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Mechanistic models of seed dispersal by wind

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Abstract Over the past century, various mechanistic models have been developed to estimate the magnitude of seed dispersal by wind, and to elucidate the relative importance of physical and biological factors affecting this passive transport process. The conceptual development has progressed from ballistic models, through models incorporating vertically variable mean horizontal windspeed and turbulent excursions, to models accounting for discrepancies between airflow and seed motion. Over hourly timescales, accounting for turbulent fluctuations in the vertical velocity component generally leads to a power-law dispersal kernel that is censored by an exponential cutoff far from the seed source. The parameters of this kernel vary with the flow field inside the canopy and the seed terminal velocity. Over the timescale of a dispersal season, with mean wind statistics derived from an "extreme-value" distribution, these distribution-tail effects are compounded by turbulent diffusion to yield seed dispersal distances that are two to three orders of magnitude longer than the corresponding ballistic models. These findings from analytic models engendered explicit simulations of the effects of turbulence on seed dispersal using computationally intensive fluid dynamics tools. This development marks a bifurcation in the approaches to wind dispersal, seeking either finer resolution of the dispersal mechanism at

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the scale of a single dispersal event, or mechanistically derived analytical dispersal kernels needed to resolve long-term and large-scale processes such as meta-population dynamics and range expansion. Because seed dispersal by wind is molded by processes operating over multiple scales, new insights will require novel theoretical tactics that blend these two approaches while preserving the key interactions across scales.

Keywords Advection–diffusion models · Ballistic models · Canopy turbulence · Large-eddy simulations · Long-distance dispersal · WALD dispersal kernel

Introduction

Seed dispersal is the predominant mechanism by which plants move in space (Ridley 1930; Harper 1977; van der Pijl 1982). Seed dispersal generates a spatial pattern of new individuals that determines the potential area of recruitment, sets the stage for processes such as predation and competition, and eventually produces a new spatial pattern of reproductive plants (Janzen 1970; Howe and Smallwood 1982; Schupp and Fuentes 1995; Nathan and Muller-Landau 2000; Levin et al. 2003). Various morphological attributes such as hairs, wings, small size and adaptive structural designs, facilitate aerodynamic transport of the diaspore (hereafter simply "seed"), essentially by lowering wing-loading (the ratio of mass to surface area) and/or increasing the roughness of the surface of the seed and thereby increase the drag force that the air exerts on the seed in flight, both of which increase travel time through the air. Species with obvious morphological adaptations for wind dispersal are common in many plant communities, comprising, for example, 10–30% on average, and up to 70%, of the flora in temperate plant communities (Willson et al. 1990).

Dispersal occurs when seeds move away from the source plant. The length of this movement, the dispersal distance D, is the measure of the dispersal process, and the distribution of dispersal distances, the seed dispersal kernel $p(x)$, is its basic statistical descriptor. The $p(x)$ is a probability density function portraying the probability that a dispersed seed arrives at a distance x away from the source. Dispersal kernels can provide the probability of seed arrival either per unit distance (the one-dimensional case) or per unit area (the two-dimensional case); for simplicity, we focus here on one-dimensional dispersal kernels, unless otherwise specified. Phenomenological dispersal kernels, fitted to functions such as the Gaussian, the negative exponential and the power-law, dominated the earlier dispersal literature (e.g., Gregory 1945; Wolfenbarger 1946). In 1989, Akira Okubo and Simon Levin argued that "the advantages of the [phenomenological] models are that they are simple, have only two parameters, and can be fit to data reasonably well. Their principal disadvantage

is that, while parameters can be fit for particular situations, such models provide no way to extrapolate from one situation to another based on independently measured physical parameters, and no understanding of the underlying mechanisms". Indeed, mechanistic models of wind dispersal have been advanced substantially in the two decades since the publication of this 1989 study, and today there is a general consensus (e.g., Cousens et al. 2008) that models of seed dispersal by wind are far more advanced than models of seed dispersal by any other vector. Reviewing all the major developments in mechanistic models of seed dispersal by wind is beyond the scope of a single paper. Instead, we focus on how the added complexity of turbulent processes and seed attributes alters the statistical features of the dispersal kernel through their strong non-linear effects and interactions. We also link different seed dispersal models, and summarize major insights into dispersal mechanisms and population dynamics. Because the mean vertical wind velocity is zero, turbulent processes are responsible for uplift and long-distance dispersal (LDD). Seed attributes control the motion capacity of the seed and represent the evolutionary adaptation of different species to facilitate seed transport by wind. Turbulence and seed attributes result in highly complex and non-linear effects that are at the cutting edge of current dispersal studies. We restrict the discussion to the primary dispersal by wind (plant to ground) and do not consider subsequent secondary movements (see, for example, Greene and Johnson 1997; Schurr et al. 2005; Thompson and Katul 2009). Although many of the models reviewed here have been used, and are appropriate, for pollen dispersal, our focus is primarily on dispersal of seeds.

Historical background of wind dispersal modeling: the simplest possible model

Dingler (1889) developed a general model for calculating the rate of fall of seeds of different morphologies based on the opposing forces that gravitation and drag exert on a particle during vertical fall. He verbally described how D can be calculated from three basic parameters: the terminal velocity (V_t) defined as the constant falling velocity of a seed in still air; the seed release height (h_r) and the mean horizontal windspeed ($\bar{u}$). This simplest ballistic equation can be easily extracted from geometric arguments, and was first formulated (though not recommended) by Schmidt (1918) to yield:

$$D = \frac{h_r \bar{u}}{V_t}. \tag{1}$$

Cremer (1971, 1977) and subsequent investigators (e.g., Augspurger 1986; Matlack 1987; Ernst et al. 1992) used Eq. 1 to compare dispersal capacity among a variety of

wind-dispersed plants. This basic ballistic model (see Fig. 1) assumes that a dispersed seed (1) reaches V_t immediately after its release so that the time it takes for the seed to reach the ground is well approximated by h_r/V_t, and (2) is horizontally transported at a velocity identical to mean wind velocity $\bar{u}$ assumed to be uniform in space and lacking any vertical component. For the seed velocity to be identical to the air velocity, the drag force between the seed and adjacent air parcels must be infinite at all times following its release. Schmidt (1918) proposed a model with a turbulence factor and argued that D is inversely correlated with V_t^2 rather than with V_t as proposed in Eq. 1. All other models of wind dispersal, including the most complicated ones, were developed to relax some or all of the basic assumptions of the simple ballistic model.

In the following sections, elaborations on the ballistic model are first presented as we progress towards a comprehensive mechanistic treatment of the theory of seed dispersal by wind. A summary of all symbols is provided in Table S1 (Supplementary Material). In the first section "Relaxing basic assumptions: seed movement in relation to airflow", the discussion commences at the finest spatial scale pertinent to $p(x)$ by presenting a technique for coping with seeds as "heavy particles" whose drag and inertia result in a difference between the instantaneous velocity vectors of the local wind field (V_a) and the seed (V_p). Then, in the section "Relaxing basic assumptions: the vertical structure of the horizontal air velocity", we discuss how variability in $\bar{u}$ along the vertical axis impacts $p(x)$ in isolation at different time scales. In the following section,

"Relaxing basic assumptions: the role of turbulence", we address how the inclusion of turbulent fluctuations in the horizontal velocity (u') and vertical velocity (w') modify the shape of the seed dispersal kernel and lead to power-law behavior even at short time scales (~1 h). Models relaxing additional features of inhomogeneous airflow include coupled Eulerian–Lagrangian approaches discussed in the section "Relaxing basic assumptions: Eulerian and coupled Eulerian-Lagrangian perspectives for inhomogeneous flow" and the more complex large-eddy simulation (LES) approach discussed in the section "Relaxing basic assumptions: moving from 'modeling' to 'simulating' turbulence". We conclude with a synthesis of the different models, summarizing the insights obtained into wind dispersal mechanisms, important implications for population dynamics, and end with a blue-print for future research.

Relaxing basic assumptions: seed movement in relation to airflow

To relax the assumption of constant fall velocity, i.e., that seeds immediately track $\bar{u}$ and fall at V_t both the inertia of the seed and the "slippage" between the seed and the surrounding air parcels must be accounted for. To do so, both the drag force on the seed $f_{D,s}$ and the timescale on which seed velocities respond to fluctuations in air velocities, the "Lagrangian Timescale" τ_s, must be determined. Once an $f_{D,s}$, τ_s and the initial conditions for V_a and V_p are determined, the temporal change in seed velocity as a function of the local air velocity, and thus seed position, can be computed iteratively, yielding a more general form of the ballistic model in which perfect coupling between the seed and air is no longer assumed.

Determination of the drag force

The acceleration of an isolated seed can be represented by the imbalance between the drag force acting on the seed and the weight of the seed. The drag force can be related to the seed properties and the flow field by

$$f_{D,s} = \frac{\rho C_{d,s} A}{m} |V_a - V_p| (V_a - V_p), \tag{2}$$

where $f_{D,s}$ is the drag force acting on the seed, m is the seed mass, V_a is the instantaneous air velocity adjacent to the seed, V_p is the seed velocity, ρ is the air density and $C_{d,s}$ is the drag coefficient acting on the seed surface area A. This formulation represents a major theoretical simplification by neglecting the seeds' shape, aerodynamic properties, and the potential for anisotropy in the drag coefficients (Burrows 1973, 1975a, b; Greene and Johnson 1989). The overall effect of the neglected factors has been shown to be
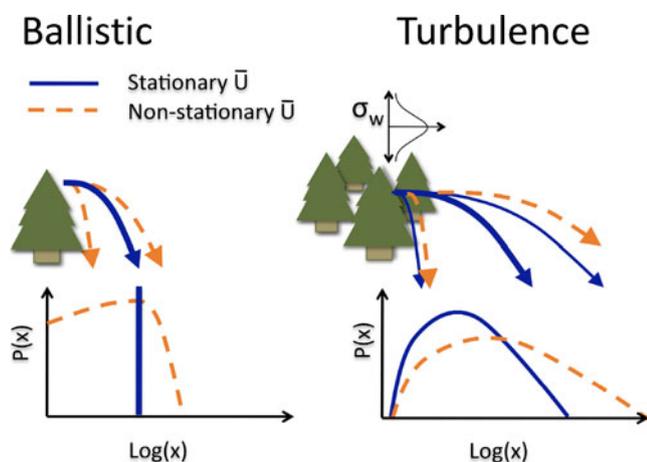

Fig. 1 Schematic of the effects of non-stationarity of mean windspeed, and turbulent fluctuations on the resulting form of the seed dispersal kernel. Non-stationarity generates a non-singular kernel in ballistic models, but is insufficient to generate power-law tails far from the seed source. Turbulence generates power-law tails for large x, and interacts with non-stationarity, meaning that the resulting dispersal kernels become dependent on the time window over which dispersed seed are monitored

small compared with Eq. 2 (Burrows 1975b; Greene and Johnson 1990).

