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Mechanistic Analytical Models for Long-Distance Seed Dispersal by Wind

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ABSTRACT: We introduce an analytical model, the Wald analytical long-distance dispersal (WALD) model, for estimating dispersal kernels of wind-dispersed seeds and their escape probability from the canopy. The model is based on simplifications to well-established three-dimensional Lagrangian stochastic approaches for turbulent scalar transport resulting in a two-parameter Wald (or inverse Gaussian) distribution. Unlike commonly used phenomenological models, WALD's parameters can be estimated from the key factors affecting wind dispersal—wind statistics, seed release height, and seed terminal velocity—determined independently of dispersal data. WALD's asymptotic power-law tail has an exponent of −3/2, a limiting value verified by a meta-analysis for a wide variety of measured dispersal kernels and larger than the exponent of the bivariate Student *t*-test (2Dt). We tested WALD using three dispersal data sets on forest trees, heathland shrubs, and grassland forbs and compared WALD's performance with that of other analytical mechanistic models (revised versions of the tilted Gaussian Plume model and the advection-diffusion equation), revealing fairest agreement between WALD predictions and measurements. Analytical mechanistic models, such as WALD, combine the advantages of simplicity and mechanistic understanding and are valuable tools for modeling large-scale, long-term plant population dynamics.

Keywords: analytical model, canopy turbulence, long-distance seed dispersal, mechanistic dispersal models, Wald distribution, wind dispersal.

The past decade witnessed a proliferation of studies that address the importance of seed dispersal in ecological processes (Clark et al. 1999; Cain et al. 2000, 2003; Nathan and Muller-Landau 2000; Wenny 2001; Nathan et al. 2002*b*; Wang and Smith 2002; Levin et al. 2003). A major emphasis in these studies is modeling seed dispersal using both the phenomenological approach (Clark 1998; Tanaka et al. 1998; Clark et al. 1999, 2001; Bullock and Clarke 2000; Nathan et al. 2000; Stoyan and Wagner 2001; Higgins et al. 2003*a*) and, especially for wind dispersal, the mechanistic approach (Greene and Johnson 1989, 1995, 1996; Okubo and Levin 1989; Horn et al. 2001; Nathan et al. 2001, 2002*a*, 2002*b*; Soons and Heil 2002; Tackenberg 2003; Tackenberg et al. 2003; Soons et al. 2004). Both modeling approaches have been shown to provide reliable predictions of observed seed dispersal patterns. However, the phenomenological approach has been favored for modeling dispersal in large-scale and long-term population studies (Levin et al. 1997, 2003; Clark 1998; Higgins and Richardson 1999; Chave 2000; Chave and Levin 2003) because of its inherent simplicity. Simplicity is important for implementation in spatially explicit population models that integrate the spatial structure of landscapes, quantify the spread of expanding populations of invasive and native species, including pests, and estimate gene flow patterns.

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Detailed mechanistic approaches, despite their advantages of being estimated independently of the dispersal data, being generally applicable, and providing insights into the underlying transport mechanism, require computer-intensive simulations of wind statistics and hence are impractical for large-scale, long-term applications.

Simplified mechanistic models that relate mean wind conditions and seed attributes to dispersal distances are based on "ballistic" models (Greene and Johnson 1989, 1995, 1996; Nathan et al. 2001, 2002*b*; Soons and Heil 2002). These models capture the mode of the dispersal curve well but fail to reproduce its tail, that is, long-distance dispersal (LDD) events (Bullock and Clarke 2000; Nathan et al. 2002*b*). In many ecosystems, LDD is a crucially important determinant of spatial spread, gene flow, and species coexistence (Levin et al. 2003). This underestimation of the tails is attributed to an underestimation in uplifting and escape of seeds from the canopy, events that play a major role in LDD (Horn et al. 2001; Nathan et al. 2002*a*).

To partially circumvent this problem, a coupled Eulerian-Lagrangian closure (CELC) model (Hsieh et al. 1997, 2000; Katul and Albertson 1998; Katul and Chang 1999; Nathan et al. 2002*a*) has recently been applied to seed dispersal by wind (Nathan et al. 2002*a*; Soons et al. 2004). This model reproduced well the observed seed dispersal data collected vertically along a 45-m-high tower for five wind-dispersed tree species in a deciduous forest in the southeastern United States (Nathan et al. 2002*a*) and horizontally for four wind-dispersed herbaceous species in grasslands in the Netherlands (Soons et al. 2004). In both cases, the model confirmed that uplifting and subsequent seed escape from the canopy is a necessary condition for LDD. Tackenberg (2003) arrived at a similar conclusion, using detailed turbulent velocity measurements.

The CELC model is computationally expensive, requiring thousands of trajectory calculations, thereby prohibiting its use in large-scale and complex ecological models. Hence, what is currently lacking is a simplified dispersal model that retains the main mechanisms in CELC (or other complex turbulent transport models) but also preserves the simplicity of phenomenological models. Recently proposed phenomenological models, such as the binomial Student *t*-test (2Dt; Clark et al. 1999) and the mixed Weibull (Higgins and Richardson 1999; Higgins et al. 2003*b*), provide good descriptions of LDD via fat tails that are typically absent in Gaussian or simple negative exponential distributions (Kot et al. 1996; Turchin 1998). However, they require dispersal data for calibration, thereby preventing their general use for any new species and environmental settings. A fast analytical solution based on a mechanistic approach thus has the decisive merit of combining the major advantages of the two modeling approaches while avoiding their major disadvantages. Additionally, it will provide the means to extrapolate from the commonly measured dispersal distances near the source (or near-field dispersion) to LDD or escape probabilities from the canopy. The latter are much more difficult to measure. Furthermore, because the parameters of such an analytical mechanistic model—seed terminal velocity, seed release height, and wind conditions—are easily interpretable and measurable, it provides the means for estimating LDD for essentially any wind-dispersed species.

In this article, we introduce a new analytic expression derived from a simplified three-dimensional stochastic dispersion model that retains the essential physics in CELC. As we explain below, this model converges to a Wald (or inverse Gaussian) distribution; hence, we call it the Wald analytical long-distance dispersal (WALD) model. We compare the new model to two other analytical mechanistic models: the tilted Gaussian plume and a solution to the advection-diffusion equation proposed by Okubo and Levin (1989). The latter two models were numerically revised to partially account for the effect of leaf area density on the vertically averaged mean velocity and turbulent diffusivity. For simplicity, we focus on one-dimensional dispersal kernels (or crosswind-integrated models) and refer to dispersal kernels as the probability density function of locating a seed on the ground (or forest floor) with respect to a point source at a given height (i.e., "distance distribution" sensu Nathan and Muller-Landau 2000). If the dispersal process is isotropic, a two-dimensional dispersal kernel (i.e., "dispersal kernel" sensu Nathan and Muller-Landau 2000) differs from its one-dimensional counterpart only by $2\pi x$, where x is the distance from the seed source.

We test the new model against several seed dispersal data sets obtained from controlled seed release experiments. Ideally, the model's capacity to predict LDD should be tested against "real" LDD data. Yet quantifying LDD remains an unaddressed challenge (Nathan et al. 2003), and its definition is still rather vague and case specific (Nathan 2005). We approached these difficulties in two ways. First, we compared the performance of WALD and some alternative models in fitting the dispersal data after setting thresholds of >5 and >10 m from the source. This procedure examines the model's ability (and robustness) to fit the low frequency of observed dispersal kernels away from the mode (Portnoy and Willson 1993). We emphasize that these release experiments were designed to encompass a wide range of influencing factors; while this approach was chosen to enhance the generality of our results, it inherently acts to reduce predictive ability. Second, we also developed an analytical expression for calculating the probability of a seed's escaping the forest canopy and tested this model against observed seed uplifting probabilities reported in Nathan et al. (2002*a*). This test is directly related to LDD because seed uplifting by vertical updrafts is crucial (or a necessary condition) for LDD.

Next, we analyze the tail properties of the predicted dispersal kernel and verify whether these emerging properties accord with a wide range of fitted power-law tails (i.e., heavy tails) from the literature. Finally, we demonstrate how to use the proposed approach to solve the so-called inverse problem—extracting biological dispersal traits and wind parameters by statistical fitting of the simplified analytical expression to measured dispersal kernels.

Theory

Thomson's Model

In this section, we provide a brief description of the essential physics in CELC as a basis for the analytical model development. The formulation of Lagrangian stochastic models for the trajectories of air particles having no mass in turbulent flows is now a well-established computational method in fluid mechanics and turbulence research (Thomson 1987; Pope 2000). These Lagrangian models must be developed to satisfy the so-called well-mixed condition. This condition states that if the concentration of a material is uniform at some time *t*, it will remain so if there are no sources or sinks. This condition is currently the most rigorous and correct theoretical framework for the formulation of Lagrangian stochastic models and ensures consistency with prescribed Eulerian velocity statistics. For this condition, the Lagrangian velocity of an air parcel is described by a generalized Langevin equation (Thomson 1987):

$$du_i = a_i(\mathbf{x}, \mathbf{u}, t)\, dt + b_{ij}(\mathbf{x}, \mathbf{u}, t)\, d\Omega_j,$$

where **x** and **u** are the position and velocity vectors of a tracer particle at time *t*, respectively. The terms a_i and b_{ij} are the drift and diffusion coefficients, respectively. The quantities $d\Omega_j$ are increments of a vector-valued Wiener process (Brownian walk) with independent components, mean 0, and variance *dt*. Here, subscripts (i, j) are used to denote components of Cartesian tensors, with implied summation over repeated indices. Both meteorological and index notations are used interchangeably throughout for consistency with both the fluid mechanics and boundary layer meteorology literature (i.e., the components of **x** are $x_1 \equiv x$, $x_2 \equiv y$, and $x_3 \equiv z$), with *x*, *y*, and *z* representing the longitudinal, lateral, and vertical axes, respectively.

