Mechanistic Analytical Models for Long Distance Seed Dispersal by Wind

Short Title: Analytical Models for 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 2-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 fatter 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 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.

Introduction

The past decade witnessed a proliferation of studies that address the importance of seed dispersal in ecological processes (Cain et al. 2000; Cain et al. 2003; Clark et al. 1999; Levin et al. 2003; Nathan et al. 2002a; Nathan and Muller-Landau 2000; Wang and Smith 2002; Wenny 2001). A major emphasis in these studies is modeling seed dispersal using both the phenomenological approach (Bullock and Clarke 2000; Clark et al. 2001; Clark 1998; Clark et al. 1999; Higgins et al. 2003b; Nathan et al. 2000; Stoyan and Wagner 2001; Tanaka et al. 1998) and, especially for wind dispersal, the mechanistic approach (Greene and Johnson 1989; Greene and Johnson 1995; Greene and Johnson 1996; Horn et al. 2001; Nathan et al. 2002a; Nathan et al. 2002b; Nathan et al. 2001; Okubo and Levin 1989; Soons and Heil 2002; Soons et al. 2004; Tackenberg 2003; Tackenberg et al. 2003). 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 (Chave 2000; Chave and Levin 2003; Clark 1998; Higgins and Richardson 1999; Levin et al. 1997; Levin et al. 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. 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, 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; Greene and Johnson 1995; Greene and Johnson 1996; Nathan et al. 2002a; Nathan et al. 2001; Soons and

Heil 2002). These models capture the mode of the dispersal curve well but fail to reproduce its tail, i.e., long-distance dispersal (LDD) events (Bullock and Clarke 2000; Nathan et al. 2002a). 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. 2002b).

To partially circumvent this problem, a *Coupled Eulerian-Lagrangian Closure* (CELC) model (Hsieh et al. 2000; Hsieh et al. 1997; Katul and Albertson 1998; Katul and Chang 1999; Nathan et al. 2002b) has recently been applied for seed dispersal by wind (Nathan et al. 2002b; 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 USA (Nathan et al. 2002b), 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 2Dt (Clark et al. 1999) and mixed Weibull (Higgins et al. 2003a; Higgins and Richardson 1999) provide good description 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 model – seed terminal velocity, seed release height, and wind conditions – are easily interpretable and measurable, such an analytical mechanistic model provides the means for estimating LDD essentially for any wind-dispersed species.

In this paper, we introduce a new analytic expression derived from a simplified 3-dimensional stochastic dispersion model that retains the essential physics in CELC. As we shall 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 cross-wind 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, 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, model's capacity to predict LDD should be

tested against "real" LDD data. Yet, quantifying LDD remains 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 meters from the source. This procedure examines the model capacity (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 develop an analytical expression for calculating the probability of a seed to escape the forest canopy, and tested this model against observed seed uplifting probabilities reported in Nathan et al. (2002b). This test is directly related to LDD since seed uplifting by vertical updrafts is crucial (or necessary condition) for LDD.

Next, we analyze the tail properties of the predicted dispersal kernel and verified whether these emerging properties accord 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

Thompson's (1987) 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 (Pope 2000; Thomson

1987). 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)

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

where $\vec{x}$ and $\vec{u}$ 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 zero, 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 $\vec{x}$ 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

$p(\vec{x},\vec{u},t)$ and must remain so for all later times. This condition requires that $p(\vec{x},\vec{u},t)$ 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 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

Additional criteria to the well-mixed condition are needed to resolve the non-uniqueness 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 account 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

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

where $b = \sqrt{C_o <\overline{\varepsilon}>}$. Moreover, with 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

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

Here, $<\overline{u_3'u_3'}> (\equiv \sigma_w^2)$ is the variance of the vertical velocity component (the coordinates are

defined so that $<\overline{u_2}> = 0$ 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 $<\overline{\varepsilon}>$ is the mean turbulent kinetic energy dissipation rate.

Note that in the previous equations $<\cdot>$ is spatial averaging (Finnigan 2000; Raupach and

Shaw 1982), and over-bar is time averaging. The vertical distribution of the flow statistics

$<\overline{u_1}>$, $<\overline{u_3'u_3'}>$, and $<\overline{\varepsilon}>$ 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

(Ayotte et al. 1999; Katul and Albertson 1998; Katul and Chang 1999; Katul et al. 2001;

Massman and Weil 1999).

It is clear that even the one-dimensional Thomson's (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:

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

$$\frac{dx_3}{dt} = (-V_t + u_3) \qquad (2)$$

$$\frac{dx_1}{dt} = <\overline{u_1}> \qquad (3)$$

with $T_L = \dfrac{2}{C_o} \dfrac{\langle \overline{u_3' u_3'} \rangle}{<\overline{\varepsilon}>}$.

Equation (2) also assumes that the seed terminal velocity is achieved instantly following a 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 non-monotonic inside canopies) and a drift term that also varies with $<\overline{u_3' u_3'}>$ 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 overbar to indicate both time and horizontal averages, and set $<\overline{u_1}> = \overline{U}$ and $<\overline{\varepsilon}> = \varepsilon$. We emphasize again that canopy turbulence is highly inhomogeneous and with large 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) in equations (1) and (2) to eliminate time, one obtains the second order process

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

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

where, $\alpha = \dfrac{C_o \varepsilon}{2\overline{U}\sigma_w{}^2}$, $\beta = \sqrt{\dfrac{C_o \varepsilon}{\overline{U}}}$, $\gamma = V_t / \overline{U}$, $\delta = 1/\overline{U}$. The corresponding Fokker-Plank

equation can also be obtained and is reported in the Appendix. If the seed settling time is

assumed much longer than the vertical velocity integral time scale (see Appendix 1), the

previous problem can be further simplified and the corresponding Fokker-Plank 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 $\sigma = \delta \dfrac{\beta}{\alpha}$.

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 $x_{3,r}$. 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 (see Appendix 1):

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

Upon defining $\mu' = \dfrac{x_{3,r}\,\overline{U}}{V_t}$ (or $\dfrac{x_{3,r}}{\gamma}$) and $\lambda' = \left(\dfrac{x_{3,r}}{\sigma}\right)^2$, 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' only depend on the wind velocity statistics (σ and $\overline{U}$), seed terminal velocity (V_t), and seed release height ($x_{3,r}$). We call this analytical solution the *Wald Analytical Long-distance Dispersal* (WALD) model, as it exhibits heavy tails for LDD, as we shall show later. It has the following statistical properties (Evans et al. 1993): Mean = μ' ; Variance = μ'^3 / λ' ;

Mode = $\mu'\left[\left(1+\dfrac{9\mu'^2}{4\lambda'^2}\right)^{1/2} - \dfrac{3}{2}\dfrac{\mu'}{\lambda'}\right]$; Skewness Coefficient = $3\left(\dfrac{\mu'}{\lambda'}\right)^{1/2}$; and Kurtosis

Coefficient = $3 + 15\dfrac{\mu'}{\lambda'}$. Here, μ' (>0) and λ' (>0) are often called the location and scale parameters. 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 $\gamma \rightarrow 0$ 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 cut-off (exponential decay) at a distance which reduces with increasing γ.