Equation 2 requires known drag coefficients and surface areas. In the following section, we will derive a formulation to approximate the drag force that is only driven by V_t, the terminal velocity in still air, and is not dependent on other physiological and aerodynamic properties of the seeds that are difficult to measure. It can be applied in the cases where $C_{d,s}$ can be treated as constant. This is a reasonable assumption when the particle Reynolds number $Re_p = \frac{d_p|V_a - V_p|}{v}$ is large ($Re_p > 10$), which is typically the case for seeds, and large pollen grains throughout most of the flight time. Orchid seeds and other particles as small as pollen and spores are characterized by $Re_p < 1$. For such small particles, d_p/v is low and therefore the viscous forces cannot be neglected; consequently, the drag force formulation is different. For example, a common formulation that can be applied to very small particles is the Stokes formulation (see Eq. 7).

The terminal velocity V_t is by definition equivalent to the vertical velocity component of the seed (w_p) when gravitational acceleration is balanced by drag. If $w_p = 0$ at $t = 0$, and $C_{d,s}$ is constant, these conditions yield:

$$V_t = w_p\big|_{\left(\frac{dw_p}{dt} = 0\right)} = \sqrt{\frac{mg}{\rho C_{d,s} A}} \cdot \tag{4}$$

Rearranging Eq. 4 results in $\frac{\rho C_{d,s} A}{m} = \frac{g}{V_t^2}$, which can be substituted into Eq. 2 to yield:

$$f_D = \frac{g}{V_t^2}|V_a - V_p|(V_a - V_p). \tag{5}$$

This provides an easy-to-parameterize alternative to Eq. 2. For small Re_p, $C_{d,s}$ increases, often in the form of $C_{d,s} \sim 1/Re_p$. Interpolating between these limits suggests that the dependence of $C_{d,s}$ on Re_p may be given by a functional relationship of the form $C_{d,s} = (a/Re_p)(1 + b\,Re_p)$, where a and b depend on the seed morphology. Note that Eq. 4 can also be used to provide constraints on the coefficients a and b (Panton 1984).

Determination of the Lagrangian relaxation time scale

To incorporate inertia in the formulation of the seed movement, few other aerodynamic parameters are needed, which cannot be explicitly measured without wind tunnel experiments. These are the Lagrangian relaxation time scale, and, for small particles, also the aerodynamic effective diameter and density of the seed required for Stokes formulation. In this section, we introduce a formulation for these properties, derived from easily observable properties of the seeds, such as mass and terminal fall velocity. The particle Lagrangian relaxation

time scale (τ_p), determines how rapidly V_p adjusts to a rapid excursion in V_a. For a large seed, τ_p may be defined as the convergence time until V_t is reached, or practically until seed velocity reaches a high proportion ϕ (e.g., $\phi = 0.99$) of V_t. For seeds starting from rest, τ_p can be derived from Eq. 2–4 as:

$$\tau_p = \frac{g}{V_t} \tanh^{-1}(\phi). \tag{6}$$

Small seeds, pollen and spores are characterized by $Re_p < 1$ meaning that viscous forces cannot be neglected and the drag force must be determined using the Stokes formulation:

$$f_D = \frac{1}{\tau_{ps}} \tag{7}$$

where τ_{ps} is the Stokes-particle Lagrangian relaxation time scale:

$$\tau_{ps} = \frac{\rho_{ps} d_{ps}^2}{18 \rho v}, \tag{8}$$

where ρ_{ps} is the Stokes-particle density and d_{ps} is the effective Stokes-particle diameter. Again, the effective aerodynamic diameter for a small seed or pollen grain can be derived from V_t as:

$$V_t = \frac{g d_{ps}^2}{18 \rho v} \left(\frac{6 m_{ps}}{\pi d_{ps}^3} - \rho \right), \tag{9}$$

where m_{ps} is the Stokes-particle mass and giving:

$$d_{ps} = \frac{m_{ps} g}{3 \pi v V_t}, \tag{10}$$

which provides an "aerodynamic" representation of the effective diameter of the small particle in terms of seed mass and fall velocity, which are easily measurable.

To summarize, f_D and τ_p are both needed to account for the effects of inertia and slippages on seed velocities, and can be estimated from mass and terminal velocity for the two limiting cases of very large or very small particle Reynold's numbers. Naturally, the instantaneous Re_p along a single seed trajectory can vary significantly, given the rapid fluctuations induced via turbulence and the slower adjustment to these rapid excursions via V_p. Hence, a single seed can experience both asymptotic extremes along its trajectory. Since the interest is on a statistical description of where the seed lands on the ground rather than the nuisances of the precise trajectory, it safe to state that the V_p time series resembles a "filtered" or "smoothed" version of the fluctuating V_a time series, where peaks in V_p are both attenuated and lagged by compared to the fluctuations in V_a.

Relaxing basic assumptions: the vertical structure of the horizontal air velocity

Independently of the treatment of wind–seed interactions given above, the description of the flow field itself can be refined in comparison to the simple ballistic case given in Eq. 1. Specifically, the assumption of a constant windspeed can be relaxed. Even for simplified flow conditions, $\overline{u}$ varies appreciably with height z above the ground. This dependence of $\overline{u}$ on z can be made explicit. For simplicity in the following derivations, we assume that the seed and air velocities are identical. A seed trajectory can then be expressed as a system of first-order differential equations:

$$\frac{dx}{dt} = \overline{u}(z) \tag{11a}$$

$$\frac{dz}{dt} = V_t \tag{11b}$$

where x and z denote horizontal and vertical directions where x is aligned with the direction of $u(z)$. Rearranging these equations to eliminate time (t) provides an equation for seed location:

$$dx = \frac{\overline{u}(z)}{V_t} dz. \tag{12}$$

Integrating this equation from the seed release height ($z=h_r$) to the ground ($z=0$) yields the horizontal travel distance:

$$x = \int_{z=0}^{z=h_r} \frac{\overline{u}(z)}{V_t} dz. \tag{13}$$

where the ground surface is referenced to $z=0$. An expression of the dispersal kernel for this ballistic model can be written as:

$$p(x) = \delta(x - x_b), \tag{14}$$

where x_b is the same as D in Eq. 1 but with $\overline{u}$ replaced by the height-averaged (effective) mean windspeed across the seed trajectory $U_{eff} = \frac{1}{h_r} \int_{z=0}^{z=h_r} \overline{u}(z)\,dz$, and δ is the Dirac-delta function ($\delta=1$ when $x=x_b$ and $\delta=0$ when $x \neq x_b$).

Although windspeeds fluctuate over a range of timescales, it has been documented in many records that fluctuations on timescales of 20 min to a few hours contribute only minimally to the variance of the overall wind time series (Van der Hoven 1957). This spectral gap, centered on temporal scales ranging from about 20 min to a few hours, is a convenient starting point to discuss the flow field properties of the wind. The existence of this "spectral gap" implies that the horizontal (u) and vertical (w) velocities can be decomposed into two components: a mean component ($\overline{u}$ or $\overline{w}$) computed on a specific averaging timescale and a fluctuating component (u' or w') associated with turbulence. The timescale defining the mean wind component is assumed to be sufficiently long to "average-out" turbulence fluctuations, but sufficiently short to permit a moving average to characterize diurnal fluctuations longer than the spectral gap. In meteorological studies, the averaging time scale for the decomposition ranges between 20 min and 1 h and this averaging timescale is implied by the use of $\overline{u}$ or $\overline{w}$ hereafter.

