
Movement of Plant Pathogens in the Crop Canopy [and Discussion]

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Movement of plant pathogens in the crop canopy

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Many spores released by plant pathogens are deposited within a few metres of their source. The distribution pattern within this zone influences the rate of spread of disease, and also controls the number of spores that leave the canopy and contribute to long-range dispersal. It would thus be valuable to develop a theory to describe the movement of spores within crop canopies, and explain the effects of airflow, crop structure, and height and mode of spore release. Conventional diffusion theory gives serious errors when used within a crop, and a random-walk theory, in which individual particle trajectories are simulated, provides a promising alternative. The three components of velocity are generated as Markov sequences with mean statistics that relate to the Eulerian windfield, and with correct Lagrangian timescales. This theory can readily incorporate the release of spores in gusts, and some implications for spore distribution are explored.

INTRODUCTION

Most foliar pathogens are transported aerielly from plant to plant, and the beginning of each spore flight must be in the complex turbulent airflow within the plant canopy. Indeed, most spores never leave the canopy but are deposited on other plants or onto the soil within a few metres of their source. Spores that escape from the crop enter the atmospheric boundary layer, and for large flat fields, at least, the airflow here is well understood, and the dispersion of spores can be described adequately by the diffusion equation (Chamberlain 1975). This paper is concerned with spore movement in the turbulent airflow within the crop canopy.

There are many practical reasons for wishing to understand the dispersal of spores among crop foliage. The build-up of an epidemic depends on spore dispersal, and an understanding of this is necessary if spraying is to be scheduled correctly. The risk of infection in fields adjacent to diseased plants also depends on the dispersal mechanism, and the chance of long-distance dispersal depends on spore release at a time when the meteorological conditions are favourable (Aylor *et al.* 1982). Small-plot fungicide tests must be interpreted with care unless inter-plot interference can be measured, or estimated (Jenkyn *et al.* 1979); and the results of such experiments need to be extrapolated to large fields. Finally, it is possible to affect the risk of disease development by some management practices, for example by planting mixtures of species resistant to different fungal strains (Wolfe *et al.* 1981), or by directly modifying the microclimate as happens when tobacco shade tents are raised (Aylor & Taylor 1982).

Measurements of plant disease gradients are difficult to interpret because they are caused by environmental inhomogeneity as well as by spore dispersal gradients (Gregory 1968), and amounts of disease are often a compound effect of several generations of spore production. In

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this paper I consider only spore dispersal gradients, and not the disease gradient that may or may not follow (figure 1) (Hirst & Stedman 1971; Bainbridge & Stedman 1979; Stedman 1980). Spore concentrations and deposition rates around a source show a very wide range of gradients (defined here by $\gamma = -d(\ln(\text{concentration}))/dx$). The diversity arises from several causes.

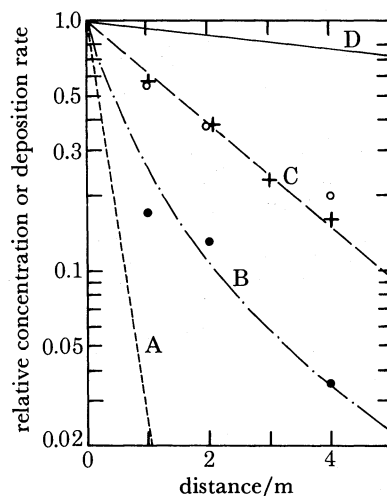


FIGURE 1. Spore dispersal gradients in crop canopies. A. Deposition of artificially splash-dispersed spores of *Lycopodium clavatum* downwind of a point source in a crop of field beans (Stedman 1980). B. (●) Concentration of naturally released *Erysiphe graminis* spores downwind of a long strip of infected barley 0.9 m tall (Bainbridge & Stedman 1979). C. (○) As for B, but when the crop was 0.45 m tall. (+) Concentration of *L. clavatum* spores that were released continuously from a line of sources at the top of a barley crop 0.9 m tall (Bainbridge & Stedman 1979). D. Concentration of pollen blowing from a field of sugar beet to an adjacent field of wheat (Hirst & Stedman 1971).

(i) There is a wide range of spore sizes (and droplet sizes where spores are released by splash dispersal). Large spores and droplets are deposited rapidly and line A, the steepest in figure 1, is for *Lycopodium clavatum* spores dispersed artificially in splash droplets (Stedman 1980). It seems likely (Fitt & Bainbridge 1983) that most splash-dispersed spores are carried in droplets with a diameter of several hundred micrometres, and these travel ballistically with little effect of wind speed. A few, however, are released in smaller droplets and become airborne.

(ii) The shape and size of the source affects the deposition gradient. In particular deposition gradients downwind from a point source are generally steeper than from a line source or from a large rectangular area.

(iii) Turbulent transport from the top of the canopy may increase or decrease a gradient depending on the height and distance of the source. The flux will be upwards near a source in the canopy (figure 1, lines B and C), causing a steepening of the gradient, but will be downwards further downwind where the cloud of spores above the crop diffuses back into the crop and makes the gradient shallower (figure 1, line D) (see also discussion by Chamberlain & Little (1981)).

(iv) The height of the source affects the relative number of spores that are lost to the ground, and the proportion that escape from the canopy (in figure 1, the *Erysiphe graminis* spores were liberated in the lower half of the canopy (line B), whereas *L. clavatum* spores were released at the top (line C)).

(v) The density and detailed structure of crop foliage determines the rate at which spores are removed by deposition.

(vi) Crop density also affects the windspeed and turbulent structure above and within the canopy, and thereby affects dispersion and the rate of spore impaction. The wind structure is also affected by temperature gradients. Legg & Long (1975) showed that changes in irradiance could, in light winds, double the turbulent exchange rate between the air above and within a wheat canopy.

