)

Two species of this rust were first seen in New Zealand in March 1973, but since then they have become widespread and have led to severe leaf
loss by the semi-evergreen Populus nigra cv 'sempervirens'. Rust is very unlikely to have come on cuttings because they are subject to strict quarantine regulations. Moreover, the pattern of spread through New Zealand suggests that the rust uredospores are readily windborne and remain infective far from their sources. First sightings at two places 450 km apart suggest an outside source. Both species had been present in Australia in February 1973, and had become widespread in New South Wales. From the size of the infection at first sighting, it seems that rust spores came to New Zealand some time between late February and early March when winds were mostly easterly over the Tasman Sea; there were westerlies only from 1 to 3 March. A forward tracking from New South Wales starting 1 March reached New Zealand after two to three days, so it seems very likely that the rust spores travelled more than 3 000 km over the sea.

There have been many studies of displacements of insects within synoptic-scale wind patterns. Most have been for middle latitudes of the northern hemisphere, over fetches of 1 000 km or more, and by many kinds of insects, such as beetles, aphids, plant-hoppers, leaf-hoppers, butterflies, moths and dragonflies. Displacements are often polewards within warm winds blowing towards higher latitudes, the more so to the east of slow-moving cyclones (or the west of anticyclones) and often for spells of up to a few days. With winds near the ground of, let us say, 10 m s⁻¹, displacements of several hundred kilometres in a day are not surprising, and could reach 1 000 km or more in a week, even with spells of settling. Swifter displacements are possible in the stronger winds likely to be blowing aloft, especially where there is a low-level jet stream (section 2.3.1; see also Wallin & Loonan, 1971). Such displacements can throw light on the causes of insect pests suddenly being seen far from known areas, even across wide stretches of open water. They can likewise cause places to be suddenly free of insects.

Many sightings at sea throw further light on the range of flight that can be kept up without a break, and by many kinds of insects, such as aphids over the North Sea (Hardy & Milne, 1937), Desert Locusts over the Atlantic and Indian Oceans (Wolff, 1960) and many species over the Pacific Ocean (Guilmette et al., 1970). Although few of these over-water flights have been linked with the synoptic-scale wind patterns at the time, a noteworthy case is that of mosquitoes seen about 170 km off the eastern coast of the U.S.A. (Curry, 1939), one of the earliest cases when synoptic weather maps were used in studies of insect displacements. The following are some of the many case studies that have been made since then:

Oriental Armyworm, Mythimna separata (Wlk.)
(See Lin et al., 1963; Li et al., 1964.)

Like the African Armyworm, this is the caterpillar of a night-flying moth (syn. Leucania separata Wlk.). It feeds on cereals and a wide range of other plants over southern and eastern Asia, the Pacific islands, eastern Australia and New Zealand. In China, where it has been known as a pest for more than 2 000 years, the moth flies in spring from southern and eastern parts into the north-east. This migration, and a return in autumn, was shown to take place during 1961–63 by marking with dye and
setting free about two million moths that had been caught after being lured to bundles of baited straw. Twelve moths were caught again after having flown straightline fetches of 600-1400 km in one to three weeks. The sudden arrival of moths in spring over north-east China cannot be attributed to an over-wintering by caterpillars or pupae, because they do not withstand the winter cold. Moreover, because moths can come suddenly to wide areas within one day, they must surely be migrating. Wind-bearing at several places in north-east China on days in spring when moths were first caught, or when there were sudden peaks in numbers, were most often from the south or south-west, supporting the idea of downwind displacement based on the catching of marked moths.

Gipsy Moth, Lymantrio dispar (L.)
(See Mikkola, 1971)

This moth is a pest of many shade, fruit and woodland trees in middle latitudes of the northern hemisphere. Leaves are stripped in the spring by caterpillars that have come from over-wintering eggs. The species is spread by young caterpillars being carried on the wind up to some tens of kilometres (section 3.1.2.5). Although the male moths are strong fliers, the females seldom, if ever, fly in Europe, North America or Japan. Eggs are laid very close to the place where the female has emerged from the pupa, so it is hardly surprising that migrations have not been observed - except in U.S.S.R., however. On the night of 25-26 July 1958 there was a huge flight of both male and female moths near Moscow, and on 28 and 29 July nine males were caught at six places in southern Finland. Weather maps show that a cyclone moved slowly north-westwards from the Black Sea between 26 and 28 July. A warm front moved west across Moscow on the night 25-26 July and across Leningrad near midday on 27 July, becoming slow-moving along the west coast of Finland by midday on 28 July. This front was followed by warm south-east winds. A back-track from Tampere (61°30'N 25°45'E), where the first of the nine moths was caught near midday on 28 July, puts the Finnish moths passing north-east of Moscow one day later than the huge flight there. This seemingly wrong timing might be due to fitful flight: it could have been mostly at night rather than by day, or largely within the converging winds of the front. The source of moths was most likely to have been about 200-300 km south-east of Moscow, among forests where the leaves of about 300,000 ha of trees had been eaten (about a third of the area stricken in the entire U.S.S.R. during 1958). The 1300 km flight to southern Finland is likely to have taken 60-90 h, on three or four nights. The moths were of a pale-coloured race seemingly unlike those from Europe, North America and Japan. The flights by females of over 1,000 km may be connected with the ending of seasonal rains in their forest habitat, where loss of leaves in spring cannot be compensated during the summer drought.
Plant-hoppers, *Sogatella furcifera* (Horc.) and *Nilaparvata lugens* (Stål) (See Kisimoto, 1976.)

These two pests of rice, the White-back Plant-hopper and the Brown Plant-hopper, are found over wide areas of south-eastern Asia, causing yellowing, dwarfing or withering of plants. In Japan they do not over-winter, but come to the paddy-fields every June or July, sometimes in mass flights. Trap catches are greatest in south-western Kyushu, supporting the view that the insects come from the south-west. Between 1600 and 2000 LT on 25 June 1969, there were large catches in tow-nets at Chikugo (33°15′N 130°25′E), mostly in the south-west winds of a warm-sector cyclone, the more so near its cold front and maybe in a low-level jet stream. The sources for this and other sightings in Japan are unknown, but may have been China, since many of the cyclones at the time of peak catches came from China across the Yellow and East China Seas.

**Cotton Stainer, *Dysdercus voelkeri* Schmidt** (See Duviard, 1977.)

This bug occurs widely throughout west Africa south of the Sahel. In summer, it is limited in the north by a mean yearly rainfall of about 500 m (which sets the northern limit of its malaceous host plants), and in the south by the northern edge of heavy rains (which kill the nymphs by drowning or inducing fungal disease). In winter, it is limited in the north by the ITCZ, and in the south by the coast of west Africa. At any one place, the bug appears suddenly in large numbers after several months' absence as a yellow form at the onset of the dry season in the south of its range, but as an orange form at the onset of the rainy season in the north of its range. In 1973, a line of traps from 5° to 1.5°N was set up in the Ivory Coast, and the variation of peak catch with rainfall suggested migration – north-eastward by the orange form on the mainly south-west winds of the monsoon, and south-westward by the yellow form on the mainly north-east winds (harmattan) of the dry season.

**Senegalese Grasshopper, *Oedaleus senegalensis* Krauss** (See Launois, 1978 and Lecoq, 1978.)

This grasshopper, like many other species in west Africa, now seems to be much more mobile than was once thought. Field observations near Ouagadougou, Upper Volta, (12°N 2°W) in 1975-77 on changes in numbers of this and other species, strongly suggest that seasonal fluctuations are due to adults flying into and out of the area as the wind changes direction with the passage overhead of the ITCZ twice a year. Adults arrive with the onset of north-east winds about October, lay their eggs and die. The eggs develop only after rain about the following May or June, when the ITCZ has moved north again. After fledging, the new generation adults move away on the monsoon south-west winds, to lay their eggs further north. These movements allow the grasshoppers to take advantage of seasonally varying habitats, and they help to explain sudden upsurges following years of drought.
Malagasy Migratory Locust, *Locusta migratoria capitata* Saussure
(See Lecoq, 1975)

Southward movements of low-density populations of solitaries of this sub-species into the southern tip of Madagascar are associated with the onset of north winds at the start of the rainy season. The north winds appear when the ITCZ moves to about 25°S, mainly in December and January, and especially when there is a cyclone in the Mozambique Channel. Such movements can also take place in north winds ahead of a cold front approaching from the south-west. Population density can increase a thousandfold over a few days in the presence of wind convergence, and may lead to the formation of swarms that later move north as the ITCZ retreats towards the Equator.

**Bush-fly, *Musca vetustissima* Walk.**
(See Hughes & Nicholas, 1974)

This bush-fly is found throughout Australia, the grubs feeding on animal dung. It can be very troublesome, pester and his animals by seeking sweat and mucus. Around Canberra there are no flies in winter and the first are seen in spring (late August–mid September). Physical changes due to age (e.g. by growth of ovaries, head width, and numbers carrying nematode worms) show that there are likely to be two or three waves of flies, bred further north on fresh dung from animals feeding on plants growing on the spring rains, arriving each spring during warm weather. Southward spread across eastern Australia occurs during spells of warm northerly winds on the western sides of subtropical anticyclones moving eastwards, the southern limit being where low temperatures stop flight.

**Six-spotted Leaf-hopper, *Macroteles fascifrons* (Stål)**
(See Nichiporick, 1965)

This insect is the main carrier of the Aster Yellows mycoplasma, the cause of a disease in vegetable crops, barley and flax, inciting a yellowing of the leaves. Insects in Manitoba, Canada, come on strong, warm south winds. The first insects at Winnipeg in all years but one from 1954 to 1964 came in May. Using weather maps showing winds near the ground and at 1 500 m, back-tracks were built up for 24-hour spells (or less if the paths went into parts where winds were lighter than five metres per second, or there was rain, or the right host plants). In 14 cases, the main sources seemed to be the Dakotas, Nebraska and Kansas - all south of Manitoba. Each spring there are spells of south winds able to bring the insects to Manitoba.

**Mosquito, *Aedes vexans* Meigen**
(See Horsfall, 1954)

In early September 1953 this mosquito spread to many parts of Illinois. Surveys between 4 and 11 September showed widespread infestations where
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no mosquitoes had been caught on several surveys in August. There had been no sites fit for breeding for two months and the most likely source was in Wisconsin, about 400 km to the north-west, where between 1 and 4 August there had been heavy rains leading to the establishment of breeding sites. At the end of August and the beginning of September the weather was hot and dry, but a cold front moved south across Wisconsin on 3 September and across Illinois the next day, and the mosquitoes seem to have spread southwards with the northerly winds that followed.

