Dispersal of spores following a persistent random walk

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A model of a persistent random walk is used to describe the transport and deposition of the spore dispersal process. In this model, the spore particle flies along straight line trajectories, with constant speed v, which are interrupted by scattering, originating from interaction of spores with the field and wind variations, which randomly change its direction. To characterize the spore dispersal gradients, we have derived analytical expressions of the deposition probability $\varepsilon(r|v)$ of airborne spores as a function of the distance r from the spore source in an infinite free space and in a disk of radius R with an absorbing edge that mimics an agricultural field surrounded with fields of nonhost plants and bare land. It is found in the free space that $\varepsilon(r|v) \sim e^{-\alpha r/l}$, with α a function of l_d/l, where l and l_d are the scattering and deposition mean free paths, respectively. In the disk, however, $\varepsilon(r|v)$ is an infinite series of Bessel functions and, exhibits three regimes: absorbing ($R<l_d$), intermediate ($R=l_d$), and deposition ($R>l_d$).

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I. INTRODUCTION

Dispersal of living organisms is a critical issue in several fields of ecological research. Living organisms need to disperse to colonize new territory, escape predators, parasites, or competitors, find trophic resources or more clement weather conditions, encounter an appropriate mate for breeding, etc. Therefore, dispersal might be one of the most important components of establishment, persistence, and evolution of populations. Several qualitative and quantitative aspects of dispersion have been addressed in two recent textbooks Refs. [1,2]. For a given organism, the geographical range of dispersal can be approximated by the dispersal function of the organism or its propagules. This function is mostly shaped by the dispersal means and behavior (when applicable) and their relations with the surrounding biotic and abiotic environment.

Several plant diseases of economic importance (e.g., cereal rusts and powdery mildews, potato late blight, and apple scab) are spread by microscopic windborne spores. In order to infect new host plants and therefore contribute to the development of an epidemic disease, spores produced on infected plants must be released by wind gusts and/or rain drops, carried away by wind currents, and finally deposed on susceptible host plants [3].

Experimental studies of spore dispersal from single infected plants or small disease foci have shown that the number of spores deposited sharply decreases with increasing distance from the spore source. The resulting curve in a given direction or after averaging data over a given space is the monotonically decreasing *spore dispersal gradient* [4]. Empirical models, such as the power law and the simple exponential models can easily be fitted to the experimental spore-dispersal gradients [5]. These models usually yield good fitting and are parameter sparse, but they are unable to explain how the gradient arose [4], even if heuristic rationales for the choice of a given distribution as the spore-dispersal function were suggested [6]. Therefore, physical models, based on an explicit description of the supposed dispersal mechanisms, are required to better understand the dispersive phases of disease [7].

Gradient transfer theory (K theory) and Gaussian plume models of turbulent dispersal have been used to describe spore dispersal [8–10]. However, such models, although relatively easy to use, cannot predict accurately spore dispersal in the complex meteorological situations that are common over diseased fields [7]. Random walk models, which simulate the trajectories of individual spores, have been applied in a few cases to spore dispersal within crop [10,11]. Parameter calibration of these models required precise measurement of several meteorological variables, such as downstream and cross-stream components of wind velocity and friction velocity [12], which might not be performed accurately in all experimental situations.

More general mechanistic models, which did not include explicit weather variables, have been used to derive a mathematical expression for the spore-dispersal gradient, there called "contact distribution" [13,14]. Considering that the distribution of moving spores follows a Gaussian density with a variance that increases linearly with time, the resulting contact distribution was found to be a Bessel function [15,16].

In this paper, we consider a persistent random walk model for spore movement where the random walk is caused by *scattering* events that change the direction of the spore trajectory from its initial direction. The scattering originates from interaction of spore particles with the field and variations in wind velocity components. To study the effect of scattering on spore-dispersal gradients, we apply the transport equation and characterize the spore-dispersal gradients in two situations: (i) an infinite homogeneous space, hereafter referred to as "free space," and (ii) a disk with absorbing edge, which might be a better representation of an agricultural field surrounded by fields of nonhost plants and bare land [17]. In the latter case, long-distance spore dispersal,

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which has been demonstrated in wind-borne plant pathogens [18,19], is not considered and all spores leaving the disk no longer contribute to the epidemic process. To complete the infection process, spores have to be deposited on susceptible plant surface. In our model, it is assumed that the deposition of spores may occur anywhere with a homogeneous probability per unit of time. Mechanisms of spore deposition, say, gravity and scrubbing by rain drops [3], are not explicitly modeled but they contribute in a random manner to spore deposition.

