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Aerial diffusion of phytopathogenic fungi

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SUMMARY. Aeriobiological studies are essential for understanding the distribution, ecology and deposition patterns of both phytopathogenic and non-pathogenic fungal spores which are carried away from their source. Many spores and conidia are devitalized during aerial transportation as a consequence of being exposed to atmospheric agents. Nonetheless, a sufficient number remain viable, causing infections of various kinds, some of which extremely serious and with an epidemic trend.

In order to predict the onset of fungi-induced diseases, it is necessary to be able to determine the inoculum source of the pathogenic agent. As air is the main vector transporting pathogenic fungal spores and conidia, periodical monitoring is required. Thus, having established the critical stages of plant infection, necessary precautionary measures can be undertaken in order to control diseases onset and development.

It is therefore necessary to gain a through understanding of spore takeoff and dispersal mechanisms so as to determine how the spores and conidia are transported by air currents onto the plants and how they cause infective impaction. Spores and conidia suspended in the atmosphere can be collected by means of appropriate traps filtering a predetermined amount of air at predetermined time intervals in order to be able to make predictions as to the possibility of plant infection. Volumetric air sampling allows not only to determine the concentration of spores and conidia in a given period of time but also to establish the hours of the day in which they are present in highest concentrations and in which therefore they are more liable to cause infection. This information may be used in estimating the incidence of disease symptoms, the duration of infection and the seriousness of the disease.

On the basis of this data, mathematical models for predicting epidemics can be worked out.

Key words: aerobiology, airborne fungi, phytopathogenic fungi, ecology.

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The air which we breathe daily almost always contains an abundance of fungi spores the number and species of which vary according to time of day, seasonal and weather conditions, geographical location and proximity to spore sources. Saprophytic or parasitic conidia proliferating on dead or decaying vegetable matter and on stored products are present in the air in higher quantities than spores originating from living vegetation.

The study of aerobiology is therefore important to understand the distribution, ecology and deposition of spores which are dispersed into the atmosphere also at considerable distances from their sources. Many spores are in fact killed during atmospheric dispersal as a consequence of exposure to atmospheric agents. Nonetheless, a number of spores remain viable, some of which may be harmless to other forms of life while others can cause diseases to plants, humans and animals as well as damage to wood, metal, bricks and stored food products.

The monitoring of the air content of conidia or spores is important for a number of reasons amongst which a better understanding of the epidemiology of plant diseases as well as for discovering the source of several allergies in humans and animals.

Aerobiological studies have therefore developed a number of spore-trapping devices which have seen the contribution of a wide range of expert including physicists, microbiologists, physicians, allergysts, veterinarians and plant pathologists. These devices are used for trapping, identifying and counting spores.

The Aerial Environment

The atmosphere around the earth comprises a series of concentric shells with different gaseous and physical characteristics. Airborne microorganisms, however, are mainly concentrated in the innermost shell, the troposphere, made up of nitrogen, oxygen and carbon dioxide. All the atmospheric phenomena leading to changes of season, cloud formation, air convection and precipitation such as rain, snow, hail and frost, originate in this zone, which can reach a height of 6 km at the poles and 17 km at the equator.

Air movements in the troposphere range from small turbulent eddies cutting across large frontal systems thousands of kilometers long and hundreds of kilometers wide to jet streams in the upper troposphere and in the stratosphere which rapidly convey air all across the surface of the planet (Fig. 1). Microorganisms can be transported and dispersed by all or any of these air movements which can occur in five distinct zones of the troposphere (Gregory, 1973). These include:

1. *The laminar boundary layer,* which represents a thin layer of still air surrounding the earth surface below which a layer of turbulence-free air streams increasing in speed with height can be found. This layer varies in thickness, according to speed and turbulence, from 1 mm to 10 cm on an overcast day up to 10 m during the night. It is into this layer, which temperature is characterized by maximum and minimum values, that the spores are initially released and only after having successfully traversed it can they become airborne;