Australian Blue Moon Butterfly, *Hypolimnas bolina nerina* (f.)
(See Tomlinson, 1973)

This butterfly is not often found in New Zealand, but many were seen at Nelson (near 41°20'S, 173°15'E) on 23 April 1971, where they stayed for several weeks but did not last out the winter. Back-tracks ending in Nelson at noon on 23 April, based on winds between 300 and 1 000 m above sea-level, show that downwind flight would have brought the butterflies from Victoria or southern New South Wales, taking about three days for the 3 000 km flight in the westerly winds that had been blowing over the Tasman Sea.

3.2.5 Displacements on the mesoscale

Airborne organisms can move 100 km a day within synoptic-scale and mesoscale wind fields. There have been only a few mesoscale studies of organisms not flying, even though some bring serious diseases.

Footh-and-mouth Disease Virus
(See Smith, 1970 and Hugh-Jones & Wright, 1970)

This virus causes a disease of cattle, pigs and sheep. It has long been thought that the disease is spread by transporting sick animals or their milk, meat or wastes, and by such carriers as people and vehicles. Even so, there are strong grounds for thinking that spread can also be on the wind. Thus, between October 1967 and January 1968 there was a very worrying outbreak in Great Britain - animals on over 2 300 farms had the disease. The outbreak started eight kilometres south-west of Oswestry (near 52°50'N 3°05'W), where sick pigs were found from 21 October onwards and were slaughtered on 26 October. The disease probably spread from this farm around the 25-26 October, when it would have been at its most contagious. The majority of the 44 outbreaks between 27 October and 1 November are likely to have come from this farm. Furthermore, most of these outbreaks were in the north-east, whilst winds between 22 and 26 October were from the south-west. Three strange things about these outbreaks suggest that standing gravity waves in the atmosphere (section 2.3.2.2) helped the spread: (a) the outbreaks were in three clusters; (b) the clusters were about 20 km apart; (c) outbreaks occurred within a week of the first (about the incubation period). Waves were most probable on the afternoon and evening of 25 October. If they did
help the spread this would explain the grouping and the long displacement downwind. Indeed, the speed of spread may have been due to the chance occurrence of standing gravity waves over a first outbreak (Tinline, 1970).

Viruses are set free in specks, mainly from the breathing tubes and can drift on the wind for several hours before being breathed in by another animal. Spread coincides with cloudy, rainy weather which can be attributed to the better chances of viruses staying alive in moist air, and perhaps to wash-out by falling raindrops (section 3.4.2.3). Wash-out is more likely to help spread the disease afar because rain would sweep up the more easily displaced small specks rather than the larger ones, which would fall out on their own nearer the source.

Once the moving of stock, people and vehicles has been banned following an outbreak, and the incubation period has passed, it is possible to obtain some idea of windborne spread, which will help in the search for new outbreaks. What is needed then is a knowledge of virus output rate (number and placing of sick animals), the wind field and humidity up to some tens of kilometres from known outbreaks, and the number and placing of healthy livestock (Sellers et al., 1973; Sellers & Forman, 1973).

Many insect species are displaced over tens of kilometres, but few of these flights have been linked to contemporaneous winds. It is likely that mesoscale wind fields, particularly sea breezes and downdraught squalls, play an important role in the hour-to-hour changes in the spread of many kinds of airborne organisms.

Weather changes at cold fronts (sections 2.1.3 and 2.3.3) have been linked with sudden sightings of moth clouds. The links are not yet clearly understood, but it is likely that strengthened winds behind a front, or at a squall line ahead of it (section 2.3.3), carry moths into any convergence zone there may be at the leading edge of the strong winds. Moreover, changes of, for example, temperature, gustiness or light at many fronts, may trigger off mass flight and lead to sudden swarming. The following three cases of insect clouds at cold fronts are from North America and Australia:

Forest Tent Caterpillar, Malacosoma disstria Hübner
(See Brown, 1965.)

Caterpillars of this moth eat the leaves of many kinds of shade and forest trees in North America. Eggs over-winter on twigs; caterpillars hatch in spring, and moths come as swarms in summer. On 13 July 1964 many moths were seen in and around Calgary, Canada (51°05'N 114°05'W), and a survey showed that moths had come suddenly to large parts of southern Alberta. Their likely source was west of Edmonton, where many moths had been seen on 11 July. Weather maps showed that a southward-moving cold front had crossed the outbreak area in the middle of the afternoon on 12 July and reached the far south of Alberta early on 13 July. Displacement of moths seems to have taken place in the northerly winds behind the front.
Eastern Spruce Budworm, *Choristoneura fumiferana* (Clem.)
(See Henson, 1962)

Like the aforementioned species, caterpillars of this moth are a pest of the northern forests of North America. They last out the winter in their early stages and feed in the spring on the leaves of end shoots, which are webbed together to form shelters where the caterpillars pupate. Moths come out of the pupae during summer and the females lay their egg masses near where they emerge. Males are strong fliers but females are only after they lay their first eggs. Flying starts as light fades towards evening, but it can also start when dark clouds dim the light. Great numbers of moths sometimes come suddenly to places far from the nearest known source, even hundreds of kilometres away. These mass flights are always in the evening or early night (the later they are, the farther the source is likely to be).

**Australian Plague Locust, Chortoicetes terminifera** Walk.
(See Clark, 1969)

This locust can be found throughout much of Australia and it eats a wide range of plants, mostly grasses and legumes. In plague years, following breeding in widespread rains, swarms vie with livestock over grazing. It flies mostly after sunset - downwind when wind speeds are near to or greater than its air speed (three to four metres per second).

Vast numbers of this locust suddenly came to light traps at Trangie, New South Wales (32°S 146°E) on 30 November 1967, the first at 2125 LT. Flights during that night were also noted at other places along a 40-km north-south line through Trangie. There were far more locusts on the ground in experimental sampling plots on the following day than before 30 November. Sources nearby could not have led to the increase in numbers, and the most likely source was about 100 km to the south, where streams of flying locusts had been seen in the preceding three days. Migrations seems likely as an analysis of food in the gut showed bits of plants not growing near Trangie at the time. If take-off on 30 November had been around dusk, giving a flight time of about three hours, downwind displacement in a southerly wind of six to seven metres per second would have been enough to bring the locusts to Trangie at the time they were seen. In fact, winds changed from west-north-west to south with the passing of a cold front across Trangie at about 1600 LT. This southerly wind had a speed of one to three metres per second at a height of two metres and could well have been six to seven metres per second at flight levels. An afternoon shower on the front gave a strip of wet ground about 70 km long and 15 km wide, lying across the path of the flying locusts. This displacement can thus be fairly put down to the onset of south winds behind the cold front. Moreover, the moistness of these southerly winds, as against the dryness of the westerlies, may well have triggered off unbroken flight after sunset, for there are grounds for thinking that such flight by this species is helped by high humidities.
LIVING THINGS IN THE AIR

Aphids can be a big pest on farms. Although they feed on plant sap, the harm they cause seems to be due mostly to the viruses they carry. Some aphids feed on only one species of host plant, but many have two or more hosts: one is often a woody shrub on which eggs are laid and over-winter, and the others are usually annuals on which summer offspring thrive. Air speeds are less than one metre per second, hence airborne aphids must almost always be carried downwind unless flight takes place in light winds, such as in sheltered places. With little wind and a flight time of a few hours, displacements would be a few kilometres at most, but in strong winds they can be hundred of kilometres. A case of the latter kind of flight is shown by the Cowpea Aphid in New South Wales, Australia:

_Cowpea Aphid, Aphis craccivora Koch_
(See B. Johnson, 1957)

This aphid feeds on a wide range of mostly leguminous plants in both tropical and middle latitudes. In New South Wales, it can be a pest of crops such as cowpeas and broad beans, feeding in great numbers on pasture and weed legumes. It may well be the carrier of bean mosaic virus. In the spring of some years, clouds of this insect come to the middle coast of New South Wales, having been brought 300 to 500 km from large sources in the north-west. In 1951 the biggest clouds came on five days, the 1 000 m wind before four of them having been north-westerly for a day (and the same was true of the other day if the cloud is taken as having come two days before insects were first seen). Wind speeds were strong enough to need flight times of less than a day. In 1948, many aphids came to the foreshore at Sydney in the early afternoon of 10 October, at a time when a north-easterly sea breeze (section 2.3.1) was blowing at about five metres per second. For a day before, upper winds had been north-westerly 10-15 m s⁻¹, so it seems likely that the aphids had come from the north-west but were taken out to sea before being brought back on the sea breeze.

_Colorado Beetle, Leptinotarsa decemlineata_ (Say)
(See Girard, 1947 and Dunn 1949.)

This potato pest is well known for its progressive spread across North America, and later across Europe. Flights are thought to be short, so that Britain, for example, is effectively immune from invasion by flight across the English Channel (about 30 km wide at its narrowest). Some idea of the distance that can be flown, however, is given by an invasion of the Channel Islands (49°N 2°W) in 1947. The first live beetles were seen in Jersey on 28 May, and in Guernsey on the next day. By 4 June, three more had been caught in Guernsey but nearly 400 in Jersey. 28 May was the first day of a week with south-east winds and afternoon temperatures above 30°C widely over north-west Europe (and even reaching 25°C in Guernsey). Because of the coincidence of dates, it seems likely that at least some beetles flew the 50-100 km from France to the Channel Islands, and some were indeed seen flying over the sea off the north-east coast of Jersey. Moreover, most catches were at the eastern end of the island. It
is probable that most of the beetles that set out from the coast of France fell into the sea for many dead ones were later washed up on the island beaches.

3.2.6 Displacements on the small scale

It is likely that many airborne organisms move for spells of an hour or less within not only mesoscale and larger-scale wind fields but also smaller ones. Although it is known that the moving eddies in a gusty wind tend to disperse a cloud (section 3.3), whereas standing eddies near a hedge or building can gather airborne organisms together (section 3.2.2), there have been far fewer studies of small-scale displacements as against those on a synoptic scale, the main exceptions being work on the drift of insects on the wingless scale.

White Pine Blister Rust, Cronartium ribicola Rabb.  
(See van Arsdale, 1965)

Spores of this fungus, widespread in Europe and North America, are set free from Ribes (currant) plants at night and carried on the wind to White Pines, Pinus strobus L., and other five-needle pines. In northern Wisconsin, Ribes grow mostly on the edges of swampy hollows whereas White Pines grow on low, sandy ridges between. There are grounds for thinking that the displacement of spores there is on weak night-time winds over a fetch of some hundred of metres:

(a) Coloured smoke showed that air drained downhill beneath the tree crowns, rose over the warm swamp water and then flowed back to the ridges;

(b) The spread of rust has a clear pattern; there is some on the tops of the tallest trees near the swamp, on the lower crowns further away, and low down on trees growing on the ridges.