II. TRANSPORT EQUATION AND DISPERSAL FUNCTIONS

Consider an ensemble of spores released at $\mathbf{r}=\mathbf{0}$ with a constant modulus of the velocity. Let θ be the angle made by the unit vector $\mathbf{u}$ of the direction in which a single spore particle moves along a fixed axis, say the x axis, and $\mathbf{r}$ and $\mathbf{v}(\theta)=v\mathbf{u}$ denote the position and velocity of the spore. To describe the motion of the spore we consider that the spore particle travels along straight line trajectories, with constant speed, which are interrupted by scattering that randomly changes its direction. Scatterings are assumed to be statistically independent events of zero duration, and the time interval between successive scattering (or the time spent moving along any given straight line without changing directions) is a random variable described by $\gamma e^{-\gamma t}$, where γ is the scattering frequency. After each single scattering, the probability density of changing the direction of the spore path from its initial direction θ_0 to θ is $p_{\mathrm{eq}}(\theta)$, assumed to be independent of θ_0.

For this type of motion, the evolution of probability density, $P(\mathbf{r},\theta,t|v)$, of finding the spore particle at $\mathbf{r}$ moving with constant speed v in the direction θ at time t can be modeled by the transport equation

$$\frac{\partial P(\mathbf{r},\theta,t|v)}{\partial t}=-\mathbf{v}(\theta)\cdot\nabla P-\gamma P+\gamma p_{\mathrm{eq}}(\theta)\int_{-\pi}^{\pi}d\theta' \times P(\mathbf{r},\theta',t|v), \tag{2.1}$$

where we assume the initial condition, $P(\mathbf{r},\theta,t=0|v)=\delta(\mathbf{r}-\mathbf{r}_0)\delta(\theta-\theta_0)$. Mathematical framework for the derivation of transport equation for dispersed objects in a fluid can be found in Refs. [20,21]. The initial value problem for Eq. (2.1) can be rewritten in integral form as

$$\begin{aligned}P(\mathbf{r},\theta,t|\mathbf{r}_0,\theta_0,v)&=e^{-\gamma t}G_0(\mathbf{r},\theta,t|\mathbf{r}_0,\theta_0,v)\\&\quad+\gamma\int_0^t dt'\int d\mathbf{r}'\int_{-\pi}^{\pi}d\theta' e^{-\gamma(t-t')}\\&\quad\times G_0(\mathbf{r},\theta,t-t'|\mathbf{r}',\theta',v)p_{\mathrm{eq}}(\theta')\\&\quad\times\int_{-\pi}^{\pi}d\theta'' P(\mathbf{r}',\theta'',t'|\mathbf{r}_0,\theta_0,v),\end{aligned} \tag{2.2}$$

where the traveling wave, $G_0(\mathbf{r},\theta,t|\mathbf{r}_0,\theta_0,v)=\delta(\mathbf{r}-\mathbf{r}_0-\mathbf{v}(\theta)t)\delta(\theta-\theta_0)$, is the solution of Eq. (2.1) in the limit $\gamma=0$. In a homogeneous space, the density $P(\mathbf{r},\theta,t|\mathbf{r}_0,\theta_0,v)$ is a function of $\mathbf{r}-\mathbf{r}_0$ such that we can set $\mathbf{r}_0=\mathbf{0}$. We are interested in what follows by the reduced probability density,

$$P(\mathbf{r},t|v)=\int_{-\pi}^{\pi}d\theta_0\int_{-\pi}^{-\pi}d\theta P(\mathbf{r},\theta,t|\theta_0,v)p_{\mathrm{eq}}(\theta_0), \tag{2.3}$$

which is the probability density of finding the spore particle at position $\mathbf{r}$ and with velocity v at time t regardless of the direction of the motion. After performing the angle average over θ_0 and θ in Eq. (2.2), we find that $P(\mathbf{r},t|v)$ satisfies the integral equation,

$$\begin{aligned}P(\mathbf{r},t|v)&=e^{-\gamma t}G_0(\mathbf{r},t|v)+\gamma\int_0^t dt'\int d\mathbf{r}' e^{-\gamma(t-t')}\\&\quad\times G_0(\mathbf{r},t-t'|\mathbf{r}',v)P(\mathbf{r}',t'|v).\end{aligned} \tag{2.4}$$