From the Fokker-Plank equation in (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)

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

Noting that a necessary condition for LDD is seed escape from the canopy (Nathan et al. 2002b), 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), 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 is this kernel to such restrictive assumptions is investigated next, after discussing the 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 1, it can be shown that

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

Unfortunately, ε is rarely measured and is difficult to model inside canopies thereby making the usage 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 constant proportional to h through a coefficient κ. For this simplification, the term involving ε can be simplified to (Poggi et al. 2004a; Poggi et al. 2004b)

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

Replacing 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 semi-empirical parameter here because all the model assumptions (including vertically homogeneous and low intensity flows, instant attainment of terminal velocity, zero inertia of seed, 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 $\dfrac{2\sigma_w^{~2}}{C_o \varepsilon} = T_L$, which is also approximately $0.3 \dfrac{h}{u_*}$ (Raupach 1989a; Raupach 1989b;

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. 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 Appendix 2 for formulation).

Model Testing

Evaluating Model Predictions by Seed Release Experiments

While the setup is described elsewhere (Nathan and Katul 2004; Nathan et al. 2002b), the salient features are reviewed. Seed release experiments were carried out in an 80 to 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, *Q. michauxii*, *Q. velutina*, *Carya tomentosa*, *C. ovata*, *Liriodendron tulipifera*, and *Liquidambar styraciflua* as canopy dominant and *Pinus taeda* as a minor component, and mostly *Ostrya virginiana*, *Carpinus caroliniana*, and *Cornus florida* in the under-story. 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 m s^{-1} to 1.89 m s^{-1} (Table 1). Seeds were manually released from a 45-m high walkup tower at 3 levels: $x_{3,r}$ =30 m, 21 m, and 12 m, above the forest floor. Each seed release lasted for about 30 minutes 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 $<\overline{u_1}>$, $<\overline{u_1'u_1'}>$, $<\overline{u_2'u_2'}>$, $<\overline{u_3'u_3'}>$, $<\overline{u_1'u_3'}>$ for each 30 minute release time. The $u_* = \left(<\overline{u_1'u_3'}>^2 + <\overline{u_2'u_3'}>^2 \right)^{1/4}$ varied roughly from 0.1 m s^{-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., 5 experiments and 3 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 height, all seeds were color-sprayed (in different colors) prior to the release. Measurements of V_t before and after spraying revealed that spraying impacted V_t appreciably (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 $<\overline{u_1}>$, $<\overline{u_1'u_1'}>$, $<\overline{u_2'u_2'}>$, $<\overline{u_3'u_3'}>$, $<\overline{u_1'u_3'}>$ within the canopy (see Appendix 2)

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, $\gamma(=V_t/\overline{U})$ 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 5 seed release experiments.

The measured 51 kernels (shown in Appendix 3) 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 3, 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 Appendix 3) resulted in a correlation coefficient (r) of 0.69. The regression analysis was conduced on $\exp(-\sqrt{p(x_1)})$ 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 $x_1 > 5m$ to reduce their effects of low probabilities near the release point and for and $x_1 > 10m$ to check the robustness of these comparisons to this arbitrary threshold. Again, this test better represents the model ability to describe relatively long dispersal events than ordinary tests; the adverse consequence is an inherent tendency to 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, and Appendix 3).

It can be argued that the kernels in Appendix 3 are not real LDD experiments as the maximum observed distance does not exceed 80 m. It is possible, however, to evaluate the "onset" of LDD by comparing measured and modeled seed escape probabilities, a necessary

condition for LDD (Nathan et al., 2002b). We compared in Appendix 4 predictions from equation (6) to the measured escape probabilities for the six species reported in Nathan et al. (2002b) (and collected at the same tower). Appendix 4 suggests good agreement between measured and modeled escape probabilities lending some confidence in WALD's ability to the necessary conditions for LDD (i.e. seed escape).

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 in Okubo and Levin (1989). These models were revised here 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 2. 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 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 (Finnigan 2000; Katul and Albertson 1998; Poggi et al. 2004b) and Large Eddy Simulations (Albertson et al., 2001).

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

$$p(x_1) = \frac{V_t}{\sqrt{2\pi}\,\overline{U}\sigma_3} \exp\left(-\frac{\left(x_{3,r} - \left(\frac{V_t x_1}{\overline{U}}\right)\right)^2}{2\sigma_3{}^2}\right) \tag{10a}$$

$$p(x_1) = \frac{V_t}{x_{3,r}\,\overline{U}\,\Gamma(1+\beta_2)} \left\{ \frac{x_{3,r}{}^2\,\overline{U}}{2(1+\alpha_2)\overline{A}x_1} \right\}^{1+\beta_2} x_1{}^{-\beta_2-1} \exp\left(\frac{x_{3,r}{}^2\,\overline{U}}{2(1+\alpha_2)\overline{A}x_1} \right) \qquad (10b)$$

where $\sigma_3{}^2 = 2\overline{A}x_1/\overline{U}$, $\overline{A} = (k\,u_*\,x_{3,r})/2$ 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), and

$\beta_2 = \dfrac{V_t}{k\,u_*(1+\alpha_2)}$ is the ratio of the terminal velocity to a characteristic vertical turbulent

velocity, and $\Gamma(.)$ is the gamma function. To revise equations (10a) and (10b), $\overline{U}$ was

computed from the Massman and Weil (1999) model (see Appendix 2), $\alpha_2 = 0$, and

$\overline{A} = \dfrac{1}{x_{3,r}} \displaystyle\int_0^{x_{3,r}} K_t(z)dz$ with the turbulent diffusivity $K_t = -l^2 \dfrac{d\overline{U}}{dz}$. Here, l approaches its rough-

wall boundary layer value ($= k\,z$, where $k = 0.4$ is the von Kármán constant) for sparse

canopies but is a constant $= \kappa\,h$ for dense canopies (Poggi et al. 2004b).

We found that the two Okubo-Levin models agree reasonably well with the data. We

also show in Appendix 3 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 originating from crosswind averaging results, while equation

(9) yields σ independent of x_1 (but is about 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. Using the same regression analysis on all the three

analytical kernels and all the data (n=459 points; see Appendix 3 for a graphical comparison

for each release height and species), WALD slightly outperformed the other models (Table 2).

Recall that the regression analysis is 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., $V_t / \overline{U} \rightarrow 0$), WALD's $p(x_1) \rightarrow x_1^{-3/2}$ for large x_1. Such asymptotic finding was also reported in Levin et al., (2003), using 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, i.e. 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 $V_t \rightarrow 0$, both the titled 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 WALD for large x_1, and as we show below, even heavier tails than 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 the 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 much of the seeds disperse near the source, which often exhibits an increase with distance rather than decrease (see Appendix 3 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:

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

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 non-extensive thermodynamics of Tsallis (Beck 2002). Also, such distributions can arise as solutions to non-linear Fokker-Plank equations and provide a unifying framework for

analyzing super-diffusion (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 (Bullock and Clarke 2000):

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

The advantage of this 4-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 equations 10a,b). It is evident that for large x_1, the above dispersal kernel (n>1) will be dominated by

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

Based on 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 likely constrained n=1 are removed, n=1.3-2.38. 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 the mixed model), the reported values of n were appreciably higher (Table 3) ranging from 2.5-7.69.