Near lakes, weak night-time land breezes (section 2.3.3) seem to carry spores over the water, but the wind aloft brings them back and deposits them in downward flow 10-15 km inland. Such a displacement would throw light on the lack of rust near the shore, as well as much disease 10-15 km inland, because spore-laden air would flow below and above crowns near the shore, but through crowns of trees on the ridges.

Bacterium Erwinia amylovora (Burr.)  
(See Glasscock, 1971)

This bacterium causes fireblight, a disease of apples and pears. There was a widespread outbreak in 1967 in the apple orchards of Kent, England. In three orchards the pattern of infection was lined up north-west to south-east, with diseased hawthorn, Crataegus, at the north-west ends. Disease development was at the same stage in all trees and therefore presumably had spread at the same time on north-west winds, but the date is unknown.
European Pine Shoot Moth, *Rhyacionia buoliana* (Schiff.)
(See Genn & Pointing, 1962)

Female moths of this species fly mostly after mating. Warm, overcast evenings trigger flight, which is from shoot to shoot or tree to tree, with stops to seek egg-laying sites. In 1956 and 1958, near Elmira, Ontario (43°35'N 80°35'W), moths in a heavily infested plantation of red pine one to three metres high were tracked by marking with numbered papers the places stopped at by each moth. At the end of each flight a moth's path was mapped and linked to the wind. When wind speed was less than the moth's air speed, flight was more or less upwind, whereas at wind speeds more than about twice the air speed, flight was mostly downwind. At other wind speeds, some flights were crosswind.

Sugar-cane Scale, *Aulacaspis tegolensis* (Zhnt.)
(See Greethe, 1972)

Like all scales, this species is a small sap-sucking insect. The females do not move, but the males can fly although they are short-lived. It is a pest in parts of east Africa and south-east Asia. The minute, wingless, first-stage nymphs, or 'crawlers', are known to be able to travel on the wind. In an experiment at Kawanda, Uganda, a line of sticky traps was set up over ploughed land up to one kilometre downwind of an area of infested sugar-cane. At one kilometre the cloud density was found to be 10^-4 m^-3, giving horizontal flows of scales more than enough to let infestations spread between fields, or even over much greater distances.

Mealybug, *Pseudococcus njalenensis* Laing
(See Cornwall, 1960)

Mealybugs are somewhat like scale insects. This species is the main carrier of a virus causing swollen shoot disease of cocoa in western and central Africa. Its airborne displacement was carefully studied by clearing a 30-m square plot of cocoa trees at Tafo, Ghana (6°15'N 0°20'W) and setting out a grid of seedlings to act as traps. The fraction of seedlings becoming infested decreased downwind to at least 30 m from the edge of a stand of infested trees, thereby showing the possibility of a spread among trees other than by crawling through the touching crowns.

Leaf-hopper, *Cicydulina storeyi* China
(See Rose, 1973)

This species is a vector of maize streak disease, found on grasses and cereals. Laboratory work has shown that long-winged forms can fly for periods of about 10 minutes and sometimes much longer. To obtain evidence for such fliers in the field, a 23-m square plot of sown grass, *Eleusine indica*, at Salisbury, Rhodesia, was kept watered during the dry season and it became infested with leaf-hoppers, coming from surrounding wild grasses that were drying out. Trap oat plants in 0.9-m squares were sown at nine places in each of the four main compass directions outwards from
the grass plot to 33.8 m, and both grass plot and trap plants were sampled by a vacuum collector. Changes in numbers of leaf-hoppers caught on oat traps were very much like those breeding in the grass — hence most of the insects caught came from the grass. Most were trapped downwind of the source, and numbers fell rapidly with distance out to about 10 m but then more slowly. These observations, together with others on the variation of trap catch with height, suggested there were some long-distance fliers present, maybe able to fly a few kilometres in winds of about five metres per second.

3.3 Dispersion* and concentration

Airborne organisms are often not alone but in large numbers that may be called a cloud. A cloud may be dense and easily seen, like some swarms of insects, or it may be thin and hard to find, as with pollen coming from many widely spaced plants. Both the shapes and densities of such clouds are likely to be constantly changing.

A cloud of organisms tends to be not only displaced downwind but also dispersed — the mean spacing tends to grow with time. Some idea of the complexity of dispersion can be obtained by watching the way a puff or plume of smoke behaves downwind from a fire. The smoke spreads through the air as it streams downwind. Plume shape and patchiness are always changing. This spread of a smoke cloud may be thought of as taking place as follows: As the wind is gusty (section 2.3.3) and mixed by eddies, threads or sheets of clear air are drawn into the cloud at the same time as threads or sheets of cloud are pulled out into clear air. The cloud is thus teased apart and grows in size. Eddies lying across the edge of a cloud thin it out, whereas those within make it less patchy. Both kinds of eddies working together lead to a cloud that is thinnest towards the edges. Downwind from a source, patchy puffs follow each other orderlessly. The spreading of most clouds of organisms is likely to happen in much the same way, although flapping flight by insects can change the rate of spread. Indeed, there are times when airborne insects are brought together, even when it might be thought that gusts would carry them apart.

There have been only a few studies of the dispersion of clouds of organisms, and almost no theoretical work. The lack of studies, however, is not surprising as it is not easy to follow a given cloud and ensure the same set of organisms is being watched as it disperses. Often, moreover, little is known about the source of a given cloud. There is a great need for case studies of dispersing clouds in many kinds and strengths of wind pattern.

How far any one kind of atmospheric disturbance might disperse a cloud depends on the length of the disturbance. Because most large disturbances last

* The word 'dispersion' is used here as in physics to mean the process of lengthening the mean spacing between particles in a cloud. In entomology, however, the word is more often used for the resulting dispersed state, and 'dispersal' is sometimes used for the process.
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longer than small ones, for a given time-span small disturbances mix more fully than large ones. The following two examples show what might happen:

(a) A cloud one metre across (for example, spores newly emitted by a lone plant): Over one minute, the cloud is likely to be dispersed by eddies less than one metre across (with life-spans of about one minute - such as eddies shed from the lee of a tree), but teased out as well as displaced by eddies greater than one metre across (such as a downslope wind). Over one hour, this same spore cloud is likely to be dispersed by disturbances up to 10 km across (with life-spans of about one hour such as cumulus convection), but teased out as well as displaced by disturbances greater than 10 km across (such as sea breezes);

(b) A cloud 200 km across (e.g. pollen from plants): Over a spell of one day, the cloud is likely to be dispersed by wind patterns less than 100 km across (with life-spans of about one day - such as upslope winds), but teased out and displaced by patterns greater than 100 km across (such as middle-latitude cyclones). Over a period of 10 days, the cloud is likely to be dispersed by, for instance, one or more tropical cyclones, but teased out and displaced by the zone of trade winds.

Studies of pollution spread should throw light on the dispersion of clouds of organisms. It is therefore perhaps worthwhile to take a short look at work that has been done on the dispersion of pollution. Much fuller reviews are given elsewhere. See Slade, 1968; Gaanady, 1973; Pasquill, 1974.

Most field studies of pollution dispersion have used tracers such as clouds of gas or smoke. Cloud density downwind of a source is often sampled with a filter or impactor. Near a ground-level, long-lasting source in open country, when the mean wind bearing does not change much with time, height and fetch from the source, the long-time mean density lessens sideways from the plume axis in a more or less normal (Gaussian) way. With a lapse rate near 10°C km⁻¹, plume width (taken between places on either side where mean density is a tenth of that on the axis) is about 40 m at 100 m from the source, and 80 m at 300 m. Rate of spread varies with gustiness, but because gustiness is seldom noted, the way a cloud spreads can be judged roughly from mean wind speed and state of sky - a method brought into use during 1958 (Pasquill, 1961; 1974). Some idea of how much a cloud disperses over larger fetches can be obtained from the drifting apart of pairs of fixed-level balloons (tetraoons) let off together. Drifts are 100 m after 1 min, 300 m after 10 min, and 3 km after 100 min (about 50 km from a source in a 10 m s⁻¹ mean wind).

Upward dispersion does not vary much with ground roughness. Plume depths from a ground source in an atmosphere with a lapse rate near 10°C km⁻¹ are about 10 m at 100 m, 70 m at 1 km and 500 m at 75 km downwind, but depth may be stunted by a capping temperature inversion. Plume depth grows downwind quicker when there is convection, but slower when the lapse rate is less than about 10°C km⁻¹ - at 100 m, the range of depth is about 25 and 5 m; at 1 km, 800 m and still only 5 m. Hence, on a clear, quiet night, or in warm air over a cool sea, the temperature inversion strongly hinders upward dispersion, as can be seen in the layering and shearing of a smoke plume at such times. Upward dispersion over a city is greater than over open country due to its greater warmth.
These sizes are for long-time mean plumes. At a given time, there will be a patchiness, often easy to see but hard to measure. Moreover, in hilly country, and where there are mesoscale and small-scale disturbances in the atmosphere, plume shapes and density patterns are more complex. Thus, smoke plumes from shore-side factories can become extremely bent when sea or land breezes are blowing.

3.3.1 Dispersion of airborne spores

3.3.1.1 Spore dispersion upwards

The volume density of a spore cloud is often smaller at greater heights. Density profiles are sometimes given in the form

$$\ln Q = \ln Q_o - k z$$  \hspace{1cm} (1),

where $Q$ is the density at height $z$ above the ground, $Q_o$ is the density at the ground, and $k$ varies with place and time. A plot of $\ln Q$ against $z$ is a straight line, and $k$ is the rate of fall of $\ln Q$ with height. Smaller densities at greater heights are not surprising where the source of spores is on the ground, and gustiness spreads them upwards against fall under their own weight, but $k$ varies with the kind of mixing. We shall now look at a simple cloud where:

(a) Density varies upwards but not sideways, hence horizontal winds cannot change the density anywhere;

(b) Mixing is such that downward flow by falling (number of spores passing through unit area in unit time) matches the upward flow by gustiness (from heights with greater density to heights with lesser);

(c) The kind of mixing (and hence $k$) does not vary with height;

(d) All spores have the same fall speed, $w$, which does not vary with height.

The cloud is in a steady state - nowhere does the density vary with time, even though there is an endless moving around of spores within the cloud. At the ground, the rate of take-off (source strength) is matched by the rate of landing. At height $z$, and density $Q$: 

- Downward flow due to weight = $Qw$ (spores m$^{-2}$ s$^{-1}$);
- Upward flow due to gustiness = $A \frac{dQ}{dz}$ (spores m$^{-2}$ s$^{-1}$);

where $\frac{dQ}{dz}$ is the upward density gradient, and $A$ is a coefficient, indicating how well the air is being mixed. Putting the sum of these flows to zero, and integrating from the ground ($z = 0$, $Q = Q_o$) to height $z$, we obtain

$$\ln Q = \ln Q_o - \frac{w}{A} z$$  \hspace{1cm} (2).