The ballistic model in Eq. 13 requires input information on the variation in $\overline{u}$ as the function of the height above the ground (z). The form of $\overline{u}(z)$ can be derived from the mean continuity and the mean momentum balance equations for incompressible flow in 2 dimensions at high Reynolds number:

$$\frac{\partial \overline{u}}{\partial x} + \frac{\partial \overline{w}}{\partial z} = 0$$
$$\frac{\partial \overline{u}}{\partial t} + \overline{u}\frac{\partial \overline{u}}{\partial x} + \overline{w}\frac{\partial \overline{u}}{\partial z} = -\frac{1}{\rho}\frac{\partial \overline{p}}{\partial x} - \frac{\partial}{\partial x}\overline{u'u'} - \frac{\partial}{\partial z}\overline{u'w'}. \tag{15}$$

For a stationary (i.e., $\frac{\partial(\cdot)}{\partial t} = 0$) and planar-homogeneous (i.e., $\frac{\partial(\cdot)}{\partial x} = 0$) flow, Eq. 15 simplifies to:

$$\frac{\partial \overline{w}}{\partial z} = 0$$
$$\overline{w}\frac{\partial \overline{u}}{\partial z} = -\frac{\partial}{\partial z}\overline{u'w'}. \tag{16}$$

Integrating the mean continuity equation with respect to z and noting that $\overline{w}(0) = 0$ (i.e., the no-slip condition at the ground) gives $\overline{w} = 0$ throughout (i.e., no subsidence). This simplification leads to a simplified momentum balance given by:

$$\frac{\partial}{\partial z}\overline{u'w'} = 0. \tag{17}$$

Integrating Eq. 17 with respect to z results in the turbulent stress $\overline{u'w'} = -u_*^2$ being constant with height. The term u_*^2 is known as the squared friction velocity. If the turbulent stress is approximated by an eddy-viscosity (or turbulent diffusivity), analogous to that used to describe viscous stresses (or molecular diffusion), then the turbulent stress may be represented as:

$$\overline{u'w'} = -K_{t,z}\frac{\partial \overline{u}}{\partial z}, \tag{18}$$

where $K_{t,z}$ is the vertical turbulent diffusivity that is much larger than the fluid viscosity ν (by virtue of the high Reynolds number flow assumption). By a scale analysis, the diffusivity can be represented as the product of two properties: a mixing length l_m and a characteristic velocity

acting over l_m given as $l_m \left| \frac{\partial \overline{u}}{\partial z} \right|$. Substituting these into Eq. 18 gives:

$$u_*^2 = l_m^2 \left(\frac{\partial \overline{u}}{\partial z} \right)^2. \tag{19}$$

When the mixing length proportionally increases with z so that $l_m = k_v(z - d)$, (where $k_v \approx 0.4$ is the Von Kármán constant and d is the zero-plane displacement), Eq. 19 yields:

$$\frac{\partial \overline{u}}{\partial z} = \frac{u_*}{k_v(z - d)}, \tag{20}$$

which upon integration results in a logarithmic mean velocity profile (Stull 1988):

$$\overline{u}(z) = \frac{u_*}{k_v} \log\left(\frac{z - d}{z_0} \right), \tag{21}$$

where z_0 is the momentum roughness length defined as the height of protrusions at which $\overline{u}(z_0) = 0$.

Simple extensions of the basic ballistic model use this logarithmic form for $\overline{u}(z)$ to define an "effective" wind velocity U_{eff} (defined above). Fields and Sharpe (1980, see also Johnson et al. 1981; Sharpe and Fields 1982) introduced the dispersal model SEDFAL that incorporates such a logarithmic profile. Nathan et al. (2001) showed that under this logarithmic profile,

$$D = \frac{u_*}{k_v V_t} \left((h_r - d) \ln\left(\frac{h_r - d}{e z_0} \right) + z_0 \right), \tag{22}$$

where e is Euler's number (≈ 2.71828). The logarithmic profile is typical of open landscapes or flow above short vegetation (e.g., Stull 1988). Within plant canopies, the vertical wind profile is typically exponential (Cionco 1965):

$$\overline{u}(z) = \overline{u}_{h_c} \exp\left(\alpha \left(\frac{z}{h_c} - 1 \right) \right) \tag{23}$$

where h_c is the height of the canopy top, $\overline{u}_{h_c}$ is $\overline{u}$ at h_c and α is the canopy attenuation coefficient (Cionco 1965), also called the canopy flow index (Cionco 1978). The attenuation coefficient tends to increase with increasing canopy density (Cionco 1978; Raupach 1988; Kaimal and Finnigan 1994); that is, the decline in horizontal windspeed from h_c downwards is most rapid in forests of high foliage and stem density (see Fig. 2). The exponential profile generally fits observed data well over flat terrain (Cionco 1978; Amiro and Davis 1988; Gardiner 1994; Kaimal and Finnigan 1994). One exception occurs when a bare-trunk layer results in a small secondary peak in windspeed at the lower half of the

canopy height (Shaw 1977) as shown in Fig. 2 for a hardwood forest canopy. This effect does not occur in stands with well-developed understory vegetation (Gardiner 1994). Nathan et al. (2002a) showed that under the exponential mean wind profile,

$$D = \frac{\overline{u}_{h_c} h_c}{\alpha V_t} \left(\exp\left(\frac{\alpha(h_r - h_c)}{h_c} \right) - \exp(-\alpha) \right). \tag{24}$$

Equations 23 and 24 form the basis of the two models, WINDISPER-L (Nathan et al. 2001) and WINDISPER-E (Nathan et al. 2002a), respectively. WINDISPER-L has been tested for various plant species and landscapes, exhibiting good agreement with local seed dispersal data (Nathan et al. 2001, 2002a; Skarpaas et al. 2004; Stephenson et al. 2007). Skarpaas et al. (2004) found that this model performed better than the model of Greene and Johnson (1989; see next paragraph for the main features of this model) and almost as well as phenomenological models such as inverse power, negative exponential and 2Dt calibrated from the dispersal data. Nathan et al. (2002a) found that both WINDISPER models predicted seed
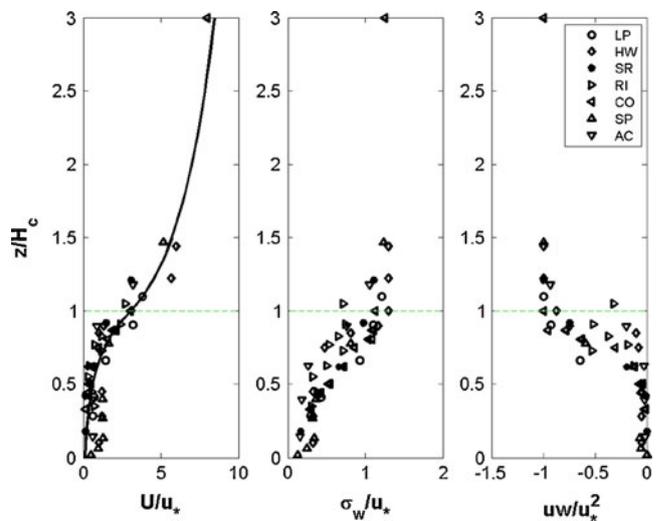

Fig. 2 Vertical variations in the bulk velocity statistics for canopies whose leaf area indices range from 2.5 to 5.0 and whose canopy heights range from 0.7 to 30 m. The horizontal windspeed standardized by friction velocity (U/u_*) tends to decline exponentially from the canopy height ($z/h_c = 1$) downwards, and to increase logarithmically upwards above the canopy. The collapse of the data here for such diverse canopies is suggestive that the canopy top (h_c) and the friction velocity (u_*) at h_c are appropriate normalizing variables (data in Katul et al. 2004). The data points are as follows: *LP* is for a southern loblolly pine stand, *HW* is for a southern hardwood forest, *SR* is for a spruce forest, *RI* is for a rice canopy, *CO* is for a corn canopy, *SP* is for a boreal scots pine, *AC* is for an alpine coniferous forest. The *solid line in the left panel* illustrates the logarithmic profile above the canopy matched to an exponential profile inside the canopy, where the matching ensures continuity and smoothness. The model is for a constant leaf area index=3.5 m^2 m^{-2}, h_c=15 m, and C_d=0.2

dispersal data collected within a dense pine stand (0–20 m from the nearest tree) well (R^2=0.81–0.90), but their performance degraded (R^2=0.57–0.59) for dispersal data collected outside the stand (20–110 m from the nearest tree). The WINDISPER models provide acceptable descriptions of the short-distance dispersal of average and relatively large seeds by wind, but they are inherently inadequate to predict dispersal at much longer distances essentially because they do not incorporate fluctuations of the vertical wind velocity, the main mechanism responsible for LDD.

Over month-long dispersal seasons, the effective wind velocity U_{eff} varies considerably and can be described by a log-normal (Greene and Johnson 1989) or Weibull probability distribution (Andersen 1991; Troen and Petersen 1989; Burton et al. 2001). At these timescales, D (in Eq. 1) or x_b (in Eq. 14) must be treated as random variables, and the shape of $p(x)$ becomes a simple transformation of the windspeed distribution (Greene and Johnson 1989; Andersen 1991). By expanding the timescale from the short (i.e., 20–60 min period) to a dispersal season, $p(x)$ evolves from a Dirac-delta (in Eq. 14) to a continuous distribution without any change in the ballistic nature of the dispersal mechanism (see the left panel of Fig. 1). This point was emphasized and exploited in the study of Greene and Johnson (1989), attributing the generation of heavy tails in $p(x)$ to such variability in the mean wind occurring over the growing season. Although Weibull and log-normal distributions describing U_{eff} are both considered "extreme-value" distributions, they do not promote the empirically observed power-law tails in $p(x)$ (Willson 1993; Portnoy and Willson 1993). We explore next why the ballistic models fail to predict LDD even though they account for the variation of $\overline{u}$ with z and for fat-tailed distribution of U_{eff}; essentially, to understand the genesis of fat tails, the role of turbulence in seed transport must be addressed.

Relaxing basic assumptions: the role of turbulence

Early attempts to account for turbulent variations in the vertical velocity were carried out by Burrows (1973a, b; 1975) and showed that w' is the most significant variable impacting a seed trajectory beyond the mean horizontal windspeed.

To show the role of w' on dispersal processes without all the complexities of seed aerodynamic shape and slippage, we re-write the seed vertical velocity component as:

$$\frac{dz}{dt} = \overline{w} + w' - V_t. \tag{25}$$

To illustrate the statistical properties of w (recall that $w = \overline{w} + w'$), Fig. 3 shows an example w time series collected over a 20 min period about 5 m above a grass surface as sampled by a triaxial sonic anemometer at 56 Hz (Katul et al. 1997). A number of features are evident in Fig. 3:

1. $\overline{w}$ (<0.05 m s^{-1}) is one to two orders of magnitude smaller than V_t of many wind-dispersed species (see "Synthesis A: Key parameters and their natural range" below), justifying its omission from Eq. 25. Nathan et al. (2001, 2002a) also discuss some of the limits and nuances of Eq. 25 when only V_t and $\overline{w}$ are considered.