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 2 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 1a 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 Figure 1a). 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 flow statistics within the canopy sublayer. Hence, based on our proposed approach, 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 (≈ -1.5), seem to well support 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 ($\approx$ 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 1b (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 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 hour period at a constant mean wind (=$\overline{U}_{eff}$) and $\sigma_{w\,eff}$. 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. 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-Clarke study.

The analysis in Figure 1b 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 utmost simplified 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 the escape probability of seeds from the forest canopy top, which were shown to be necessary conditions for LDD in other studies (Nathan et al. 2002b).

We tested the realism and applicability of the WALD model by comparing simulated data 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 whether 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 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 WALD when $V_t \rightarrow 0$. 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 the canopy is a passive source of seeds and does not alter the flow field within the canopy; hence, their resulting mixing length was linear, and their second moment (e. g. $<\overline{u'w'}>$ and $<\overline{w'w'}>$) 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 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.

APPENDIX-1:

As earlier stated, upon substituting equation (3) in equations (1) and (2) to eliminate time, the corresponding Fokker-Plank equation becomes

$$\frac{\partial p}{\partial x_1} = -\gamma \frac{\partial p}{\partial u_3} + \frac{1}{2}\sigma^2 \frac{\partial p}{\partial x_3}$$

(A1)

with "initial" conditions $p(x_3; x_1 = 0) = \delta(x_3 - x_{3,r})$ and boundary condition $p(x_3 = 0; x_1) = 0$.

The following second-order stochastic process can be obtained as

$$du_3 = -\alpha u_3 dx_1 + \beta d\Omega_l$$

(A2)

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

where, $\alpha = \dfrac{C_o \varepsilon}{2\overline{U}\sigma_w^2}$, $\beta = \sqrt{\dfrac{C_o \varepsilon}{\overline{U}}}$, $\gamma = V_t / \overline{U}$, $\delta = 1/\overline{U}$, and $d\Omega_l$ is a delta-correlated zero-mean Gaussian process. The evolution of the probability density function, $p(x_3, u_3; x_1)$ is given by the Fokker-Plank equation (van Kampen 1992, p. 242)

$$\frac{\partial p}{\partial x_1} = -\gamma \frac{\partial p}{\partial x_3} + \delta u_3 \frac{\partial p}{\partial x_3} + \alpha \frac{\partial p}{\partial u_3} + \alpha p + \frac{1}{2}\beta^2 \frac{\partial^2 p}{\partial u_3^2}$$

(A3)

In the context of seed dispersal, the release is assumed to take place at $x_{3,r}$ with zero vertical velocity and the "initial" condition is $p(x_3, u_3; x_1 = 0) = \delta(x_3 - x_{3,r})\delta(u_3)$ as before. Assuming that the seed movement stops once it reaches the ground surface (i.e., no re-suspension), the relevant boundary condition at $x_3 = 0$ is an absorbing boundary with $p(x_3 = 0, u_3; x_1) = 0$. The solution of the above second-order problem and especially the solution of the distribution of the position x_1 of seeds reaching the ground is quite complicated (Masoliver and Porra 1995).

However, the problem can be considerably simplified by noticing that the stochastic equation for the velocity u_3 is the well-known Ornstein-Uhlenbeck process, whose long-term

solution is a Gaussian probability density function with zero mean, variance $\frac{\beta}{\alpha}$, and

autocorrelation function equal to $e^{-\alpha\tau}$. Therefore with the assumption

that α may be considered to be large enough so that the effects of the correlation of u_3 are

negligible relative to the setting time in the evolution of x_3, the second-order process can be

reduced to the following first-order one,

$$dx_3 = -\gamma\, dx_1 + \sigma\, d\Omega_l,\tag{A4}$$

where $\sigma = \delta\dfrac{\beta}{\alpha}$ (Gardiner 1990). The corresponding Fokker-Plank equation is

$$\frac{\partial p}{\partial x_1} = -\gamma\frac{\partial p}{\partial u_3} + \frac{1}{2}\sigma^2\frac{\partial p}{\partial x_3}\tag{A1}$$

with "initial" conditions $p(x_3; x_1 = 0) = \delta(x_3 - x_{3,r})$ and boundary condition $p(x_3 = 0; x_1) = 0$.

The above equation represents a classic diffusion process (Brownian motion) with constant

downward drift that can be solved analytically using standard stochastic calculus procedures

(Cox and Miller 1965).

Note that upon replacing the estimates of α, β, and δ in $\sigma = \delta\dfrac{\beta}{\alpha}$, we obtain

$$\sigma = \frac{2\,\sigma_w^{\,2}\,\overline{U}^{-1/2}}{\sqrt{C_o\varepsilon}}.$$

APPENDIX-2:

To estimate the WALD parameters, the vertically averaged mean velocity and standard deviation of the vertical velocity are needed from wind speed measurements above or at the top of the canopy. Here, we show how the profiles of the velocity statistics $<\bar{u}>$, $<\overline{u'w'}>$, σ_u, σ_v, and σ_w can be computed. Vertically averaging σ_w and $<\bar{u}>$ yields the desired flow variables for the WALD parameters. Given the mean velocity at the canopy top ($<\bar{u}(h)>$), the Massman and Weil (1999) model (MW99) predicts the velocity statistics at any depth z inside the canopy to be

$$\frac{<\bar{u}(z)>}{<\bar{u}(h)>} = e^{-n\gamma(z)}$$

$$\frac{<\overline{w'u'}(z)>}{u_*^2} = e^{-2n(\gamma(z))}$$

$$\frac{\sigma_u}{u_*} = A_u \, \upsilon_1 \frac{\sigma_e(z)}{u_*}$$

$$\frac{\sigma_v}{u_*} = A_v \, \upsilon_1 \frac{\sigma_e(z)}{u_*}$$

$$\frac{\sigma_w}{u_*} = A_w \, \upsilon_1 \frac{\sigma_e(z)}{u_*}$$

where:

$$\frac{\sigma_e}{u_*} = \left[\upsilon_3 e^{-\Lambda\varsigma(h)\gamma(z)} + B_1\left(e^{-3n\gamma(z)} - e^{-\Lambda\varsigma(h)\gamma(z)}\right)\right]^{1/3},$$

$$\gamma(z) = 1 - \frac{\varsigma(z)}{\varsigma(h)},$$

$$\varsigma(z) = \int_0^z C_d a(z)dz \text{, and the constants are given by } n = \frac{1}{2}\left(\frac{u_*}{<\bar{u}(h)>}\right)^{-2} \varsigma(h),$$

$$B_1 = \frac{-9\dfrac{u_*}{<\bar{u}(h)>}}{2\alpha\upsilon_1\left[\dfrac{9}{4} - \Lambda^2 \dfrac{u_*^4}{(<\bar{u}(h)>)^4}\right]} , \quad \Lambda^2 = \frac{3\upsilon_1}{\alpha^2} , \quad \upsilon_1 = (A_u^2 + A_v^2 + A_w^2)^{-1/2} ,$$

$$\upsilon_3 = (A_u^2 + A_v^2 + A_w^2)^{3/2} \text{, and } \upsilon_2 = \frac{\upsilon_3}{6} - \frac{A_w^2}{2\upsilon_1} .$$