(vii) The spore release mechanism may also influence dispersal patterns, as spores released only during gusts will initially travel faster and be more likely to be deposited by impaction (figure 1; *E. graminis* spores would have been released in gusts, but *L. clavatum* spores were released continuously).

Each of the seven factors listed is able to change the deposition gradient by at least a factor of two, and for some a factor of ten; so it is not surprising that the range shown in figure 1 differs by as much as 60 times.

With so many factors affecting spore dispersion there is clearly a need for a physical theory to predict gradients for each of the practical situations that occur. There is the added bonus that such a theory will also be useful to describe the dispersion of pollen, spray drops, and gaseous and particulate pollutants, and so be valuable in many areas of agricultural research.

The aim of this paper is to outline the main features of airflow in crop canopies, to describe spore release and deposition, and to explore possible theories of dispersion in turbulent airflow. Finally, a very simple Markov chain model is used to show the effect of high turbulent intensity and gust release on deposition gradients close to a point source.

AIRFLOW IN CROP CANOPIES

There have been several detailed reviews of airflow among crop foliage (Raupach & Thom 1981; Legg & Monteith 1975; Bradley & Finnigan 1973; Thom 1975), and here only a few of the major features are presented.

Firstly, the airflow is highly turbulent. To describe the flow u , v and w are defined as the instantaneous velocities in the downstream (x), cross stream (y) and vertical (z) directions. An overbar indicates a time average, and a prime indicates the departure therefrom. I shall consider \bar{v} and \bar{w} to be zero, though this is not strictly true in a crop unless a space average is also taken (see Raupach & Shaw 1982). It is important to consider also the instantaneous horizontal speed of the air, given by $s = (u^2 + v^2)^{1/2}$, and the standard deviations of all these quantities, denoted by σ_u , σ_v , σ_w and σ_s . Turbulent intensities i_u , i_v , i_w and i_s are defined here as σ_u/\bar{u} , σ_v/\bar{u} , σ_w/\bar{u} and σ_s/\bar{s} respectively.

In much early work the distinction between u and s was not made, for the very practical reason that cup anemometers and vertical hot wire anemometers measure s and not u . Provided that i_u and i_v are small it follows that $\bar{s} \approx \bar{u}$ and $\sigma_s \approx \sigma_u$, correct to first order. But Shaw *et al.* (1974) and Wilson (1980) used a servo-controlled split-film anemometer to measure unambiguously the three wind components in a maize canopy. Shaw *et al.* made measurements in a rather open senescing canopy and found i_u and i_v to be *ca.* 0.7 at mid-canopy. Wilson, working in a denser canopy, found i_u and i_v to increase from 0.7 at the top of the canopy to 4.0 near the ground! The ratio σ_w/σ_u was 0.9 in mid-canopy, and 0.5 at the top and bottom.

In such highly turbulent flow there is no simple equation to relate \bar{s} and σ_s to \bar{u} , σ_u and

σ_v , but for independent Gaussian fluctuations in u' and v' , and with σ_u equal to σ_v , the relation is shown in table 1. It is particularly interesting to note that although i_u may have any value, σ_s/\bar{s} is constrained to be 0.52 or less. Thus many measurements of σ_s/\bar{s} of about 0.5 (Cionco 1972) show merely that i_u was greater than 0.6. Turbulent intensities of 4.0 may be extreme, but we must conclude that values of 1.0 and above are probably normal.

Secondly, the probability distribution for speed, s , is positively skewed. Even with a Gaussian distribution for u and v , s may have a skewness of 0.6 (table 1), primarily because s cannot

TABLE 1. VALUES OF \bar{s}/\bar{u} , σ_s/σ_u , σ_s/\bar{s} , AND SKEWNESS OF s GIVEN THAT $\sigma_u = \sigma_v$ AND u' AND v' HAVE INDEPENDENT GAUSSIAN DISTRIBUTIONS

$i_u = \sigma_u/\bar{u} \dots$	0	0.25	0.5	0.75	1.0	1.5	2.0	3.0	4.0	5.0
\bar{s}/\bar{u}	1.00	1.03	1.14	1.30	1.55	2.1	2.7	3.9	5.1	6.3
σ_s/σ_u	1.00	1.00	0.94	0.83	0.78	0.72	0.70	0.67	0.66	0.66
σ_s/\bar{s}	0	0.25	0.41	0.48	0.50	0.51	0.52	0.52	0.52	0.52
s^3/σ_s^3	0	0.03	0.21	0.44	0.51	0.56	0.58	0.61	0.62	0.63

$$\begin{aligned} \text{If } \bar{u} = 0, \bar{s}/\sigma_u &= (\frac{1}{2}\pi)^{\frac{1}{2}} && \approx 1.25; \\ \sigma_s/\sigma_u &= (2 - \frac{1}{2}\pi)^{\frac{1}{2}} && \approx 0.66; \\ \sigma_s/\bar{s} &= (4/\pi - 1)^{\frac{1}{2}} && \approx 0.52; \\ s^3/\sigma_s^3 &= 2\pi^{\frac{1}{2}}(\pi - 3)/(4 - \pi)^{\frac{3}{2}} && \approx 0.63. \end{aligned}$$

be negative, but Finnigan (1979) measured a skewness of 2 to 4 for u in a wheat canopy. Thus the flow is characterized by frequent quiescent periods punctuated by strong gusts. This distribution of windspeed has been described by Shaw *et al.* (1979) who estimated that in a maize canopy speeds of 4.4 times the mean occurred on at least 10 separate occasions during one hour. Raupach & Thom (1981) also discuss the skewness of velocity distributions in canopies, and link this with the transport of momentum into the crop during gusts or sweeps. They argue, furthermore, that local diffusion theory is unlikely to be valid where skewness is large ($\text{Sk}(w) \gg 0.2$).

Thirdly, the flow in crops is very heterogeneous vertically, with \bar{u} , σ_u , σ_v , σ_w and shear stress, $\overline{u'w'}$, decreasing by almost an order of magnitude with depth in the canopy (Wilson 1980). Thus simple models of dispersion in which the flow is assumed to be homogeneous can be expected to have only limited applicability.

