A mechanistic model for seed dispersal

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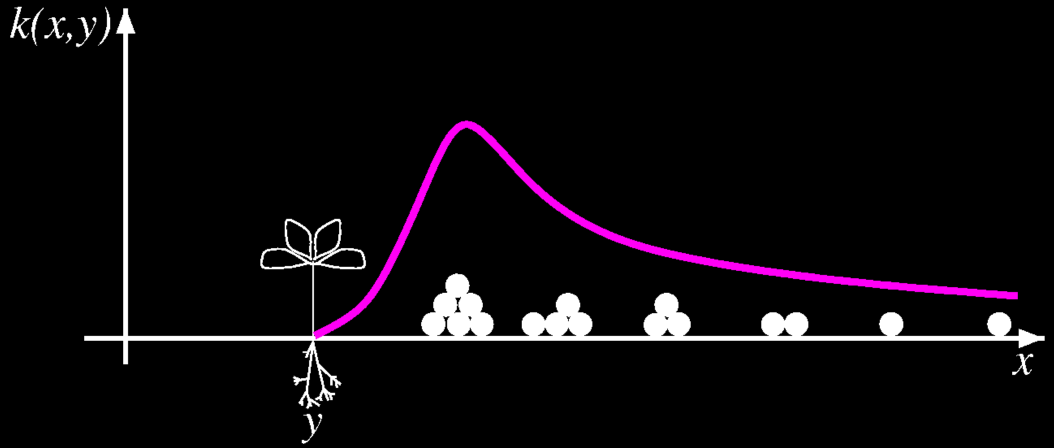
Outline

- Biological Background
- Model for wind dispersed seeds
- Model results
- Summary

Biology: Introduction



- Consider a terrestrial plant species
- Seeds are released seasonally
- What is the dispersal kernel, $k(x, y)$, for the species:
  k is the probability of a seed landing at x given that it was released at y.

Biology: Why?

- Local dispersal – Mode of $k(x, y)$:
  - Spatial patterning
  - Species persistence
- Long-distance dispersal – Tail of $k(x, y)$:
  - Genetic mixing within/between species
  - Species persistence (habitat degradation)
  - Spread rates (invasive species)
  - Migration rates (changes in the global climate)

Biology: Needs. . .

- A mechanistic model for seed dispersal
- A mechanistic understanding of previous models
- A model that is simple and easy to use/understand
- A model that can be scaled to the landscape/population level

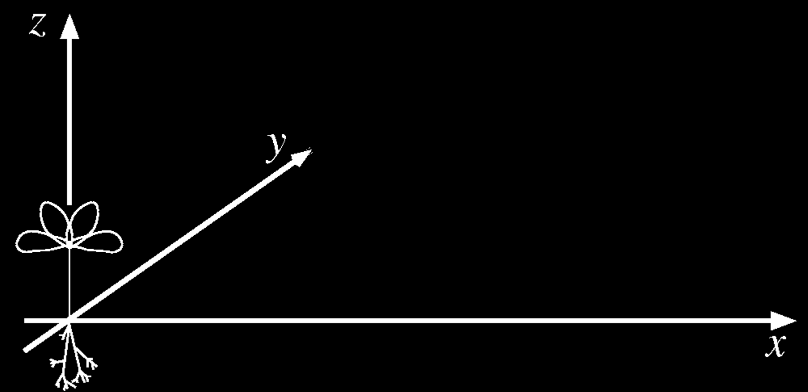
Biology: Goals

- SIMPLE!
  (Computer model that runs on a laptop in a few moments)
- Mechanistic basis
- Able to describe multiple data sets
- Have an analytic form for k
  (ideally with 2 or 3 independently measured parameters)
- Use as a tool to identify important mechanisms

Individual Based Model: Assumptions

- The plant is assumed to be point source
- Seeds are passively release into the wind flow
- Seeds are passively advected by the wind
- Seeds are biased toward the ground due to gravity
- One a seed hits the ground it remains there for all time, i.e., there is no secondary dispersal