The MW99 computes the zero displacement height from the centroid of the momentum sink using:

$$\frac{d}{h} = 1 - \int_0^1 \left(\frac{<\overline{u'w'}(r)>}{u_*^2}\right) d(r) \text{, where } r = z/h .$$

Above the canopy, the flow is assumed to attain its atmospheric surface layer state with

$$\frac{\overline{u'w'}}{u_*^2} = -1 , \quad \frac{\bar{u}}{u_*} = \frac{1}{k_v}\log\left[\frac{z-d}{z_o}\right] \text{, and } \frac{\sigma_u}{u_*} = A_u \text{ , } \frac{\sigma_v}{u_*} = A_v \text{ , } \frac{\sigma_w}{u_*} = A_w \text{, where}$$

$$\frac{z_o}{h} = \left(1 - \frac{d}{h}\right)e^{-k_v\frac{\bar{u}_h}{u_*}} .$$

For this study, we used the long-term sonic anemometer data above the canopy during the dispersal seasons and determined that $A_u = 2.1$, $A_v = 1.8$, and $A_w = 1.1$.

In WALD, vertically averaged mean velocity and vertical velocity standard deviation are computed via $\dfrac{1}{h}\int_0^h \overline{U}(z)\,dz$ and $\dfrac{1}{h}\int_0^h \sigma_w(z)dz$, respectively.

APPENDIX – 3:

In this appendix, we show graphically all 51 measured dispersal kernels from the Duke Forest seed release experiments along with the predicted kernels by the three models (Figure 2). The experimental conditions along with the computed vertically averaged mean wind velocity and σ_w for each kernel is summarized in Table 1 and the regression analysis used to assess the model performance is shown in Table 2. The panels in Figure 2 are organized by species type and release height. In these experiments, all the inputs affecting WALD parameters are varied - release height varied by a factor of 2.5, wind speeds varied by a factor of 9, LAI varied by a factor of 4, and terminal velocity varied by a factor of 2. It is no trivial matter that a simple analytical model with no tunable parameters like WALD captures the variations of all these factors.

APPENDIX – 4:

Uplifting probabilities, mean seed release height, and seed terminal velocities for *Pinus taeda*, *Liriodendron tulipifera, Liquidambar styraciflua, Carpinus caroliniana*, *Fraxinus americana* were reported in Nathan et al. (2002b) at the same tower location used in the manual seed release experiments. Using the measured time series of u_* for the period reported in Nathan et al. (2002b), we estimate a time-averaged u_*=0.3 m s^{-1} (see Figure 3). We then employed the model in Appendix 2 to estimated σ and $\overline{U}$ needed for equation (6). For each of the 5 species, we estimated the probability of uplifting from equation (6) based the reported mean seed release height and terminal velocities in Nathan et al. (2002). The overall agreements between measured and modeled uplifted probabilities are shown in Figure 3. Using linear regression analysis ($\hat{y} = m\,\hat{x} + b$; where $\hat{x}$ and $\hat{y}$ are modeled and measured variables) for the 5 points in Figure 3, we found a coefficient of determination $r^2 = 0.99$, $m = 0.88$, $b = 0.00035$, and a standard error of estimate SEE=0.002. Given that WALD has no "tunable" parameters, the agreement between measured and modeled seed uplifting probabilities is encouraging and suggests that WALD can model necessary conditions for the occurrence of LDD.

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Table 1: Summary of seed release experiments including the species (acne=*Acer negundo*, acru=*Acer rubru*m, acsa=*Acer saccharinum*, acsr= *Acer saccharum*, caca = *Carpinus caroliniana*, fram=*Fraxinus americana*, frpe=*Fraxinus pennsylvanica*, litu=*Liriodendron tulipifera*). The measured release height ($x_{3,r}$), terminal velocity (V_t), the leaf area index (LAI), and friction velocity above the canopy (u_*) are also shown. The modeled depth-averaged mean velocity ($\overline{U}$) and vertical velocity standard deviations (σ_w) within the canopy are also shown. The values of V_t here are higher than earlier published values (Nathan et al. 2002b) because seeds of different species were color-sprayed for enhancing detection and recovery.

Date of Release	Species	V_t^* (m s^{-1})	LAI (m^2 m^{-2})	$x_{3,r}$ (m)	u_* (m s^{-1})	$\overline{U}$; σ_w (m s^{-1})
Nov. 2/00[*]	*litu,*	1.50	1.2	30	0.16	0.23; 0.09
	frpe,	1.43		21	0.16	0.23; 0.09
	acne,	1.50		12	0.16	0.23; 0.09
	caca	1.89				
Nov. 28/00	Same as	Same as	0.9	30	0.89	1.55; 0.61
	above	above		21	0.89	1.55; 0.61
				12	0.63	1.10; 0.44
May13/01	*acsa,*	1.10	4.9	30	0.60	0.56; 0.27
	acru	0.67		21	0.62	0.58; 0.28
				12	0.61	0.57; 0.27
June 25/01	*acsa,*	Same as	4.9	30	0.25	0.23; 0.11
	acru,	above		21	0.20	0.19; 0.09

	caca,			12	0.27	0.23; 0.11
	frpe					
July 20/01	*acsr*	1.74	4.9	30	0.27	0.25; 0.12
	fram	1.21		21	0.32	0.31; 0.15
	caca	Same as above		12	0.25	0.23; 0.11

[*]Terminal velocity was measured for spray-marked seeds

[**]In this particular experiment, all the seeds were simultaneously released from the source. Hence, the 30-minute 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-minute period at each level.

Table 2: Comparison between measured and modeled dispersal kernels for all data points (n) using regression analysis. The regression model $\hat{y} = m\hat{x} + b$ is used; where $\hat{x}$ and $\hat{y}$ are modeled and measured variables, respectively. Since 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 the $\exp\left(-\sqrt{p(x_1)}\right)$ rather than $p(x_1)$ (see Figure 2f). 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 m and x_1 exceeding 10 m to separate the effects of low $p(x_1)$ near the source from the low $p(x_1)$ at further 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 zero. We found that 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.