2) *The local eddy layer,* which is characterized by surface roughness causing eddies originating after turbulences or depressions;

3) *The turbulent boundary layer,* which, in the presence of projecting objects, is characterized by turbulence diminishing with height and temperature, thus deviating air currents both outwards and upwards. The thickness of this layer increases with wind speed and is thickest, reaching up to 150 meters, in hot weather and on sunny days and thinnest in clear weather or during still nights;

4) *The transitional zone,* reaching up to a height of 500-1000 m, in which turbulence diminishes with altitude, disappering altogether

with diurnal changes. The particles and air impurities from the lower layers are conveyed up to the upper limits of this zone by the underlying turbulence;

5) The convective layer, in which airborne particles can be transported only by convection currents upon air being heated close to the ground and moving upwards to the cooler layers thereby causing eddies and air streams. During summer, warm air bubbles carrying a considerable number of microorganisms may form in areas of 1.25 sq.km every 6 to 15 minutes.

Precipitation can be conducive to both spore liberation and deposition. The form of precipitation and its intensity depend on various factors but the most frequent form of spore transporting precipitation is represented by rain drops. Rain drops are usually 1-2 mm in diameter, although they can also be much smaller, from between 0.2 to 0.5 mm in diameter, in case of drizzle and also much larger, up to 5 mm, in case of thunder storms.

Factors affecting the survival of airborne conidia include, amongst others, ultraviolet radiation, particularly harmful at higher altitudes, as well as freezing and desiccation, which may be harmful but can also actually offer protection against radiation. The effects, however, of these various factors on the survival of airborne conidia is still at present largely uninvestigated.