The specification of the drift and diffusion terms is sufficient to determine how air parcels move. While b_{ij} can be uniquely determined by requiring that the Lagrangian velocity structure function match predictions from theories of locally homogeneous and isotropic turbulence, the determination of a_i is much more complex and requires the use of the well-mixed condition. Thomson (1987) showed that for high Reynolds numbers, typical of atmospheric flows, the well-mixed condition requires the distribution of air parcels in position-velocity space to be proportional to the Eulerian probability distribution function $p(\mathbf{x}, \mathbf{u}, t)$ and to remain so for all later times. This condition requires that $p(\mathbf{x}, \mathbf{u}, t)$ must be a solution to the generalized Fokker-Planck equation

$$\frac{\partial p}{\partial t} + \frac{\partial}{\partial x_i}(u_i p) = -\frac{\partial}{\partial u_i}(a_i p) + \frac{\partial^2}{\partial u_i \partial u_k}\left(\frac{1}{2} b_{ij} b_{jk} p\right).$$

The solution of the above Fokker-Planck equation for Gaussian turbulence provides the probability distribution for the velocity components. For two- and three-dimensional turbulence, Thomson (1987) showed that the drift term, $a_i(x, u, t)$ can be constrained (but not completely determined) by requiring consistency with prescribed Eulerian velocity statistics.

Simplifications

Criteria in addition to the well-mixed condition are needed to resolve the nonuniqueness of the drift coefficients in two and three dimensions. Furthermore, the resulting set of three equations derived by Thomson (1987) for the velocity fluctuations (not shown here but used in the CELC model) cannot be solved analytically. Therefore, further simplifications are needed to reduce the model to arrive at an analytic dispersal kernel. We consider the one-dimensional case of turbulent flows for very low turbulent intensity as a basis for building the simplified model. Our intent is to develop a dispersal kernel that recovers the most elementary turbulent flow physics and then progress to accounting for vertical inhomogeneity and high intensity by modifying the simplified solution. Within such a conceptual framework and idealized conditions, the Langevin and the Fokker-Planck equations reduce to, respectively,

$$du_3 = a(z, u_3, t)\, dt + b(z, u_3, t)\, d\Omega$$

and

$$\frac{\partial p}{\partial t} + \frac{\partial}{\partial z}(u_3 p) = -\frac{\partial}{\partial u_3}(ap) + \frac{1}{2}\frac{\partial^2}{\partial u_3^2}(b^2 p),$$

where $b = (C_0 \langle \varepsilon \rangle)^{1/2}$. Moreover, a Gaussian $p(z, u_3, t)$ given by

$$p(z, u_3, t) = (2\pi)^{-1/2}\langle\overline{u_3'u_3'}\rangle^{-1/2}\exp\left[-\frac{1}{2}\frac{u_3^2}{\langle\overline{u_3'u_3'}\rangle}\right],$$

results in a drift coefficient

$$a(z, u_3, t) = -\frac{u_3}{T_{\mathrm{L}}} + \frac{1}{2}\left(1 + \frac{u_3^2}{\langle\overline{u_3'u_3'}\rangle}\right)\frac{\partial\langle\overline{u_3'u_3'}\rangle}{\partial z}.$$

Here $\langle\overline{u_3'u_3'}\rangle$ ($\equiv \sigma_w^2$) is the variance of the vertical velocity component (the coordinates are defined so that $\langle\overline{u_2}\rangle = 0$, as is common in atmospheric flows), T_{L} is the integral time scale (a measure of temporal coherency of turbulent eddies), C_0 (~5.5) is a similarity constant (related to the Kolmogorov constant), and $\langle\overline{\varepsilon}\rangle$ is the mean turbulent kinetic energy dissipation rate. Note that in the previous equations, angle brackets denote spatial averaging (Raupach and Shaw 1982; Finnigan 2000) and an overbar is for time averaging. The vertical distribution of the flow statistics $\langle\overline{u_1}\rangle$, $\langle\overline{u_3'u_3'}\rangle$, and $\langle\overline{\varepsilon}\rangle$ needed to drive the Thomson (1987) model can be readily computed from Eulerian second-order closure models, which require as input the mean velocity above the canopy, the leaf area density, and the drag coefficient of the canopy (Katul and Albertson 1998; Ayotte et al. 1999; Katul and Chang 1999; Massman and Weil 1999; Katul et al. 2001).

It is clear that even the one-dimensional Thomson (1987) model cannot be solved analytically. We consider the previous formulation for the case where the flow is vertically homogeneous. Under this assumption, the change in the position and velocity of an air parcel transporting a seed with terminal velocity V_{t} (and zero inertia) is given by the stochastic differential equations

$$du_3 = \left[-\frac{C_0\langle\overline{\varepsilon}\rangle}{2}\left(\frac{u_3}{\langle\overline{u_3'u_3'}\rangle}\right)\right]dt + \sqrt{C_0\langle\overline{\varepsilon}\rangle}\,d\Omega, \tag{1}$$

$$\frac{dx_3}{dt} = -V_{\mathrm{t}} + u_3, \tag{2}$$

and

$$\frac{dx_1}{dt} = \langle\overline{u_1}\rangle, \tag{3}$$

with $T_{\mathrm{L}} = (2/C_0)(\langle\overline{u_3'u_3'}\rangle/\langle\overline{\varepsilon}\rangle)$.

Equation (2) also assumes that the seed terminal velocity is achieved instantly after seed release. While equations (2) and (3) are analogous to the Lagrangian model proposed by Andersen (1991), equation (1) drastically differs from his model, given that the dispersion term is dependent on a turbulent kinetic energy dissipation rate (which is nonmonotonic inside canopies) and a drift term that also varies with $\langle\overline{u_3'u_3'}\rangle$, both modeled using second-order closure principles (described later). Note that when $u_3 \approx 0$, the simplest ballistic model is recovered.

For notational simplicity, we use an overbar to indicate both time and horizontal averages and set $\langle\overline{u_1}\rangle = \overline{U}$ and $\langle\overline{\varepsilon}\rangle = \varepsilon$. We emphasize again that canopy turbulence is highly inhomogeneous and of high turbulent intensity; hence, these simplifications are only adopted to arrive at a simplified version of the Thomson (1987) model that can be solved analytically, and we later modify the solution to account for high intensity and vertical inhomogeneity through appropriate adjustments of its coefficients.

Analytical Solution

Substituting equation (3) into equations (1) and (2) to eliminate time, one obtains the second-order process

$$du_3 = -\alpha u_3\, dx_1 + \beta\, d\Omega_1,$$

$$\frac{dx_3}{dx_1} = -\gamma + \delta u_3,$$

where $\alpha = (C_0\varepsilon/2\overline{U}\sigma_w^2)$, $\beta = (C_0\varepsilon/\overline{U})^{1/2}$, $\gamma = V_{\mathrm{t}}/\overline{U}$, and $\delta = 1/\overline{U}$. The corresponding Fokker-Planck equation can also be obtained and is reported in appendix A in the online edition of the *American Naturalist*. If the seed settling time is assumed to be much longer than the vertical velocity integral timescale (see app. A), the previous problem can be further simplified, and the corresponding Fokker-Planck equation becomes

$$\frac{\partial p}{\partial x_1} = -\gamma\frac{\partial p}{\partial x_3} + \frac{1}{2}\sigma^2\frac{\partial p}{\partial x_3}, \tag{4}$$

where $\sigma = \delta(\beta/\alpha)$.