Equations (1) and (2) are the same if $k = w/A$. Because some density profiles are of the form of equation (2) it is probable they come from more or less steady-state
clouds. The coefficient $A$ is unlikely to change much with height to about 100 m (above the surface boundary layer, or constant flux layer), when there is no convective gustiness (as at night, or above the daytime convective layer). At such times, $A$ is also likely to be small (weak mixing). Hence profiles like those given by equation (1) are most likely to be found at night, or by day above the convective layer.

Across a temperature inversion that caps a convective layer there may be little or no upward flow of spores. There is likely to be a sharp top to the spore cloud, judged by the well-marked haze top often seen near the base of an inversion. Such inversions very probably cause the sudden falling off of cloud density sometimes found at greater heights. Moreover, air above an inversion has often had a path quite different from that of the air below. Thus, the higher air may have few spores because it has been washed by rain in the last few days (section 3.4.2.3) and then saved by the inversion from touching ground sources, whereas the lower air, being next to the ground, may have had many spores mixed into it over several days.

In the lowest 100 m or so of the atmosphere, where drag by the ground is strong, the coefficient $A$ may be taken roughly to vary with height like $A = az$, where $a$ is greater for rougher ground and for a larger lapse rate. Since $A$ is found to be about 1 m$^2$ s$^{-1}$ at 100 m, $a$ is of the order $10^{-2}$ m s$^{-1}$. For this lowest part of the atmosphere, and for a steady-state cloud:

$$\ln Q = \ln Q_0 - \frac{w}{a} \ln z \quad \text{or} \quad Q = Q_0 e^{-w/a} \quad (3).$$

Density profiles are perhaps of this form within the surface boundary layer. From both equations (2) and (3), $\ln Q$ is seen to go to $\ln Q_0$ as either $w$ goes to zero or $A$ goes to infinity; hence $Q$ changes little with height when fall speeds are slow (small spores) or when the air is well stirred (in strong winds and bright sunshine). For a layer which is less well stirred the change of $A$ with height is little understood, although it may well be greatest at a height of some hundreds of metres. Because changes of $A$ with height and lapse rate are in question, a general relation between $Q$ and $z$ cannot be given, even for a steady-state cloud.

Because real sources are clumped and fitful, spore clouds are seldom in a steady state; there may not have been enough time, take-off rate may differ from deposition rate, eddies may die away so that up- and-down flows of spores no longer match, and there may be sideways gradients. It is no wonder, then, that profiles are less simple than those given by equations (2) and (3); moreover, they vary with time.

3.3.1.2 Spore dispersion downwind

Like smoke from a fire, a cloud of organisms displaced from its source by the wind can be thought of as a plume (when the source is long-lasting) or a puff (when it is fleeting). We first look at a point source, and take no account of changes in density brought about by landing (section 3.4). Time-meaned density profiles across the wind, both upwards and sideways (along $z$ and $y$) at a given place downwind of a source are rendered quite well given by a normal (Gaussian) equation
CHAPTER 3

\[ Q = Q_0 \exp\left(-A^2\right) \exp\left(-Bz^2\right) \]  \hspace{1cm} (4),

where \( A \) and \( B \) vary with place and time (and are not easy to find), and \( Q_0 \) is the density at the centre of the puff, or on the axis of the plume. Time-meaned density varies downstream exponentially, \( Q = Q_0 \exp\left(-x/k\right) \), where \( k \) is the decay distance, which varies with species but is often tens or hundreds of metres. Some pollen can be taken much further and is of significance if out-crossing is to be avoided in growing a seed crop. (See Raynor et al., 1973, for pollen plume studies.) The following is a similar study for a plume of bacteria.

Bacteria plume from sewage
(See Raygor & Mackay, 1975)

Air bubbling through an activated sludge tank at a sewage treatment works near San José, California, was sampled for bacteria over a nine-day period at 10 m intervals out to 100 m, and along radii every 30°. This network showed the mean plume density had a Gaussian profile. The source strength, from a tank of area 1 200 m², was only about \( 10^4 \) organisms s⁻¹, a small fraction of the organisms carried up to 5 cm by the bursting bubbles, because the wind was unable to carry most of them over the raised tank edge.

Equation (4) of course cannot give a more or less well-marked edge to a puff or plume, such as it undoubtedly has at any one time, because densities fall away exponentially to zero. Close to a long-lasting area source, or a line source lying across the wind, density changes more strongly upwards than across the plume. A group of point sources should give a patchy plume, like smoke from many fires in a forest, but far downwind the plume becomes more like that from a lone source. A plume can also be patchy because the kind or strength of source changes with time from day to night - thus, with a 10 m s⁻¹ wind, each part would be about 500 km long (see section 3.2.4). Over rolling country, plumes in strong winds or bright sunshine can be thought of as flowing more or less straight; but at night under clear skies, plumes are more likely to flow along the contours of the ground such that a valley source gives a plume close to the valley bottom whereas a hill source gives a plume that may flow across-valley. Moreover, a downslope wind at night may carry a plume from a hill source down into a valley, whereas an upslope wind by day may carry a plume from a valley source into the hills.

When take-off rate is less than landing rate, the ground acts as a sink. Where the downward flow of organisms is slow, the greatest cloud density can be at some height above the ground. This often happens with spore and pollen clouds over the ocean, for organisms falling onto the ocean surface are unlikely to take off again. Similarly over cities, clouds coming from the country are likely to be densest away from the ground. Near coasts, sea-breeze air, with few airborne organisms, underlies land air - again leading to greatest density aloft. More broadly, wherever the wind changes markedly with height, profiles are unlikely to be simple. Layering is striking wherever there is shear together with a small lapse rate, for mixing is then weak.
3.3.2 Dispersion of airborne insects

Dispersion of flying insects is harder to understand than that of airborne organisms not flying actively, because it can be strongly tempered by the kind of flight, which may be, for instance, towards or away from the ground, a light or other insects of its kind. Densities of insect clouds have been measured most surely by using suction traps, the more so for small insects in quiet weather, when the rate of catching does not vary much with air speed. Traps that lure insects give only a hint of the real density for their ways of working are still not well understood. (For studies of trapping see Southwood, 1966; Bowden, 1975.)

The density of airborne insects is changed not only by take-off and landing, but also by displacement and dispersion. Because each of these is known to vary with the weather (wind, temperature, humidity and light intensity - sometimes several together), it follows that the causes of changes in both cloud density and numbers flying are complex; at any one time they are likely to be largely unknown.

3.3.2.1 Insect dispersion upwards

Vertical profiles of airborne insect density, \( Q \), averaged over spells of an hour or more, can often be written as

\[
Q = Q_o \left( \frac{z}{b} + 1 \right)^c
\]

(5),

where \( z \) is height above ground, and \( b \) and \( c \) vary with time, place and species (Johnson, 1957). Because equation (5) is the same as (3) when \( z \) is much greater than \( b \) (and when \( c = w/a \)), it is probable that such profiles are due to a matching of: (a) upward flow of insects due to gustiness (sometimes helped or hindered by the up or down parts of flapping flight) and (b) downward flow due to fall under their own weight. Near the ground, where \( z \) is about as small as \( b \), densities given by equation (5) are less than those given by equations like (3). Thus, a simple theory of eddy mixing offset by gravity sinking does not show how insect cloud density profiles arise near the ground. This is not surprising, bearing in mind that these profiles will probably be modified by goal-seeking that varies with time, place and species. Steady-state profiles can be taken, however, as being built of two parts: an upper one, with a profile like that of equation (3); and a lower one in which density varies little with height. For small, slow-flying insects the change in profile slope is found to be at a height near which wind speed and air speed are the same (Taylor, 1974) - the top of the insect boundary layer (section 3.2.2).

There do not seem to be any theoretical studies in which airborne insect density profiles are linked to insect behaviour and the strength and depth of eddy mixing, even for the simple case of a steady-state cloud above a lasting and very wide source.

Profiles can be far from that given by equation (5), even when an almost steady state has been reached. Thus, when there is a temperature inversion from the ground upwards, the greatest densities are sometimes near the heights with greatest temperature (up to several hundred metres above the ground). Such a profile is to be sought when an evening ground source has weakened and night-flying insects seem to
stay in the warmest air (perhaps where flight is easiest) by up-and-down flight. Moreover, the greatest height at which there can be flapping flight is likely to be set by a threshold temperature that varies with species and is greater than the air temperature (section 3.2.2). As long as updraughts are slower than fall speeds, insects can stay below heights too cold for flight, but in stronger updraughts, as in some cumulus convection, insects can be taken to greater heights, where the cold may even kill.

Profiles are unlike those given by equation (4) if two or more clouds overlap and are not thoroughly mixed. Thus, a lower cloud may have come from a nearby source and not have had time, perhaps, to reach a steady state, whereas an upper cloud may have come from faraway sources and been mixed to a near-steady state over a long time. Greatest density may be at some height where strong wind shear upwards has stretched an insect cloud so that part of it lies above air having few or no insects. Schaefer (1976) gives some cases of such density profiles found by radar.

Profiles are likely to be least simple among and downwind of, clumped and fitful sources.

3.3.2.2 Gathering together of airborne insects

Time changes in density of airborne insects just above the ground have been studied, but it is seldom possible to judge to what extent they are due to dispersion, rather than displacement, take-off or landing. Moreover, there may well be downward displacements from unseen insects flying at greater heights. Because observed density changes seldom refer to the same set of insects, almost nothing is known about the dispersion of an insect cloud. On the other hand, there are grounds, although not straightforward, for thinking there can sometimes be a concentration, or a gathering together, of flying insects in a cloud. Such gathering together has been studied on a wide range of scales - from windbreaks to continents.

Most crop shelter on farms in temperate Europe and North America is given by hedges or rows of trees, but artificial windbreaks (e.g. made of cane, straw or netting) are more widely used to shelter small areas of valuable crops. Field work using suction traps has shown that airborne insects gather near windbreaks, especially downwind. Rate of change of density downwind depends on such things as gustiness and strength of the wind, height and openness of the windbreak and its lie across wind, and the kind of insect (e.g. night-fliers such as lace-wings and moths tend to gather closer to a windbreak than day-fliers such as thrips and parasitic wasps). Changes in density can be found as far downwind as ten times the height of a windbreak, but the greatest densities (up to ten times those upwind) are mostly at only one to four times the height. Moreover there can be similar density profiles on the ground or plants, at least for weak fliers, with peak densities in places similar to those where blowing snow or dust gather. Windbreaks gather insects in this way probably because they lead to standing eddies, with patches where winds are light. Leeward gatherings of insects on crops can lead to damage or disease starting in particular places. For example, aphids may be found on the leeward side of outer rows on the upwind edge of a crop, and a crop with gaps or uneven top is more likely to gather airborne organisms than a crop with an unbroken and smooth top. A result is that sampling for first arrivals may be best carried out in the sheltered zones.
Damson-hop Aphid, *Phorodon humuli* (Schrank)  
(See Campbell, 1977)

Observations in hop-gardens in Kent, England, showed that there were more aphids on leeward than on windward strings (two or four strings to a plant). Because this species rarely, if ever, gives winged forms able to reinfest hops, this pattern of distribution reflects settling after primary spring flights, and is probably due to the pattern of sheltering.