Individual Based Model: General Model



$$\frac{dX}{dt} = u \; ; \qquad X(0) = x_0$$
$$\frac{dY}{dt} = v \; ; \qquad Y(0) = y_0$$
$$\frac{dZ}{dt} = w - W_s \; ; \qquad Z(0) = h$$

- $X = X(t)$, $Y = Y(t)$ and $Z = Z(t)$ are the position of the seed,
- u, v and w are the wind velocities in the x-, y- and z-directions
- W_s is the terminal velocity of the seed

Wind Velocity Model: Assumptions

- The wind velocity has a *Reynolds decomposition*

$$
\begin{aligned}
u &= \bar{u} + u' \\
v &= \bar{v} + v' \\
w &= \bar{w} + w'
\end{aligned}
$$

  where

  - $(\bar{u}, \bar{v}, \bar{w})$ denote the average wind velocities
  - (u', v', w') denote fluctuations about the mean

- During seed flight, the mean wind flow is *stationary* in time and directed along the x-axis

- The wind is assumed to be *statically neutral* during seed flight

Wind Velocity Model: Mean Wind Speed

- If the wind is *statically neutral*, then the mean wind profile in the x-direction is

$$\bar{u}(z) = \begin{cases} 0 & \text{if } z < z_d + z_0 \\ \dfrac{u_*}{\kappa} \ln\left\{\dfrac{z - z_d}{z_0}\right\} & \text{if } z \geq z_d + z_0, \end{cases}$$

  where
  - $\kappa = 0.41$ is the von Kármán constant
  - u_* is the friction velocity characterizing the ground surface
  - z_d is the displacement height of the vegetation
  - z_0 is the roughness length of the vegetation

- $\bar{v} = 0$

- The *statically neutral* assumption and Thomson's *well-mixed principle* implies that

$$\bar{w} = \kappa u_*$$

Wind Velocity Model: Wind Fluctuations

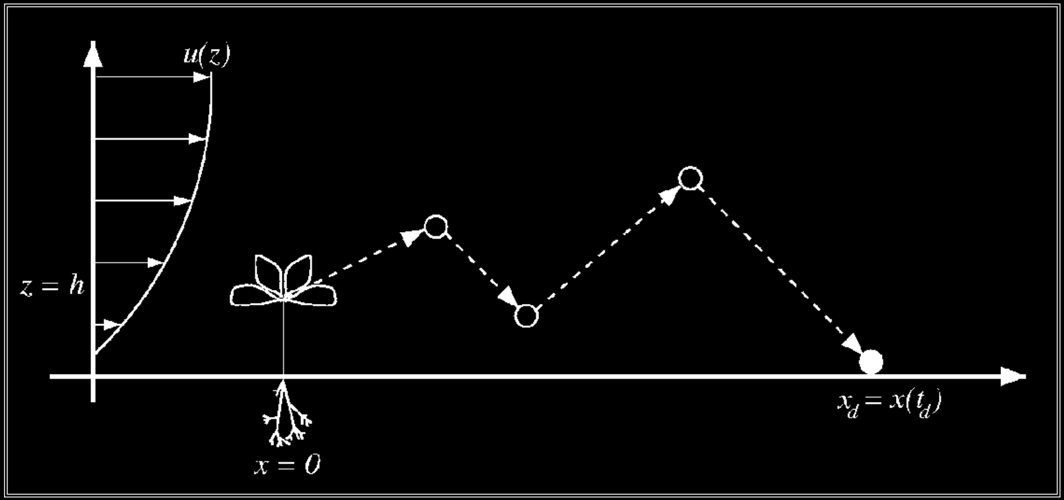
- We assume that $u' \ll \bar{u}(z)$, so that $u' = 0$
- Considering the cross-wind integrated seed distribution, $v' = 0$
- From Taylor's diffusion equation, we have the discrete time equation