The solution of equation (4) with the specified initial and boundary conditions is well known (Cox and Miller 1965, p. 221). More importantly, the probability distribution of a seed reaching the ground can be obtained by noticing that it is equivalent to the probability of crossing the absorbing boundary $x_3 = 0$ starting from $x_{3,\mathrm{r}}$. Following the standard procedure for the calculation of the first passage times (Cox and Miller 1965, p. 221), the final kernel of seed dispersal can be obtained as

$$p(x_1) = \frac{x_{3,\mathrm{r}}}{\sigma\sqrt{2\pi x_1^3}}\exp\left[-\frac{(x_{3,\mathrm{r}} - \gamma x_1)^2}{2\sigma^2 x_1}\right] \tag{5a}$$

(see app. A). When we define $\mu' = (x_{3,\mathrm{r}}\overline{U})/V_{\mathrm{t}}$ (or $x_{3,\mathrm{r}}/\gamma$) and $\lambda' = (x_{3,\mathrm{r}}/\sigma)^2$, equation (5a) reduces to a Wald (or inverse Gaussian) distribution of the form

$$p(x_1) = \left(\frac{\lambda'}{2\pi x_1^3}\right)^{1/2} \exp\left[-\frac{\lambda'(x_1 - \mu')^2}{2\mu'^2 x_1}\right]. \tag{5b}$$

The inverse Gaussian distribution, known as the first passage time distribution of Brownian motion with positive drift, was first derived by Schrödinger (1915) and is now routinely used to model positively skewed data (Wald 1947). Note that the dispersal kernel parameters μ' and λ' depend only on the wind velocity statistics (σ and $\overline{U}$), seed terminal velocity (V_{t}), and seed release height ($x_{3,\mathrm{r}}$). We call this analytical solution the Wald analytical long-distance dispersal (WALD) model, as it exhibits heavy tails for LDD, as we show below. It has the following statistical properties (Evans et al. 1993): mean $= \mu'$; variance $= \mu'^3/\lambda'$; mode $= \mu'\{[1 + (9\mu'^2/4\lambda'^2)]^{1/2} - (3/2)(\mu'/\lambda')\}$; skewness coefficient $= 3(\mu'/\lambda')^{1/2}$; and kurtosis coefficient $= 3 + 15(\mu'/\lambda')$. Here μ' (>0) and λ' (>0) are often called the location and scale parameters, respectively. The WALD kernel has finite variance, is positively skewed, and has a kurtosis coefficient much bigger than that of a Gaussian distribution (3).

For values of $\gamma \to 0$, equation (5) exhibits power-law decay (i.e., fat-tail distribution) with exponent $-3/2$, a signature of long-distance dispersal. For finite γ, the fat tail presents a cutoff (exponential decay) at a distance that decreases with increasing γ.

From the Fokker-Planck equation (4), one can also derive analytically the escape probability from the canopy top as a function of canopy height h. This is given by Cox and Miller (1965):

$$\Pr(x_{3,\mathrm{r}} > h) = \frac{\exp(2\gamma x_{3,\mathrm{r}}/\sigma^2) - 1}{\exp(2\gamma h/\sigma^2) - 1}. \tag{6}$$

Noting that a necessary condition for LDD is seed escape from the canopy (Nathan et al. 2002*a*), equation (6) provides an unambiguous upper limit on the fraction of seeds that can "potentially" undergo or experience LDD as a function of the key dispersal determinants.

In summary, the WALD kernel derived here makes several restrictive assumptions about canopy turbulence, including low turbulent intensity flows, instant attainment of terminal velocity (and thus zero inertia of seed), and negligible effects of the correlation of u_3 relative to the settling time, in addition to all the simplifications to the classical Thomson (1987) model, including Gaussian fluctuations, and the use of Kolmogorov scaling within the inertial subrange to arrive at b_{ij}. How robust this kernel is to such restrictive assumptions is investigated next, after a discussion of kernel parameter estimation from determinants of seed dispersal.

Estimation of Model Parameters

For equation (5) to be readily usable, it is necessary to estimate σ from wind statistics typically observed or available above the canopy. From appendix A, it can be shown that

$$\sigma^2 = \left(\frac{2\sigma_w^2}{C_0\varepsilon}\right) \times \left(\frac{2\sigma_w^2}{\overline{U}}\right). \tag{7}$$

Unfortunately, ε is rarely measured and is difficult to model inside canopies, thereby making the use of equation (7) not practical. Equation (7), however, can be further simplified when the mixing length (or effective eddy sizes responsible for dispersion) inside the canopy is assumed to be constant and proportional to h through a coefficient κ. For this simplification, the term involving ε can be simplified to

$$\frac{2\sigma_w^2}{C_0\varepsilon} = \kappa\frac{h}{\sigma_w} \tag{8}$$

(Poggi et al. 2004*a*, 2004*b*, 2005).

Substituting equation (8) into equation (7) gives

$$\sigma^2 = \kappa h\left(2\frac{\sigma_w}{\overline{U}}\right), \tag{9}$$

where $\kappa \in [0.3, 0.4]$. The coefficient κ, while bounded and qualitatively connected to a mixing length, must be considered as a semiempirical parameter here because all the model assumptions (including vertically homogeneous and low-intensity flows, instant attainment of terminal velocity, zero inertia of seed, and the negligible effects of the correlation of u_3 relative to the settling time) and all simplifications in the original Thomson (1987) model (including a Gaussian $d\Omega$) affect this coefficient.

The lower limit on κ can be derived by noting that near the canopy top $\sigma_w \approx u_*$ and that $2\sigma_w^2/C_0\varepsilon = T_{\mathrm{L}}$, which is also approximately $0.3h/u_*$ (Raupach 1989*a*, 1989*b*; Raupach et al. 1996) for dense and extensively uniform canopies (i.e., $\kappa = 0.3$). The upper limit is constrained by the fact that eddies within the canopy, even for very sparse canopies, cannot geometrically exceed the classical mixing length scale at the canopy top (i.e., $\kappa = k = 0.4$, the von Kármán constant).

Finally, the values $\overline{U}$ and σ_w can be estimated from wind speed measurement above the canopy in numerous ways.

Table 1: Summary of seed release experiments

Date of release, species[a]	LAI (m^2 m^{-2})	$x_{3,\mathrm{r}}$ = 30 m			$x_{3,\mathrm{r}}$ = 21 m			$x_{3,\mathrm{r}}$ = 12 m		
		u_* (m s^{-1})	$\overline{U}$ (m s^{-1})	σ_w (m s^{-1})	u_* (m s^{-1})	$\overline{U}$ (m s^{-1})	σ_w (m s^{-1})	u_* (m s^{-1})	$\overline{U}$ (m s^{-1})	σ_w (m s^{-1})
November 2, 2000:[b] litu (1.50), frpe (1.43), acne (1.50), caca (1.89)	1.2	.16	.23	.09	.16	.23	.09	.16	.23	.09
November 28, 2000: litu (1.50), frpe (1.43), acne (1.50), caca (1.89)	.9	.89	1.55	.61	.89	1.55	.61	.63	1.10	.44
May 13, 2001: acsa (1.10), acru (.67)	4.9	.60	.56	.27	.62	.58	.28	.61	.57	.27
June 25, 2001: acsa (1.10), acru (.67), caca (1.89), frpe (1.43)	4.9	.25	.23	.11	.20	.19	.09	.27	.23	.11
July 20, 2001: acsr (1.74), fram (1.21), caca (1.89)	4.9	.27	.25	.12	.32	.31	.15	.25	.23	.11

Note: The measured release height ($x_{3,r}$), terminal velocity (V_t), leaf area index (LAI), friction velocity above the canopy (u_*), modeled depth-averaged mean velocity ($\overline{U}$), and vertical velocity standard deviations within the canopy (σ_w) are also shown. acne = *Acer negundo*, acru = *Acer rubrum*, acsa = *Acer saccharinum*, acsr = *Acer saccharum*, caca = *Carpinus caroliniana*, fram = *Fraxinus americana*, frpe = *Fraxinus pennsylvanica*, litu = *Liriodendron tulipifera*). The values of V_t here are higher than previously published values (Nathan et al. 2002*a*) because seeds of different species were color sprayed to enhancing detection and recovery.

[a] For each species, V_t, measured for spray-marked seeds, is shown in parentheses (m s^{-1}).

[b] In this particular experiment, all the seeds were simultaneously released from the source. Hence, the 30-min friction velocity u_* need not represent the correct mean wind conditions of the few seconds in which dispersal occurred. In the remaining four experiments, seeds were released over a 30-min period at each level.

One approach is to use simplified analytical models (Massman and Weil 1999) driven by the wind speed above the canopy to compute the flow statistics inside the canopy and then vertically average the computed profiles to obtain $\overline{U}$ and σ_w (see app. B in the online edition of the *American Naturalist* for formulation).

Model Testing

Evaluating Model Predictions by Seed Release Experiments

While the setup is described elsewhere (Nathan et al. 2002*a*), the salient features are reviewed here. Seed release experiments were carried out in an 80–100-year-old oak-hickory forest within the Blackwood division of the Duke Forest near Durham, North Carolina. The stand is composed primarily from mixed hardwood species, with *Quercus alba*, *Quercus michauxii*, *Quercus velutina*, *Carya tomentosa*, *Carya ovata*, *Liriodendron tulipifera*, and *Liquidambar styraciflua* as canopy dominant, *Pinus taeda* as a minor component, and mostly *Ostrya virginiana*, *Carpinus caroliniana*, and *Cornus florida* in the understory. The tree density is 311 ha^{-1}, the basal area is 26.3 m^2 ha^{-1}, the mean canopy height is 33 m, and the leaf area index (projected foliage area per ground area) varies from 0.9 m^2 m^{-2} (leafless conditions) to 4.9 m^2 m^{-2} (full foliage).