Now Laplace-Fourier transforming this equation and solving the resulting equation for the reduced probability distribution, we get

$$\overline{P}(\mathbf{k},s|v)=\frac{\overline{G}_0(\mathbf{k},s+\gamma|v)}{1-\gamma\overline{G}_0(\mathbf{k},s+\gamma|v)}, \tag{2.5}$$

where the Laplace-Fourier transform of any function $f(\mathbf{r},t)$ is defined as $\overline{f}(\mathbf{k},s)=\int_0^\infty d\mathbf{r}e^{i\mathbf{k}\cdot\mathbf{r}}\int_0^\infty dt e^{-st}f(\mathbf{r},t)$, and thus,

$$\begin{aligned}\overline{G}_0(\mathbf{k},s+\gamma|v)&=\int_0^\infty d\mathbf{r}e^{i\mathbf{k}\cdot\mathbf{r}}\int_0^\infty dt e^{-(s+\gamma)t}\int_{-\pi}^{\pi}d\theta_0\\&\quad\times\int_{-\pi}^{-\pi}d\theta G_0(\mathbf{r},\theta,t|\mathbf{0},\theta_0,v)p_{\mathrm{eq}}(\theta_0)\\&=\int_{-\pi}^{\pi}d\theta\frac{p_{\mathrm{eq}}(\theta)}{(s+\gamma)-i\mathbf{k}\cdot\mathbf{v}(\theta)}\\&=\int_{-\pi}^{\pi}d\theta\frac{p_{\mathrm{eq}}(\theta)}{(s+\gamma)-ikv\cos(\theta)}.\end{aligned} \tag{2.6}$$

For isotropic scattering, i.e., $p_{\mathrm{eq}}(\theta)=1/(2\pi)$, the integration can be readily performed to give

$$G_0(k,s+\gamma|v)=[(s+\gamma)^2+(\gamma kl)^2]^{-1/2}, \tag{2.7}$$

where the scattering mean free path $l=v/\gamma$ is the average distance a spore travels before scattering, i.e., before changing its flight direction. For anisotropic scattering, however, a fairly good approximation of G_0 can be obtained from Eq. (2.7) provided that l is replaced by the transport mean free path $l^*=l/[1-\langle\cos(\theta)\rangle]$, which is the length scale beyond which the scattering angles are randomized. In what follows, we will restrict ourselves to the isotropic case.

Now, we consider that the spore particles are stopped and deposited anywhere with a homogeneous probability $\mu=\mu(v)$ per unit of time. It may be worthwhile to mention at this stage that the spore deposition rate is in general a func-

tion of velocity as $\mu=\mu_s+v/l_c$, where μ_s represents the sedimentation rate constant and l_c the compaction length over which the deposition of spores increases as their velocity gets larger. Similarly, we define the mean deposition or capture length $l_d=v/\mu$ as the average distance a spore travels before deposition. The object we are after to is the contact density function or the spore-dispersal density function defined as

$$\begin{aligned} C(\mathbf{r}|\mathbf{0},v) &= C(\mathbf{r}|v) \\ &= \mu\int_0^\infty e^{-\mu t}P(\mathbf{r},t|v)dt \\ &= \mu\overline{P}(\mathbf{r},\mu|v) \\ &= \frac{\mu}{2\pi}\int_0^\infty e^{-i\mathbf{k}\cdot\mathbf{r}}\overline{P}(\mathbf{k},\mu|v)d\mathbf{k}. \end{aligned} \tag{2.8}$$