Living windbreaks such as hedges and tree-belts give not only shelter to crops but also feeding and breeding places for insects, some of which can be predators or parasites of those that are brought to the crop on the wind. The downwind density variation of insects coming from afar is then changed by insects coming from the hedge- or tree-belt. An artificial barrier, however, may well encourage field pests to gather without being able to harbour their hedge-living enemies, but it is not yet known if windbreaks are in general harmful or useful. Each windbreak and crop must be judged individually until more is known of the ways by which it gathers insects.

Airborne insects gathered near a tree-belt  
(See Lewis, 1970)

A 300-m north-south belt of trees, mostly pine about 20 m tall and 12-14 m wide at the top (but only 8 m at the base, where there was much hawthorn between the tree stems), was used on 16 days with westerly winds during June and July 1969 to discover how airborne insects gathered behind shelter. There was a sheep pasture on the windward side, and a wheat-field to leeward. Suction traps were put in the field along a line out from the trees. The kinds of insects in the trees were found by beating and, in the wheatfields, by taking samples along lines through the traps at fixed distances from the trees. The belt was 34 per cent open, leading to greatest shelter (60 per cent – found by a line of sensitive cup anemometers) at 40 m from the belt. Insects blown on the wind from elsewhere (such as aphids) had a profile peaked in much the same place as the amount of shelter, perhaps because they had been blown over the trees and down to leeward. Insects blown from the trees (such as leaf-hoppers) had their greatest density close to or within 40 m of the trees. Faster-moving, dung-feeding flies from beneath the trees and to windward had a sharp peak in the density profile at 10-20 m. The downwind distribution of cereal thrips in early July almost certainly came about from the pattern of flight in early June, when the winged females would have left their wintering sites in grass, litter and bark to be blown by the wind onto the wheat, where they would have laid their eggs and become less willing to fly. First females are sparse and not easily visible, unlike their numerous male offspring, which are wingless, and stay on the plants where they hatch.

Concentration can be looked for in those parts of the atmosphere where there is convergence of the horizontal wind (section 2.3.1). In such places there is a net inflow of air. Within synoptic-scale wind patterns, areas of greatest wind
convergence (or divergence) are hundreds of kilometres wide, often changing greatly in setting, size and strength from day to day, and even from hour to hour. They can also move through the atmosphere, at speeds unlike those of the winds, rather like waves moving through running water. The patterns of wind convergence and divergence in some kinds of disturbances are known only sketchily. Convergence patterns in synoptic-scale disturbances can be worked out daily for many parts of the world, and for heights up to many kilometres above sea-level.

If there is wind convergence close to the ground the air must rise, and at speeds growing with height through the converging layer. Greatest upward speeds are therefore at the top of the layer, sometimes at heights of many kilometres. Upward speeds at a height of one kilometre come from convergence with strengths often found in the various scales of disturbance. Air sinks at other places where there is wind divergence close to the ground. In some areas which are small set against that of a whole disturbance, or for spells much shorter than the life of a disturbance, there can be convergence and divergence, and therefore up or down winds, many times greater than the mean for the whole disturbance.

Many airborne organisms fall so slowly they can be taken aloft within areas of wind convergence. Volume density does not then change much during the lifting. But an insect stops flapping flight when it becomes too cool and, unless there are strong enough updraughts, it tends to fall into warmer air where flying may start again. In this lower air the volume density therefore grows. It has been thought that ways such as this might have helped bring about the dense clouds of locusts seen within some areas of wind convergence on both the synoptic scale and the mesoscale, such as the intertropical convergence zone (section 2.3.1) and sea-breeze fronts (section 2.3.3), where the strongest convergence often occurs in long, narrow strips. Long-lasting zones may act as traps for airborne locusts; they may also be traps for other insect species. A case from east Africa links mass arrivals of moths with the passing overhead of a long-lived convergence zone.

Mass arrival of Spodoptera exempta (Walk)
(See Haggis, 1971)

On the night of 9-10 March 1970 swarms of many kinds of moths were seen at Muguga (01°20'S 36°30'E), north-west of Nairobi, Kenya. A Robinson light-trap, modified to record hourly, caught 1 400 moths of the night-flying species Spodoptera exempta in the seventh hour after sunset. The trap then failed but about another 7 000 moths would probably have been caught, judging by the 42 000 caught in a nearby standard light-trap (the highest nightly catch in seven years' trapping) and the usual ratio of catches in the two traps. Hourly winds showed a change from east to west, at 2250 GMT on 9 March. Weather maps showed these westerlies were the leading part of an airflow spreading eastwards from Zaire across Uganda, reaching an approximate line north-south near Narok and Dodoma by 1200 GMT on 9 March. In the 200 days between 1 December 1969 and 18 June 1970 there were 17 nights with spells of westerlies. On 5 of these 17 there were catches of 1 000 moths or more in the standard light-trap, but there were similar catches on only 21 of the remaining 183 nights (when there were only easterly winds), on nine of which there
had been westerly winds within 18 hours of the catches. The evidence
suggests the gathering of moths at the wind shift between east and west
winds.

Shorter-lived convergence zones, such as fronts (section 2.3.3) and the
leading edges of downdraughts from convective storms, may also gather airborne insects
in much the same way.

Using a small radar to study airborne insects, Roffey (1972) found pat-
terns over New South Wales, Australia, that seem to show the gathering of day-flying
insects into the walls of convection cells (section 2.3.3). Dense clouds were also
seen along a night-time wind-shift line at least 50 km long. Rainey (1973) has also
found, by trapping from an aircraft, the density of an insect cloud within the ITCZ
over Sudan, seen at the same time by radar, and containing the plague grasshopper
Aiolopus simulatrix Walk. (a pest of Sorghum millet) in numbers great enough to be
worth controlling. Rainey (1976) also gives several other cases where insect clouds
have been found (both from aircraft searches and by biogeographical mapping) in
zones of wind convergence.

Some idea of the rate at which airborne insects might be concentrated in
an area of wind convergence may be found as follows: Consider the insects within a
volume of horizontal area $A$ m$^2$ and fixed depth $d$ m. Let the horizontal convergence,
$C$ s$^{-1}$, be the same over the whole area such that $\frac{dA}{dt}$ shrinks with time. Convergence is
the rate of shrinking of unit area with time:

$$ C = - \frac{1}{A} \frac{dA}{dt} \quad (6) $$

As $A$ shrinks so the volume density should grow. The time $t_c$ so taken for, let us say,
a tenfold growth in density will therefore be the same as the time taken for the
area to shrink to a tenth; it can be obtained by integrating equation (6):

$$ t_c = -\frac{1}{C} \int_{A_0}^{A_0/10} \frac{dA}{A} = \frac{2.3}{C}. $$

Thus, the time needed for a tenfold growth in density is simply 2.3 divided by the
convergence. For synoptic-scale convergence, of the order $10^{-5}$ s$^{-1}$, $t_c$ is of the
order $2.3 \times 10^5$ s (a few days), but $2.3 \times 10^3$ (about one hour) for small-scale
convergence (of the order $10^{-3}$ s$^{-1}$). The time $t_c$ is about the same as the life-time
of a disturbance, no matter what size; on average, therefore, the convergent part of
any one disturbance can bring about a tenfold growth in density.

On a given day, some idea of the rate of concentration can be obtained
from the coming together of the tracks of a network of points moved with the wind
fields. Points become crowded into zones of wind convergence. (See Coohame, 1965,
for this method of finding concentration rate, and a synoptic-scale case for locusts
in India and Pakistan.)

When a cloud becomes dense enough it may lead to a change in the way that
an insect flies, which in turn could lead to a change in density growth-rate. Thus,
if there is a threshold density beyond which insects fly towards each other, then those parts of a cloud of airborne insects that have been concentrated beyond the threshold may not disperse when they later move into divergent areas.

Where flying insect pests are concentrated in wind convergence zones, new ways of killing them can be devised. Insects gathered into an easily visible cloud, may be killed more easily as:

(a) Less work is needed to seek and find wind convergence zones in a given area than to search the whole of that area;
(b) The cost of killing decreases as density grows.

3.4 Landing

Airborne organisms land in ways that can be called either 'active' or 'passive'. In active landing, a site is sought, such as by a flying insect, whereas passive landing is a chance event, such as falling to the ground, or bumping into something that blocks the way, or being gathered up by a raindrop.

3.4.1 Active landing

The causes of active landing are little understood. It can take place only within an insect's boundary layer, where there is no chance of a crash landing. Close to the ground, there will almost always be some places with winds light enough for a landing, especially behind plants, windbreaks and such like that are in the path of the wind. The following is a case study of landing near a windbreak:

Lettuce Root Aphid, *Pemphigus bursarius* L.
(See Lewis, 1965)

This aphid sucks lettuce roots, thereby causing wilting and sometimes death. In Britain, winged adults fly during early summer from galls on poplar trees (*Populus*) to land on the lettuce plants and give birth to nymphs that burrow through the soil to the roots. Winged aphids are produced on lettuce only in the autumn, and since wingless aphids are unlikely to wonder far in the soil, the pattern of wilting in a crop shows where the first winged aphids landed.

A lettuce crop was sown on 9 June 1964 in rows about 0.6 m apart along the line and on both sides of an east-west windbreak formed of a metre-high, wooden, slotted fence with 45 per cent open spaces. Seedlings sprouted between 17 and 23 June, and plants were fully grown by 14 August. Suction traps caught flying aphids 22-29 June in winds from between south-west and north-west, mostly on 24 June. Wilting started on 25 July, and each row was checked on 30 July, and on 5, 14 and 21 August. Wilting was greatest along a line 2-3 m to leeward of the windbreak, the line thus showing where a heightening of density of airborne aphids in June is likely to have occurred due to sheltering by the windbreak.
An insect lands when its mood for flight gives way to a mood for settling. The change of mood may come about after a long flight, or when the weather becomes too cool or windy, or when the insect is lured towards, for example, food, a mate or an egg-laying site. One flight may last anything from seconds to days but, at least for the species so far studied, the longer the flight, the longer the rest that follows. Landing may be followed immediately by further flight. If the air becomes too cold for flapping flight, an insect may glide or simply fall with closed wings. Flying insects have often been seen landing when clouds cover the sun for a while, or during spells of rain. Late in the afternoon, flying may end when day-time convective mixing dies away and there are no longer any buoyant updraughts (section 2.3.3), but this may not happen over some warm spots such as rocky areas or openings in forests from where updraughts may persist.