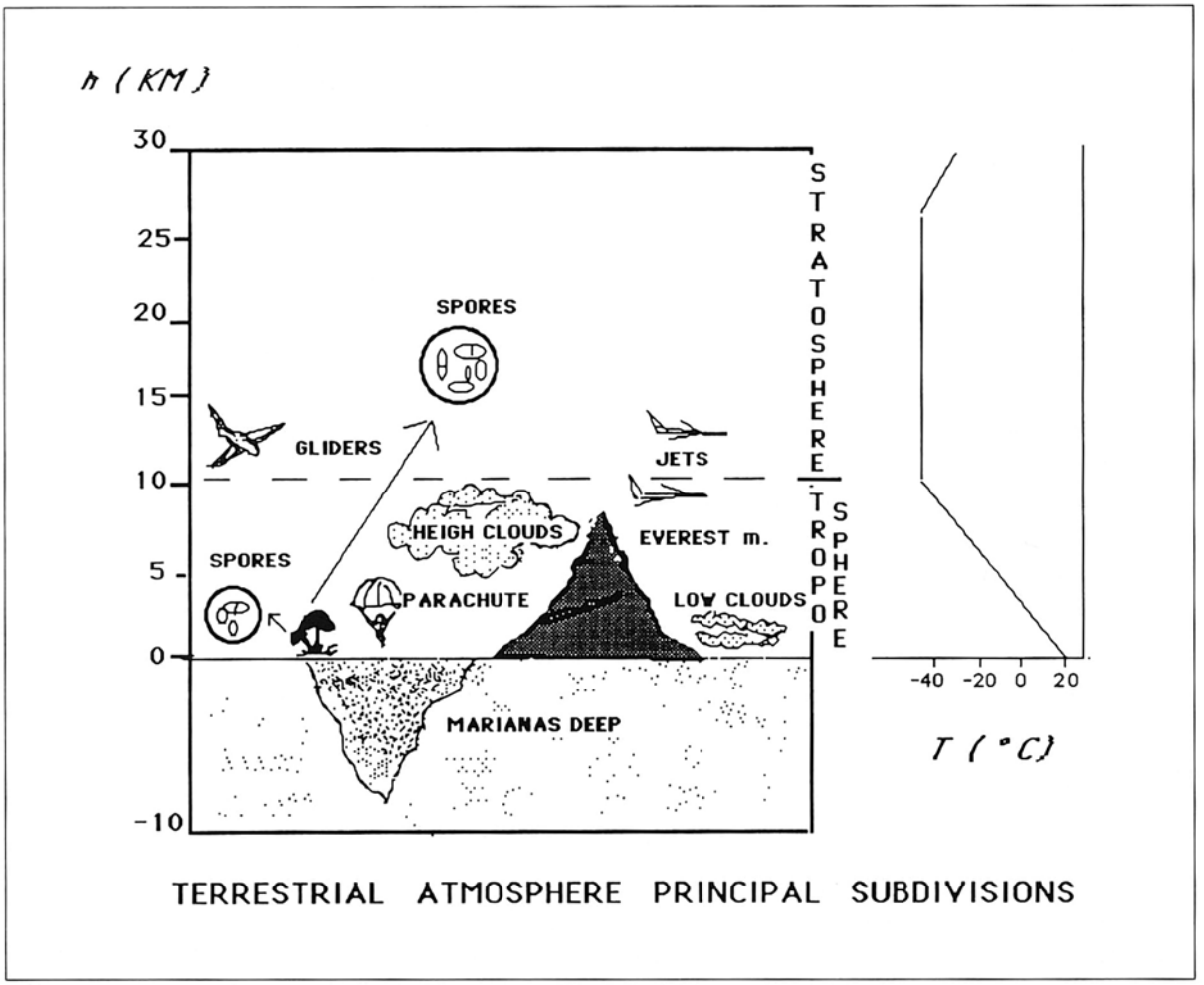

Figure 1. Spores are to be found at altitudes of 5 to 20 km in both the troposphere and the stratosphere, together with higher clouds, jets and gliders. The height of Everest is compensated for by the depth of the Mariana trench.

Spore population in the aerial environment

The study of spore populations in the aerial environment has been carried out in various parts of the world but the general significance of the findings is difficult to evaluate given the considerable differences in trapping methods employed, exposure times, number and frequency of daily samplings and duration of study. Comparisons of results, therefore, are also extremely difficult. In the majority of cases, spore assays have been conducted by daily exposing open Petri dishes for brief periods of time to the aerial environment being studied. Other frequently used methods include the exposure of slides for 24-hr periods in the rain shelters as well as the use of special suction traps employing a pump to draw air in onto vaseline treated slides. The latter methods is particularly helpful as it provides a clear indication as to time of spore deposition on the slide which is carried forward at a rate of 2 mm an hour across an aperture through which spore-containing air flows. Every method, however, presents its advantages and disadvantages and the technique chosen depends on the purpose of the study.

As has already been pointed out, spore numbers and types vary depending on the time of the day, season, weather conditions, geographical location and proximity to spore sources. In fact, conidium, ascospore, basidiospore, yeast, rust and smut spore numbers can vary considerably ranging between less than 200 to more than 2 million/m^3 air but the daily average number is between 10,000 and 20,000/m^3, with peaks of up to 200,000 for brief periods. These peaks are particularly significant as they indicate conditions especially favourable to the formation and liberation of numerous types of spores such as the ballistospores of basidiomycetes. Deuteromycetes have rarely been recorded in such large numbers under normal conditions.

Airborne spores tend to be found in greater quantities in temperate and tropical regions and in lesser quantities at high latitudes and in desert areas. In latter environments, in fact, fungal colonization is severely curtailed due to high temperatures and sparse vegetation. In polar and subarctic regions peak concentrations are usually below 10,000 spores/m^3 of air, and 70% of these are ascospores and basidiospores (Rantio-Lehtimaki, 1977).