This function gives the density of spores deposited at distance $\mathbf{r}$ from the source when released with the initial velocity v. However, it may be more convenient for practical purposes to deal with the probability $\varepsilon(\mathbf{r})$ that a spore is deposited at distance greater than or equal to $\mathbf{r}$ from the source,

$$\varepsilon(\mathbf{r}|v)=\int_{\mathbf{r}}^\infty C(\mathbf{r}'|v)d\mathbf{r}'. \tag{2.9}$$

In the absence of any absorbing obstacles, the conservation of the probability implies that $\varepsilon(\mathbf{0}|v)=1$ and $\varepsilon(\mathbf{r}\to\infty|v)=0$. However, when there is a loss of probability due to absorbing boundaries, for instance, $\varepsilon(\mathbf{0}|v)=\mu\tau<1$, where τ is the lifetime of the spore particle in the field before either deposition or escape from the area under observation. Indeed, the spore lifetime τ in the presence of absorbing boundaries is smaller than the lifetime $1/\mu$ in the absence of absorbing boundaries because of additional loss of spore at absorbing boundaries. This results in less spores deposited in the field. These features will be illustrated in the following sections.

III. DISPERSAL IN FREE SPACE

As an application of the above formula, we consider the isotropic dispersion of spores in an infinite homogeneous field. In this case, the probability density of spores is

$$\overline{P}_0(k,s|v)=\frac{1}{\sqrt{(s+\gamma)^2+(\gamma kl)^2}-\gamma}. \tag{3.1}$$

Laplace-Fourier inversion of this expression is given in Ref. [22] as,

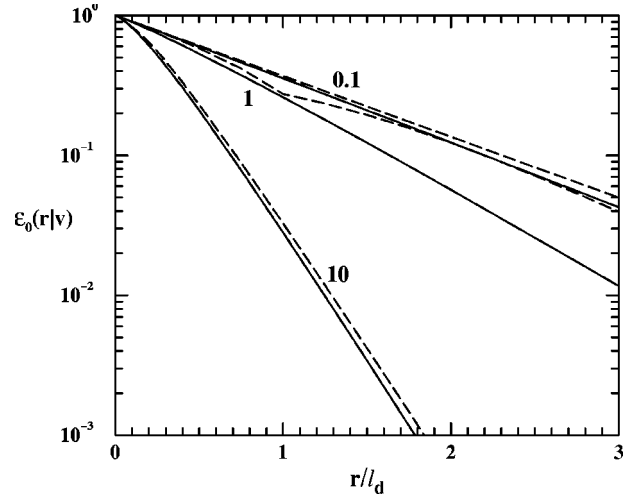

FIG. 1. Probabilities in Eq. (3.4) (solid lines) and in Eq. (3.8) (dashed lines) as a function of the reduced distance r/l_d from the focal for various values of l_d/l as quoted in the figure.

$$\begin{aligned} P_0(r,t|v) &= \frac{\delta(r/l-\gamma t)}{2\pi lr}e^{-\gamma t} \\ &\quad + \frac{\exp[-\gamma t+\sqrt{(\gamma t)^2-(r/l)^2}]}{2\pi l^2\sqrt{(\gamma t)^2-(r/l)^2}}H(\gamma t-r/l), \end{aligned} \tag{3.2}$$

where $H(z)$ is the Heaviside step function defined as $H(z)=1$ for $z>0$ and $H(z)=0$ for $z<0$. The spore-dispersal density and the deposition or captured probability are readily obtained from integrations of Eq. (3.2) as follows:

$$\begin{aligned} C_0(r|v) &= \frac{\exp[-(1+l_d/l)r/l_d]}{2\pi l_d r} \\ &\quad + \int_1^\infty dx\frac{\exp\left\{-\frac{r}{l_d}\left[\left(1+\frac{l_d}{l}\right)x-\frac{l_d}{l}\sqrt{x^2-1}\right]\right\}}{(2\pi l l_d)\sqrt{x^2-1}}, \end{aligned} \tag{3.3}$$

and

$$\varepsilon_0(r|v)=\int_{r/l_d}^\infty dx\exp\left[-\left(1+\frac{l_d}{l}\right)x+\frac{l_d}{l}\sqrt{x^2-\left(\frac{r}{l_d}\right)^2}\right]. \tag{3.4}$$

Figure 1 shows that this function (solid lines) decays exponentially as a function of r/l_d with a rate depending on l_d/l. That is to say, $\varepsilon_0\sim e^{-r/l_d}$ for $l_d\ll l$ and $\varepsilon_0\sim e^{-r/\sqrt{ll_d}}$ for $l_d\gg l$.