Five manual seed release experiments were conducted from November 2, 2000 to July 20, 2001. Eight wind-dispersed species were used in those releases, with mean V_t ranging from 0.67 to 1.89 m s^{-1} (table 1). Seeds were manually released from a 45-m-high walk-up tower at three levels: $x_{3,\mathrm{r}}$ = 30, 21, and 12 m above the forest floor. Each seed release lasted for about 30 min, with seeds released every 30 s. A CSAT 3 (Campbell Scientific, Logan, UT) sonic anemometer situated at 40 m above the forest floor recorded the mean flow statistics $\langle \overline{u_1} \rangle$, $\langle \overline{u_1'u_1'} \rangle$, $\langle \overline{u_2'u_2'} \rangle$, $\langle \overline{u_3'u_3'} \rangle$, and $\langle \overline{u_1'u_3'} \rangle$ for each 30-min release time. The $u_* = \left(\langle \overline{u_1'u_3'} \rangle^2 + \langle \overline{u_2'u_3'} \rangle^2\right)^{1/4}$ varied roughly from 0.1 to 0.9 m s^{-1}, with a concomitant $\overline{U}$ variation from 0.3 to 3.3 m s^{-1} just above the canopy, within the ensemble of the 15 (i.e., five experiments and three release heights per experiment) manual seed releases (see table 1). To facilitate the detection of seeds on the forest floor and to distinguish between seeds of the same species released from different heights, all seeds were color sprayed (in different colors) before the release. Measurements of V_t before and after spraying revealed that spraying increased V_t appreciably (from 12% to 112%). Hence, the measured after-spraying V_t values were used in the calculations.

For each u_*, the local leaf area density $a(z)$ was measured (or estimated), and the second-order closure model (Massman and Weil 1999) was used to calculate the vertical profiles of $\langle \overline{u_1} \rangle$, $\langle \overline{u_1'u_1'} \rangle$, $\langle \overline{u_2'u_2'} \rangle$, $\langle \overline{u_3'u_3'} \rangle$, and $\langle \overline{u_1'u_3'} \rangle$ within the canopy (see app. B) using the measured flow statistics above the canopy (table 1). These flow statistics were then vertically averaged to estimate $\overline{U}$ and σ_w, and hence, γ ($= V_t/\overline{U}$) and $\sigma^2 = 2\kappa h \sigma_w/\overline{U}$ for each species and each seed release. All in all, an ensemble of 51 seed dispersal kernels was measured in the five seed release experiments.

The 51 measured kernels (shown in app. C in the online edition of the *American Naturalist*) were compared to the predicted kernels for a wide range of leaf area index (factor of 4), release height (factor of 2.5), terminal velocity (factor of 2), and friction velocity (factor of 9), as evidenced by table 1. From appendix C, the agreement between WALD's calculations and the measurements is reasonably good despite all the simplifying assumptions. Using regression analysis on the 459 data points (i.e., all the points for all release dates shown in app. C) resulted in a correlation coefficient (r) of 0.69. The regression analysis was conducted on $\exp\left\{-[p(x_1)]^{1/2}\right\}$ rather than $p(x_1)$ to increase the regression sensitivity for low $p(x_1)$ (<0.2). Since low values are typically observed at both tails of the distribution (i.e., near and away from the source), we repeated the regression analysis for $x_1 > 5$ m to reduce the effects of low probabilities near the release point and for $x_1 > 10$ m to check the robustness of these comparisons to this arbitrary threshold. Again, this test represents the model's ability to describe relatively long dispersal events better than ordinary tests; the adverse consequence is an inherent tendency toward lower fits due to amplified noise in the measurements. Given that WALD involves no parameter tuning, and given the uncertainty of the data in terms of small probabilities, the overall agreement between measured and modeled dispersal kernels is quite encouraging (table 2; app. C).

It can be argued that the kernels in appendix C are not real LDD experiments, because the maximum observed distance does not exceed 80 m. It is possible, however, to evaluate the "onset" of LDD by comparing measured and modeled probabilities of seed escape, a necessary condition for LDD (Nathan et al. 2002*a*). In appendix D in the online edition of the *American Naturalist*, we compare predictions from equation (6) with the measured escape probabilities for the six species reported in Nathan et al. (2002*a*) from data collected at the same tower. Appendix D suggests good agreement between measured and modeled escape probabilities, lending some confidence in WALD's ability to estimate the necessary conditions for LDD (i.e., seed escape).

Table 2: Comparison, using regression analysis, between measured and modeled dispersal kernels for all data points

Data points, model	m	b	r	RMSE
All points ($n = 459$):				
WALD (proposed)	.77	.21	.69	.066
Tilted Gaussian	.69	.28	.55	.077
Advection-diffusion	.72	.26	.56	.075
Gaussian	.69	.27	.58	.077
$x_1 > 5$ m from source ($n = 408$):				
WALD (proposed)	.76	.21	.69	.059
Tilted Gaussian	.67	.31	.64	.066
Advection-diffusion	.72	.27	.67	.062
Gaussian	.61	.36	.62	.071
$x_1 > 10$ m from source ($n = 357$):				
WALD (proposed)	.68	.31	.67	.051
Tilted Gaussian	.58	.41	.59	.058
Advection-diffusion	.62	.38	.61	.057
Gaussian	.56	.42	.64	.057

Note: The regression model $\hat{y} = m\hat{x} + b$ is used, where $\hat{x}$ and $\hat{y}$ are modeled and measured variables, respectively. Because the kernels are all bounded between 0 and 1, and to increase the sensitivity of this comparison at small probabilities, thereby avoiding the mode, we compared $\exp[-p(x_1)^{1/2}]$ rather than $p(x_1)$ (see app. C). The correlation coefficient (r) and the root mean squared error (RMSE) are also shown. We also report the same model comparisons for distances x_1 exceeding 5 and 10 m, to separate the effects of low $p(x_1)$ near the source from the low $p(x_1)$ at greater distances. We also conducted a Student t-test to evaluate the hypothesis that the regression slope is different from unity and the correlation coefficient is different from 0. We found the resulting p values for both hypotheses and both variables to be $<10^{-6}$, indicating significant correlation but also significant bias in the slope from unity at the 95% confidence level. WALD = Wald analytical long-distance dispersal model.

Comparison with Other Analytical Model Kernels

The Duke Forest experiments also permit us to evaluate other analytic kernels computed from the tilted Gaussian plume model and the advection-diffusion equation model of Okubo and Levin (1989). We revised these models to include the depth-averaged velocity $\overline{U}$ and the depth-averaged eddy diffusivity computed using the second-order closure model of Massman and Weil (1999), as described in appendix B. This revision was necessary because the Okubo-Levin models do not consider any canopy effects on the velocity statistics. Rather, they assume that the mean velocity and eddy diffusivity are described by their boundary layer values (the boundary here being the forest floor) and that the canopy is simply a passive source of seeds. Canopy turbulence significantly differs from the classical boundary layer turbulence in that the second-order statistics all vary appreciably with height (within the canopy) and the mean velocity profile has an inflection point near the canopy top (unlike power-law or logarithmic functions), as revealed by numerous canopy experiments (Katul and Albertson 1998; Finnigan 2000; Poggi et al. 2004*a*) and large-eddy simulations (Albertson et al. 2001).

In their original derivation, these two models are given, respectively, by

$$p(x_1) = \frac{V_\mathrm{t}}{\sqrt{2\pi}\,\overline{U}\sigma_3}\exp\left\{-\frac{[x_{3,\mathrm{r}} - (V_\mathrm{t}x_1/\overline{U})]^2}{2\sigma_3^2}\right\} \quad (10a)$$

and

$$p(x_1) = \frac{V_\mathrm{t}}{x_{3,\mathrm{r}}\overline{U}\Gamma(1+\beta_2)}\left[\frac{x_{3,\mathrm{r}}^2\overline{U}}{2(1+\alpha_2)\overline{A}x_1}\right]^{1+\beta_2}$$

$$\times\ x_1^{-\beta_2-1}\exp\left[\frac{x_{3,\mathrm{r}}^2\overline{U}}{2(1+\alpha_2)\overline{A}x_1}\right], \quad (10b)$$

where $\sigma_3^2 = 2\overline{A}x_1/\overline{U}$, $\overline{A} = (ku_*x_{3,\mathrm{r}})/2$ is the mean eddy diffusivity (assuming a boundary layer flow rather than a canopy turbulence flow), α_2 is the power-law exponent of the mean velocity profile in a rough-wall boundary layer, $\alpha_2 = 1/6$ to $1/7$ (Katul et al. 2002), $\beta_2 = V_\mathrm{t}/[ku_*(1+\alpha_2)]$ is the ratio of the terminal velocity to a characteristic vertical turbulent velocity, and $\Gamma(\ldots)$ is the gamma function. To revise equations (10a) and (10b), $\overline{U}$ was computed from the Massman and Weil (1999) model (see app. B), α_2 was set to 0, and $\overline{A}$ was set to $(1/x_{3,\mathrm{r}})\int_0^{x_{3,\mathrm{r}}} K_\mathrm{t}(z)\,dz$, with the turbulent diffusivity $K_\mathrm{t} = -l^2(d\overline{U}/dz)$. Here, l approaches its rough-wall boundary layer value (kz, where $k = 0.4$ is the von Kármán constant) for sparse canopies but is a constant κh for dense canopies (Poggi et al. 2004*a*).