$$w'(Z,t) = R(\Delta t)w'(Z(t-\Delta t), t-\Delta t) + \sqrt{1 - R^2(\Delta t)}\sigma_{w'}(Z(t))\xi(t)$$

where

  - Δt is the discrete time step
  - $R(\Delta t) = \exp\{-\Delta t/T_L\}$ is the Lagrangian autocorrelation function
  - $\sigma^2_{w'}(z) = 2\kappa u_* z/\Delta t$ is the height dependent variance of the vertical wind fluctuations
  - $\xi(t)$ is a Gaussian random variable with mean zero and variance one, i.e., $\xi(t) \sim \mathrm{N}(0,1)$ and uncorrelated on all positive time scales Δt

Individual Based Model: Discrete-Time Model



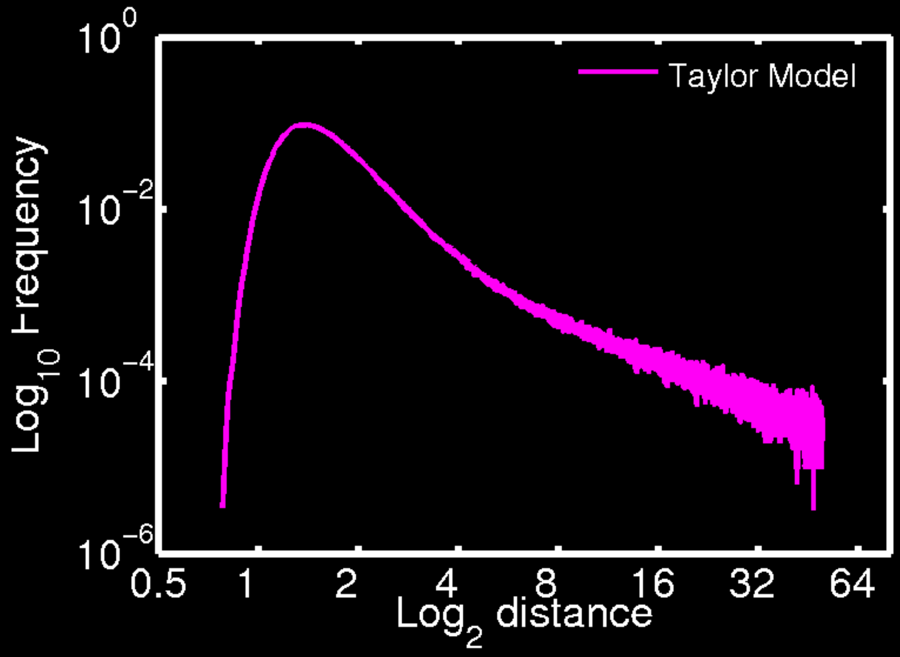
- The discrete time model for the seed position is

$$
\begin{aligned}
X(t + \Delta t) &= X(t) + u(Z(t))\Delta t \\
Z(t + \Delta t) &= Z(t) + [\kappa u_* - W_s + w'(Z,t)]\Delta t
\end{aligned}
$$

- And the initial conditions

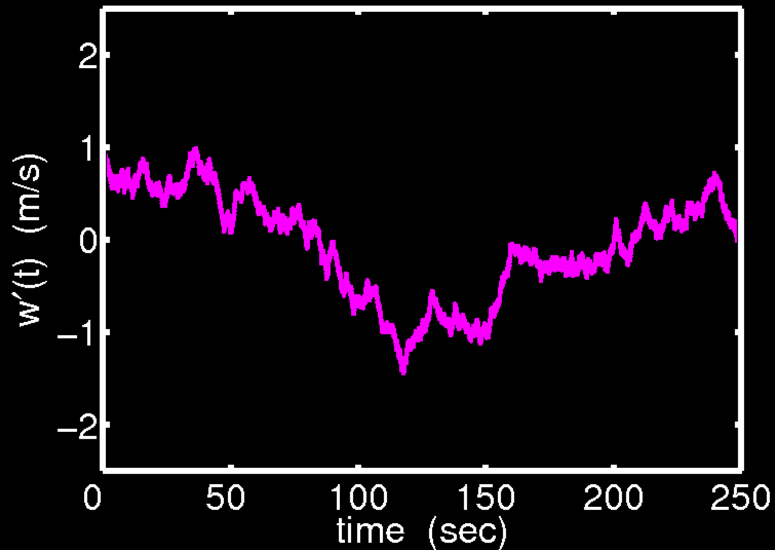
$$
\begin{aligned}
X(0) &= x_0 \\
Z(0) &= h
\end{aligned}
$$