This behavior can also be understood by considering the ballistic and diffusion regimes of the spore motions. Indeed, the mean square displacement of a spore particle is

$$\langle r^2\rangle = \int_0^\infty 2\pi r^3 P(r,t)dr = 2l^2[e^{-\gamma t}+\gamma t-1] \simeq \begin{cases} (l\gamma t)^2, & \gamma t<1 \\ 4Dt, & \gamma t>1, \end{cases} \quad (3.5)$$

where $D=\gamma l^2/2$ is the diffusion constant. It follows from this expression that the spore motion can be approximated by a ballistic motion for times $t<1/\gamma$ and by a diffusive motion for times $t>1/\gamma$. This is the equivalent of writing

$$P_{\rm app}(r,t|v) = H(1-\gamma t)P_{\rm b}(r,t|v) + H(\gamma t-1)P_{\rm d}(r,t|v), \quad (3.6)$$

where $P_{\rm b}(r,t|v)=\delta(r-vt)/(2\pi r)$ and $P_{\rm d}(r,t|v) = e^{-r^2/4Dt}/(4\pi Dt)$ are the probability densities for ballistic and diffusion motions, respectively. Now, using this approximate expression of $P(r,t|v)$ into Eq. (2.8), and carrying out the integration, we obtain the approximate spore-dispersal density function as

$$C_{\rm app}(r|v) = \frac{\exp(-r/l_d)}{2\pi l_d r}H(l-r) + \int_{l/r}^\infty \frac{dx}{2\pi l l_d x}\exp\left\{-\frac{r}{l_d}\left(x+\frac{l_d}{2lx}\right)\right\}. \quad (3.7)$$

It is an easy matter to show that when $r<l$ we have $C_{\rm app}(r)=[1/(2\pi l_d r)]e^{-r/l_d}$ like for wave propagation in ballistic motion, while for $r>l$ it is $C_{\rm app}(r) =[1/(2\pi l l_d)]K_0((2r^2/ll_d)^{1/2})$ like for the diffusion [16]. Similarly, the probability $\varepsilon_{\rm app}(r|v)$ is given by

$$\varepsilon_{\rm app}(r|v) = [e^{-r/l_d}-e^{-l/l_d}]H(l-r) + \frac{r}{l_d}\int_{l/r}^\infty dx \exp\left\{-\frac{r}{l_d}\left(x+\frac{l_d}{2lx}\right)\right\}. \quad (3.8)$$

This function (dashed line) is compared to $\varepsilon_0(r|v)$ in Fig. 1. It is clear that the approximate formula describes very well the exact probability $\varepsilon_0(r|v)$ in the limit of $l_d \ll l$ and $l_d \gg l$. As a check, we have $\varepsilon_{\rm app}\simeq\exp(-r/l_d)$ when $r<l$ (ballistic regime) and $\varepsilon_{\rm app}\simeq(2r^2/ll_d)^{1/2}K_1((2r^2/ll_d)^{1/2})\sim\exp(-2r/\sqrt{2ll_d})$ when $r>l$ (diffusion regime).

IV. DISPERSAL INSIDE A DISK WITH ABSORBING EDGE

In this section, we investigate the effect of boundaries on the spore-dispersal density function and the deposition probability. To this end, we consider the isotropic dispersion of spores within a disk bounded by an absorbing edge. This latter mimics the escape of spores leaving the disk. To determine the expression of $\overline{P}(r,s)$ for the disk with absorbing boundary, we consider the expansion

$$\overline{P}(r,s|v) = \sum_{n=1}^\infty \overline{A}_n(s|v)\psi_n(r), \quad (4.1)$$

where the eigenfunction $\psi_n(r)=\sqrt{2}J_0(\alpha_n r/R)/[RJ_1(\alpha_n)]$ and $J_i(\cdots)$ is a Bessel function of first kind of order i and α_n are zeros of $J_0(\cdots)$ [23]. The eigenfunctions $\psi_n(r)$ are normalized such that $\int_0^R r\psi_n(r)\psi_m(r)dr=\delta_{nm}$. Thus, it follows that