Fourthly, there is a bewildering choice of turbulence length scales, from the size of individual foliage elements, at which wake turbulence is produced, to the depth of the atmospheric boundary layer which influences the frequency between gusts both above and within the canopy. For vertical transport the dominant length scale is likely to be of the order of the height of the crop, but other scales contribute.

SPORE RELEASE AND DEPOSITION

Although the airflow in crop canopies is highly turbulent, each element of foliage has a boundary layer around it in which the flow is laminar with intermittent turbulence. The layer is of the order of 1 mm thick, and if fungal spores are to escape from the host plant they must first escape from the boundary layer. For some fungi, such as ascomycetes and those releasing ballistospores there is an 'active' mechanism in which the spores are projected away from the

host. Although the distance of discharge is short, typically only 0.1–0.2 mm (Ingold 1971), it is enough to ensure that some spores do escape. For many other fungi the spores are held away from the leaf surface on sporophores, as for *Helminthosporium maydis*, or in chains, as for *E. graminis*, and are released passively as wind gusts penetrate the boundary layer (Aylor 1978), or as leaves flap (Bainbridge & Legg 1976) or rub against one another. Yet other spores, such as *Puccinia hordei* and *Rhynchosporium secalis*, are released when rain drops or drips from higher leaves shake them free, or project them into the air in small drops of water.

The spore release mechanism thus influences the manner in which spores enter the airflow, and as Aylor (1978) argues, this may influence the dispersal pattern. The most obvious effect is for spores that are splash-dispersed where the droplet is much larger than the spore that it contains, and it is the fall speed of the droplet, not the spore, that determines the dispersal distance. But the mode of release is also important for dry-dispersed spores. Active release operates independently of windspeed, and so spores become entrained in airflow that represents the full range of windspeeds. However, passively released spores, whether dislodged by rubbing, shaking, or directly by wind drag, are all blown away from the host considerably faster than the mean wind speed; how much faster may vary considerably from spore to spore. Aylor (1978) contends that *H. maydis* has a wind threshold of some 5 m s^{-1} and will wait for several days if necessary for that threshold to be reached, but chains of *E. graminis* spores weaken progressively with time (Bainbridge & Legg 1976) and can be dislodged by very low speeds or gentle shaking after several hours in still air. Although *E. graminis* spores do not have a well defined threshold for release they are still dislodged primarily during gusts, and Aylor *et al.* (1981) obtained evidence that the speed at which spores are released is approximately twice the true mean windspeed.

In laminar airflow spores or water drops may be deposited to solid surfaces by sedimentation, impaction or diffusion, and for simple objects the three processes can be described theoretically. For complex vegetative surfaces and turbulent airflow the subject is not so simple, but has been reviewed by Chamberlain & Little (1981). For spores of most pathogens (of diameter greater than $1 \mu\text{m}$) molecular diffusion is negligible, and the deposition rate is often expressed as the sum of sedimentation and impaction. This rather simplistic model of deposition was used by Legg & Powell (1979) with some support from Gregory's (1973) wind-tunnel experiments. In field crops the vertical wind component is comparable with the two horizontal components, and most leaves are neither horizontal nor vertical but inclined at some intermediate angle. But there is unlikely to be a more realistic theory until experimental work becomes more accurate.

The rate of sedimentation depends only on the area density of leaf surface projected vertically, A_v , and the fall speed of the spore, f (defined to be positive), and is independent of windspeed. Thus if sedimentation were the only deposition process the rate of depletion of a cloud of spores of concentration c drifting through a crop at a steady speed s would be

$$dc/dt = -cA_v f;$$

therefore

$$dc/dx = (1/s) dc/dt = -cA_v f/s,$$

and

$$c(x) = c(0) \exp(-\gamma_s x), \quad (1)$$

where $\gamma_s = A_v f/s$ and is the extinction coefficient due to sedimentation.

The rate of impaction, however, depends on the speed of the particle: increasing the speed

increases the rate at which leaves or stalks are encountered, and also increases the efficiency of impaction, $E_1(s)$. Thus

$$dc/dt = -cA_h sE_1(s),$$

where A_h is the leaf and stem area density projected horizontally, and assumed to be independent of direction. Therefore

$$c(x) = c(0) \exp(-\gamma_1 x), \quad (2)$$

where $\gamma_1 = A_h E_1(s)$.

The efficiency of impaction is a function of the Stokes number $St = (fs)/(gL)$, where g is the acceleration due to gravity, and L is the length scale of the target defined variously as the radius or diameter for cylindrical objects. $E(St)$ is an increasing function of windspeed (Chamberlain & Little 1981) and for many practical situations may be considered to increase linearly with windspeed above a certain threshold. For a barley mildew spore ($f \approx 12 \text{ mm s}^{-1}$) moving among barley stems (radius *ca.* 4 mm) the threshold speed is approximately 0.5 m s^{-1} .

If total deposition is expressed as the sum of sedimentation and impaction we have

$$c(x) = c(0) \exp(-(\gamma_s + \gamma_1)x), \quad (3)$$

where γ_s dominates at low windspeeds and decreases with increasing windspeed, and γ_1 dominates at higher windspeeds and increases with windspeed (figure 4*a*).

Spore release and deposition both depend critically and nonlinearly on the instantaneous windspeed. Theories of dispersion that use only mean windspeeds and mean concentrations are thus likely to be in serious error, and other approaches must be sought.