2. At certain points in time, w' exceeds 1 m s^{-1}, a vertical velocity comparable to or exceeding V_t of many wind-dispersed species.

3. The probability distribution of w' is near-Gaussian, although non-Gaussian behavior at the tails (or extremes) is also evident, especially in the positive tail.

4. The durations of the w' excursions are coherent and rather long, about 10 s for the series in Fig. 3. This duration can be quantified by the autocorrelation function $\rho_\tau(\tau) = \frac{\overline{w'(t)w'(t+\tau)}}{\sigma_w^2}$, where τ is the time lag ($\rho_\tau(0)$=1 when τ=0 s), and $\sigma_w^2 = \left(\overline{w'w'}\right)^2$ is the vertical velocity variance. The internal correlation in w' can be approximated by the lag when $\rho_\tau(\tau)$ first crosses zero. This time lag is a measure of the degree of coherence, memory, or organization of the w' time series. Note that the 10-s lag time is much shorter than the averaging interval employed in determining $\overline{u}$ (20–60 min), but much longer than the sampling frequency (1/56 s). At very short time scales (<0.1 s), the turbulent fluctuations are random, locally homogeneous and isotropic, and do not exhibit organization.

The significance of the long autocorrelations in w' lies in their ability to alter the trajectory of a falling seed. When the correlation time of the w' excursions is comparable to or larger than the gravitational settling time of a seed (=h_r/V_t), seeds caught by an "updraft" (a sustained and coherent $w' > 0$) also experience coherent positive vertical velocity excursions. These excursions (1) significantly increase the flight time of the seed, and (2) increase the effective horizontal velocity by uplifting the seed into regions where $\overline{u}$ is higher, potentially even to points where $z > h_r$. Seeds in a downdraft experience the converse, shortening their journey.

Tackenberg (2003) presented the wind dispersal simulation PAPPUS that incorporates w' and u' time series measured in one location at a single height above the ground, and generates dispersal distances in excess of 100 m. Yet, the statistics of w' and u' vary with height (z), as does $\overline{u}$. Since measuring wind statistics is only feasible at few heights, a general model for the vertical velocity acceleration of air parcels is needed to account for the

Fig. 3 Canonical features of a w' time series sampled over a 20 min period. **a** The measured time series (sampled at 56 Hz); **b** a 60 s zoom-in on this series to illustrate the coherency time scale of a typical updraft (~10 s); **c** the signatures of all such coherent events in the autocorrelation function $\rho(\tau)$; **d** the probability density function of this w' time series (open circles, spanning roughly four decades of probability) and its Gaussian approximation
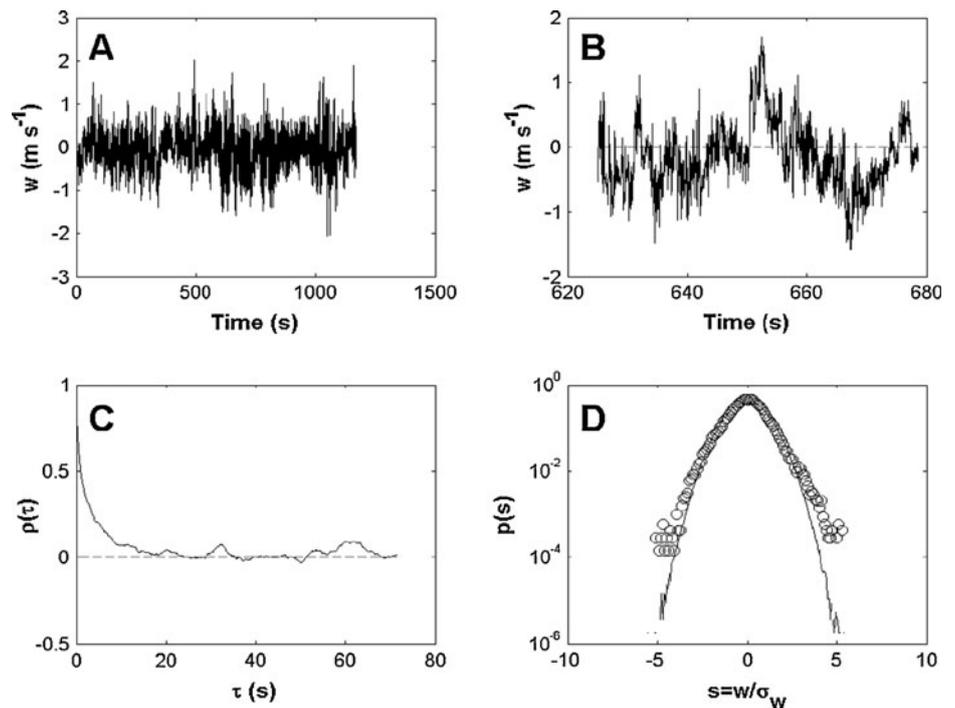
effect of correlations in w' at various locations along a seed trajectory. One such model (Katul et al. 2005) consists of linear drift and dispersion, expressed as:

$$dw' = -\alpha_w \left(\frac{w'}{\sigma_w^2} \right) dt + \beta_w d\Omega, \qquad (26)$$

where $d\Omega$ is a Gaussian random variable with mean zero and variance dt. To preserve the turbulent kinetic energy (TKE) at any point in the flow, the drift must be set to $\alpha_w = \frac{1}{2C_0\varepsilon}$ and the dispersion to $\beta_w = \sqrt{C_0\varepsilon}$, where C_0 is the Kolmogorov constant, and ε is the turbulent kinetic energy dissipation rate. When the stochastic differential Eq. 26 is combined with the system of equation in Eq. 11a, 11b, the dispersal kernel can be solved analytically (see Katul et al. 2005) as:

$$p(x) = \sqrt{\frac{\lambda}{2\pi x^3}} \exp \left[-\frac{\lambda(x-\mu)^2}{2\mu^2 x} \right], \qquad (27)$$

which is an inverse-Gaussian (or Wald) kernel a with a scale parameter $\mu = \frac{xV_t}{U_{\text{eff}}}$ and a shape parameter $\lambda = \left(\frac{h_r}{\sigma} \right)^2$, where

$$\sigma = \frac{2\sigma_w^2}{\sqrt{C_0\varepsilon}U_{\text{eff}}}. \qquad (28)$$

Because $C_0\varepsilon$ is difficult to quantify, especially inside canopies, Eq. 28 may be further simplified when the

effective mixing length is assumed constant. Poggi et al. (2004) demonstrated that, assuming that l_m is constant inside the canopy and proportional—by the turbulence coefficient κ—to the canopy height (i.e., $l_m = \kappa h_c$), the approximation

$$\frac{2\sigma_w^2}{C_o\varepsilon} = \kappa \frac{h_c}{\sigma_w}, \qquad (29)$$

could be made, resulting in:

$$\sigma^2 = 2\kappa h_c \frac{\sigma_w}{U_{\text{eff}}}. \qquad (30)$$

The turbulence coefficient κ encodes all the uncertainty in C_0 inside canopies and its precise estimation remains elusive (Poggi et al. 2008a). It is plausibly bounded between 0.3 and 1.0, and is likely to vary with leaf area density. Equation 27 is known as the Wald analytical long distance (WALD) model. WALD does not account for the non-Gaussian behavior in w' alluded to in Fig. 3, but assumes that the Gaussian distribution of w' is given by:

$$p(w') = \frac{\exp \left[-\frac{w'^2}{2\overline{w'w'}} \right]}{\sqrt{2\pi \overline{w'w'}}}, \qquad (31)$$

which is also shown in Fig. 3d for reference.

The WALD approach can also be used to compute the probability of a seed uplifting above a canopy of mean height h_c when released at h_r, given by:

$$\Pr(z > h_c) = \frac{\exp\left[2\frac{h_r V_t}{\sigma^2 U_{\text{eff}}}\right] - 1}{\exp\left[2\frac{h_c V_t}{\sigma^2 U_{\text{eff}}}\right] - 1} \qquad (32)$$

$$\approx \exp\left[2\frac{V_t}{\sigma^2 U_{\text{eff}}}(h_r - h_c)\right].$$

This expression places an upper bound on the fraction of seeds released at h_r that can potentially escape the canopy in a given 20–60 min time interval, and this escape is a necessary condition for undergoing LDD (Nathan et al. 2002b). In the ballistic models, $\Pr(z > h_c) = 0$ if the seed is released inside the canopy ($h_r < h_c$).

The contrasts between WALD, the ballistic models, and phenomenological models such as the 2Dt (Clark et al. 1999) elucidate the effect of turbulence (encoded in w') on the shape of $p(x)$. When $\frac{V_t}{U_{\text{eff}}} \to 0$ in Eq. 31, $p(x) \sim x^{-3/2}$ for large x. Thus, three critical differences become apparent: first, in stark contrast to the ballistic kernel in Eq. 14, WALD exhibits a power-law behavior with un-bounded variance (i.e., as $x \to \infty$, the kernel variance is also infinite). This surprising and powerful result is true even if U_{eff} is constant over a 20–60 min period. Second, WALD highlights turbulent updrafts as providing a mechanistic basis for the emergence of power-law tails in the dispersal kernel far from the seed source. This power-law is then "censored" by a multiplicative (rather than additive, ctr. Bullock and Clarke 2000) exponential cutoff when gravitational effects are significant (through $\frac{V_t}{U_{\text{eff}}}$). Third, if it is assumed that U_{eff} is sampled from a Weibull distribution, WALD and ballistic predictions for this U_{eff} distribution may be compared, allowing the interactions of turbulence and mean wind at the dispersal season time scale to be "fingerprinted" (Thompson and Katul 2008; Nathan et al. 2011). The addition of vertical turbulent fluctuations can result in seeds traveling more than 1 km while their ballistic counterpart with only mean flow variability accounted for travel on the order of only 20 m (Fig. 4). Clearly, accounting for vertical turbulence is necessary for estimating LDD.