We found that the two Okubo-Levin models agree reasonably well with the data. We also show, in appendix C, the kernel in equation (10b) with σ_3 estimated from equation (9) rather than $\sigma_3^2 = 2\overline{A}x_1/\overline{U}$. The difference between these two estimates is that in equation (10a), a distance-dependent σ originates from crosswind averaging results, while equation (9) yields σ independent of x_1 (but about a factor of 10 larger than σ_w). Hence, $p(x_1)$ computed using equation (10a) with a constant σ recovers the classic Gaussian kernel (Levin et al. 2003) and is also shown for reference in figures C1–C5. Using the same regression analysis on all the three analytical kernels and all the data ($n = 459$ points; see app. C for a graphical comparison for each release height and species), WALD slightly outperformed the other models (table 2). Recall that the regression analysis was constructed to be hypersensitive to the variability in $p(x_1)$ for $p(x_1) < 0.2$ (i.e., long-distance probability).

Meta-Analysis of Asymptotic Tails

The rate of decay of $p(x_1)$ for large x_1 determines the level of LDD estimated by the dispersal kernel. It is clear that when $\gamma \rightarrow 0$ (i.e., $V_\mathrm{t}/\overline{U} \rightarrow 0$), WALD's $p(x_1) \rightarrow x_1^{-3/2}$ for large x_1. Such an asymptotic finding was also reported by Levin et al. (2003), who used a similar approach. The $p(x_1) \rightarrow x_1^{-3/2}$ is also consistent with other Lagrangian dispersion analyses conducted on spores and pollen (Stockmarr 2002). When γ is large (e.g., heavy seeds or low winds), the power-law behavior of $p(x_1)$ is limited to an intermediate region beyond which the decay of $p(x_1)$ is faster than a power law, that is, exponential.

For large x_1, the asymptotic behavior of the tilted Gaussian model is $p(x_1) \sim x_1^{-1/2}$ and the advection-diffusion equation is $p(x_1) \sim x_1^{-1-\beta_2}$ ($\beta_2 > 0$). In Okubo and Levin (1989), the minimum $\beta_2 = 0.15$ (calculated here), and hence, the minimum exponent (or the heaviest-tail behavior) is $p(x_1) \sim x_1^{-1.16}$. In short, when $V_\mathrm{t} \rightarrow 0$, both the tilted Gaussian (i.e., $p(x_1) \sim x_1^{-1/2}$) and the solution to the advection-diffusion equation ($p(x_1) \sim x_1^{-1}$) yield tails "heavier" than those from WALD for large x_1, and as we show below, even heavier than those from almost all other empirical models constructed for the singular purpose of explaining heavy tails. Because they exhibit such a heavy tail, both the tilted Gaussian model and the solution to the advection-diffusion equation do not have finite variances as $x_1 \rightarrow \infty$. It is for this reason that the meta-analysis below is restricted to the WALD kernel.

A logical but indirect test is to assess whether other empirical models or dispersal data result in tails that decay slower than $p(x_1) \sim x_1^{-3/2}$. If so, then WALD's decay rate, $p(x_1) \sim x_1^{-3/2}$, will certainly underestimate LDD for such a species. We compared this asymptotic behavior with recent studies that used power-law-type distribution to seed trap–measured kernels, and we find that virtually all studies resulted in a power-law decay with absolute exponent larger than 1.5 (table 3). That is, the exponent of WALD is sufficient to capture the tails for the majority of species that were measured in dispersal experiments (table 3). We emphasize that in this particular comparison we test predicted versus observed agreement on the asymptotic behavior of the tail, which is different from the tests using the release experiments data, in which we compared predicted versus observed dispersal frequencies at the tail of the dispersal kernel. It should also be noted that LDD is very difficult to measure, and in most dispersal studies the measured dispersal distances did not exceed several tens of meters.

Other studies recognized that estimating the tails from seed dispersal data is complicated by the fact that many of the seeds disperse near the source, and hence the kernel often exhibits an increase with distance rather than a de-

Table 3: Reported exponent of power-law dispersal kernel for wind-dispersed seeds

Species	Power-law decay	Notes
Pinus halepensis	−1.63 to −1.94	Obtained by fitting a power-law distribution to measured kernels (Nathan et al. 2000); maximum distance ∼120 m
Acer rubrum, *Betula lenta*, *Fraxinus americana*, *Liriodendron tulipifera*, *Pinus rigida*, *Tilia americana*, *Tsuga canadensis*	−2.0 to −3.0	Obtained from fitting the 2Dt model to measured kernels (Clark et al. 1999); maximum distances not reported
Cryptantha flava, *Senerio jacobaea*, *Apocymum sibrica*, *Cirsium undulatum*, *Liatris aspera*, *Senecio jacobaea*, *Solidago rigida*, *Penstemom digitalis*, *Cassia fasciculata*, *Geranium maculatum*		Data selected from Willson (1993) for the following two criteria: the dispersal mode is at least 1 m away from the source, and good statistical power-law fits ($r^2 > .6$); maximum distance >150 m[a]
	−1.51 to −4.24	For species with special devices for wind dispersal
	−1.62 to −3.79	For species dispersed without special morphological devices or mechanisms
	−4.29 to −7.96	For species with ballistic dispersal
Calluna vulgaris	−4.7 to −10.3	Obtained from fitting power laws to measured kernels across different directions and for a wide range of wind speeds (Bullock and Clarke 2000)
Erica cinerea	−2.85 to −4.43	Obtained as for *Calluna* above

[a] An exception is *Tussilago farfara*, with a reported exponent of −0.59 and maximum dispersal distance exceeding 4,000 m reported for a pasture.

crease (see app. C for examples from the Duke forest data). This recognition leads to several approaches aimed at introducing kernels with fat tails. Two proposed phenomenological models employed different types of fat-tailed distributions. The first, a bivariate Student *t*-test (2Dt) distribution (Clark et al. 1999) is given by

$$p(x_1) \sim \frac{1}{\left[1 + (x_1^2/u)\right]^{n+1}},$$

which for large x_1 (and finite u) yields a $p(x_1) \sim x_1^{-2(n+1)}$. The use of this distribution has been advocated recently in the interpretation of turbulent fluctuations in connection with the nonextensive thermodynamics of Tsallis (Beck 2002). Also, such distributions can arise as solutions to nonlinear Fokker-Planck equations and provide a unifying framework for analyzing superdiffusion (or anomalous diffusion) in such stochastic differential equations. According to Clark et al. (1999), for wind-dispersed species of temperate deciduous forests, $n < 0.5$, suggesting that the asymptotic behavior of the 2Dt model is $p(x_1) \sim x_1^{-2}$ (for $n \rightarrow 0$) and $p(x_1) \sim x_1^{-3}$ (for $n = 0.5$). In both cases, WALD has power-law tails that decay slower than those predicted by the 2Dt model (at least for $\gamma \rightarrow 0$).

The second approach uses a superposition of two kernels, often referred to as the mixed model, which yields

$$p(x_1) \sim a' \exp(-b'x_1) + c'x_1^{-n}$$

(Bullock and Clarke 2000). The advantage of this four-parameter model is that the near-field dispersion primarily affects the exponential term, while long-distance dispersal events affect the power law. Furthermore, this mixed model assumes that these two effects are additive, not multiplicative (as derived by WALD and eqq. [10a], [10b]). It is evident that for large x_1, the above dispersal kernel ($n > 1$) will be dominated by

$$p(x_1) \sim \frac{1}{x_1^n}.$$

On the basis of data sets for two species (*Calluna vulgaris* and *Erica cinerea*) and for a wide range of wind conditions, Bullock and Clarke (2000) reported n ranging from 1.0 to 2.39. We note that n was obtained by optimizing the parameters of the mixed model to fit their measured kernels, with, apparently, $n = 1$ a constrained condition (i.e., the optimization may have forced $n = 0$). If the probably constrained $n = 1$ are removed, then $n = 1.3$ to 2.38. Given the overall uncertainty, the lower limit is sufficiently close to 1.5, suggesting some confidence in the WALD-modeled lower limit. We also note that when Bullock and Clarke fitted a power-law distribution across the entire data set (rather than using the mixed model), the reported values