3.4.2 Passive landing

Very small airborne organisms such as spores and pollen grains can land in many ways, mainly by fall-out (sedimentation), bumping (impaction) and wash-out in raindrops (scavenging). It is not known if passive landing ever occurs with insects in flapping flight, but it does with fleas and click-beetles after jumping.

3.4.2.1 Fall-out

Downward settling onto the upper side of a leaf, say, is the main way of falling out when there is little or no wind. Within the viscous boundary layer it is the only way but elsewhere it is more or less offset by gustiness of the wind because updraughts can be stronger than the fall speed of the organism. Any given body falls through still air at a fixed speed when its weight is matched by drag on the air. For a round body, this fall speed (settling or terminal velocity), $v_s$, is given by:

$$\frac{4}{3} \pi r^3 \rho g = 6 \pi \eta r v_s; \quad \text{i.e.} \quad v_s = \frac{2r^2 \rho g}{9 \eta}$$

(weight \hspace{1cm} drag)

(as long as no eddies are shed from the wake behind the body), where $r$ = body radius, $\rho$ = its density (much greater than that of air), and $\eta$ = air viscosity (about $1.8 \times 10^{-4}$ g cm$^{-1}$ s$^{-1}$ at 20°C). For $\rho = 1$ g cm$^{-3}$, this gives the following fall speeds:

<table>
<thead>
<tr>
<th>$r$ (µm)</th>
<th>1</th>
<th>5</th>
<th>10</th>
<th>50</th>
</tr>
</thead>
<tbody>
<tr>
<td>$v_s$ (cm s$^{-1}$)</td>
<td>$10^{-2}$</td>
<td>0.2</td>
<td>1</td>
<td>20</td>
</tr>
</tbody>
</table>

In most winds, updraughts and downdraughts are stronger than these fall speeds; hence fall-out should often be overwhelmed by mixing between eddies, but a full study has yet to be made. Updraughts can also carry airborne organisms to the underside of leaves.

3.4.2.2 Bumping

Windborne organisms can bump into anything standing on both windward and leeward sides. When a wind comes up to such a body, it passes around and the flow
may join again downwind, with or without a wake. A windborne organism will also tend to be carried around, but because of its mass is not pushed sideways as far as the air and may bump. Small organisms in light winds are less likely to bump than large ones in strong winds. Organisms with radii less than 2 μm are unlikely to bump at all. It is not surprising, therefore, that spores of leaf pathogens such as Phytophthora and Helminthosporum are larger and bump more easily than the spores of fungi growing on the ground or on dead plants or animals, which must therefore land in a way other than bumping, or even fall-out. Medium-sized spores such as cereal rusts, with radii of about 20 μm, can bump into the finer parts of plants, such as flowers, rather than stems and leaves. Many kinds of airborne pollen grain, too, are large enough to bump into the stigmas of flowering plants. Neither spores nor pollen will grow if they bounce off, but the bareness and stickiness of stigmas of many wind-pollinated flowers lower the chances of bounce-off after bumping. Likewise, for example, wetting a plant helps a bumping spore to stick. On the one hand, large bodies like tree trunks can be bumped by large spores, such as those of the lichen Pertusaria, which have 50-μm radii. On the other hand, even very small spores are caught on hairs only 100 μm thick - which is maybe why hairy leaves catch more spores than do wet leaves. Perhaps many spores and pollen grains have radii of about 5 μm because such a size provides a good chance of bumping, whilst not allowing dispersion to lead to volume densities too small to find a growth site. The pattern of deposition on a plant varies very much with its small-scale anatomy – preferred sites are hairs, spines, upstanding leaf veins, upwind leaf edges, and leaf stalks.

Over rough ground in gusty winds, fall-out and bumping go on together as deposition. A deposition velocity, $v_d$, can then be found:

$$v_d = \frac{\text{flow rate to ground (organisms m}^{-2}\text{ s}^{-1})}{\text{airborne density (organisms m}^{-3}\text{) near the ground}}.$$  

This velocity can be much greater than the fall speed in still air, $v_s$. Hence, ground roughness, particularly that caused by plants, can quickly clear organisms from the air, as long as the volume density is not too small.

Because deposition velocity increases with both gustiness and mean wind speed it has a diurnal variation - a maximum can be expected in the afternoon (sections 2.3.2 and 2.3.3). Presumably, a forward-tumbling eddy brings down more spores or pollen grains than it takes up again because the viscous boundary layer at the leaf surface is briefly stripped off. Within a vegetation canopy, deposition velocity will vary with stage of growth (e.g. summer or winter for deciduous trees), and is probably greatest in the upper canopy. Although winds are much lighter in a canopy than over bare ground, deposition velocity can be greater there because the catchment area is so large. Numerical models of deposition within a canopy are now being tested. For example, Legg & Powell (1979) have compared one with results from a barley field where spores of barley mildew, Erisyphe graminis, and of Lycopodium were set to drift on the wind. Agreement for Lycopodium was good but not for Erisyphe, maybe because its spores were clumped and fell faster than expected.
3.4.2.3 Wash-out

Around a falling raindrop the air flows in such a way that some of the airborne organisms in the drop's path will bump, and some will stick. A long-lasting spell of rain therefore tends to thin a cloud of organisms. The rate of thinning varies with the size both of the organism and of the drop as the smaller organisms are unlikely to be caught - in much the same way as when a cloud is carried among plants. The ratio of number caught by a drop to the number lying in its path (the collection efficiency) is much less than 1:0 for small spores, as has been found in the laboratory:

Collection efficiency for spores and pollen by falling drops
(See Starr & Mason, 1966)

Spores of the puff-ball fungus Lycoperdon and barley smut, Ustilago nuda (Jens.) Rostr., and pollen of the paper mulberry Broussonetia Papyrifera were shot into a chamber of known size, through which water drops were allowed to fall. Drops were caught and the number of grains in each counted; volume density of the spore cloud was obtained by allowing all the grains to settle and counting them. Results were as follows:

<table>
<thead>
<tr>
<th>Grains (volume density)</th>
<th>Collection efficiency for drop (radius in μm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(100)</td>
</tr>
<tr>
<td>Lycoperdon</td>
<td>(r = 2.25 μm, ρ = 0.73 g cm⁻³)</td>
</tr>
<tr>
<td>Ustilago</td>
<td>(r = 2.6 μm, ρ = 0.56 g cm⁻³)</td>
</tr>
<tr>
<td>Broussonetia</td>
<td>(r = 6.4 μm, ρ = 1.1 g cm⁻³)</td>
</tr>
</tbody>
</table>

The table shows that collection efficiency is greatest with drops of radii 400 μm, and is least for the smaller grains.

For given sizes of organism and raindrop, the rate of cloud thinning by wash-out varies with volume density, Q. The latter therefore lessens with time exponentially:

\[ Q = Q_0 e^{-At} \]

where \( Q_0 \) is the starting density and \( A \) is the wash-out coefficient (or Langmuir's factor), the part swept out in unit time. Raindrop sizes are seldom known; it is therefore useful to see how \( A \) varies with the more easily found rainfall rate. This
can be done if it is known how the rainfall rate varies with drop size (or better, drop spectrum, because drops in a given rainfall have a range of sizes). Times can then be found that are needed to wash out a given part of a cloud. For Lycopodion spores (radius 2.25 μm), Starr (1967) showed that λ increased from 0.4 × 10^{-4} s^{-1} for light rain (1 mm h^{-1}) to 1.5 × 10^{-4} s^{-1} for heavy rain (5 mm h^{-1}), with times needed to thin a cloud to half its starting density lessening from four hours to one. For pollen of paper mulberry (Broussonetia papyrifera, radius 6.4 μm), λ is 2.5 and 9.1 × 10^{-4} s^{-1}, and the half-thinning times are 1 and 0.25 h for these two rainfall rates. An airborne cloud may take up to 10 h to pass through a spell of persisting rain, and in so doing is therefore likely to be greatly thinned.

Wettable spores swept up by falling rain are taken inside the drops whereas unwettable spores stay on the outside. When a spore-laden drop rolls over an unwettable leaf some of the unwettable spores are left behind as a trail, but none of the wettable spores are left. Splash droplets from a spore-laden drop are likely to spread through a leaf canopy any spores picked up from the air or from the place of splashing (Davies, 1961). Ascospores of Eutypa armeniacae Hansf. & Carter, a pathogen of apricot, Prunus armeniacæ, are shed in clumps of eight and carried on the wind, but rain separates the clumps, splash-spreading the spores through the trees.

Organisms with radii less than 2 μm are unlikely to be washed out of the air by falling raindrops. How these smallest of organisms leave the air is still in doubt. Nevertheless, wash-out may well be the quickest way by which most spores and pollen grains leave the air, well away from where they took off. In a deep, sparse cloud of organisms, fall-out and bumping into plants are likely to be very slow.

3.4.3 Thinning of a cloud

A cloud of organisms moving downwind becomes thinner by both dispersion and landing. Far from a source, thinning by dispersion is slower than by landing (and the same is true even nearby, if the source is a line or an area), because the cloud width changes only slowly downwind. However, the rates of fall-out and wash-out are not the same. Some idea of their size can be gained from a simple model of a steady-state plume with a right-angled cross-section, width L and depth h, and with density Q unchanging across the axis (Scriven and Fisher, 1975). The flow rate of organisms through the upwind side of an upright slice of the plume is \( u \alpha L \), where \( \alpha \) is the horizontal wind. Hence the rate of loss from the slice is \( u \alpha L \frac{dQ}{dx} \delta x \), where \( \delta x \) is the downwind thickness of the slice. The rates of landing are:

- By fall-out \( \frac{v}{g} \delta x Q \)
- By wash-out \( \alpha L \delta x Q \)

Since \( u \alpha L \frac{dQ}{dx} \delta x = -(v_a + \alpha \lambda) \delta Q \),

\[ Q = e^{-x/x}, \]

where \( x = u/(\frac{v}{g} + \lambda) \) is the average decay distance, i.e. the distance a part of the
plume moves while its density lessens by 1/e. The average decay time is $\bar{\tau} = \bar{x}/u$. For small spores in a plume of depth 1 km (trapped, for example, below a temperature inversion), borne over grassland on winds of speed $u = 5$ m s$^{-1}$, then $\bar{x} = 1$ cm s$^{-1}$ and $\Lambda = 10^{-4}$ s$^{-1}$. Hence the average decay distance for deposition alone is 500 km (with decay time about one day), and for wash-out alone is 50 km (decay time about 2 h); hence wash-out overwhelms deposition. But this will not be true for a plume that is sufficiently shallow. The change-over depth is given by $\Lambda = \bar{v}/a$; hence, for the above plume, $a = 100$ m. Such shallow plumes are most probable with a temperature inversion on the ground; otherwise, eddies mix the plume to greater heights.