Model	m	b	r	RMSE
All points (n=459)				
WALD (proposed)	0.77	0.21	0.69	0.066
Tilted Gaussian	0.69	0.28	0.55	0.077
Advection-Diffusion	0.72	0.26	0.56	0.075
Gaussian	0.69	0.27	0.58	0.077
$x_1 > 5$ m from source (n=408)				
WALD (proposed)	0.76	0.21	0.69	0.059
Tilted Gaussian	0.67	0.31	0.64	0.066
Advection-Diffusion	0.72	0.27	0.67	0.062
Gaussian	0.61	0.36	0.62	0.071

	$x_1 > 10\ m\ from\ source\ (n=357)$			
WALD (proposed)	0.68	0.31	0.67	0.051
Tilted Gaussian	0.58	0.41	0.59	0.058
Advection-Diffusion	0.62	0.38	0.61	0.057
Gaussian	0.56	0.42	0.64	0.057

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

Species	Power-law decay
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, and 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, and	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 ($r^2>0.6$). Maximum distance >150 m.
Geranium maculatum	-1.51 to –4.24 for species with special devices for wind dispersal[1]. -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 *Calluna* above

[1]An exception is *Tussilago farfara*, with a reported exponent = –0.59 and maximum dispersal distance exceeding 4000 m reported for a pasture.

Table 4: Estimated parameters (μ' and λ') for WALD shown in Figure 1a. Using these two parameters, the effective mean wind speed $\overline{U}_{eff}$ and vertical velocity variance $\sigma^2_{w,eff}$ responsible for the measured tails are inferred along with the escape probability from the canopy (Pr(z>h)) assuming h=0.41 m.

	Species Calluna	Erica
Variable		
V_t (m s^{-1})	1.14	1.58
$x_{3,r}$ (m)	0.14	0.12
μ' (m)	1.02	1.04
λ' (m)	0.060	0.064
$\overline{U}_{eff}$ (m s^{-1})	8.4	13.7
γ	0.14	0.12
σ_{eff} (m$^{1/2}$)	0.57	0.47
$\sigma_{w,eff}$ (m s^{-1})	2.7	3.0
Pr(z>h)	0.22	0.19

Table 5: The estimated parameters (μ' and λ') for WALD shown in Figure 1b. Using these two parameters, the effective mean wind speed $\overline{U}_{eff}$ and vertical velocity variance $\sigma^2_{w,eff}$ 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).

Variable	*Species*	Cirsium dissectum	Hypochaeris radicata	Centaurea jacea	Succisa pratensis
V_t (m s^{-1})		0.38	0.33	4.36	2.12
$x_{3,r}$ (m)		0.99	1.03	1.01	0.97
μ' (m)		3.68	3.18	0.28	0.54
λ' (m)		0.58	3.31	0.74	0.70
$\overline{U}_{eff}$ (m s^{-1})		1.41	1.02	1.19	1.18
$\overline{U}_{eff}$ (m s^{-1}) at z=10 m		3.9	2.9	5.3	2.6
γ		0.27	0.32	3.66	1.79
σ_{eff} (m$^{1/2}$)		1.30	0.57	1.17	1.16
$\sigma_{w,eff}$ (m s^{-1})		2.39	0.33	1.64	1.60

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

Figure 1b: Measured (open circles) and modeled kernels (lines) for the grassland ecosystems described in Soons et al. (2004). The solid line represents the fitted WALD obtained by first and second moment matching to the measured distances. The solid dashed lines represented the modeled kernels for $\overline{U} = 6.9$ m s^{-1}, $h = 0.5$ m, $x_{3,r}$ and V_t shown in Table 4. For reference, we also show the modeled kernels for the lowest wind speeds ($\overline{U} = 0.1$ m s^{-1}). For *Centaurea jacea* and *Succisa pratensis*, the resulting modeled kernels for $\overline{U} = 0.1$ m s^{-1} are about < 1 cm from the source and are not shown for clarity.

List of Figures for Appendix 3:

Figure 2a: Comparison between modeled (line) and measured (open circle) dispersal kernels for seed releases in November 2, 2000. The models include WALD (thick-solid), tilted Gaussian (dotted), advection-diffusion equation (dot-dashed), and the Gaussian (thick-dashed). All seeds were released at once from a given level. The modeled kernel was computed using a 30 minute averaged u∗ for each seed release height. For species abbreviations, see Table 1.

Figure 2b: Same as Figure 2a but (1) seeds were released in small clusters every 30 seconds during the 30 minute u_* averaging interval, and (2) experiment carried out on November 28, 2000.

Figure 2c: Same as Figure 2b but for May 13, 2001.

Figure 2d: Same as Figure 2b but for June 25, 2001.

Figure 2e: Same as Figure 2b but for July 20, 2001.

Figure 2f: Comparison between measured and modeled $\exp(-p(x_1))$ for all 51 kernels ($n = 459$). The regression statistics are presented in Table 2.