Comparisons between field-measured and WALD-modeled $p(x)$ for a number of species appear to be in good agreement at 20–60-min time scales (Katul et al. 2005). Field measurements were made following seed release experiments in which seeds of various wind-dispersed species were manually released from a meteorological tower inside a 33-m canopy at h_r=30, 21, and 12 m each over half-hour intervals (Fig. 5). The agreement between WALD and the measured kernels illustrates that models that account for h_r, V_t, the autocorrelation time scale of w' and

the flow statistics ($\bar{u}$ and σ_w) reproduce the bulk properties of the measured $p(x)$ for stationary $\bar{u}$. Skarpaas and Shea (2007) measured dispersal patterns of thistle seeds in large open fields, and found that WALD, parameterized independently of the thistle data, fit the empirical patterns as well as phenomenological models (exponential, log-normal, and half-Cauchy) calibrated from thistle data. Stephenson et al. (2007) found that WINDISPER-L tended to give better predictions than WALD for distances of up to 100 m, whereas for longer distances model performance was difficult to compare; yet, they set their measured mean windspeed well above the canopy to U_{eff} in the WALD calculations, which yields an over-estimation of their dispersal mode, reflected in the bias in their results. Using an inverse modeling approach, Schurr et al. (2008) found that WALD best fits seed dispersal data collected in a pine forest and adjacent scrubland, compared to the exponential power, 2Dt and the log-normal phenomenological models.

Relaxing basic assumptions: Eulerian and coupled Eulerian-Lagrangian perspectives for inhomogeneous flow

The mechanistic approaches so far utilized vertical averaging approaches and effective parameters to account for the vertical structure of the flow field (e.g., by defining U_{eff}). The
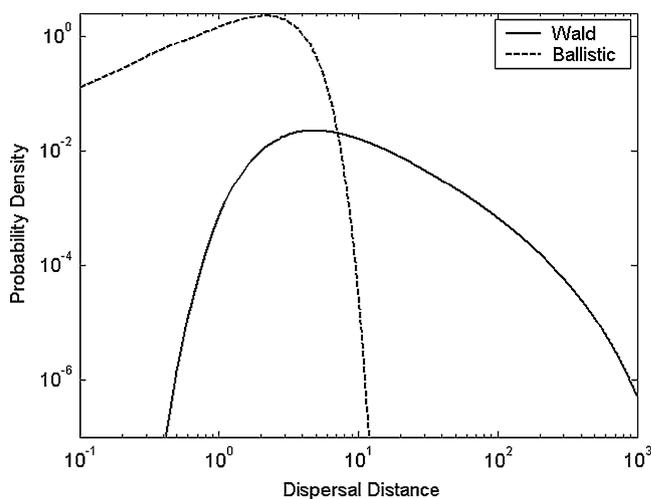

Fig. 4 Comparison of WALD and Ballistic kernels. Kernels are shown for annual time scales and dispersal parameters estimated for Green Ash (*Fraxinus pennsylvanica*). The Ballistic kernel considers only advection of a seed falling with terminal velocity V_t and being advected by the mean windspeed, whose distribution is taken from the Weibull parameters. The WALD kernel accounts for turbulence (including its vertical velocity components) in addition to advection, and results in finite probabilities of dispersion at length scales two orders of magnitude greater than those of the Ballistic kernel (from Thompson and Katul 2008)
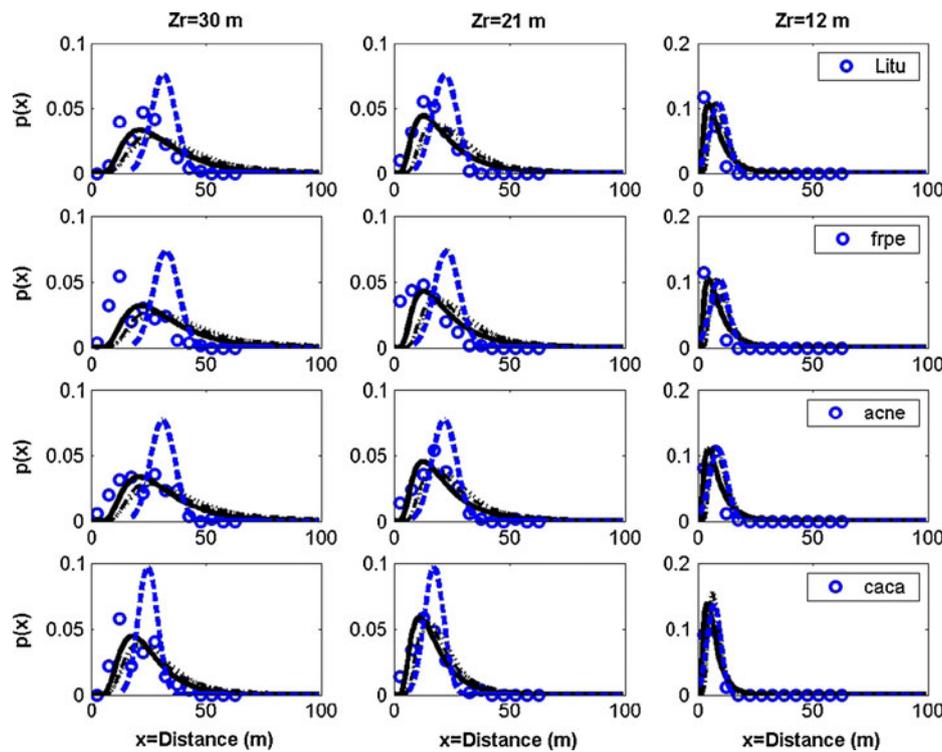
Fig. 5 Comparison between modeled (*line*) and measured (*open circle*) dispersal kernels for seed releases in November 28, 2000 from three heights. The models include WALD (*thick solid*), tilted Gaussian (*dotted*) and the advection–diffusion equation (*dot-dashed*) proposed by Okubo and Levin (1989), and the Gaussian (*thick dashed*) is shown for reference. Seeds were released in small clusters every 30 s during the 30-min averaging interval. The modeled kernel was computed using a 30-min averaged friction velocity u_* for each seed release height h_r (u_*=0.89 m s^{-1} for h_r=30 m and 21 m, and u_*=0.6 m s^{-1} for h_r=12 m). The species abbreviations are *acne*, *Acer negundo*; *caca*, *Carpinus caroliniana*; *frpe*, *Fraxinus pennsylvanica*; *litu*, *Liriodendron tulipifera*. The seed terminal velocities are V_t=1.50 (litu), 1.43 (frpe), 1.50 (acne), 1.89 (caca)m s^{-1}

generalization of these approaches, however, needs to account for vertical variations in all the velocity statistics. In a seminal study, Okubo and Levin (1989) pioneered the use of an advection–diffusion (AD) approach, analogous to those used in the derivation of WALD, for addressing seed dispersal problems. The budget equation for seed concentration (S, seeds per cubic meter) at any height z and position x away from a seed source is given by (Okubo and Levin 1989):

$$\frac{\partial S}{\partial t} + \overline{u}(z)\frac{\partial S}{\partial x} - V_t\frac{\partial S}{\partial z} = -\frac{\partial}{\partial z}\left(\overline{w's'}\right)$$
$$\approx \frac{\partial}{\partial z}\left(K_{t,z}\frac{\partial S}{\partial z}\right). \tag{33}$$

This approach anticipated the stochastic properties of seed transport in a turbulent flow field via the vertical turbulent diffusivity $K_{t,z}$, using the assumption that the flow field through a forested canopy resembled a boundary layer, namely that the canopy acts as a passive seed source without altering the flow. For stationary conditions $\left(\frac{\partial S}{\partial t} = 0\right)$ and uniform flow conditions, and when $K_{t,z}$=0 in Eq. 33, the basic ballistic model is recovered. Okubo and Levin (1989) also modeled $K_{t,z}$ with a linear height-dependent diffusion coefficient. This second assumption implies that the vertical dispersion has an effective "memory" or autocorrelation time scale on the order of $\frac{k_v z u_*}{\sigma_w^2}$ (see Fig. 3). The mean longitudinal velocity was assumed to be a power-law of the form $\overline{u}(z) = u_{h_c}\left(\frac{z}{h_c}\right)^\psi$ which approximates well the logarithmic profile (Eq. 10) with exponent $\psi \approx 1/7$ (see Katul et al. 2002). The dispersal kernel solution is given by

$$p(x) = \frac{V_t}{h_r U_{eff}\,\Gamma(1 + \xi)}\left(\frac{h_r U_{eff}}{k_v u_*(1 + \psi)}\right)^{1+\xi^2} x^{-\xi-1}\exp\left[-\frac{h_r U_{eff}}{x k_v u_*(1 + \psi)}\right], \tag{34}$$

where $\xi = \frac{V_t}{k_v u_*(1+\psi)}$ and $\Gamma(.)$ is the Gamma function. Again, the outcome here is a power-law tail that depends on V_t and the flow conditions (u_*) "censored" by an exponential cutoff.

The comparison of WALD kernel predictions with experimental seed release data (Fig. 5) also shows the comparable predictions made by the Okubo–Levin's AD approach and their simpler tilted Gaussian-plume model. The similarities between WALD and the AD predictions are evident, but the AD contains less probability mass at the tails of the distribution. Similar findings were presented in Andersen (1991), who also compared a Lagrangian particle trajectory approach to the AD approaches, and found the Lagrangian approach performs best for dispersal data on *Sonchus oleraceus*.