A plume flowing among plants is thinned by bumping as well as fall-out. As a plume comes to a forest edge it broadens sideways and upwards and tends to split into two: one part rises over the forest, and the other passes between the tree trunks. Within the forest there is mixing through the tree crowns but little sideways spread. The rate of change of density downwind is greater than in open country, but this is not so just inside the upwind edge (Raynor et al., 1975).

### 3.4.4 Forecasting changes in cloud density

Perhaps the main work of aerobiologists is the understanding and forecasting of changes in volume density of harmful airborne organisms. With such forecasts, sound ways can be sought to help suppress outbreaks of both crop pests and illnesses in man and animals.

Clouds of airborne organisms often come from clumped and fitful sources—spores from sickly crops, pollen from widely scattered flowers, insects from patchy host plants. Moreover, sources may be hundreds of kilometres wide. Day-to-day and hour-to-hour changes in cloud density are manifold. To understand them means seeking links with changing weather patterns: not just wind patterns on all scales, but also changes in temperature, humidity, cloudiness and rainfall. Trying to link density changes with changes in only one weather element is unlikely to be helpful. To show this, we may look at the ways in which the passing of a cold front (section 2.1.3) might change the density of a cloud of organisms over a given place. A cold front often gives a spell of rainy weather, and a sudden change in wind with strong convergence, and is followed by falls of temperature and relative humidity. Spore and pollen cloud density may rise or fall at the onset of rain because the local rate of take-off may rise or fall whereas wash-out will start. With the wind change, new upwind sources spread their plumes and the rates of take-off may rise or fall as temperature and humidity change and convective mixing heightens dispersion. Insect cloud density may also rise or fall at the onset of rain because of a changing rate of both take-off and landing. As the wind changes there could be a big increase of density in the convergent winds, but soon there is a decrease and the density may drop to less than it was at first, because not only have the upwind sources changed but also the rate of take-off, following the changes in temperature, humidity and light strength.

For airborne pests and disease organisms found only at certain times of the year, forecasts of initial outbreaks can be very helpful in planning survey and control. Such forecasts are really of times when cloud density is likely to become large enough to cause worrying losses after landing, and they are based on: (a) the
likelihood of there being enough organisms ready for take-off, and (b) there being days when they can take off and spread, maybe downwind. Thus, the onset of hay-fever can be forecast from mean temperatures during the few weeks when pollen grows, and then, when it is ready, by watching for days suitable for take-off and spread.

Forecasting changes in cloud density among clumped and fitful sources is not easy. These changes vary in manifold ways with the weather. Rate of density change with time varies with changes in gustiness, temperature, etc., as can be given, in principle, by the 'transport equation' (or 'concentration equation'), which has terms for take-off, displacement, dispersion and landing. Analytical solutions of this equation in air-pollution studies can be found only for simple situations; otherwise numerical methods are used (see Shir and Shieh, 1974). Similar ways could be used with clouds of airborne organisms, but so far this has not been done. Moreover, movement through the air (as by falling or by flapping flight) rather than with it needs to be kept in mind. Even if enough is known about the weather during the spread of a given cloud of organisms, it is unlikely that take-off rate will be known - there may not be simple answers to the question: "Where are the sources and how do their strengths vary with time?" Answers could be obtained by a network of sampling places from which a set of maps could be drawn showing time changes among the sources (such as grassy places giving pollen, or crops harbouring insects or fungal diseases). Volume density over a place set among many sources could be obtained by modelling the sources into a grid network of squares, each square being taken as an evenly spread source (its strength being based on all the real sources in the square). Volume density could then be given by the sum of the plume densities from all upwind squares, although often only the nearest squares need be taken because those further upwind give only thin plumes. This would also allow for changes in wind and lapse rate with time. An even simpler method could be used when it is possible to lump the sources into one large area within which strength varies little with place, and wind bearing does not change with time, for then volume density, \( Q \) organisms m\(^{-3} \), is given by

\[
Q = C \frac{s}{u},
\]

where \( s \) is the mean source strength (organisms m\(^{-2} \) s\(^{-1} \)), \( u \) is the mean wind speed (m s\(^{-1} \)), and \( C \) (which varies with lapse rate and fetch from the upwind edge of the source) needs to be found by experiment. At the downwind edge of such a source the density would be given by

\[
Q = \frac{sI}{ud},
\]

where \( I \) is the fetch across the source, and \( d \) is the cloud depth at the downwind edge (some idea of which can be drawn from \( I \) and lapse rate).

3.5 Death in the air

An airborne organism will eventually die if it does not reach a place where it can thrive. Many, maybe most, pollen grains and fungal spores never reach such a place. An airborne organism may be killed, for instance, by some toxic part of the air, by drying out at low relative humidities, by sudden wetting, by sunshine, or by being caught and devoured. Even if it is not killed, there may be changes that lead to unusual behaviour during growth.
A rate for death in the air has not been found for even one species of insect; nor has there been any study of the causes of such death. Hence it is not clear how the weather might kill - some insects no doubt die of cold after being taken far aloft.

California Red Scale, *Aonidiella aurantii* (Mask.)
(See Willard, 1973)

Laboratory work measured the survival periods of crawlers of this citrus pest at various temperatures and relative humidities by their ability afterwards to feed and form scales on pieces of lemon leaf. Mean periods were:

<table>
<thead>
<tr>
<th>Temperature</th>
<th>Survival Periods</th>
</tr>
</thead>
<tbody>
<tr>
<td>15°C</td>
<td>17 h at 70%</td>
</tr>
<tr>
<td>25°C</td>
<td>10 h at 70%</td>
</tr>
<tr>
<td>35°C</td>
<td>7 h at 70%</td>
</tr>
</tbody>
</table>

These long periods leave little doubt that crawlers could withstand wind-borne movement for 100 km or more.

A great deal of doubt still persists about how airborne organisms are killed. Hardy ones, like pollens, spores and encysted protozoa, may well be able to live much longer than others such as pathogens carried on the air in droplets and breathed in by people or animals living in close proximity indoors. Oxygen may be toxic to some; others are killed by very small amounts of a substance in the air (the 'open-air factor'), one source of which seems to be a chemical reaction between ozone and olefins shed into town air, most probably from petrol (Druett, 1973).

Organisms carried high in the air may be harmed by ultra-violet sunshine, but some may be kept from harm by colouring, or by being hidden in rafts formed of other particles. Low temperatures and relative humidities sometimes seem able to help keep organisms alive, perhaps by slowing down the rate of chemical change.
CHAPTER 4

CONCLUSIONS AND RECOMMENDATIONS

The types of questions most likely to be asked of an aerobiologist are, for example: "How is this harmful, airborne pest (or disease organism), going to spread?", "Where, how quickly and in what numbers - and where has it come from?" The answers will vary with the means by which the species of organism enters and leaves the air, and is carried on the wind. Because there are many such ways, some of which were shown in Chapter 3, it is not easy here to make more than a few general comments on the kind of work that might be carried out to help provide an answer.

Forecasts of likely spread are now being made operationally for several species of airborne pest and disease organisms, mostly in Europe and North America, months or seasons ahead. They are based on knowing both the distribution of the organism and, from past records, its probable changes with the weather. The present distribution is judged from on-going field surveys, using samples often taken at more or less fixed times and places, in much the same way as weather is sampled at synoptic stations. These surveys give a more or less clear idea of how sources and sinks change in time and space; they are also used to heighten awareness of changes that have already occurred. Maps of the spread and severity of, for example, crop loss can also be drawn, showing up links between the organism and the losses it causes.

Such forecasts of the likely spread of an airborne organism, or the harm it causes, are used in planning the control of numbers of that organism and the mitigation of damage, but knowledge of how winds bring about the spread is not necessary. For forecasts of windborne spread for only days ahead, however, as well as an understanding of how an organism has reached a given place, such knowledge is essential because the weather can change greatly from day to day, and it is unwise to use only the average for the time of year that a forecast is being made. It is here that the meteorologists can play a role in both forecasting and back-tracking, but he needs to know the probable sources and sinks, all available information about the organisms in the air at the time, and on a space scale at least as large as the likely windborne displacements. It would also help to know how damage is linked to cloud density, and below which threshold density it becomes of little concern (although it should be borne in mind that occasionally a threshold density is too small to be measured).

There are many gaps in the knowledge of how most species of airborne organisms enter and leave the air, and how they are carried on the wind. These gaps are more or less well known among aerobiologists, and are listed in the next section.

4.1 Conclusions

Apart from a few, but nevertheless very harmful, species (amongst insects, notably aphids, locusts and armyworms), little or nothing is known about the ever-
changing sources and sinks of pest and disease organisms on a scale needed for forecasting and back-tracking windborne spread. Much still needs to be learned to answer such basic questions as:

(a) How are take-off, landing and death in the air linked to weather changes?
(b) How does the density of a cloud of organisms vary in space and time?
(c) How is that cloud dispersed, particularly where the organisms can fall or fly through the air?
(d) How far can the cloud spread at densities great enough to be worrying?
(e) How does cloud density vary downwind among a host of fitful sources?

4.2 Recommendations for further work

There are two basic requirements for a better understanding of the windborne spread of any species of pest or disease organism at any given time: (a) a knowledge of where the species is at that time, and (b) an understanding of how its later spread is likely to be engendered by the wind. The former calls for an information service which sends reports of field samples to an analysis centre in good time for the formulation of warnings and forecasts; the latter calls for a programme of research as to how the organism behaves in the air, aimed at answering such questions as those set out in section 4.1.

4.2.1 Information services

An information service should be able to provide answers to such questions as: "Where are the organisms now?", "How have numbers been changing?", "How are numbers likely to change?". An analysis centre is fed with field data on the sites and strengths of all known sources and sinks of the organism via a network of sampling points manned with staff who (a) know the organism well; (b) use the same sampling methods, and (c) send their reports in time to be used. The network may at first be small and sparse, but as knowledge and resources grow so can the network — in size, density and usefulness. Moreover, other surveying methods might be added, such as the use of aircraft and satellites to scan the ground for signs of change in sources and sinks. Data flowing to the analysis centre can be used not only for warnings and forecasts, but also for research, and for the training of field observers and forecasters.