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Figure 3: Comparison between measured (circle) and calculated (star) seed escape probabilities (from equation 6) for the 5 species in Nathan et al. (2002b). The ordinate axis is the normalized seed release height (normalized by the canopy height h=33 m) and the abscissa is the seed escape probability ($\Pr(z>h)$). The time series of u_* above the canopy along with its time average are also shown.
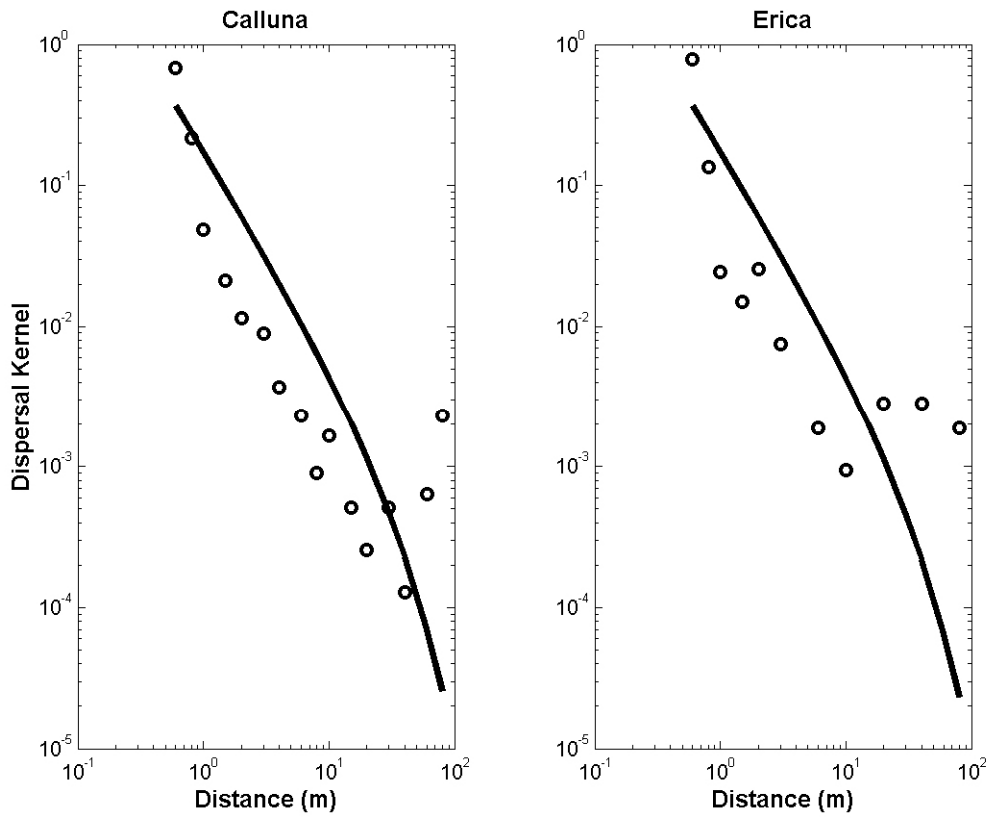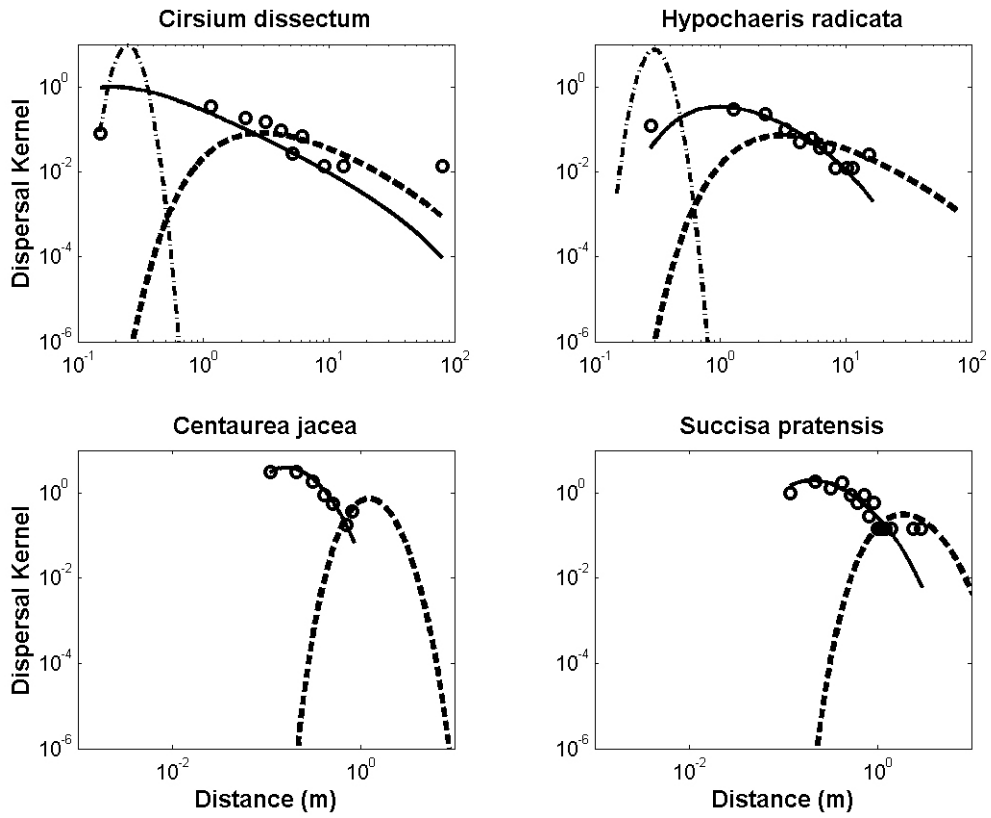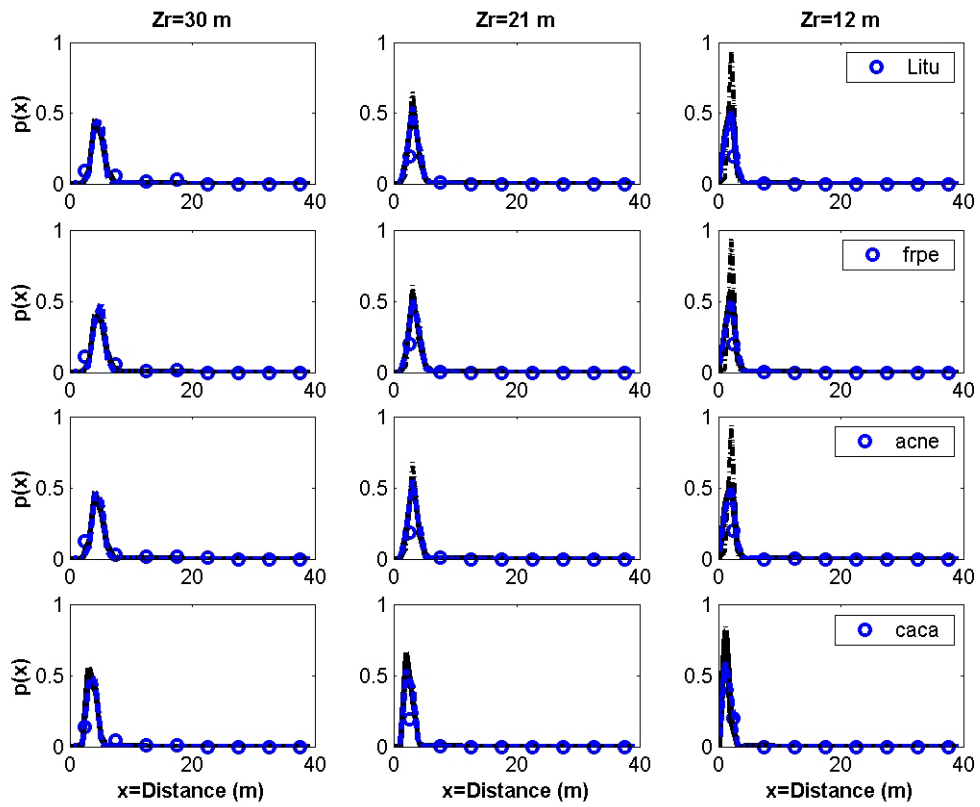
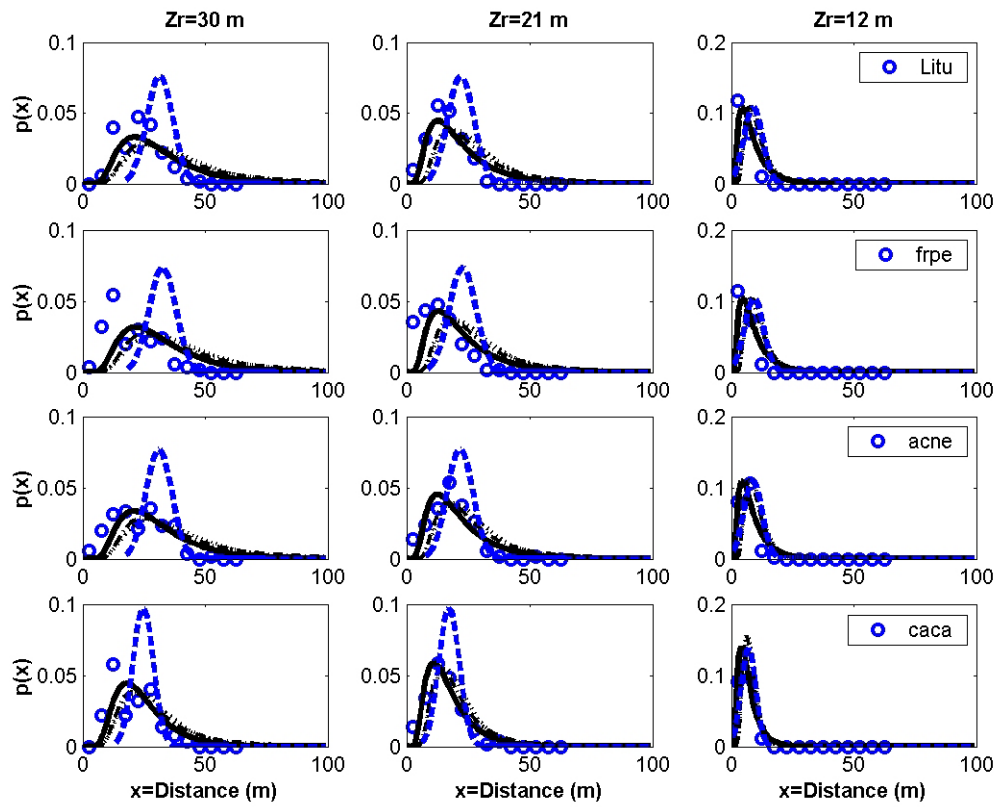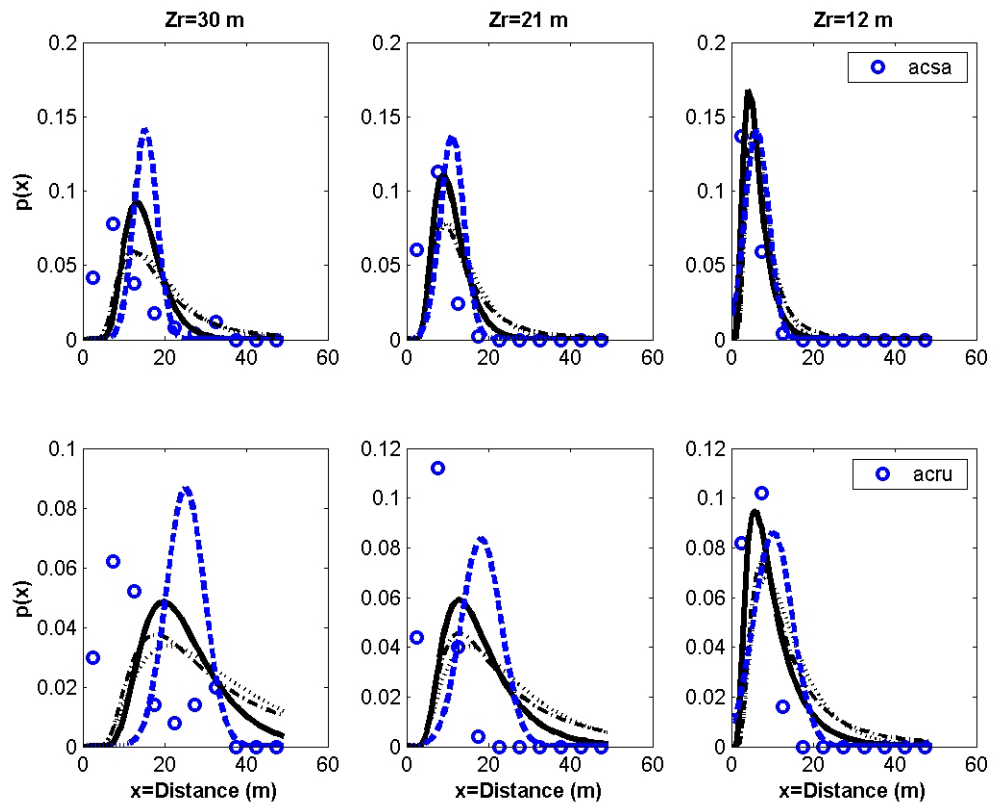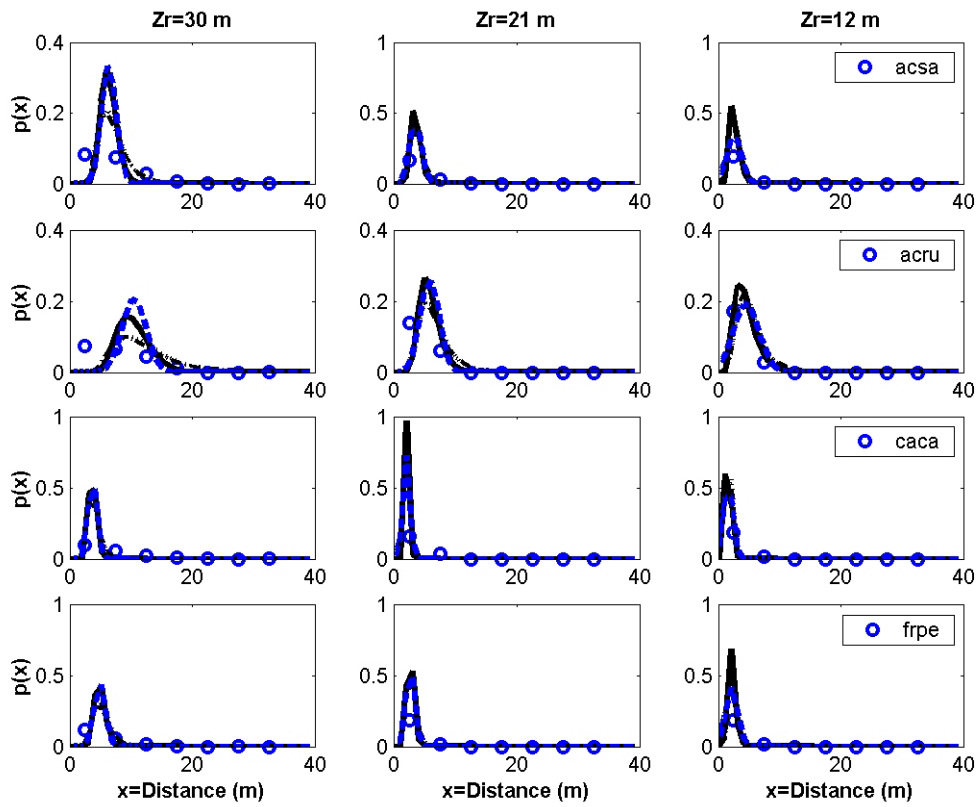Figure 1a: Katul et al.