A coupled Eulerian-Lagrangian perspective for inhomogeneous flow

The distinction between two otherwise comparable approaches—WALD and AD—can be understood in terms of two effects:

1. The inhomogeneity of canopy flow statistics in the vertical direction is parameterized in WALD by incorporating canopy turbulence into vertical averaging, but is assumed to resemble boundary layer flows (i.e., the vertical structure of the canopy does not impact the flow statistics beyond z_o) in the AD models. The inhomogeneity within vegetated canopies can be significant with the canopy modulating some flow statistics by an order or magnitude (see Fig. 2). Inside the canopy, the mean flow is approximately exponential (Eq. 23), $\overline{w'u'}$ is no longer constant at $-u_*^2$ (as in Eq. 17) due to a canopy drag force, and the second-order statistics are attenuated but nearly constant with height above the canopy (as is the case for boundary layers). Figure 2 also shows that considering the canopy height h_c and u_* at h_c collapse canopy turbulence data quite well given that the data in Fig. 2 span a wide range of forested and agricultural ecosystems. Improved turbulence and trajectory models must account for such inhomogeneities in their description of the flow field. Although the simplifying assumption of the AD model is quantitatively comparable to the full WALD treatment for dispersal below the canopy height, the WALD model adds and interprets parameters of turbulence more realistically.

2. The seed turbulent flux $\left(= \overline{w's'}\right)$ in Eq. 33 was modeled as $K_{t,z}\frac{\partial S}{\partial z}$, a model known to fail inside canopies (Denmead and Bradley 1985; Raupach 1988, 1989; Katul and Albertson 1998). Such a model, conventionally labeled as "flux-gradient" or "gradient-diffusion" approximation already introduced in Eq. 18 for relating the momentum flux to the mean velocity gradient, fails inside canopies because the non-local transport of seeds (encoded in terms such as $\partial\overline{w'w's'}/\partial z$) can be significant. For gradient-diffusion approximation to hold, the vertical gradient in this "triple covariance" term must be small.

One model that expands on Eq. 26 by accounting for turbulent fluctuations (and their correlations) for all three velocity components and their covariances (e.g., $\overline{w'u'}$) is the Coupled Eulerian–Lagrangian Closure (CELC) model (Nathan et al. 2002b). The model describes Lagrangian trajectories in three dimensions for each of the three velocity components using equations for the fluid particle acceleration resembling those employed for WALD. It accommodates vertical inhomogeneities in the flow statistics such as those reported in Fig. 2 using Eulerian higher-order closure formulations described elsewhere (Katul and Albertson 1998; Massman and Weil 1999). Due to the Eulerian–Lagrangian coupling implemented in CELC, this model compensates for the failure of the gradient-diffusion in both the flow field computation and the seed transport equations. In the flow field generation calculations, CELC models the triple moments while providing conservation equations for the first and second moments of the flow in a manner that is consistent with the leaf area density profile (Nathan and Katul 2005). For the Lagrangian trajectory calculations, the formulation used by CELC accounts for differences in turbulent diffusion behavior near and far from the seed source, with the latter recovering the gradient-diffusion behavior and the former accounting for the disturbances from it. The mathematical details of the CELC model are presented elsewhere and are not repeated here (Nathan et al. 2002b; Soons et al. 2004a; Nathan and Katul 2005; Wright et al. 2008). Predictions of the CELC model agreed well with dispersal data collected in a vertical array of seed traps at Duke Forest (Nathan et al. 2002b; Nathan and Katul 2005) and with data from individually tracked seeds of grassland forbs in the Netherlands (Soons et al. 2004a). In the latter study, CELC performance was significantly better than WINDISPER-L for short-distance dispersal, and markedly so for LDD.

Relaxing basic assumptions: moving from "modeling" to "simulating" turbulence

The next level of realism in mechanistic modeling is represented by LES. Ideally, the three-velocity-component

conservation of momentum equations (referred to as the Navier–Stokes equations or N–S) should be solved in three-dimensional space at scales ranging from the height of the atmospheric boundary layer (~1 km), to the distance at which the air viscosity becomes significant (<0.1 mm). Such computations require a three-dimensional computational grid that includes on the order of $(10^7)^3$ grid nodes to resolve all these dynamically relevant spatial scales, a number that is beyond the computational capacity of supercomputing systems for the foreseeable future. Instead of resolving all such scales, spatial filtering is applied to the N–S equations that govern the air flow so that the large and energetic eddies are explicitly resolved while the smaller eddies are parameterized. Because the spectrum of these large-scale eddies is explicitly resolved (rather than modeled by a canonical length or time scale as done in CELC), the term "simulation" is used. This approach is in stark contrast to Reynolds-Averaged Navier–Stokes expressions used in Eq. 15, where time-averaging was employed and the effects of turbulence on the key flow statistics (e.g., $\overline{u'w'}$) were modeled as in Eq. 18. However, LES are not free from uncertainties and assumptions. The "spatial filtering" of the N–S equations gives rise to subgrid-scale (SGS) flux terms that must be modeled. These terms represent the effect of small eddies, which are filtered out by such spatial averaging, on the resolved scales of motion (Bou-Zeid et al. 2004). An important effect of the small eddies is to pass the cascading energy to smaller and smaller scales until that energy can be dissipated by molecular viscosity, a phenomenon that was mathematically presented by Kolmogorov (1941a,b). This phenomenon is not explicitly resolved in LES and needs to be parameterized by the SGS TKE scheme, and remains an active research topic in the computational turbulence community (e.g., Stoll and Porté-Agel 2006; Yang et al. 2006). In an LES, the three-dimensionally resolved field of the airflow is represented by the flow at the centers of the discrete cells that make up the numerical mesh of the model. However, unlike the air itself, which can be approximated by discrete, Eulerian, control volumes; moving particles need to be described in Lagrangian motion terms following the continuous particle movement along its path. To simulate the movement of particles in Eulerian flow fields that are generated by LES, a combined Eulerian–Lagrangian approach is needed and is analogous in formulation to the one used in CELC (Thomson 1987). Under this approach (also called Lagrangian–Stochastic or L–S), each particle has its location tracked in small increments and moved by the Eulerian flow field to a new location, and has its velocity augmented by a random amount to account for the SGS turbulent motion. The Lagrangian track is then completed for the simulated particle, which and can also accommodate seed inertia (Reynolds 1999; Weil et al. 2004).

LES with heavy-particle L–S have only recently been applied to seed dispersal (Fig. 6). Using an LES, Kuparinen et al. (2007a) showed that the complexity at which seeds are represented in the model (as simpler ideal particles versus as heavy particles) affects the resulting interactions between seed dispersal and atmospheric boundary layer structure. They determined that lighter seeds could be more accurately described as ideal particles whose momentum can be ignored. This assumption is commonly used for simulations of pollen dispersal with LES (e.g., Kuparinen et al. 2007b). LES models, incorporating L–S approach for dispersal of seeds as heavy particles, were used to study the effects of canopy structure heterogeneity on LDD of seeds. Bohrer et al. (2008) used the Regional Atmospheric Modeling System-based Forest LES (RAFLES) to show the existence of seed ejection hot spots above short trees surrounded by taller ones (Fig. 6). RAFLES is unique among LES models in resolving the effects of drag and surface fluxes of 3-D heterogeneous canopy and accounts for the volume and aperture restriction that the vegetation imposes on the air inside the canopy. Because they explicitly resolve the wind conditions at the assumed seed location at high resolution, LES can also be used to study the effect of seed release timing and abscission conditions (Bohrer et al. 2008).
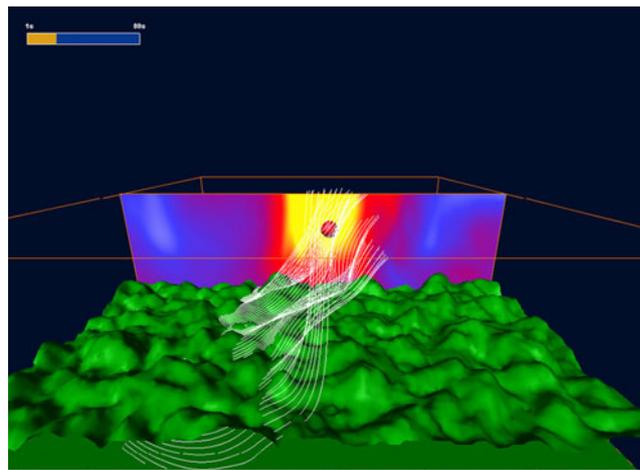

Fig. 6 A puff of simulated seeds (*red ball*) dispersing from a virtual canopy (*green surface illustrates the canopy tops*, Bohrer et al. 2007) in a computer-based experiment using RAFLES (Bohrer et al. 2008). The illustrated domain is $300 \times 300 \times 100$ m^3 and the maximal canopy height is 40 m. The vertical wind velocity is projected in color on a vertical cross-section through the canopy center, with strong updraft (greater than 1 m/s) in *yellow* through downdraft (less than −1 m/s) in white. 3-D wind velocities are illustrated by streamlines, originating from a line along the canopy, at the canopy mean height (29 m) and 50 m upwind of the seed release location. The seeds were released at an ejection hot-spot, above short trees surrounded by tall ones, during a momentum ejection event

Over the last two decades, the usage of LES has proliferated in ways that benefits dispersal studies. LES results have been reported for wind over tree canopies (Shaw and Patton 2003; Dupont and Brunet 2008); windbreaks (Patton et al. 1998); individual plant crowns (Yue et al. 2007; Bohrer et al. 2009); and surface heterogeneity (Li and Avissar 1994; Scanlon and Albertson 2003), fine scaled heterogeneous landscapes including gaps (Bohrer et al. 2009), and hilly terrain covered by canopies (Patton and Katul 2009). However, LES are limited by computational power constraints, and typically can only resolve domains not larger than several kilometers and for short periods (a few hours). For these reasons, LES cannot be used directly to study regional and seasonal dispersal at the population and landscape scale, but they can be used as a powerful tool to explore the sensitivity of dispersal, and particularly LDD, to specific interactions between turbulence, wind, atmospheric conditions, land surface heterogeneity and canopy structure. They can be used to generate hypotheses about mechanisms that act at the small scale but have large and/or non-linear effects on seed dispersal, such as biasing the launch of seeds into updrafts that rise above the canopy, allowing them to exploit power-law kernels for LDD. Future developments in LES can be utilized to further broaden our mechanistic modeling capacities—and perhaps to derive effective parameters for the analytical schemes earlier described. Moreover, LES can be employed as a computational laboratory that incorporates both topography and canopy heterogeneity, permitting detailed assessments of how the tails of $p(x)$ are impacted by such combined heterogeneity. Is the canonical shape of $p(x)$ dramatically altered from its uniform-flat world counterpart? Can the perturbations from the uniform-flat world representation be accommodated via extra dispersive terms in an equivalent one-dimensional representation of the ecosystem as was done for WALD and AD? SGS parameterization inside the canopy is another field with active developments and a need for future improvements. Exploring these combined effects on wind flow and on seed dispersal patterns is the next challenge for LES.