Not all airborne spores are viable, their viability depending on species, catch time and perhaps also on the interval between spore formation, liberation and sampling as well as on solar radiation intensity, environmental dryness and sensitivity to light. With regard to spore species, viability can differ considerably, for example, 80% for *Alternaria*, 70 to 90% for *Cercospora* and 20 to 30% for *Cladosporium*. With regard to deuteromycete fungi such as *Cladosporium*, even fragments of these can germinate and rapidly generate up to 20 conidiophores and conidia.

The greatest spore numbers have been recorded during the day despite the unfavourable effects on their concentration of factors such as air turbulence, wind speed, convection and temperature inversions. The periodical distribution of spores has been determined by estimating their concentration at 2-hour intervals during daylight hours using continuously exposed spore traps.

As has been recorded for several species of fungi, maximum spore concentration occurs between 07.00 and 10.00 hrs due to rapid change or decrease in relative humidity. For others, maximum concentration has been recorded between 10.00 and 13.00 hrs due to increase in temperature and wind speed and turbulence around midday. Peak concentrations for some spore species have been found to occur twice during the hotter hours of the day, the reason for this pattern being still a source of specula-

tion. For a few other species, maximum concentration has been recorded between 20.00 and 22.00 hrs, the cause being perhaps ascribable to an increase in humidity, although the phenomenon has not yet been studied thoroughly. Basidiospores and ascospores show maximum concentrations between 02.00 and 04.00 hrs but with low concentration of conidia being recorded. This is probably due to the fact that these species require high degrees of humidity for both spore formation and liberation (Fig. 2).

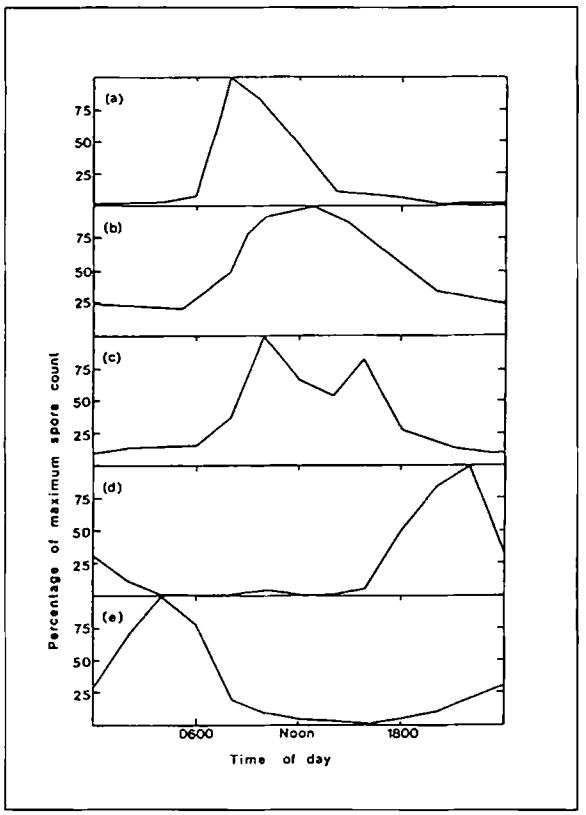

Figure 2. Mean diurnal periodicities of airborne spores illustrating different patterns of release (Lacey, 1981). (a) Early morning pattern, Nigrospora spp.; (b) midday pattern, Cladosporium spp.; (c) double-peak pattern, Tetraploa spp.; (d) postdusk pattern, tretraspore type; (e) night pattern, Pyricularia grisea. (After Hirst, 1953; Meredith, 1962a,b; Sreeramulu and Ramalingam, 1966; Shenoi and Ramalingam, 1975.).

Other crucial factors in the growth and sporulation of fungi and the liberation, dispersion and deposition of their spores are seasonal variations in relation to relative humidity, dew point, temperature, wind speed and especially rainfall. Light rainfall, for example, considerably favours the growth of Cladosporium, Alternaria and Erysiphe (Hirst and Stedman, 1963) while ascospores and the spores of other species prefer dry damp air conditions. Most airborne spores are removed by heavy and prolonged rain.