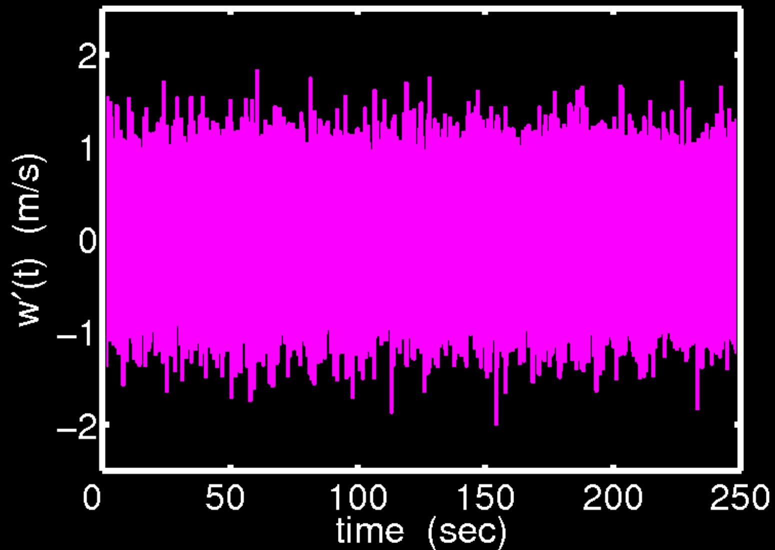
Individual Based Model: Taylors Model



- Realize the discrete time model 5,000,000 time
- Generate a normalized frequency plot of first hitting locations
- Variation in the tail of the dispersal kernel?

Eulerian Model: Wind Fluctuation Model





- Assume that the time scale over which the wind fluctuations are correlated goes to zero

$$\lim_{T_L \to 0} R(\Delta t) = \lim_{T_L \to 0} \exp\left\{\frac{-\Delta t}{T_L}\right\} = 0$$

so that

$$w'(Z,t) = \sigma_{w'}(Z(t))\xi(t)$$

Eulerian Model: SDE Model

- Assume that

$$\Delta t \to 0 \qquad \text{so that} \qquad \frac{-\Delta t}{T_L} \to -\infty$$

- Then the discrete time model reduces to the Stochastic Differential Equation (SDE) model

$$\begin{aligned} dX_t &= u(Z_t)dt \\ dZ_t &= \left[\kappa u_* - W_s\right] dt + \tilde{\sigma}_{w'}(Z_t) d\omega_t \end{aligned}$$

where

- X_t and Z_t are the position of the seed, parameterized by t
- $\tilde{\sigma}_{w'} = \sigma_{w'} \Delta t$ is the instantaneous variance of the vertical wind fluctuations
- $d\omega_t$ is an uncorrelated, Gaussian random variable with mean zero and variance dt