THEORIES OF TURBULENT TRANSPORT

The problem of predicting turbulent dispersion from a knowledge of crop structure and mean windspeed above the crop can conveniently be considered in two stages: first, that of predicting profiles of mean windspeed and turbulence statistics within the crop, and secondly that of predicting the dispersion of spores that are 'passive', i.e. do not affect the airflow in any way. In this paper only the second of these two is discussed: it is assumed that all relevant properties of the airflow can be measured, or calculated by other means. I also assume that the dispersion of fungal spores is equivalent to the dispersion of air parcels with the addition of a steady fall of the spores under gravity. Csanady (1963) discusses the dispersion of heavy particles, and concludes that the dispersion of particles does not differ from that of gases provided that two conditions are satisfied: first, that the particles should be light enough to follow the fastest eddies that contribute to dispersion, and secondly that the particles fall slowly enough that they do not 'fall out' of an eddy before that eddy decays. These two conditions, can, with several reasonable assumptions, be expressed as $f \ll gL_z/\sigma_w$ and $f^2 \ll 2\sigma_w^2/\beta^2$, where L_z is the vertical length scale of transporting eddies, and $1/\beta$ is the ratio of the Eulerian scale length to the product of the Lagrangian timescale and σ_w , and is probably between 0.25 and 1.0. (Eulerian properties of the flow are those relating to measurements made at a fixed point; Lagrangian properties relate to particles being carried along by the flow.) In a crop where L_z and σ_w may be 0.1 m and 0.3 m s^{-1} respectively, the first condition becomes $f \ll 3 \text{ m s}^{-1}$ and is readily satisfied for fungal spores. The second condition is probably satisfied for particles with an effective diameter less than $40 \text{ }\mu\text{m}$, but it depends on the values of σ_w and β . Neither condition

is satisfied for droplets of several hundred micrometres diameter, but for these it may be adequate to calculate the ballistic trajectory with allowance for the mean wind.

From previous sections it follows that a realistic theory of fungal spore dispersal must allow for the release of spores by wind gusts, or by the shaking or rubbing together of leaves that occurs during gusts. The theory must therefore incorporate the following features. (1) After release, spores travel at a speed that may be a factor of two or more above the mean windspeed for a distance of about $s_r \tau_{Lu}$, where s_r is the speed of release, and τ_{Lu} is the Lagrangian timescale for horizontal fluctuations in speed. (2) After time τ_{Lu} the air parcel carrying the spore 'forgets' its initial speed and is dispersed in the highly turbulent and heterogeneous flow through or above the crop canopy. (3) At any time during its flight through the crop the spore may be deposited to the ground or to foliage.

Several theories of dispersion are worth considering.

(a) *Diffusion theory*

Diffusion theory is analogous to the molecular diffusion of gases, and it is assumed that the flux of spores at any point is proportional to the local concentration gradient. For turbulent dispersion the 'diffusion coefficient' may take the full three-dimensional tensor form, and may also be a function of height. This theory has been widely used in the past (e.g. by Legg & Powell (1979) and Aylor & Taylor (1983)) but has limitations for dispersion in crop canopies (Raupach & Thom 1981). First, diffusion theory is known to be invalid close to a source of dispersed material (Taylor 1921); ideally the distance should be greater than $\tau_L \bar{s}$, where τ_L is the Lagrangian timescale for vertical or lateral fluctuations. For vertical velocity fluctuations at the top of the crop $\tau_{Lw} \approx 0.3(h-d)/\sigma_w$, where h is crop height and d is the zero plane displacement. Thus $\tau_{Lw} \bar{s} \approx 0.2$ m for crop 1 m tall, and seems unlikely to cause serious error in dispersion patterns; but for spores released in gusts $\tau_{Lw} s_r$ may 1 m or more.

Secondly, diffusion theory is valid only where the scale length of transporting eddies is less than the scale in which the concentration gradient changes. This condition is rarely satisfied in crop canopies where there is a source or sink of the material being dispersed. The most conspicuous effect of large scales of turbulence is seen when counter-gradient fluxes occur; for example there is a wind speed maximum in the lower part of many canopies but momentum must be transferred downwards at all heights. Counter-gradient heat fluxes have also been observed in the lower half of a forest of Ponderosa pine (E. F. Bradley, O. T. Denmead & G. W. Thurtell, personal communication) where the mean temperature increased with height, but eddy correlation measurements showed the mean heat flux to be upwards. Close examination of the results showed that the heat flux was large and positive for short periods during gusts, when the temperature gradient was temporarily negative; but for long periods between gusts the temperature gradient was positive, and the heat flux was small and downwards.

Thirdly, diffusion theory has been used and tested in flows with low turbulence intensity, $i_u \leq 0.2$, where streamwise diffusion can be neglected in comparison with advection. As we have seen, i_u can be as high as 4.0 within crop canopies, so streamwise diffusion cannot be neglected, and to estimate dispersion in three dimensions the full tensor form of the diffusion coefficient must be used. The solution is no longer straightforward, and because of the multiplicity of length and velocity scales (Raupach & Thom 1981) it seems unlikely that the components of the diffusivity tensor can be estimated with any accuracy.

Fourthly, it is usual to assume that the cloud of spores is advected at the mean wind velocity \bar{u} . But this is not acceptable when turbulence intensity is high and impaction depends nonlinearly on the instantaneous windspeed. It is even less acceptable if spores are released and deposited during gusts.

It can be seen that diffusion theory is not well suited to describe dispersion within crop canopies. It may be possible to improve it by semi-empirical adjustments, such as averaging concentration gradients over height intervals that correspond to the mean mixing length. Aylor (1978) has adapted an 'advected Gaussian puff' diffusion model to allow for gust release: puffs of air carry spores only if the speed of the puff exceeds the threshold speed for release, and the speed then decays exponentially to the mean windspeed. This method successfully predicts the increased rate of impaction caused by gust release (Aylor 1982), but it is not easy to see how it could be extended to describe the full dispersion process in the heterogeneous turbulence above and within crops.