Plant growth, together with seasonal conditions, also affects the numbers of spores in the aerial environment. Maximum concentration in temperate regions is encountered during maximum plant growth period, with peaks between June and August. The aerial environment in this period is almost always characterized by the presence of plant pathogenic spores and conidia such as Erysiphe, Polythrincium, Helminthosporium (Hamilton, 1956) and Venturia (Govi, 1955; 1961).

Assays carried out with airborne spore traps have shown that the upward movement of spores is mainly due to atmospheric turbulence and convection (Gregory, 1973). The highest concentration of airborne spores has been recorded close to ground where they are continuously replenished by the liberation of new spores. Concentration has been found to diminish logarithmically with height in unstable air environments unless temperature inversions prevent upward air movement, which increases as convection increases (Fulton, 1966).

Microbial concentrations reported by Fulton were on average around 200 spores/m^3 with about 50% fungi at 690 meters altitude, 60 spores/m^3 at 1600 meters above sea level and 30 spores/m^3 at 3127 meters above sea level, with around 10% of fungi being recorded between 12.00 and 18.00 hrs when air convection was greatest. Only 45, 25 and 23 spores/m^3 were found by Fulton at various times during the morning between 06.00 and 12.00 hrs.

0.03 to 0.14 microorganisms per m^3, about half of which fungi, have been reported at altitudes of approx. 20 km above sea level (Meier, 1936; Bruck, 1967).

Apart from the outdoor aerial environment, the indoor environment also contains fungus spores and conidia, albeit in lesser numbers. Concentration in these cases depends on the activities and on the overall conditions of these indoor environments. Air conditioning, for example, facilitates spore dispersion form one room to another. Large numbers of spores can be found in areas in which organic substances are handled, processed or stored such as rooms containing fruit, seeds, animal products or fodder storage areas such as silos, barns, and so on. Building activity is also another environment favourable to spore concentration given the high amounts of dust produced or the humidity caused by paints being applied to walls in scarcely ventilated rooms. While aspiration and ventilation systems can be adopted in industrial plants in order to reduce spore concentration, this is rarely feasible in farm buildings given their large volume.

Spore liberation and dispersion

Diffusion of airborne spores takes place in three stages, namely:

1. *Liberation and takeoff*, which depends on the capacity of the spore or the conidum to overcome the adhesive forces holding it to the conidiophore or to the sterigma and to cross the laminar boundary layer, thus entering the turbulent boundary layer;

2. *Dispersal*, during which stage the liberated spore or conidium reaches the air currents from the source to other parts of the troposphere;

3. *Deposition*, which corresponds to the spores and conidia coming to rest on the surface where they will germinate and grow.

A large number of fungi are endowed with tall conidiophores penetrating through the laminar boundary layer or with special liberation mechanisms capable of launching the spores into these layers.

Spore liberation and takeoff can also take place thanks to a number of passive mechanisms such as falling under gravity onto underlying vegetation, transportation in upward air currents due to convection, vectoring by external carriers such as insects or other animals or by rain drops with subsequent dispersal through humid currents.

The active mechanism of spore liberation and takeoff mainly involves conidiophore or sterigma contraction due to variations in environmental humidity or to cell turgidity occurring especially during early morning hours as has been observed by Jarvis (1962) and Meredith (1966) for *Botrytis cinerea* and *Alternaria porri*. Another active mechanism especially observed in ascomycetes depends on spore sac bursting due to pressure exerted by cell turgidity.