$$\overline{A}_n(s|v) = \int_0^R r\psi_n(r)\overline{P}(r,s|v)dr = \frac{\psi_n(0)}{2\pi}\overline{P}_0(k=\alpha_n/R,s|v), \quad (4.2)$$

where $\overline{P}_0(k,s|v)$ is given in Eq. (3.1). This gives

$$\overline{P}(r,s|v) = \sum_{n=1}^\infty [\sqrt{(s+\gamma)^2+(\alpha_n\gamma l/R)^2}-\gamma]^{-1} \times \frac{J_0(\alpha_n r/R)}{\pi R^2 J_1^2(\alpha_n)}. \quad (4.3)$$

Using this expression in Eq. (2.8) leads to

$$C(r|v) = \frac{l}{l_d}\sum_{n=1}^\infty [\sqrt{(1+l/l_d)^2+(\alpha_n l/R)^2}-1]^{-1} \times \frac{J_0(\alpha_n r/R)}{\pi R^2 J_1^2(\alpha_n)}, \quad (4.4)$$

and, after integration of this latter expression with respect to r we obtain

$$\varepsilon(r|v) = \frac{l}{l_d}\sum_{n=1}^\infty [\sqrt{(1+l/l_d)^2+(\alpha_n l/R)^2}-1]^{-1} \times \frac{2}{\alpha_n J_1(\alpha_n)}\left[1-\frac{rJ_1(\alpha_n r/R)}{RJ_1(\alpha_n)}\right]. \quad (4.5)$$

This function is displayed in Fig. 2. It is clear from the figures that due to the additional absorbing edge the spore lifetime τ in the disk is smaller than $1/\mu$ as $\varepsilon(0|v)=\mu\tau<1$. Three different regimes can be drawn.

Absorbing regime, $R<l_d$. This case is dominated by the loss of spores escaping from the disk. The lifetime of spores in the disk increases with the ratio l_d/l indicating that the more the spore motion is diffusive (i.e., $R\gg l$) the more spores are deposited in the field.

Intermediate regime, $R=l_d$. As a result of equal length scales for the absorption (or escaping) and deposition, the lifetime of spores in the disk is enhanced and the deposition probability has the same general trends as a function of l_d/l like in the absorbing regime, i.e., larger $\varepsilon(r|v)$ corresponds to spore diffusive motions.

Deposition regime, $R>l_d$. In this case, the depletion of spores is dominated by the deposition in the field rather than by the escape or absorption. As above, the lifetime of spores in the disk is larger than in the intermediate regime but with different general behavior. Almost all spores are deposited in the field for diffusive ($R\gg l$ and $l_d\gg l$) spore motions while a small fraction is absorbed when spores undergo ballistic motions ($R\leqslant l$ and $l_d\leqslant l$).