(b) *Second-order closure models*

One approach to modelling turbulent dispersion that avoids the local diffusion assumption is to manipulate the equations of conservation of matter (concentration, c) and momentum (Navier–Stokes equations) to give four equations for \bar{c} , $\overline{u'c'}$, $\overline{v'c'}$, and $\overline{w'c'}$ (Donaldson 1973) (further equations are needed for buoyant or stable flow). These equations contain third moments, such as $\overline{u'w'c'}$, and also terms for pressure–concentration correlations. By making suitable approximations it is possible to reduce all terms to second order and obtain a set of equations that can be solved. The possible use of second-order closure models in crop canopies is reviewed by Raupach & Thom (1981); here it need only be said that although such methods have been shown to give plausible results, and to be capable of predicting counter-gradient diffusion (Wilson & Shaw 1977), the equations are complex to solve, and contain so many unknown constants that they are unlikely to be used for some time for spore dispersion in crops.

(c) *Walk on a random field*

In this method a three-dimensional array of velocity vectors is generated to define the airflow pattern in the space through which the spores will move. These velocities are then varied in time in a pseudo-random fashion, so that the velocity statistics and spatial correlations match those of the real world. Spores are released into the matrix and carried by the turbulent flow. The method is in principle 'rather straightforward' (Lamb 1981), but 'not well suited to most applied studies because it requires a considerable amount of computer time to generate the ensemble of velocity fields and large amounts of computer memory to store them'. This method has not yet been attempted for dispersion in crop canopies, and it seems unwise to do so until more progress has been made in simpler situations.

(d) *Markov chain simulation*

Here the trajectories of individual fluid particles are simulated as a random walk, and spores are assumed to follow the same path, but with an additional downwards velocity equal to their fall speed. The velocities for successive time steps, of length Δt , are not independently random, but retain a 'memory' so that the velocity autocorrelation timescale assumes the correct value: the Lagrangian integral timescale. For homogeneous turbulence the vertical velocity sequence for an air parcel can be generated as a first-order Markov sequence

$$w_{n+1} = \alpha_w w_n + \beta_w \sigma_w \xi_n, \quad (4)$$

where w_n and w_{n+1} are vertical velocities during steps n and $n+1$, ξ_n is a random number taken from a distribution with zero mean and unit variance, and α_w and β_w are constants. It can readily be shown (Hall 1975) that this generates a velocity sequence with an exponential autocorrelation function, and by choosing $\alpha_w = \exp(-\Delta t/\tau_w)$ and $\beta_w = (1 - \alpha_w^2)^{\frac{1}{2}}$, the timescale equals τ_w , and the velocity variance equals the Eulerian variance.

Most previous Markov chain models (see, for example, Hall 1975; Wilson *et al.* 1981) have included fluctuations in vertical velocity only, and assumed streamwise advection at the mean velocity \bar{u} . This is clearly not acceptable close to or within crops where streamwise diffusion is comparable with advection, and where spore release and deposition are nonlinearly related to the instantaneous windspeed. Legg (1983) extended these early models to include streamwise turbulence and proposed an additional equation for the movement of air parcels in a boundary layer in which the timescales vary with height but σ_w , σ_u and $\overline{u'w'}$ are constant:

$$u'_{n+1} = \alpha_u u'_n + \beta_u \sigma_u \zeta_n, \quad (5)$$

where u'_{n+1} is the departure of the instantaneous windspeed from the local mean wind at the height of the air parcel. The coefficients α_u and β_u are defined as $\exp(-\Delta t/\tau_u)$ and $(1 - \alpha_u^2)^{\frac{1}{2}}$, where τ_u may be loosely identified with the Lagrangian timescale for streamwise velocity fluctuations, but is not rigorously equal to it. The timescale τ_u is not generally proportional to τ_w , so α_u and β_u vary with height. The pseudo-random number ζ_n is taken from a Gaussian distribution, but chosen so that

$$\overline{\xi_n \zeta_n} = \overline{u'w'} (1 - \alpha_u \alpha_w) / (\sigma_u \sigma_w \beta_u \beta_w) \quad (6)$$

to maintain the correlation between u'_n and w_n .

This model was used to predict the mean temperature and heat flux profiles in the plume of heat downwind from a cross-stream elevated line heat source in a wind-tunnel boundary layer (Legg 1983). The computed centroid height and depth of the plume agreed with measurements, and the profile of streamwise heat flux (figure 2) was also predicted correctly close to the source. The flux is seen to be positive below the source where the negative covariance $\overline{u'w'}$ brings down fast hot air, but negative above the source where rising air moves slower than the mean windspeed. The ability of the model to predict streamwise fluxes is particularly encouraging because the correlation between windspeed and spore concentration is believed to have an important influence on the dispersion of fungal pathogens, especially those released in gusts.

So far I have assumed that σ_w , σ_u and $\overline{u'w'}$ are constant, but this is not so in crop canopies where magnitudes of all three increase with height. Wilson *et al.* (1981) showed that (4) cannot be used in crops, or fluid particles accumulate in the region of small σ_w . From the mean momentum equation Legg & Raupach (1982) showed that a gradient of σ_w is associated with a vertical pressure gradient, and they modified (4) to

$$w_{n+1} = \alpha_w w_n + \beta_w \sigma_w \xi_n + (1 - \alpha_w) \tau_w \partial \sigma_w^2 / \partial z. \quad (7)$$

Similarly, a gradient in $\overline{u'w'}$ is associated with a pressure gradient $\partial \bar{p} / \partial x = -\rho \partial (\overline{u'w'}) / \partial z$, and (5) becomes

$$u'_{n+1} = \alpha_u u'_n + \beta_u \sigma_u \zeta_n + (1 - \alpha_u) \tau_u \partial (\overline{u'w'}) / \partial z. \quad (8)$$

For lateral velocity fluctuations,

$$v_{n+1} = \alpha_v v_n + \beta_v \sigma_v \chi_n, \quad (9)$$

where α_v and β_v are related to the timescale for lateral fluctuations, and χ_n is a random number with zero mean and unit variance, and is independent of ξ_n and ζ_n . By adding the fall speed of the spore we now have the necessary set of equations to describe three dimensional dispersion within a crop canopy.