Both the make-up and the working of an information service are very much like those of a national weather service; hence the establishment of an information service for a given pest or disease organism would be enhanced by advice from those who have set up Meteorological Services.

4.2.2 Research

The following recommendations for research are based on the five main gaps in knowledge and understanding listed in section 4.1. All require the cooperation of biologists and meteorologists.
4.2.2.1 Weather thresholds and triggers

Field and laboratory studies are needed on the weather thresholds that allow take-off and landing, and the flapping flight of insects. They are also needed to see how changes in temperature, humidity, wind, cloudiness, rain, etc., induce take-off and landing. Although mechanisms are known for some organisms (see the case studies in sections 3.1 and 3.4), their outcome on a given day (such as needs to be known to forecast the likely place and time of take-off and landing, and the numbers airborne) is largely unknown. The causes of death in the air and the way weather changes affect flight - especially insect air speed, heading and height - also need to be studied. Advice from agrometeorologists and biometeorologists could help in understanding and forecasting the growth of organisms until they are ready for take-off, whereas the synoptic meteorologist could assist, for example, in forecasting those weather changes that lead to take-off and spread, or in detailing the killing weather that may have struck whilst a given cloud was airborne, or in forecasting weather that may lead to landing.

4.2.2.2 Trap efficiency

Field and laboratory studies are needed as to how most kinds of traps work, how well they sample the passing cloud of organisms, and how weather changes vary their catch. Micrometeorologists might advise on how wind flow around a trap changes its catch.

4.2.2.3 Upward spread

Theoretical and field studies are needed as to how upward spread by airborne organisms varies with lapse rate and ground roughness. It would be enlightening to start with simple sources or with radar which could be used to follow insects taking off as a plume from a known source. More studies are also needed on the ways whereby airborne organisms are gathered together, maybe leading to denser clouds in, for example, standing eddies or other zones of wind convergence. Micrometeorologists could advise on the ways that atmospheric diffusion helps upward spread.

4.2.2.4 Air paths

Although there have been many studies to show that airborne organisms can move over a very wide range of fetches (see the case studies in sections 3.2.3 to 3.2.6), there is much need for work on how often clouds of a certain density move over a given fetch; such knowledge is needed to find the chance of an outbreak of a pest or disease arriving on the wind as opposed to any other means. There is also a need to list those wind patterns most likely to bring about displacement (the more so on the mesoscale and the synoptic scale, and for the smaller organisms). Displacement studies are best made by marking where there are several probable sources - by affixing a marker at source (e.g. dye or radioactivity) or by using an inbred marker (e.g. some peculiarity of shape or of biochemistry, gut content, or even the presence of parasites). Synoptic meteorologists can build up paths based on the changing wind field, but need to note the time and place of take-off or landing in order to identify the start or end of a path.
4.2.2.5 Cloud thinning

Field and theoretical studies are needed of the downwind thinning of clouds of organisms amongst clumped and fitful sources, in both open country and among stands of plants. These sheared and teased clouds call for the use of numerical models, and for the help of systems mathematicians, micrometeorologists and synoptic meteorologists (particularly those working on air pollution). It is through the use of such models that forecasts can be made in sufficient detail for the planning and use of methods to restrict the numbers of harmful organisms. Moreover, models force the researcher to state his problems more clearly, thereby highlighting those gaps in knowledge and understanding which require further research.
CHAPTER 5

BIBLIOGRAPHY

This bibliography lists the works quoted in the text, and gives others which may be useful for further reading or as sources of references. It is in two parts:

(a) Section 5.1 - Books and review papers, in both meteorology and aero-biology;

(b) Section 5.2 - Articles, mostly from journals, giving examples of take-off, displacement, dispersion and landing by living things.

5.1 Books and review papers

5.1.1 Meteorology

There are many works that may be used to supplement the brief outline given in Chapter 2. The following are some of the more recent, chosen because they are partly or wholly descriptive; many of them have long bibliographies.

5.1.2 Aerobiology


5.2 Articles

Each entry is headed by an identifier that can be used to obtain a separation under the following headings.

T - Take-off; P - Path in relation to wind; G - Displacement on the global scale; Sy - Displacement on the synoptic scale; M - Displacement on the mesoscale; Sm - Displacement on the small scale; D - Dispersion and concentration; Su - Survival in the air; L - Landing.

Most entries briefly show their content. Those entries referring to case studies in the text are also marked *.

(Spread put down to aphid flights of about 100 m downwind from weeds)

(Autumn flight direction of Gulf Fritillary independent of wind)

(Possible sources of ship catches)

(Landing of ragweed pollen on maize by bumping at crop top, but by fall-out within the crop)

(Laboratory work with centrifuge and small air jet)

(Wind changes in laboratory studies blew away dry fragments)

(Detailed studies in relation to wind)

(Spore release by shake-off due to wind gusts)
(Swarms of blackflies coming from a source 80 km away)
(Catches in a suction trap at 300 m, and in a trap towed by aircraft at 600 m)
(Arrivals associated with weather)
(Crosswind heading during flights up to 400 km)
Sm Brown, C.E., 1958: Dispersal of the Pine Needle Scale, Phenacoccus pinifolii (Fitch) (Hom.: Diaspididae). Can. Ent., 90, 685-690. (Crawlers trapped up to 3 km downwind of source)
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(Deposition on twigs in a wind tunnel.)


(Effects of wind speed and wetness of cereal plants and soil on bumping and bouncing of *Lycopodium* spores tagged with radioactive markers.)


(Likely changes in small plume with static stability can explain observed diurnal variation of flight activity.)


(Displacements above the convective layer.)


(Two-day crossing of Tasman Sea inferred from estimated arrival dates and weather maps.)


(G. Effects of convergence on insect cloud density.)


(Seasonal movements related to seasonal winds.)


(D. Types of spore profiles in relation to local and distant sources.)


(Early use of weather maps to study insect movement - mosquitoes 150 km offshore.)


(Laboratory experiments with droplets, radii 4-105 μm.)
(Experiments with spore-laden drops)

(10 years of grass-pollen counts in London related to weather)

(Uniformity of enzyme systems supports hypothesis of migration.)


(Temperature thresholds)


(Airborne spiders trapped over vegetation)


(Windborne displacement over Norway in spring)


(Discussion of possible mechanisms)

(Five swarm movements on hot north winds, sometimes leading to death at sea)

(Butterflies, moths and bush-flies came on two days on north-west winds between easterlies.)

(Many Australian moths and butterflies come to New Zealand on west or north-west winds.)


(Introduction to earlier work on many kinds of insects)

(Surface weather favourable to fungus growth affected by stability of Rossby waves)

(Two case studies of arrivals on the wind)


(Many Aedes dorsalis carried up to 100 km inland)


(Insects flying far out at sea)

(Head hairs respond to air flow stronger than 1 m s⁻¹.)

(Laboratory studies of changes in take-off rate with temperature and humidity)

(Over-wintering caterpillars cannot account for the early spring peak catches in light traps; windborne flight seems likely.)


(Can fly 200 km in 3 days when helped by wind.)


(Flight in warm south winds ahead of a cold front)

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   (Invasion of Illinois on warm south winds)
   (Back-tracks from Morocco)
   (Includes three case studies on migration)
   (Review of mechanisms)
   (Effects of temperature, humidity and wind speed)
T Jarvis, W.R., 1962: The dispersal of spores of Botrytis cinerea Fr. in a raspberry plantation.
   (Prolific take-off with rapid rises or falls of relative humidity)
   (Traps on balloon tether to find profile of insect-cloud density)
   (Discusses transatlantic displacement of both flying and non-flying organisms)
   (Kinds of spores related to air path)
   (Review of mechanisms)
   (Wind tunnel with patterned, movable floor suggests moths respond to apparent movement of pattern caused by wind.)
(Field studies of upwind tracks by Myzus persicae in light winds, and wind-tunnel studies of upwind heading and control of air speed by Aphis fabae)
(Numbers trapped in Yugoslavia related to south-east winds)
(Optimum rainfall for take-off)
T Leach, C.M., 1976: An electrostatic theory to explain violent spore liberation by Drechsleria turcica and other fungi. Mycologia, 68, 63-86.
(Electrostatic charging related to water-vapour exchange)
(Effects of sunlight and temperature on take-off by the Colorado potato beetle)
(Numerical model tested against field records)
(In Chinese, with English summary)
(In Chinese, with English summary)
(Mark and recapture of these flies showed displacement little related to the wind.)

(Experiments with resting spores, not airborne)


(Invasion on warm south winds)

(Pollen caught up to top of haze layer over New Mexico)

(Flight level related to forming night-time inversion)

(Gas bubble suddenly forms in drying cell.)

(Field studies with a grid of traps out to 3 m from a release point)

(100 migrations by 52 species, mostly on S or SE winds from U.S.S.R.)

(Likely flight on warm south-west winds)


(Flight against wind on warm days)

(Back-track from Caspian Sea to Scandinavia)


(Track in relation to wind)

(Inferred egg-laying dates followed spells with warm sector winds.)

(Midge swarm studied by cinematography)

(Spread of sugar-beet yellows by swarms of aphids coming on south winds to Sweden and Finland)

(Spores at high latitudes)


(Invasion on warm south winds)

(Pine pollen in summer at Spitzbergen - hundreds of kilometres from sources)

(Atlantic samples)

(Most of these moths fly no higher than 60 m.)

(Marked mosquitoes caught up to 40 km downwind)

(Laboratory studies show take-off rate increases with decreasing relative humidity.)

(Mark and recapture)
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(Crawlers caught up to 4 km from an infestation)


(Invasion on warm south winds)


(Examples and implications of airborne concentration)


(Several swarms of this cricket seen up to 900 km from land, off the west coast of Africa)


(Effects of wind and rain on take-off by uredospores)


(Network of samplers around the tank)


(Extension of work of Raynor et al., 1973)


(Mean plume structure found from grid of samplers on masts)


(Pollen cloud density profiles related to lapse rate)


(Downwind movement up to 150 km)


(Radar tracking of flight against wind)


(At Resolute, 74°N 95°W, most pollen came more than 1 500 km.)


(Mark and recapture mostly downwind)


(Examples of insect cloud structure by day and night)

(Two flights over 500-1 000 km in warm south winds)


(Examples of use of small 3-cm radar to study insect-cloud density in relation to atmospheric stability and wind convergence, and identification and movement of individual insects)


(Mark and recapture)


(Shows parts played by various mechanisms in spreading the virus)


(Source likely to be skin rather than breath)


(Culicoides midges probably brought from Morocco by unusual southerly winds)


(Application of method of Bassett & Wilson, 1963 (q.v.))


(Estimates of rate of thinning of spore and pollen clouds by falling rain drops)


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