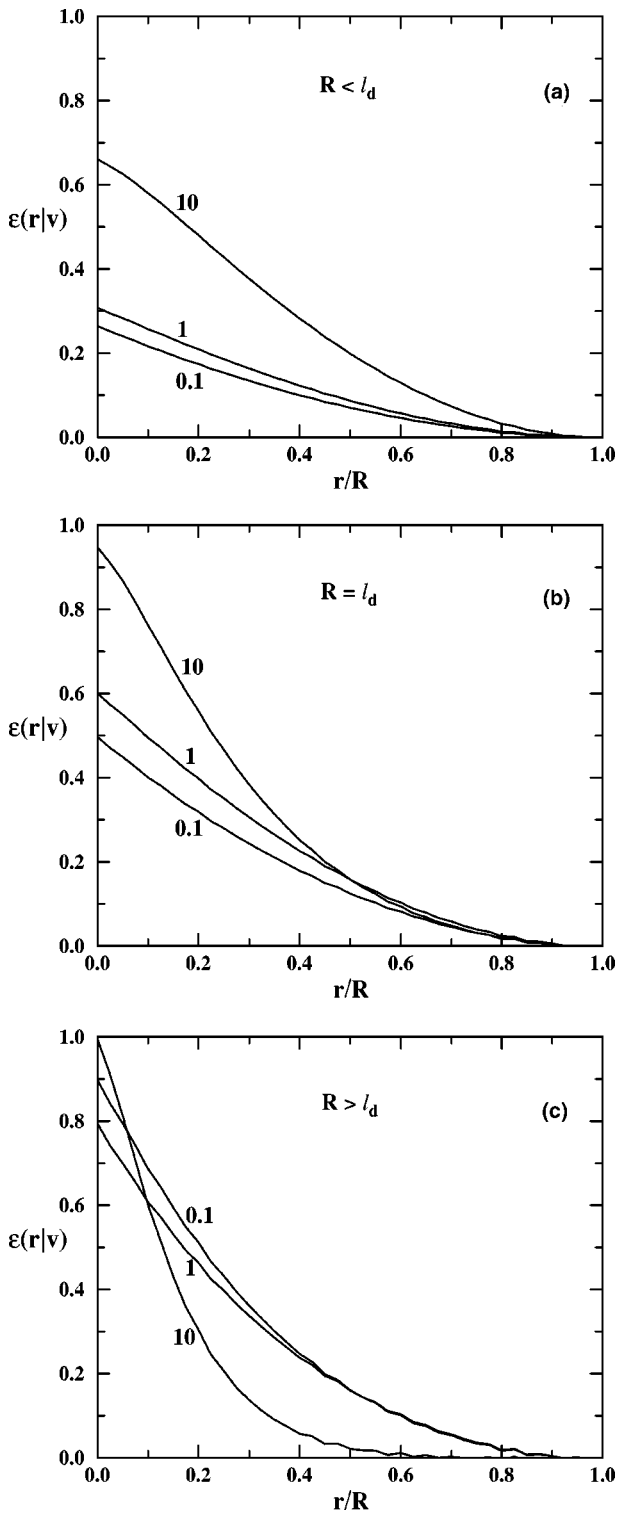

FIG. 2. Probability in Eq. (4.5) as a function of the reduced distance r/R from the focal for various values of l_d/l as quoted on the figure. Panels (a), (b), and (c) correspond to $R/l_d=0.5$, 1, and 2, respectively. $n=50$ values of α_n have been used to compute $\varepsilon(r|v)$.

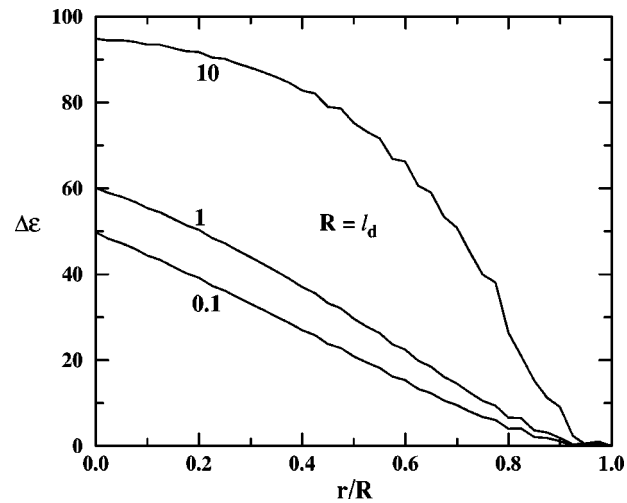

FIG. 3. Fraction in percentage of deposited spores in Eq. (4.6) as a function of r/R for various values of l_d/l as quoted in the figure.

To gain some insight in the discrimination between deposition and absorption to the total spore depletion, one can estimate the fraction of deposited spores from the relation

$$\Delta\varepsilon(r|v)=\frac{\varepsilon(r|v)}{\varepsilon_0(r|v)}, \tag{4.6}$$

where $\varepsilon_0(r|v)$ and $\varepsilon(r|v)$ are given in Eqs. (3.4) and (4.5), respectively. $\Delta\varepsilon(r|v)$ is the fraction of spores which are deposited at the distance r from the source out of 100% of spores reaching that distance; the corresponding fraction of absorbed spore is simply $1-\Delta\varepsilon(r|v)$. Figure 3 shows that the fraction $\Delta\varepsilon(r|v)$ decreases with r approaching R and when the spore motion goes from diffusive to ballistic one. Combination of Figs. 2 and 3 indicates that the fraction of deposited spores at a given distance r decreases on going from deposition to absorbing regimes.