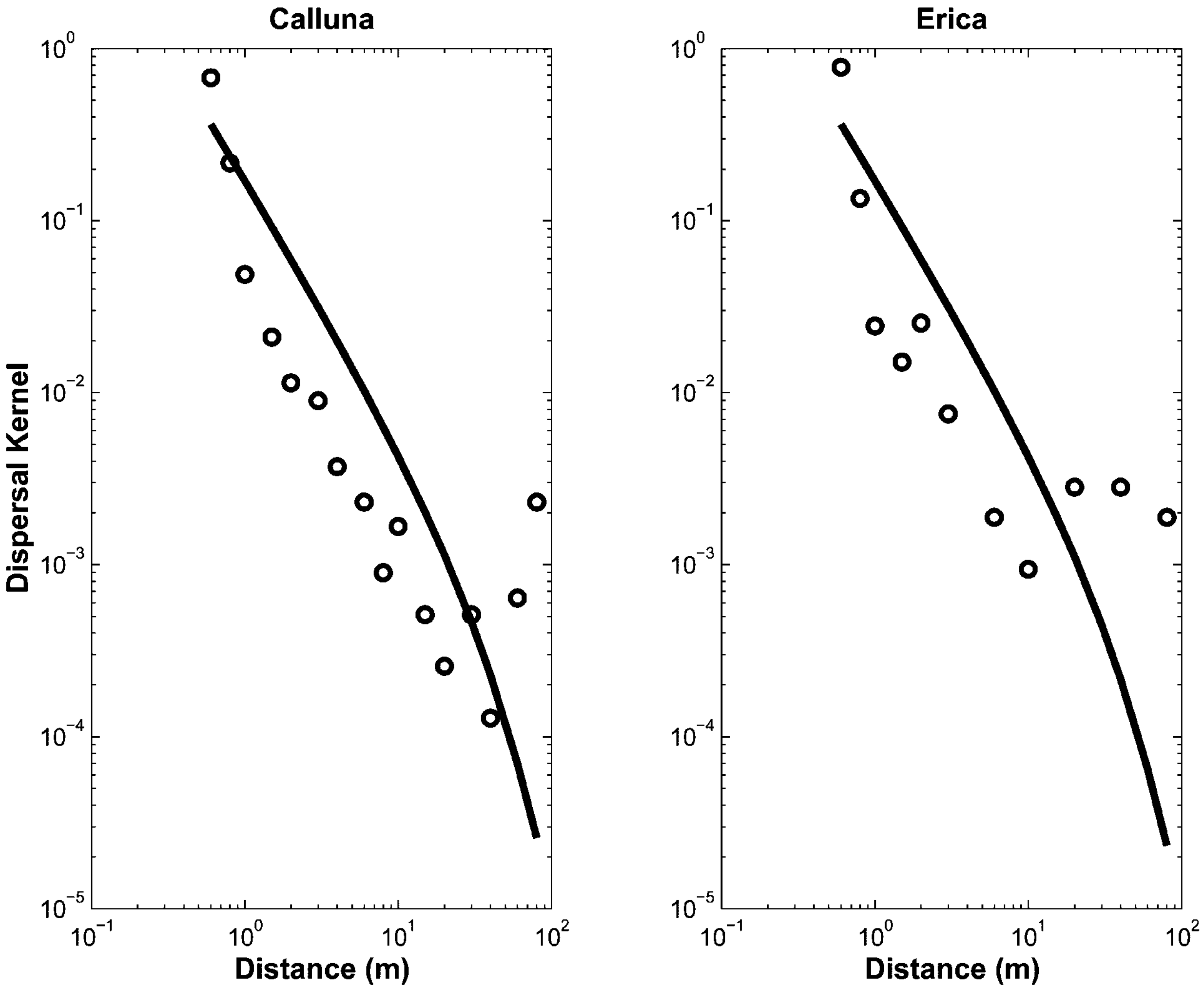

Figure 1: Determining μ', λ', and the concomitant effective mean wind for the Bullock and Clarke (2000) experiments. Measured dispersal kernels (*circles*) are derived by summing seeds from all seed traps along all directions. The solid lines (model) are for μ' and λ' shown in table 3 obtained by a moment-matching method between the Wald analytical long-distance dispersal distribution and the measurements.

of n were appreciably higher (table 3), ranging from 2.5 to 7.69.

The Inverse Problem

To contrast our proposed mechanistic model with the results from typical ballistic models, especially at the tails, we consider again the study of Bullock and Clarke (2000). These authors concluded that a wind speed of 633 m s^{-1} is needed (at the seed release height) for their simple ballistic model to transport *Calluna* seeds some 80 m distance from the source. Such a wind speed exceeds typical gusty winds by about two orders of magnitude and is about an order of magnitude larger than damaging hurricanes. We combined the seed trap measurements for all wind directions for *Calluna* and *Erica* in the Bullock and Clarke (2000) study and fitted equation (5b) to the resulting kernels in figure 1 to determine μ' and λ' (table 4) and hence determine the effective winds needed to transport these seeds. Using the computed μ' and λ', we estimated γ and σ and then estimated $\overline{U}$ and σ_w to determine the effective wind speed and vertical velocity standard deviation that best reproduce the measured kernels (see fig. 1). We found that effective wind speeds on the order of 10 m s^{-1} and concomitant σ_w on the order of 3 m s^{-1} are sufficient to reproduce the measured distributions for both *Calluna* and *Erica*. We note that just above the canopy (Raupach et al. 1996), $\overline{U}/u_* \sim 3.3$ and $\sigma_w/u_* \sim 1.1$, so that $\sigma_w/\overline{U} \sim 0.33$. For a wind speed of 10 m s^{-1}, a $\sigma_w = 3$ m s^{-1} is quite reasonable and consistent with what is established about

Table 4: Estimated parameters for WALD shown in figure 1

Variable	*Calluna*	*Erica*
V_t (m s^{-1})	1.14	1.58
$x_{3,r}$ (m)	.14	.12
μ' (m)	1.02	1.04
λ' (m)	.060	.064
$\overline{U}_{\mathrm{eff}}$ (m s^{-1})	8.4	13.7
γ	.14	.12
σ_{eff} (m$^{1/2}$)	.57	.47
$\sigma_{w,\mathrm{eff}}$ (m s^{-1})	2.7	3.0
$\Pr(z > h)$	.22	.19

Note: From the parameters μ' and λ', the effective mean wind speed $\overline{U}_{\mathrm{eff}}$ and vertical velocity variance $\sigma^2_{w,\mathrm{eff}}$ responsible for the measured tails are inferred along with the escape probability from the canopy ($\Pr(z > h)$), assuming $h = 0.41$ m. WALD = Wald analytical long-distance dispersal model.

flow statistics within the canopy sublayer. Hence, in our proposed model, both *Calluna* and *Erica* seeds can travel 80 m for typical gusts encountered at the site. We iterate here that equation (5) is derived for a single source and need not represent the near-field dispersal kernel of the Bullock-Clarke study. However, the approximate power-law decay of the data (ca. -1.5) seems to support well the results of our proposed simplified model.

We repeated a similar exercise on four other grassland species (*Cirsium dissectum*, *Hypochaeris radicata*, *Centaurea jacea*, and *Succisa pratensis*), with V_t now ranging from 0.33 to 4.3 m s^{-1} and with all seeds released above the main canopy (Soons et al. 2004). In Soons et al. (2004), individual seeds were released at different mean wind speeds (∼0.1–6.9 m s^{-1}), and hence, one-to-one direct comparisons between model calculations and measurements (as was done for the Duke Forest seed release experiments) are not possible. Only qualitative statements about the plausibility of WALD explaining the dispersal data can be made. When WALD is fitted to the kernels in figure 2 (*line*), the effective resulting mean velocity is well within the range reported by Soons et al. (2004) and close to the hourly average value (table 5). However, for such an effective velocity, the model clearly underestimates the tails for all four species. We note that fitting WALD assumes that all seeds were released during a 1-h period at a constant mean wind ($\overline{U}_{\mathrm{eff}}$) and $\sigma_{w,\mathrm{eff}}$. That is, the model clearly does not reflect the conditions of the Soons et al. (2004) experiments in which seeds were released over the entire range of $\overline{U}$ (i.e., 0.1–6.9 m s^{-1}). Not withstanding those limitations, when the model was used to compute the dispersal kernels for $\overline{U} = 6.9$ m s^{-1} (i.e., the maximum recorded mean wind speed), the measured dispersal kernel tails were well captured by the model, suggesting that those events are, in fact, associated with the high mean wind speed conditions encountered during the experiment similar to the Bullock and Clarke (2000) study. The analysis in figure 2 is an indirect confirmation that the proposed model can reproduce the asymptotic behavior of the tails for small and large V_t, even for seeds released above the canopy, without requiring unrealistic wind conditions.

Conclusions

We have developed and tested an analytical mechanistic model for wind dispersal of seeds based on the simplest possible representation of canopy turbulence. This analytical solution maintains mechanistic properties and has a shape of a Wald (inverse Gaussian) distribution. The resulting model (WALD) provides, for the first time, an analytical expression for calculating probability that seeds escape from the forest canopy top, which was shown to be a necessary condition for LDD in other studies (Nathan et al. 2002*a*).

We tested the realism and applicability of the WALD model by comparing simulated to measured data from several different data sets, including data on forest trees, heathland shrubs, and herbaceous grassland plants. For each data set, the WALD model predicted realistic dispersal patterns whether the model was used to predict seed dispersal distances from measured plant and wind parameters or the inverse approach was used, predicting wind parameters from measured dispersal distances. We conclude from our results that the WALD model adequately describes seed dispersal by wind and performs better than previously existing analytical mechanistic models. It should be noted, however, that all measured dispersal data do not include rare LDD events and that no mechanistic model, analytical or not, has been tested against measured LDD data so far.