The great strength of the Markov chain theory of dispersion is its versatility. It satisfies the criteria specified earlier in this section of being usable in highly turbulent and heterogeneous flows, it is valid at any distance from a point source, and it can be adapted to describe the trajectories of spores released in gusts. It can also be adapted for flow in which the velocity distributions are skewed (Legg 1983), and could be used for splash-dispersed spores carried by airborne droplets that are evaporating and diminishing in size.

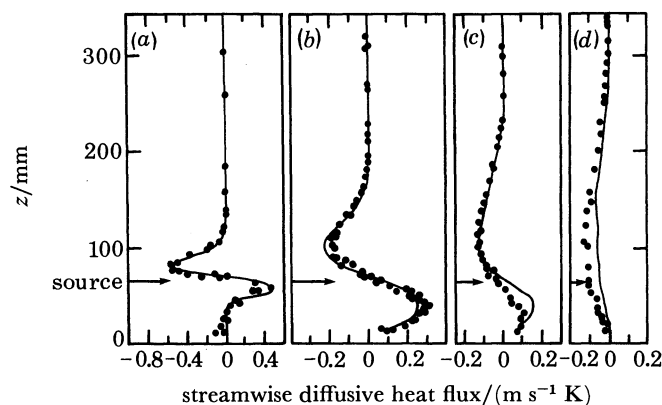


FIGURE 2. Streamwise diffusive heat flux at distances of (a) 0.15 m, (b) 0.45 m, (c) 0.90 m and (d) 1.80 m downstream from an elevated heat source in a wind-tunnel boundary layer. Symbols: (●), experimental results; the line is the flux predicted by Markov chain simulation (Legg 1983).

It must be emphasized, however, that this theory has not yet been tested in the complex airflow in crops, and from previous experience it seems likely that some further developments will be necessary. For example, with so many length scales and timescales contributing to the turbulence it is possible that the assumption of an exponential autocorrelation function, implicit in first-order Markov models, will prove to be inadequate. This could be accommodated by higher-order models in which the velocity for each step is related not only to the previous step but to several earlier steps, but such refinement cannot be justified yet. The equipment necessary to test the theory for gaseous dispersion, including sonic anemometers and rapid response gas analysers, now exists, and it is to be hoped that such experiments will soon be done.

THE EFFECTS OF TURBULENCE AND GUST RELEASE ON SPORE DISPERSION PATTERNS

Until experiments have proved that the theory is valid, it is too early to attempt a full three-dimensional Markov chain simulation of spore movement and deposition in a crop. But it is instructive to calculate deposition patterns for a very simple situation and to see from this the effects of turbulence in the flow, and of gust release of particles. The example chosen is that of dispersion in two dimensions in homogeneous turbulence. Vertical movement is omitted except that spores may be deposited by sedimentation at their normal fall speed. The mean

velocity \bar{u} is in the streamwise, x , direction, and there are velocity fluctuations u' and v' in the x and y directions. This example corresponds roughly to dispersion of spores released near the middle of a tall uniform crop: all spores are deposited by sedimentation or impaction to the foliage, and none are deposited on the soil or removed from the top of the crop by vertical dispersion.

The detailed assumptions are that u' and v' have a Gaussian distribution and are independent of one another, but both have the same Lagrangian timescale τ . For continuous release the initial values of u' and v' are taken at random from a Gaussian distribution and thereafter varied in a Markov sequence. During each step there is a probability of deposition by sedimentation, P_s , or impaction, P_i , where

$$P_s = fA_v \Delta t$$

and

$$P_i = E_i(s) A_h s \Delta t. \quad (10)$$

Sedimentation occurs when a random number, chosen from a distribution that is uniform between 0 and 1, is less than P_s , and impaction occurs if a second random number is less than P_i . Spores can be released from points in an area of any shape or size, and the deposition pattern for sedimentation and impaction is given. Unfortunately the results cannot be presented in a way that applies universally, as sedimentation depends only on the fall speed of the spore, and impaction depends on the instantaneous speed of the spore and physical dimensions of the leaf or stem. So we must choose one specific example and use that to illustrate the main principles involved. The example chosen is that of the dispersion of mildew spores, fall speed = 12 mm s⁻¹, from a point source in a barley crop with $A_v = 4.0$ m⁻¹, $A_h = 4.0$ m⁻¹ and a mean radius of stems and leaves of 4 mm. Initially it is assumed that spores are released continuously, so their flights start with the full range of windspeeds. Simulations were run with $\bar{u} = 0.05, 0.10, 0.20, 0.30, 0.50$ and 1.0 m s⁻¹ and with turbulent intensities $i_u = i_v = 0, 1, 2.5$ and 5 . The choice of τ was not easy: Lagrangian properties are difficult to measure and there have been no estimates of the Lagrangian timescale for fluctuations in horizontal windspeeds in crops. One possible clue comes from Finnigan (1979), who measured the windspeed in a wheat crop and found that gusts arrived at intervals of about 5 s and lasted for about 1 s. The measurements were made by fixed instruments, but suggest that the Lagrangian timescale is of the order of 1–10 s. To cover this range, and also illustrate the sensitivity of the dispersion pattern to τ , all simulations were repeated with $\tau = 1$ and 10 s.

It was shown earlier that for a cloud of spores moving at a constant speed the concentration, and hence the deposition rate, decreases exponentially with distance. For a point source with spores leaving in various directions but at constant speed there is a dilution effect, and it is the total number of spores deposited in an annulus of unit width that decreases exponentially; this may alternatively be written as $2\pi rD$, where D is the mean deposition rate per unit area at a radius of r . For this simple situation rD decreases exponentially, and

$$(rD)_r = (rD)_0 \exp(-(\gamma_s + \gamma_i) r), \quad (11)$$

where γ_s and γ_i are given by (1) and (2). For turbulent flow rD need not decrease exponentially, but for all the simulations tried it was approximately exponential in the range for which $(rD)_r/(rD)_0$ decreased to *ca.* 0.01, e.g. figure 3*a*. For simplicity a straight line was fitted through the linear portion so that deposition could be characterized by a single extinction coefficient, $\gamma (= \gamma_s + \gamma_i)$.