Figure 1b: Katul et al.

Figure 2a: Katul et al.

Figure 2b: Katul et al.
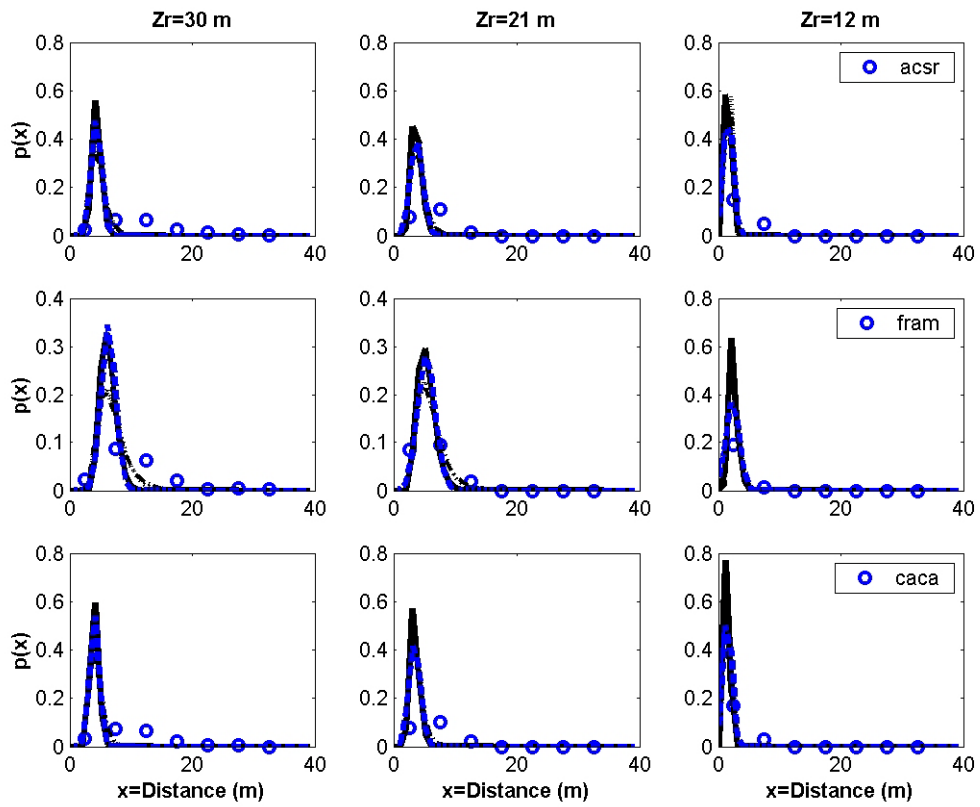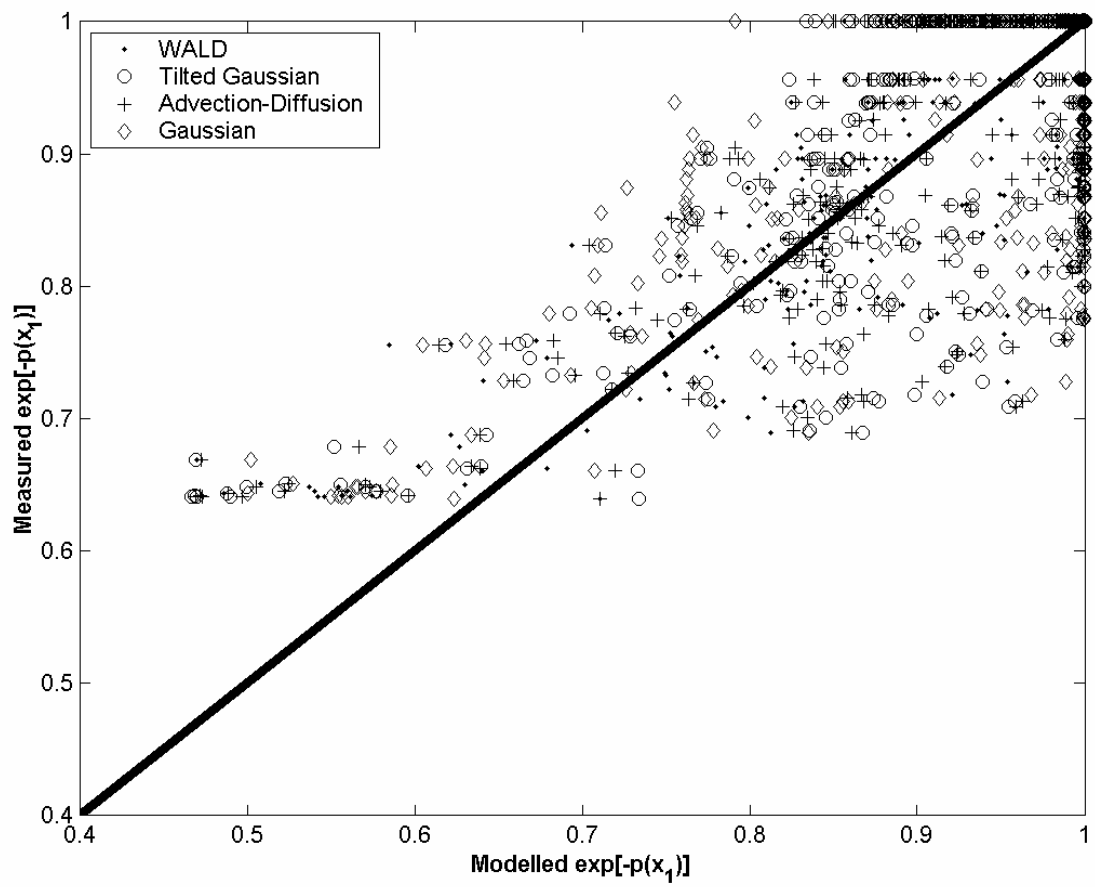
Figure 2c: Katul et al.

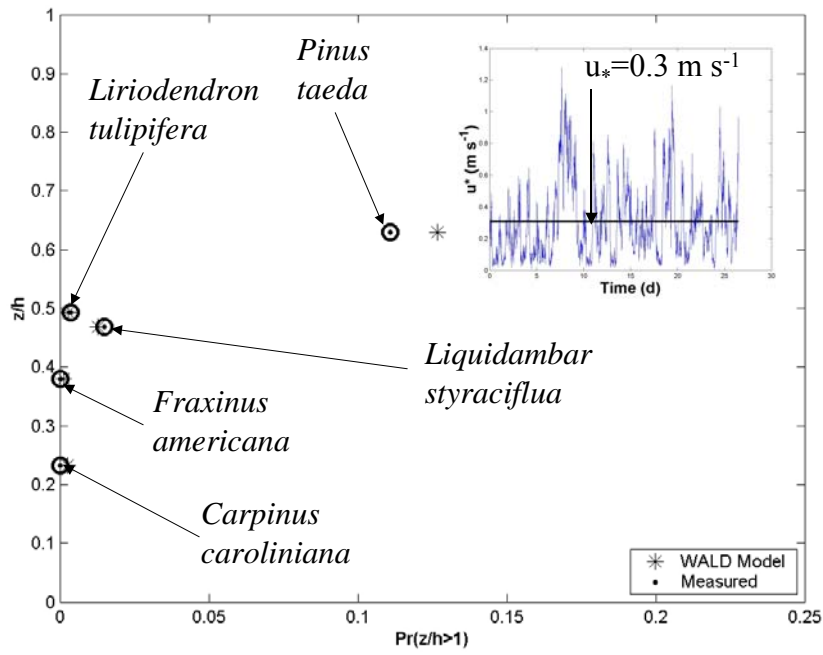Figure 2d: Katul et al.

Figure 2e: Katul et al.

Figure 2f: Katul et al.

Figure 3: Katul et al.