We also showed that the asymptotic behavior of WALD for large distances from the seed source can be fat tailed. We noted that other analytical models, such as the tilted Gaussian plume (with x-dependent σ_3) and the solution to the advection-diffusion equation, exhibit tails that are "heavier" than those from WALD when $V_t \to 0$. However, those models do not admit a finite variance for (infinitely) large distances. For finite σ (i.e., turbulent flows), the WALD kernel admits a finite variance for large distances.

We note that the other models were derived assuming that the canopy is a passive source of seeds and does not alter the flow field within the canopy; hence, their resulting mixing lengths were linear, and their second moments (e.g., $\langle \overline{u'w'} \rangle$ and $\langle \overline{w'w'} \rangle$) were constant inside the canopy. The WALD derivation uses second-order closure principles to estimate how foliage density modulates these flow statistics inside the canopy and how this modulation affects the parameters of the dispersal kernel. The advantage of

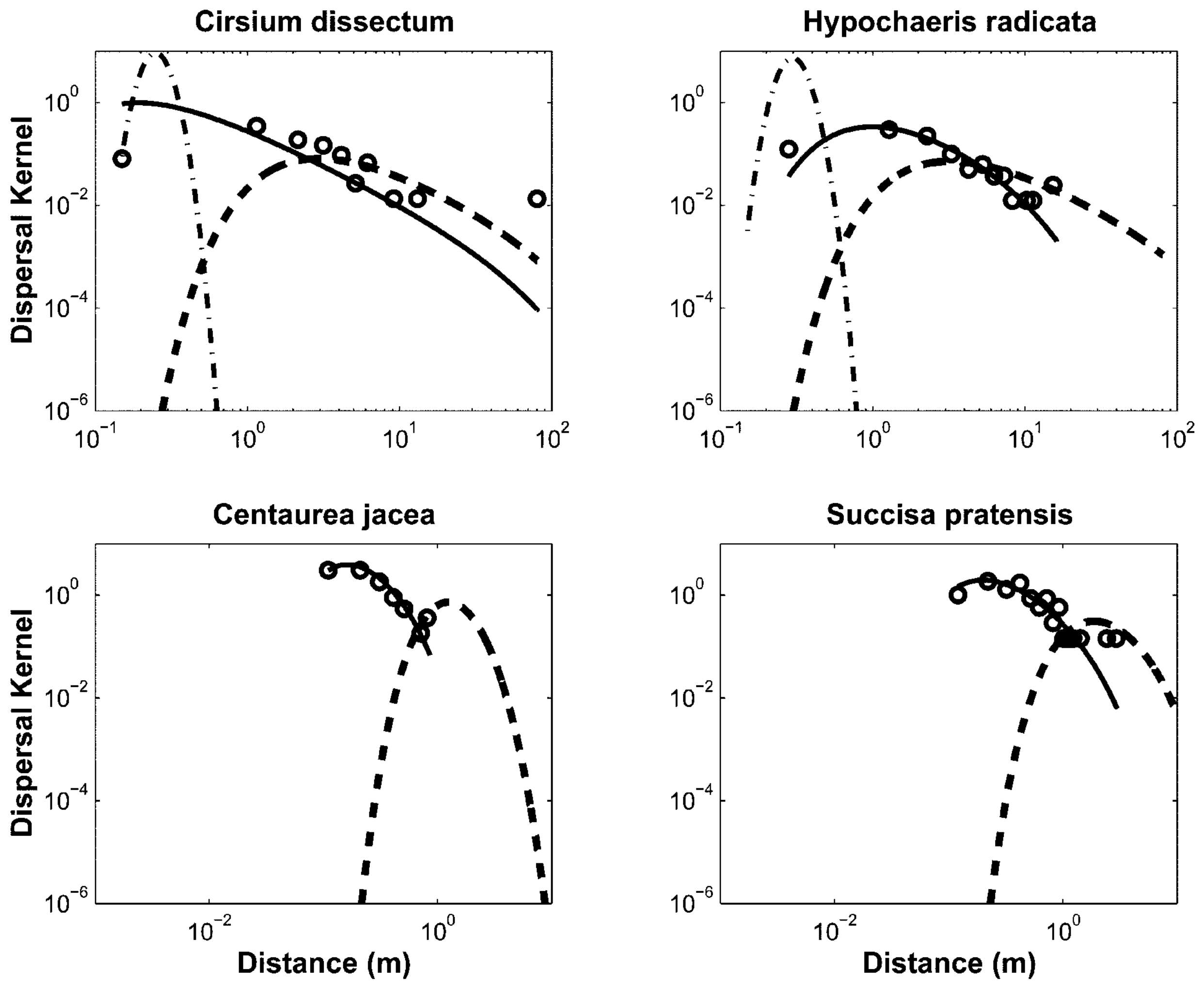

Figure 2: Measured (*circles*) and modeled (*lines*) kernels for the grassland ecosystems described in Soons et al. (2004). The solid line represents the fitted Wald analytical long-distance dispersal model obtained by first- and second-moment matching to the measured distances. The dashed lines represent the modeled kernels for $\overline{U} = 6.9$ m s^{-1}, $h = 0.5$ m, $x_{3,r}$ and V_t shown in table 5. For reference, we also show the modeled kernels for the lowest wind speeds ($\overline{U} = 0.1$ m s^{-1}; *dot-dashed lines*). For *Centaurea jacea* and *Succisa pratensis*, the resulting modeled kernels for $\overline{U} = 0.1$ m s^{-1} are ≤ 1 cm from the source and are not shown for clarity.

the WALD model over other analytical models is that it can be applied to a wide variety of wind-dispersed species and ecosystems and can be used to delve into the process of seed dispersal by wind. While this is a known advantage of mechanistic dispersal models over phenomenological models, phenomenological models have been favored for modeling seed dispersal in large-scale and complex ecological models because previous mechanistic models were computationally too slow and impractical in estimating dispersal kernels over large domains. WALD maintains all the major strengths of the mechanistic modeling approach for seed dispersal while resolving its major weakness of reliance on intensive computations. Even though the model was developed with several restrictive assumptions, we conclude that the good agreement between measured and modeled kernels is quite encouraging and suggests robustness to these simplifications.

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Table 5: Estimated parameters for WALD shown in figure 2

Variable	*Cirsium dissectum*	*Hypochaeris radicata*	*Centaurea jacea*	*Succisa pratensis*
V_{t} (m s^{-1})	.38	.33	4.36	2.12
$x_{3,\,\mathrm{r}}$ (m)	.99	1.03	1.01	.97
μ' (m)	3.68	3.18	.28	.54
λ' (m)	.58	3.31	.74	.70
$\overline{U}_{\mathrm{eff}}$ (m s^{-1})	1.41	1.02	1.19	1.18
$\overline{U}_{\mathrm{eff}}$ (m s^{-1}) at $z = 10$ m	3.9	2.9	5.3	2.6
γ	.27	.32	3.66	1.79
σ_{eff} (m$^{1/2}$)	1.30	.57	1.17	1.16
$\sigma_{w,\,\mathrm{eff}}$ (m s^{-1})	2.39	.33	1.64	1.60

Note: From the parameters μ' and λ', the effective mean wind speed $\overline{U}_{\mathrm{eff}}$ and vertical velocity variance $\sigma^2_{w,\mathrm{eff}}$ responsible for the measured tails are inferred. For neutral conditions, the mean wind speed at $z = 10$ m, the reference height, is 2.8 times the mean wind speed at the release height. The reported mean velocity range is 0.1–6.9 m s^{-1}, with an hourly mean wind speed of 3.8 m s^{-1} at the reference height (Soons et al. 2004). WALD = Wald analytical long-distance dispersal model.

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Literature Cited

Albertson, J. D., G. G. Katul, and P. Wiberg. 2001. Relative importance of local and regional controls on coupled water, carbon, and energy fluxes. Advances in Water Resources 24:1103–1118.

Andersen, M. 1991. Mechanistic models for the seed shadows of wind-dispersed seeds. American Naturalist 137:476–497.

Ayotte, K. W., J. J. Finnigan, and M. R. Raupach. 1999. A second-order closure for neutrally stratified vegetative canopy flows. Boundary-Layer Meteorology 90:189–216.

Beck, C. 2002. Generalized statistical mechanics and fully developed turbulence. Physica A 306:189–198.

Bullock, J. M., and R. T. Clarke. 2000. Long distance seed dispersal by wind: measuring and modelling the tail of the curve. Oecologia (Berlin) 124:506–521.

Cain, M. L., B. G. Milligan, and A. E. Strand. 2000. Long-distance seed dispersal in plant populations. American Journal of Botany 87:1217–1227.

Cain, M. L., R. Nathan, and S. A. Levin. 2003. Long-distance dispersal. Ecology 84:1943–1944.

Chave, J. 2000. Spatio-temporal dynamics of the tropical rain forest. Annales de Physique 25:1–184.

Chave, J., and S. Levin. 2003. Scale and scaling in ecological and economic systems. Environmental and Resource Economics 26: 527–557.

Clark, J., L. Horvath, and M. Lewis. 2001. On the estimation of spread rate for a biological population. Statistics and Probability Letters 51:225–234.

Clark, J. S. 1998. Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. American Naturalist 152: 204–224.