In figure 4a the deposition extinction coefficients for $\tau = 1.0$ s are shown as a function of \bar{s} , the mean windspeed. The mean speed, rather than \bar{u} , was chosen because it is equal to \bar{u} for the simple case of no turbulence, and is a more suitable parameter in very intense turbulence where it represents the speed at which spores leave the source and also the mean speed at which spores are impacted. It also has the merit of being easy to measure. For non-turbulent flow γ is simply the sum of γ_s and γ_i , as expected. As the turbulence intensity increases the dispersion changes in two ways, and both increase γ . First, the range of speeds means that faster spores are deposited more rapidly by impaction and very slow spores are liable to be lost by sedimentation close to the source. Secondly, if the time of flight exceeds τ , particles cease to

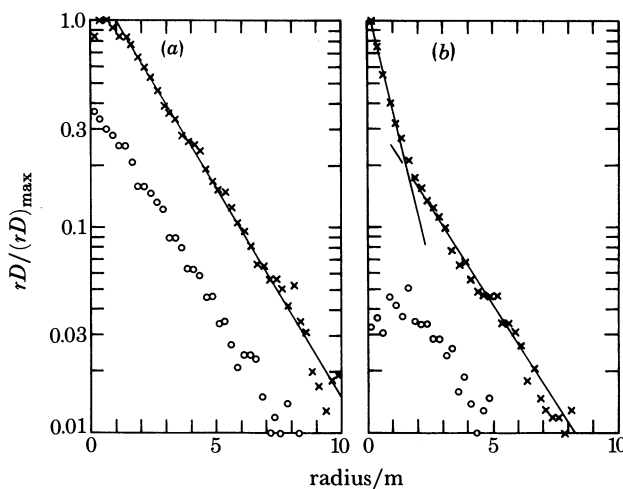


FIGURE 3. Estimated deposition of barley mildew spores around a point source, showing the linear relations between $\ln(rD)$ and radius, r . Symbols show deposition by impaction (\times) and by sedimentation (\circ); the straight lines were fitted by eye. The model used $\bar{u} = 0.5$ m s $^{-1}$, $\sigma_u = \sigma_v = 0.5$ m s $^{-1}$, giving $\bar{s} = 0.78$ m s $^{-1}$, and $\tau = 1.0$ s. The threshold for spore release was (a) 0.0 m s $^{-1}$ and (b) 1.55 m s $^{-1}$.

move in straight lines and leave the source by diffusion. For pure diffusion r increases as only the square root of time, so deposition occurs nearer to the source and γ is larger. For a wide range of \bar{s} , values of γ calculated on the basis of no turbulence will be too small by a factor of 1.5 to 2.0 if $i_u = 1.0$, and a factor of 3 or more if $i_u = 2.5$, as found by Wilson (1980) in maize.

If the Lagrangian timescale is set to 10 s (figure 4b) there is less variation in γ caused by increasing turbulence intensity. This is because the distance $\bar{s}\tau$ for which particles move in straight lines is now greater than $1/\gamma$, the distance within which most spores are deposited. There is an increase in γ due to the spread of spore speeds, but very little increase due to diffusion.

The ratio of the number of spores deposited by impaction to the total deposition is also affected by \bar{s} (figure 4c). For non-turbulent flow this ratio is given simply by the ratio $P_i/(P_i + P_s)$ (equation (10)). The presence of turbulence generally increases the proportion lost by impaction due to the nonlinearity of $E_i(s)$, but this is not always so.

The final question is how much γ is affected if spores are released only above a certain threshold speed s_t . The answer depends on the relative magnitudes of $s_t\tau$, the distance that spores move before 'forgetting' their take-off speed, and $1/\gamma(s_t)$, the deposition scale length

at the threshold speed. If $s_t \tau \ll 1/\gamma(s_t)$, most spores will slow down to the mean windspeed before being deposited, and γ will be unchanged (figure 4a, Δ). If $s_t \tau \gg 1/\gamma(s_t)$, most spores will be deposited at their take-off speed and the dispersion pattern will be dependent on s_t , not \bar{s} (figure 4a, \bullet ; and figure 4b, $\blacktriangle, \blacktriangledown, \bullet$). For $s_t \approx 1/\gamma(s_t)$, spores will be deposited at a rate dependent on s_t near to the source (figure 4a, \blacktriangledown), and on \bar{s} beyond $s_t \tau$ (figure 4a, ∇), so γ changes at a distance of $ca. s_t \tau$. The double slope is shown in the graph of $\ln(rD)$ against r in figure 3b for dispersion in flow with $\bar{s} = 0.78 \text{ m s}^{-1}$, $s_t = 1.55 \text{ m s}^{-1}$, $i_u = i_v = 1.0$ and $\tau = 1.0 \text{ s}$. For gust release the proportion impacted is also a function of distance, decreasing