Synthesis A: key parameters and their natural range

Key parameters of the simplest and all subsequent wind dispersal models are the seed terminal velocity (V_t), the seed release height (h_r) and the mean horizontal windspeed ($\overline{u}$). Terminal velocity varies widely between species, ranging from 0.07 (for *Epilobium angustifolium*) to 6.19 m s^{-1} (for *Phaseolus coccineus*), with a median of 2.27 m s^{-1} for all 1,327 species for which V_t data are available in the LEDA plant trait database (Kleyer et al.

2008). In LEDA, 64 species (5%) are listed with $0.07 \leq V_t < 0.3$ m s^{-1}, indicating a good potential for uplift by wind-shear or convection-generated updrafts given that vertical fluctuations (w') at this magnitude are fairly common (Stull 1988; see also Fig. 2). Thus, seeds of these species, which include mostly orchids and a few other herbs and tree species (e.g., *Salix* spp. and *Populus nigra*), have the potential to be dispersed over very long distances. Seeds of another 746 species (56%) have $0.3 \leq V_t < 2.5$ m s^{-1}, indicating that they could be uplifted during strong prolonged updrafts (Stull 1988). Seeds of the remaining 39% species with $2.5 \leq V_t < 6.2$ m s^{-1} can be uplifted only by exceptional excursions of high w' that might occur in storms; indeed, under unusually strong winds that occur in less than 0.02% of half-hour wind observations, even hickory nuts with mean V_t of 7.84 m s^{-1} are predicted to be uplifted and transported up to 650 m by wind (Higgins et al. 2003b). In most plant species (except the minority exhibiting dispersal dimorphism), V_t varies much less within species than between species, with coefficient of variation ranging from 10 to 20% within trees and herbaceous plant species (Greene and Johnson 1992; Augspurger and Franson 1987; Horn et al. 2001; Soons and Heil 2002; Katul et al. 2005). Plant population size, isolation, and local nutrient status have been shown to affect variation in V_t within species (Cody and Overton 1996; Soons and Heil 2002; Riba et al. 2009), either through genetic or environmental effects.

Seed release height varies between almost at the ground surface and the height of the tallest trees, up to ca. 100 m. Inter-specific differences are thus potentially very large. Seed release height can be conveniently expressed as the product of the easily measured mean plant height and the proportional height in which seeds are distributed. For North American wind-dispersed tree species, the former varies from 5 to 72 m ($n=154$; Nathan et al. 2011), whereas the latter has been generalized as 0.75 (Greene and Johnson 1996), and measurements for a few additional species revealed similar values (Nathan et al. 2002b, 2011). Consequently, variation in mean tree height has much greater impact, compared to variation in the proportional height, on dispersal distances, both within (Nathan et al. 2001) and between (Nathan et al. 2011) species. For grassland forbs, natural variation in h_r (0.09–0.96 m) was found to be more important than the somewhat larger variation in V_t (0.34–4.33 m s^{-1}) in determining dispersal distances (Soons et al. 2004a). For North American tree species, inter-specific variation in V_t (0.4–3.4 m s^{-1}, $n=54$) has a greater impact on tree spread rate than inter-specific variation in tree height (see above), and both had much greater impact than the vertical distribution of seeds along tree height (Nathan et al. 2011). Several intra-specific

>comparisons found that h_r is more important than V_t in determining seed dispersal distances (Nathan et al. 2001; Soons et al. 2004a). In more sophisticated models, where canopy height is included, it is not release height per se but the difference between release height and canopy height that determines seed dispersal distances, as anticipated from Eq. 32.

Hourly averaged surface windspeed data is usually measured in relatively open landscapes 10 m above the ground. Surface wind data collected during 21 years (1979–1999) from 776 weather stations across North America fitted a Weibull distribution well, with mean scale and shape parameters of 4.69 and 2.04, respectively, implying that hourly averaged windspeed ranges between 0.25 and 26.47 m s^{-1} (Nathan et al. 2011). The variation in hourly averaged vertical windspeed is much lower. In general, $\overline{w} = 0$ and sites that experienced long coherent periods of positive or negative $\overline{w}$ are often situated on complex terrain (e.g., Nathan et al. 2001; Shannon et al. 2002). Detailed measurements or LES-based assessment of how idealized topographic variability (cosine hill) impacts the flow statistics governing WALD, for example, are discussed elsewhere (Poggi and Katul 2008; Patton and Katul 2009). Most of the studies examining the sensitivity of dispersal distance to natural variation in basic physical and biological wind dispersal parameters were performed at the within-species level, revealing, without exception, that variation in $\overline{u}$ is considerably more important than the intra-specific variation in either h_r or V_t (Greene and Johnson 1992; Horn et al. 2001; Nathan et al. 2001; Soons et al. 2004a; Nathan and Katul 2005). One inter-specific comparison, however, showed that the variation in V_t among North American wind-dispersed tree species has a similar impact on predicted spread rate compared to $\overline{u}$ and a stronger impact compared to σ_w (Nathan et al. 2011).

Synthesis B: insights into wind dispersal mechanisms

Models of different complexity levels have yielded new insight into the process of seed dispersal by wind. First and foremost, uplift is a critical mechanism that is responsible for LDD (Nathan et al. 2002b; Tackenberg 2003; Soons et al. 2004a; Nathan and Katul 2005; Bohrer et al. 2008). Seed release experiments and model simulations showed that uplift above the canopy top is sufficient and necessary to LDD; hence, uplift events provide the means to define LDD quantitatively. Because the long-term mean of vertical windspeed is (close to) zero, the turbulence statistics of the vertical wind fluctuations, including its probability distribution and integral time scale, govern these uplift events.

Other compounding mechanisms affect dispersal and LDD in particular. Buoyancy-driven turbulence, from heating of the ground surface, increases the fluctuation of vertical velocity and the uplift components, and will affect the dispersal distance and LDD (Tackenberg 2003; Soons et al. 2004a; Wright et al. 2008; Kuparinen et al. 2009). This effect could be enhanced by land surface heterogeneity and patterns of land use. Other land-cover effects are mediated by tree canopies. Canopy structure interacts with the wind inside and above the canopy. The leaf area density plays an important role in this interaction by determining the strength of the drag force that the canopy exerts on the air. Sparser canopies in late fall and early spring were found to promote uplift and LDD (Nathan and Katul 2005). Spatial heterogeneity of the canopy, particularly in the organization of canopy top heights leads to increased uplift above particular areas, termed hot spots of dispersal (Bohrer et al. 2008, 2009). These ejection hot-spots are characterized as gaps or relatively short trees surrounded by taller ones. In this LES-based study, LDD was exclusively achieved by seeds that were ejected above the canopy. The release height of the seed relative to the canopy height also proved to be a critical variable in determining dispersal distance and LDD rates (Soons et al. 2004a; Bohrer et al. 2008).

The physiological processes that lead to seed abscission and detachment from the branch/fruit or release from the seed pod also play an important role in determining LDD. The abscission conditions bias the interaction of the seed dispersal with the wind statistics. By targeting particular release conditions instead of an unbiased sample of the vertical windspeed, a seed can be dispersed in a very narrow range of wind conditions that may be conducive for LDD (Kuparinen et al. 2007a; Bohrer et al. 2008; Wright et al. 2008). Specifically, seeds of various wind-dispersed plant species have been shown to be released predominantly during gusts, hence sampling relatively high horizontal and vertical windspeeds (Greene 2005; Soons and Bullock 2008). Also, higher turbulence conditions (which occur more frequently at higher windspeeds but also depend on the local site characteristics) have been found to promote seed abscission from flower heads (Skarpaas et al. 2006; Jongejans et al. 2007), indicating that during gusts and turbulent conditions seeds are preferentially released. As high windspeeds and turbulent conditions also promote LDD (e.g., Nathan et al. 2002b; Kuparinen et al. 2007a), biased (windspeed-dependent) seed abscission can increase LDD and give rise to much faster spread (Soons and Bullock 2008; Nathan et al. 2011). Despite its recognized importance, deriving general rules about biased seed abscission remains a difficult challenge, due to the large

variety of biological and environmental processes that affect the timing of seed ripening and release mechanisms in a rather case-specific manner.