Eulerian Model: Fokker–Plank Model

- If we consider an ensemble average of the SDE model, we have the Fokker–Plank

$$\frac{\partial \rho}{\partial t} = \frac{\partial}{\partial z}\left\{\tilde{\sigma}_w \frac{\partial \rho}{\partial z}\right\} - u(z)\frac{\partial \rho}{\partial x} + W_s \frac{\partial \rho}{\partial z}$$

where $\rho = \rho(x, z, t | x_0, h, 0)$ is the expected airborne seed density

- With the initial condition

$$\rho(x, z, 0) = \rho_0 \delta(x - x_0)\delta(z - h)$$

and boundary conditions

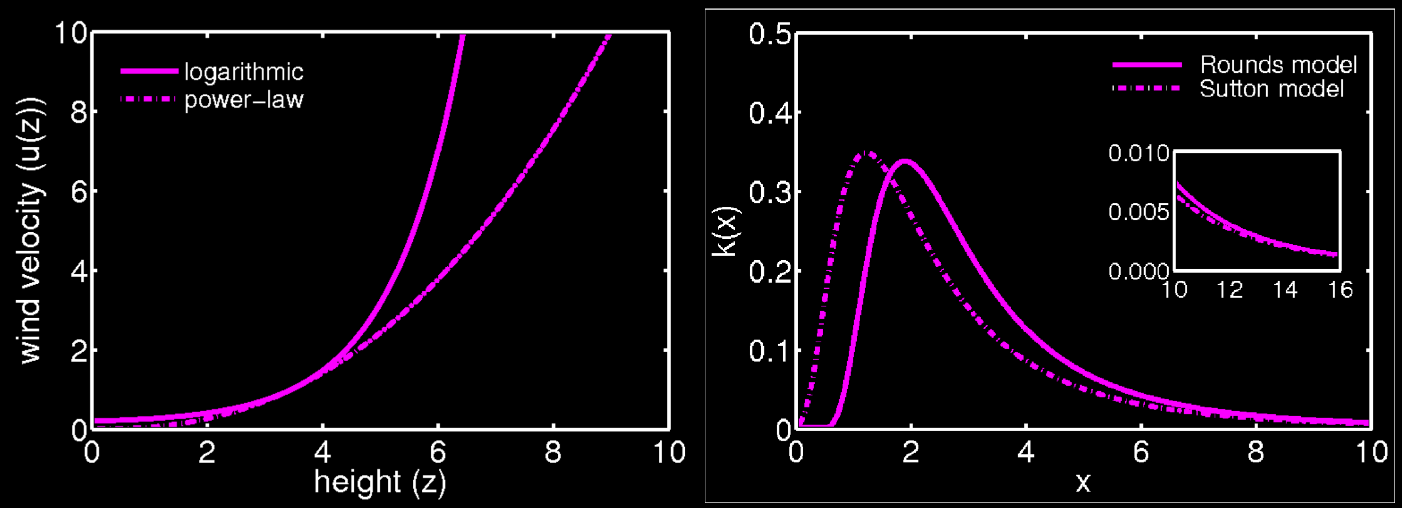
$$\rho(x, z, t) \longrightarrow 0 \quad \text{as} \quad |x|, z \longrightarrow \infty$$

$$\tilde{\sigma}_w \frac{\partial \rho}{\partial z} + W_s \rho = W_s \rho \quad \text{as} \quad z \longrightarrow 0$$

- The dispersal kernel is defined by the seed flux into the ground

$$k(x; x_0, h, u) = \int_0^\infty W_s \rho(x, z, t | x_0, h, 0) dt \quad \text{as} \;\; z \longrightarrow 0.$$