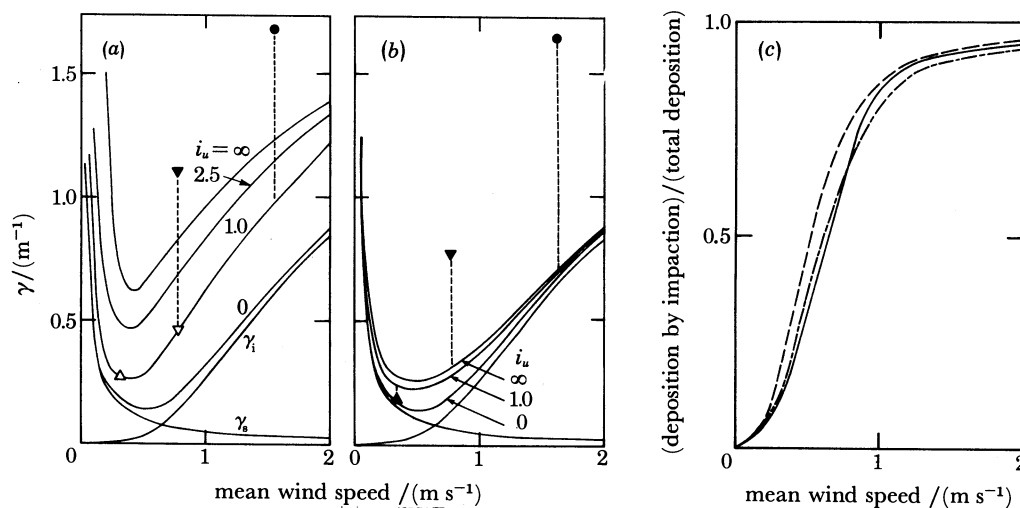


FIGURE 4. (a, b) The estimated extinction coefficient, γ , for *E. graminis* spores in a barley crop as a function of the mean windspeed, \bar{s} , and turbulence intensity. The timescale for horizontal velocity fluctuations was (a) 1.0 s and (b) 10.0 s. The lines are for a zero threshold velocity and $i_u = i_v = 0, 1.0, 2.5$ and ∞ ; symbols $\blacktriangle, \Delta, \blacktriangledown, \nabla$ and \bullet are for a release threshold of $2.0 \bar{s}$ and $i_u = 1.0$. (c) The ratio of the number of spores deposited by impaction to the total deposition, as a function of mean wind speed for: (—), non-turbulent flow; (---), $i_u = i_v = 2.5$ and $\tau = 1.0 \text{ s}$; (-·-·-), $i_u = i_v = 2.5$ and $\tau = 10 \text{ s}$.

in this instance (figure 3b) from 0.96 close to the source to 0.81 at 3.0 m. The relation between spore concentration and deposition rate also changes with distance from the source as the mean speed of spores decreases.

Further simulations have been done to show the extinction coefficient, γ , for spore deposition per unit area adjacent to a large rectangular source of spores, analogous to an infected plot. Graphs of γ against \bar{s} (not given here) are very similar to figure 4; for non-turbulent flow γ is formally identical to that for a point source, and for very turbulent conditions γ for the rectangular source is larger than for a point source by a factor of 1.0–1.5.

CONCLUSIONS

Of the theories available to describe turbulent dispersion, Markov chain simulation is the most suitable to describe the dispersal of plant pathogen spores within crops. Although the theory awaits field tests it seems able to cope with very turbulent heterogeneous flows, and also with the release of spores in gusts, and their deposition to plant surfaces. To apply the theory in crops it is necessary to know the turbulent velocity variances and the Lagrangian timescale

for vertical and horizontal wind fluctuations. The Lagrangian timescales cannot be measured directly, but may be estimated from plumes of inert gas released from a point source in a crop. There is also scope for wind-tunnel work to find the relation between Lagrangian and one-point and two-point Eulerian timescales.

A simple two-dimensional Markov chain model was used to simulate spore dispersal in flow with streamwise and cross-stream (but not vertical) velocity fluctuations. It showed that at a given mean windspeed the presence of horizontal velocity fluctuations could increase the extinction coefficient for spore deposition by as much as a factor of 4. Releasing spores only in gusts of double the mean windspeed also increased the extinction coefficient by as much as a factor of 2. It has not been possible to test the model rigorously against deposition gradients in earlier experiments because measurements of air flow were inadequate. But Bainbridge & Stedman (1979) measured the concentration of barley mildew spores downwind of an infected strip of crop (figure 1, lines B and C), and their results, with a mean windspeed of about 0.4 m s^{-1} , correspond to an extinction coefficient of $0.5\text{--}1.5 \text{ m}^{-1}$. These values are higher than those in figure 4, but as our model does not allow for loss of spores from the top of the crop or to the ground the agreement is satisfactory.

Early work on spore dispersal in crops has suffered for lack of a theoretical framework to explain the results. Markov chain simulation appears to provide a suitable model, and future studies should be accompanied by the necessary meteorological and crop measurements to test it. Only by developing such models can we hope to predict dispersal patterns for the great diversity of spore sizes and release mechanisms, of crop structure, and of meteorological conditions that are of practical importance.

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Discussion

C. WALL (*Rothamsted Experimental Station, Harpenden, U.K.*). In our work on the dispersal of insect pheromones from point sources over distances of the order of tens to hundreds of metres in wheat fields, we have shown that pheromone molecules are adsorbed onto the wheat plants downwind of the source and then released in sufficient quantities for the insects to respond to them. Thus male moths can orient to the position of the original point source for several hours after its removal.

Are there any parallels in the dispersal of other agents from point sources? Is there any evidence that fungal spores, bacteria or virus particles that have become impacted or deposited on vegetation can be blown back into the air by gusts? If so, what importance does this have for existing models of dispersal from point sources?

B. J. LEGG. It is possible that in strong winds some spores may impact onto plants and bounce off, as was shown by A. C. Chamberlain for *L. clavatum* spores impacted onto barley heads in a wind tunnel. In the present model bounce-off could be accommodated quite simply by

decreasing the impaction coefficient at high windspeeds. It is rather unlikely that the spores of foliar pathogens will be dislodged after coming to rest on a plant surface, especially for spores that are sticky. If spores can be resuspended, however, the rate of release would presumably depend on the numbers of spores that had already settled, and would increase with time. Thus the present Markov chain model, that describes only the steady-state concentration and deposition rates resulting from a continuous source, could not be used without modification. Eventually an equilibrium might be reached in which the rate of resuspension equalled the deposition rate, and the mean spread of the spore plume could then be calculated by assuming no further deposition.