Clark, J. S., M. Silman, R. Kern, E. Macklin, and J. HilleRisLambers. 1999. Seed dispersal near and far: patterns across temperate and tropical forests. Ecology 80:1475–1494.

Cox, D. R., and H. D. Miller. 1965. The theory of stochastic processes. Methuen, London.

Evans, M., N. Hastings, and B. Peacock. 1993. Statistical distributions. Wiley, New York.

Finnigan, J. 2000. Turbulence in plant canopies. Annual Review of Fluid Mechanics 32:519–571.

Gardiner, C. W. 1990. Handbook of stochastic methods for physics, chemistry and the natural sciences. Springer, Berlin.

Greene, D. F., and E. A. Johnson. 1989. A model of wind dispersal of winged or plumed seeds. Ecology 70:339–347.

———. 1995. Long-distance wind dispersal of tree seeds. Canadian Journal of Botany 73:1036–1045.

———. 1996. Wind dispersal of seeds from a forest into a clearing. Ecology 77:595–609.

Higgins, S. I., and D. M. Richardson. 1999. Predicting plant migration rates in a changing world: the role of long-distance dispersal. American Naturalist 153:464–475.

Higgins, S. I., R. Nathan, and M. L. Cain. 2003*a*. Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? Ecology 84:1945–1956.

Higgins, S. I., J. S. Clark, R. Nathan, T. Hovestadt, F. Schurr, J. M. V. Fragoso, M. R. Aguiar, et al. 2003*b*. Forecasting plant migration rates: managing uncertainty for risk assessment. Journal of Ecology 91:341–347.

Horn, H. S., R. Nathan, and S. R. Kaplan. 2001. Long-distance dispersal of tree seeds by wind. Ecological Research 16:877–885.

Hsieh, C. I., G. G. Katul, J. Schieldge, J. T. Sigmon, and K. K. Knoerr. 1997. The Lagrangian stochastic model for fetch and latent heat flux estimation above uniform and nonuniform terrain. Water Resources Research 33:427–438.

Hsieh, C. I., G. Katul, and T. Chi. 2000. An approximate analytical model for footprint estimation of scaler fluxes in thermally stratified atmospheric flows. Advances in Water Resources 23:765–772.

Katul, G. G., and J. D. Albertson. 1998. An investigation of higher-order closure models for a forested canopy. Boundary-Layer Meteorology 89:47–74.

Katul, G. G., and W. H. Chang. 1999. Principal length scales in second-order closure models for canopy turbulence. Journal of Applied Meteorology 38:1631–1643.

Katul, G. G., R. Leuning, J. Kim, O. T. Denmead, A. Miyata, and Y. Harazono. 2001. Estimating CO_2 source/sink distributions within a rice canopy using higher-order closure model. Boundary-Layer Meteorology 98:103–125.

Katul, G., P. Wiberg, J. Albertson, and G. Hornberger. 2002. A mixing layer theory for flow resistance in shallow streams. Water Resources Research 38:1250.

Kot, M., M. A. Lewis, and P. van den Driessche. 1996. Dispersal data and the spread of invading organisms. Ecology 77:2027–2042.

Levin, S. A., B. Grenfell, A. Hastings, and A. S. Perelson. 1997. Mathematical and computational challenges in population biology and ecosystems science. Science 275:334–343.

Levin, S. A., H. C. Muller-Landau, R. Nathan, and J. Chave. 2003. The ecology and evolution of seed dispersal: a theoretical perspective. Annual Review of Ecology Evolution and Systematics 34: 575–604.

Masoliver, J., and J. M. Porrà. 1995. Exact solution to the mean exit time problem for free inertial processes driven by Gaussian white noise. Physical Review Letters 75:189–192.

Massman, W. J., and J. C. Weil. 1999. An analytical one-dimensional second-order closure model of turbulence statistics and the Lagrangian time scale within and above plant canopies of arbitrary structure. Boundary-Layer Meteorology 91:81–107.

Nathan, R. 2005. Long-distance dispersal research: building a network of yellow brick roads. Diversity and Distributions 11:125–130.

Nathan, R., and H. C. Muller-Landau. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in Ecology & Evolution 15:278–285.

Nathan, R., U. N. Safriel, I. Noy-Meir, and G. Schiller. 2000. Spatiotemporal variation in seed dispersal and recruitment near and far from *Pinus halepensis* trees. Ecology 81:2156–2169.

Nathan, R., U. N. Safriel, and I. Noy-Meir. 2001. Field validation and sensitivity analysis of a mechanistic model for tree seed dispersal by wind. Ecology 82:374–388.

Nathan, R., G. G. Katul, H. S. Horn, S. M. Thomas, R. Oren, R. Avissar, S. W. Pacala, et al. 2002*a*. Mechanisms of long-distance dispersal of seeds by wind. Nature 418:409–413.

Nathan, R., H. S. Horn, J. Chave, and S. Levin. 2002*b*. Mechanistic models for tree seed dispersal by wind in dense forests and open landscapes: seed dispersal and frugivory: ecology, evolution and conservation. CABI, Wallingford.

Nathan, R., G. Perry, J. T. Cronin, A. E. Strand, and M. L. Cain. 2003. Methods for estimating long-distance dispersal. Oikos 103: 261–273.

Okubo, A., and S. A. Levin. 1989. A theoretical framework for data analysis of wind dispersal of seeds and pollen. Ecology 70:329–338.

Poggi, D., A. Porporato, L. Ridolfi, J. Albertson, and G. Katul. 2004*a*. The effect of vegetation density on canopy sublayer turbulence. Boundary-Layer Meteorology 111:565–587.

Poggi, D., G. G. Katul, and J. D. Albertson. 2004*b*. Momentum transfer and turbulent kinetic energy budgets within a dense model canopy. Boundary-Layer Meteorology 111:589–614.

———. 2005. Scalar dispersion within a model canopy: measurements and three-dimensional Lagrangian models. Advances in Water Resources (forthcoming).

Pope, S. B. 2000. Turbulent flows. Cambridge University Press, Cambridge.

Portnoy, S., and M. F. Willson. 1993. Seed dispersal curves: behavior of the tail of the distribution. Evolutionary Ecology 7:25–44.

Raupach, M. R. 1989*a*. Applying Lagrangian fluid-mechanics to infer scalar source distributions from concentration profiles in plant canopies. Agricultural and Forest Meteorology 47:85–108.

———. 1989*b*. A practical Lagrangian method for relating scalar concentrations to source distributions in vegetation canopies. Quarterly Journal of the Royal Meteorological Society 115:609–632.

Raupach, M. R., and R. H. Shaw. 1982. Averaging procedures for flow within vegetation canopies. Boundary-Layer Meteorology 22: 79–90.

Raupach, M. R., J. J. Finnigan, and Y. Brunet. 1996. Coherent eddies and turbulence in vegetation canopies: the mixing-layer analogy. Boundary-Layer Meteorology 78:351–382.

Schrödinger, E. 1915. Zür theorie der Fall-und Steigversuche an Teilchenn mit Brownsche Bewegung. Physikalische Zeitschrift 16:289–295.

Soons, M. B., and G. W. Heil. 2002. Reduced colonization capacity in fragmented populations of wind-dispersed grassland forbs. Journal of Ecology 90:1033–1043.

Soons, M. B., G. W. Heil, R. Nathan, and G. G. Katul. 2004. Determinants of long-distance seed dispersal by wind in grasslands. Ecology 85:3056–3068.

Stockmarr, A. 2002. The distribution of particles in the plane dispersed by a simple 3-dimensional diffusion process. Journal of Mathematical Biology 45:461–469.

Stoyan, D., and S. Wagner. 2001. Estimating the fruit dispersion of anemochorous forest trees. Ecological Modelling 145:35–47.

Tackenberg, O. 2003. Modeling long-distance dispersal of plant diaspores by wind. Ecological Monographs 73:173–189.

Tackenberg, O., P. Poschlod, and S. Kahmen. 2003. Dandelion seed dispersal: the horizontal wind speed does not matter for long-distance dispersal—it is updraft! Plant Biology 5:451–454.

Tanaka, H., M. Shibata, and T. Nakashizuka. 1998. A mechanistic approach for evaluating the role of wind dispersal in tree population dynamics. Journal of Sustainable Forestry 6:155–174.

Thomson, D. J. 1987. Criteria for the selection of stochastic-models of particle trajectories in turbulent flows. Journal of Fluid Mechanics 180:529–556.

Turchin, P. 1998. Quantitative analysis of movement. Sinauer, Sunderland, MA.

van Kampen, N. G. 1992. Stochastic processes in physics and chemistry. North Holland, Amsterdam.

Wald, A. 1947. Sequential analysis. Wiley, New York.

Wang, B. C., and T. B. Smith. 2002. Closing the seed dispersal loop. Trends in Ecology & Evolution 17:379–385.

Wenny, D. G. 2001. Advantages of seed dispersal: a re-evaluation of directed dispersal. Evolutionary Ecology Research 3:51–74.

Willson, M. 1993. Dispersal mode, seed shadows, and colonization patterns. Vegetatio 108:261–280.

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