Synthesis C: insights into population-level processes and environmental changes

Dramatic advances in modeling wind dispersal of seeds and pollen have been motivated in recent decades by an increasing need to understand and predict ecological and evolutionary processes in plant populations. Short-distance dispersal serves as the spatial template for recruitment processes in a population. Our ability to model wind dispersal in detail provides the means to estimate the nearest neighbors distances between dispersed seeds (including inter-sibling distances, Wright et al. 2008), contributing to our knowledge of the competitive environment of each seed and the generation of spatial vegetation patterns (Nathan and Muller-Landau 2000). The larger scale of LDD is intimately related to the regional spreading of a population (e.g., Higgins and Richardson 1999; Clark et al. 2001; Higgins et al. 2003a) and its ability to colonize and to connect available habitat patches (e.g., Bohrer et al. 2005; Soons et al. 2005; Damschen et al. 2008). Seed and pollen dispersal co-determine the rate of gene flow between populations (e.g., Ellstrand 1992). All of these processes have recently become of a particular interest, not only to understand fundamental drivers of dynamics and genetics of populations, but also to provide practical applications to ameliorate environmental changes and human-induced disturbances (Kuparinen et al. 2007b, 2009).

Climate change is forecasted to increase average temperatures (Meehl et al. 2007), leading to poleward shifts of species ranges (Fischlin et al. 2007). Additionally, increasing land-use activities are expected to cause further habitat fragmentation, leading to increasingly patchy landscapes (Fischlin et al. 2007). Seed dispersal ability, especially over long distances, therefore becomes a key trait determining how well species can track their shifting ranges and colonize new habitats (e.g., Clark et al. 2001; Soons et al. 2005; Nathan et al. 2011). Various distribution models raised concerns about the (insufficient) ability of plants to spread as fast as their viable ranges are expected to shift (Thomas et al. 2004; Thuiller et al. 2005). However, wind dispersal itself, as well as seed production and establishment of dispersed seeds, can be modified by climate change and fragmentation, due to changes in wind conditions (Soons et al. 2004b; Meehl et al. 2007; Kuparinen et al. 2009; Nathan et al. 2011), in atmospheric CO_2 concentrations (LaDeau and Clark 2001) and in post-

dispersal survival (Nathan et al. 2011). Approaches accounting for these features still remain rare, but the few existing studies suggest that even though future LDD rates are likely to increase with climate change (e.g., through increased occurrence of extreme windspeeds) these increases will remain moderate (Soons et al. 2004b), and estimated increases in spreading rates will not be sufficient alone to compensate for forecasted shifts in the species ranges (Kuparinen et al. 2009; Nathan et al. 2011). To deepen the knowledge of the effects at the population-level, mechanistic wind dispersal models should be complemented by equally powerful tools to quantify post-dispersal processes. For population spread, this challenge is now beginning to be addressed by applying modeling approaches such as spatial integro-difference models (Jongejans et al. 2008), integro-differential equation models (Thompson et al. 2009), and order statistics (Nathan et al. 2011) that combine wind dispersal models such as the WALD model (Katul et al. 2005) with demographic models. The promise of such fully mechanistic modeling approaches, which explicitly account for the key mechanisms underlying both dispersal and demographic processes, lie in their ability to incorporate prospective changes in these key influential factors based on existing empirical evidence and theoretical projections. Yet, given the high uncertainty in forecasting future conditions, the predictions from such models should be repeatedly re-examined once further empirical evidence becomes available (Nathan et al. 2011). Empirical field studies, particularly transplantation experiments (e.g., Savolainen et al. 2007) are likely to provide useful insights into species responses to different environments and, particularly, feedbacks of maladaptation and phenotypic plasticity on vital demographic parameters.

Even though plant populations' responses to climate change are typically viewed from the perspective of their spreading potential via seed dispersal (Higgins and Richardson 1999; Clark et al. 2001; Higgins et al. 2003a), pollen dispersal also plays an important role by affecting the ability of plants to adapt evolutionarily to changing conditions in their habitats (Savolainen et al. 2007). For instance, gene flow from populations adapted to warmer temperatures will aid populations in colder environments to adapt to increasing temperatures in their habitats (Davis and Shaw 2001; Kuparinen et al. 2010). Traditional models and accounts of LDD by pollen have been discounted by assuming low viability during travel in the air (e.g., Aylor 2004). However, recent findings suggest that pollen can disperse over tens of kilometers and still remain viable (Bohrerova et al. 2009). In natural populations, such gene flow is often beneficial as it promotes genetic diversity of

local populations and thereby their adaptability (Reed and Frankham 2003), but in an agricultural context this may not be the case. Pollen-mediated introgression of transgenes into non-modified and wild varieties, or the escape of the entire transgenic plants into cultivated lands and natural habitats via seed dispersal are both of a great public concern, thus warranting a careful risk assessment (e.g., Snow et al. 2005). To this end, mechanistic wind dispersal models are particularly useful as they provide proxies of how far and at which rates seeds and pollen are expected to disperse (Nathan et al. 2002b; Tackenberg 2003; Soons et al. 2004a), as well as how stochastic the dispersal processes can be (Kuparinen et al. 2007b).

Future directions

Traditionally, phenomenological models were favored to describe dispersal kernels because data on canopy morphology and wind statistics were very difficult to acquire. This situation has changed dramatically on both fronts over the past decade. In terms of canopy attributes, remote sensing platforms from aircraft, such as canopy LIDAR systems, and characterizations of vegetation by differential spectroscopy from satellites, are now capable of mapping vegetation height, the three-dimensional variation of the leaf area density, and topography at unprecedented resolution of few meters (Lefsky et al. 2002). The MODIS satellite system now provides estimates of leaf area index over a 30 m-by-30 m pixel on an 8-day cycle, which can be used to describe changes in phenology (Miller et al. 1997; Myneni et al. 2002; Clark et al. 2008). Regarding wind statistics, the FluxNet program has in excess of 400 sites providing globally detailed wind velocity measurements (e.g., u_*, σ_w, and sensible heat) across numerous biomes and climates (Baldocchi et al. 2001; Stoy et al. 2009). Many of its participating sites can now boast in excess of 5 years of detailed turbulence measurements above the canopy, and for some of the sites, within the canopy as well.

Unlike phenomenological models, mechanistic models are positioned to take advantage of all these monitoring advancements. Analysis of the asymptotic behavior of WALD and AD models revealed that accounting for vertical turbulent transport of seeds leads to a power-law dispersal kernel far from the seed source that is censored by an exponential cutoff. The exponent of the power-law tail and the degree of censoring imposed by the exponential cutoff are both dependent on the parameterizations of the vertical structure of the flow field inside the canopy and V_t/u_* (or V_t/U_{eff}). The implications of these tails for LDD is significant when combined with the fact that u_* or U_{eff} are themselves derived from "extreme-value" distributions such

as a Weibull. The compound effects of the tails in u_* or U_{eff} distribution and those induced by turbulent dispersion (whether predicted via WALD or AD) lead to seed dispersal distances that are up to two to three orders of magnitude larger than their ballistic counterparts driven by the same u_* or U_{eff} and for the same V_t, which has enormous consequences for predicted colonization potential and species spread rates (Nathan et al. 2011).

Because the AD and WALD demonstrated that the power-law emerges when accounting for vertical turbulent diffusion, it is natural that the next level of complexity would aim at resolving the entire turbulent flow field. LES are well-established computational tools that explicitly simulate rather than model the effects of turbulence on seed dispersal. Current LES schemes can resolve many interactions between air flow and complex geometries imposed by natural heterogeneities (e.g., fine-scale variations in leaf area, forest edges, topography) that impact the dispersal process. Because of this resolution, we can now finally begin to grasp dispersal mechanisms and resulting seed deposition patterns in realistic, spatially heterogeneous landscapes. Particularly, a number of important unresolved dispersal hypotheses such as differential arrival of seeds into gaps, the effects of landscape fragmentation and complex topography on the generic shape of the dispersal kernel can now be explored. However, it is also inconceivable that this type of model would be used to generate long-term predictions due to the intensive computational power and time it requires. The need for some intermediate approach that bridges the detailed investigation to generate kernel shapes usable for studying long-term ecological processes remains essential, especially for biological questions that deal with larger spatial and temporal scales, such as species range expansion (Nathan et al. 2005).

This challenge has been partially addressed by adjustments of simple models (Greene and Johnson 1996; Tackenberg 2003; Nuttle and Haefner 2005). Recently, models of intermediate complexity such as CELC have been modified to account for landscape heterogeneity for studying processes at large spatial scales and over long terms. For example, new mechanistic models of wind flow on gentle forested hills (Poggi et al. 2008b), supplemented by a simplified derivation of the turbulence statistics, have been incorporated into the Eulerian module of CELC to yield a simplified mechanistic dispersal model for a hilly scenario (Trakhtenbrot 2010). The main attributes of the modeled wind field over a gentle forested cosine hill (covered by homogeneous canopy) are acceleration of the topography-following mean wind component uphill and its deceleration downhill to the point that a recirculation zone is formed within the canopy (Finnigan and Belcher 2004; Poggi and Katul 2007; Poggi et al. 2008b). By accounting for the effects of this acceleration, deceleration, and

recirculation on dispersal, these intermediate complexity approaches can yield spatially non-homogeneous dispersal kernels without the expensive computational costs incurred by LES.

The dialogue between the modeling approach seeking detailed understanding of dispersal mechanisms and the one seeking simplification for investigating large-scale and long-term processes should be extended to the design of empirical research on wind dispersal. Sensitivity analyses of the models will help to distinguish those parameters that need detailed measurement from those that can be safely estimated. Spatiotemporal fluctuations in model behavior can help to optimize the placement and monitoring designs for seed traps; for example, by proposing a more detailed sampling design in areas where seed deposition is expected to vary along steep spatial gradients (e.g., across canopy gaps or other landscape transitions) or during periods when more LDD is expected. Conversely, the degree of non-randomness of seed abscission needs to be quantified empirically (e.g., Wright et al. 2008; Marchetto et al. 2010), and the corresponding dispersal kernel measured, so that models can predict LDD under appropriately filtered wind conditions. Ultimately a true understanding of dispersal will require continual bi-directional interplay between models and data, between theory and reality.

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