V. CONCLUDING REMARKS

The model we developed in this paper describes the deposition probability of airborne spores according to the distance from the spore source. Although it is known that source geometry (height and area of diseased part of a crop) might dramatically shape spore-dispersal gradients [4], we have considered only the transport and deposition subprocesses involved in the overall spore-dispersal process. Biophysical mechanisms affecting spore dispersal (i.e., removal, transport, and deposition of the spores) have been extensively characterized: removal of wind-borne spores has been shown to occur mostly during short wind gusts causing high turbulence [24], which have been characterized in various crop and weather situations [25,26]. Explicit models of spore dispersal in relation to turbulence have been validated and applied to practical phytosanitary problems [27–29]. In our model, we do not characterize explicitly the biophysical environment within which spores are traveling. Though, we develop in a first approximation a simple model of transport

for description of complex processes occurring in real situations. Our goal is to establish simple relations between probability of spore dispersal and a few parameters of biological significance (Figs. 1 and 2). As far as we are aware, the present model is the first attempt to apply concepts of statistical physics to phytopathology and to consider airborne spores as particles submitted to swift changes in flight direction and random deposition, without any explicit description of weather factors.

Among the parameters used in the model, those with the most straightforward biological interpretation are R and l_d, the radius of the field and the average distance traveled by a spore before deposition, respectively. The latter parameter can be estimated for several pathosystems by fitting a simple function, such as a negative exponential function, to experimental plant disease or spore-dispersal gradient [4,5]. As shown in Fig. 2, the simulated pattern of spore deposition is dramatically affected by the ratio R/l_d. This ratio can also be related to the two opposed mechanisms of autodeposition and allodeposition by which spores produced in a given area, whatever its unit and size, are deposited on the very same area and outside the area, respectively. The frequency of allodeposition ϕ is one of the most important parameters in models of plant disease spread within genetically heterogeneous crops [30]. When restricting for instance the ''field'' to a single plant, autodeposition on the source plant should occur for $R \leqslant l_d$, while allodeposition occurs for a field with several plants when $R > l_d$. The biophysical determinism of autodeposition vs allodeposition, which would help to evaluate the parameter ϕ, is still not fully understood.

The ratio l_d/l (Figs. 1 and 2) of the average distance a spore traveled before deposition to the average distance a spore traveled before scattering would be more difficult to evaluate in field conditions. Increased turbulence may increase scattering and therefore decrease l, but its effect on l_d might be more complex. The average distance a spore traveled before deposition depends on several other factors. For instance, occurrence of rain will cause an increase in spore deposition by washing off the air [3], and therefore a decrease in l_d. Experimental assessment of spore scattering could anyway be attempted, at least in controlled conditions, using flow visualization technology [31]. This model discussed above considers both ballistic ($l_d \ll l$) and diffusive ($l_d \gg l$) spore motions. Most models of passive dispersal of spores by wind (e.g., Refs. [6,13,15]) consider spore motions to be a diffusive process. Ballistic motion would be more appropriate for spores forcibly discharged from fruiting bodies, such as *Sporobolomyces* ballistospores [32], which have a very restricted dispersal range.

Although initially designed for studying spore dispersal, our model could be already useful for a broader range of spreading organisms. Scattering is a component of random walk models used for insects, but occurs in this case on much larger time and space scales [33]. In the case of smaller, wind-borne propagules, such as spores, pollen grains [34], or small seeds [35], dispersal was supposed in most cases to be driven by the main wind direction, and changes in the flight direction before deposition were not addressed. Such changes might be of relevance when considering long-distance dispersal [36–38] and contribute to the difficulty of assessing correctly the tails of dispersal gradients.

However, this work can be extended in number of directions. Indeed, we have assumed up to now that the spore particles travel with a constant velocity. The next improvement of the model will be to include the velocity dynamics in assuming, for instance, that the spore velocity undergoes a diffusion process. This leads to a spore-dispersal process with fluctuating mean free path. Another issue is to deal with the turbulence by using the appropriate distribution function of time interval between successive scattering. Such extending works are underway.

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