Basidiospore liberation takes place in the following sequence. Shortly before takeoff, an inflation can be observed on the dorsal side around the point of attachment of the spore to the sterigma. Before launching, this inflation hase been observed to either increase, diminish or disappear altogether (Prince, 1943; Corner, 1948). The inflation itself is surrounded by a membrane which, in basidiomycetes, can be considered a flexible extension of the wall of the sterigma (Wells, 1965). Different interpretations are given as to the contents of this membrane. According to some authors, the membrane contains liquids while others favour gas. The former assumption would appear to be born out by the fact that a droplet has often been observed to come off together with the spore (Buller, 1933) as well as by the fact that immediately after takeoff the spore is surrounded by liquids (Muller, 1954). Be it as it may, the droplet or the infiltration attached to the basidiospore have been seen to exert an active initial pressure on the

basidiospore itself upon it becoming detached from the sterigma, thus launching it away from the source. Spore takeoff can however occasionally take place without droplet formation. Moreover, in some species such as Cronartium ribicola, no droplet formation has been observed (Bega and Scott, 1966). In conclusion, therefore, it is not unjustified to assume that the droplet itself may in fact play no essential role in the takeoff mechanism. On the basis of this assumption, several other contributing factors have been hypothesized in order to explain basidiospore takeoff mechanism.

Dispersal

The second event marking spore diffusion can be characterized according to both the fate of each single spore and the overall behaviour pattern of the spore cloud. Both these aspects are interrelated as they depend on the size, shape and roughness of the spore as well as air viscosity, conditions of the laminar boundary layer, convection, wind gradients close to ground and dispersal capacity of circulating air streams. The spores themselves are in fact heavier than the surrounding air and therefore would normally tend to sediment. This tendency, however, is counteracted by upward air movements originating from air turbulence and convection currents while the turbulence itself disperses the spore clouds according to eddy diffusion patterns. It is therefore the interaction of all these wind factors, subject to limitations of precipitation and deposition phenomena, which determines the distance and direction a single spore or group of spores will travel.

Spore dispersion into the atmosphere can be considered according to spread criteria. Spores can in fact be dispersed at short distances from the source, such as in the dispersion of spores within the limited area of a specific crop affecting the epidemiology of plant diseases, or over large distances across various regions. Given the difficulty in identifying a small number of spores originating at considerable distances, the grater part of aerobiological studies have concentrated on short-distance spreads.

Small spore clouds dispersed in the atmosphere only carry a small amount of spores from between 5 to 10% of the original cloud at large distances from source. Moreover, in some cases, rather than the fully developed spore itself it is the sporangium which is dispersed. This is observed for example in oomycetes species such as *Phytophthora infestans*, which causes downy mildew in potato and tomato crops. The sporangia of this species are attached to a peduncle and are dispersed by rain, being transferred from infected to healthy leaves where they germinate thus releasing the zoospores which cause the infection.

The *Pilobolus* species, frequently encountered in herbivorous animal dung, employ an active launching mechanism dispersing the sporangia several meters from the source. The closely related *Pilaira* species, also found in herbivorous animal dung, employs a different mechanism for dispersing the sporangia. These, in fact, attach themselves, together with their peduncle, to surrounding grass stems by means of sticky and slimy substances.

Ascomycetes present limited cases of ascospore dispersal while these are still contained in the spore sac. Examples include types of *Podosphaera* species which cause powdery mildey. Each single spore sac is launched at long distances from the source by means of an elastic action of the inflated walls of the ascocarp. Another example of ascomycetes ascospore dispersion is represented by truffles. The carpophores are in fact eaten by rodents which subsequently expel the spore sacs together with the ascospores. It has even been hypothesized that the spores themselves can only germinate after having actually passed through the digestive tract of

the animal. Other instances of spore dispersal occuring together with a variety of spore protective coatings are encoutered in gasteromycetes. In the *Sphaerobolus* species, for example, which produces round spore-bearing organs of about 2 mm in diametre on dry plants and animal dung, the basidiospores and other reproductive cells called «gems» are contained in a dark slimy lump and are launched at distances of between 5 to 6 metres. In the *Cyathus* species the basidiospores are contained in a kind of lenticular peridium attached to the inner side of a funnel shaped spore-bearing organ by means of a sort of spiral spring called funiculus. The funiculus ligaments are detached by splashes of rain water after which the funiculus is dispersed together with the peridium to distances of over a meter, thus allowing the funiculus and the peridium to wrap around and attach themselves to the surrounding vegetation.

The study of short-distance spore dispersal in certain phytopathogenic funghi has yielded information relevant to long-distance spread as well. This is the case when the spores have been assayed before onset of disease in localized crops, which has allowed to identify the source of these spores by plotting wind trajectories. Early catches of *Puccinia graminis* urediniospores accompanied by *Alternaria* conidia thus occurred in the southern regions of Great Britain only when wind trajectories had passed over the wheat-growing areas of continental Europe, taking off rust spores from these.

The extension of the geographical range of fungi is often related to the distance between the source and the point of impaction. *Peronospora tabacina*, for example, employs four years to travel across Europe and *Puccinia polysora* the same time to cross Africa. On the other hand, *P. graminis* f. sp. *tritici* can cover the distance separating Europe from North America in a single season (Gregory, 1963; Zadoks, 1967). Another factor contributing to spore dispersal is represented by modern air travel as spores of many species have been found on the shoes and luggage of aircraft passengers.

The deposition or sedimentation of spores on a surface represents the final event or airborne spore dispersal. Spores are thus deposited on the ground where they can begin colonizing new substrates. Several different processes are involved in spore sedimentation, amongst which spore crossing through the boundary layer, wind turbulence, impaction and rain washout (Tab. I).

Table I. This table shows the massive presence of conidia in several organic substances, whereby the pathogens of various plant species are conveyed into the atmosphere (Lacey, 1981).

Predominant Conidial Fungi in Organic Substrates and Associated Air Spora

Substrate	*Fungi*
Hay	*Aspergillus fumigatus, A. nidulans, A. versicolor, A. glaucus* group, *Humicola lanuginosa*
Cereal grains	As hay plus *Penicillium* spp., *Thermoascus (Paecilomyces) crustaceus*
Malting barley	*Aspergillus clavatus, A. fumigatus*
Straw	As hay plus *A. terreus, A. flavus, Cladosporium* spp., *Penicillium* spp.
Mushroom compost	*Scytalidium thermophilum, Humicola grisea, A. fumigatus, Penicillium* spp., *Doratomyces stemonitis*
Maple logs	*Cryptostroma corticale*
Cork	*Penicillium frequentans, P. granulatum, Aphanocladium album, Monilia sitophila*
Red wood sawdust	*Aureobasidium pullulans, Graphium* sp.
Cheese	*Penicillium casei*
Sugarcane bagasse	*A. fumigatus, A. niger, Penicillium* spp., *Chrysosporium thermophilum, Paecilomyces varioti*
Cotton	*A. niger, A. ochraceus, A. versicolor, A. nidulans, Fusarium moniliforme, Cladosporium* spp.
Citrus fruits	*Penicillium digitatum, P. italicum*

A large number of studies have been conducted on the aerobiology of plant pathogens in relation to both their local spread within crops

and their long-distance spread into new crops and areas. These studies have been essential in gaining a better understanding of the epidemiology of related diseases and in predicting their onset, development and diffusion as they provide information as to the numbers of pathogenic spores and conidia in the air and their sedimentation patterns which depend on weather conditions and on dispersion gradients.

These findings ca be usefully employed in developing mathematical models for forecasting plant disease epidemics.

Knowledge concerning the numbers and types of spores present in the atmosphere and their interaction with the environment, the substrate and the area of deposition has considerably widened in recent years. Despite this progress, however, many areas of the world have as yet not been investigated from an aerobiological point of view and others, albeit variously studied, have yielded unreliable results due to the inadequate methods employed.

An important objective for future studies, therefore, is a greater coordination of research efforts, methods and results on a worldwide scale especially with regard to spore trapping procedures and techniques. It is only by working within an international framework of reference that appropriate and general models of fungi diffusion applicable to areas with similar environmental conditions can be developed.

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