Eulerian Model: Rounds Model



- If the logarithmic wind profile is approximated by the power-law profile

$$u(z) \approx u_{\mathrm{pl}}(z) = u_h \left(\frac{z}{h}\right)^{\eta}$$

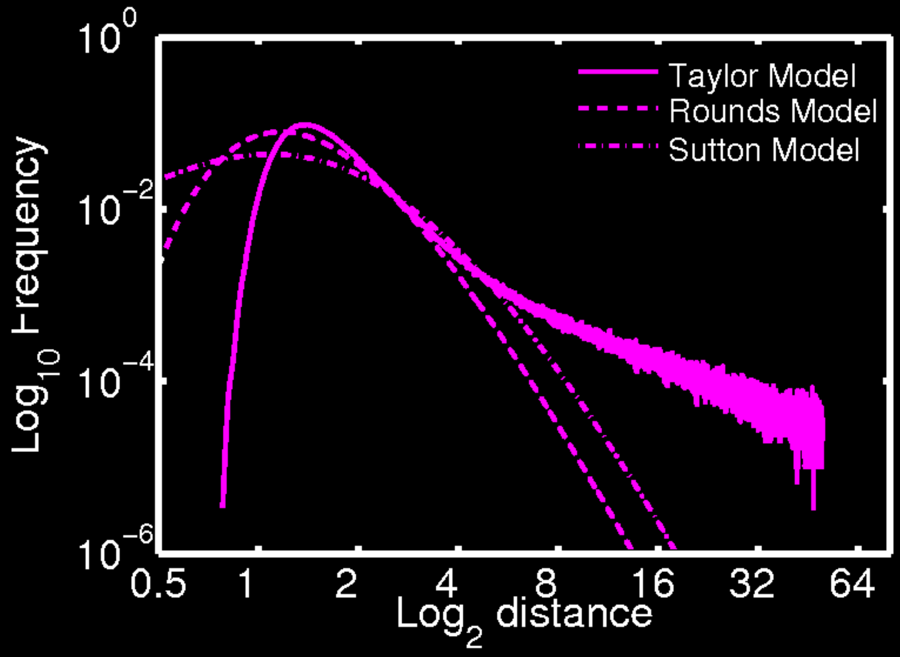
then the analytic solution for the dispersal kernel is

$$k_{\mathrm{R}}(x; x_0, h, u_{\mathrm{pl}}) = \frac{W_s}{\hat{u}\Gamma(1+\beta)} \left[\frac{\hat{u}}{\kappa u_*(1+\eta)(x-x_0)}\right]^{1+\beta} \exp\left\{\frac{-\hat{u}}{\kappa u_*(1+\eta)(x-x_0)}\right\}$$

where

- $\hat{u} = u_h h^{1+\eta}/(1+\eta)$ and $\beta = W_s/[\kappa u_*(1+\eta)]$

Model Comparison



- More weight in the tail for the IBM model
- The Rounds model has more weight in the tail than the Sutton Model
- Change in con-cavity for IBM model

Generalized Model

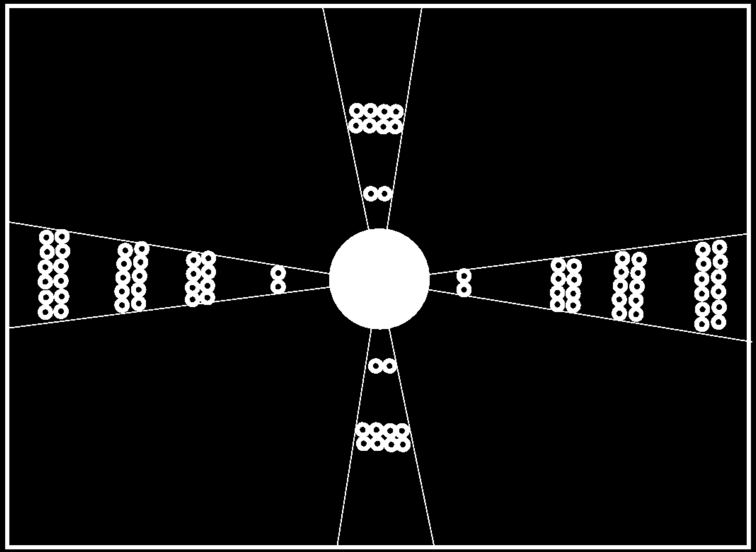
- Taking into account different source geometries and varying wind conditions, the generalized dispersal kernel is

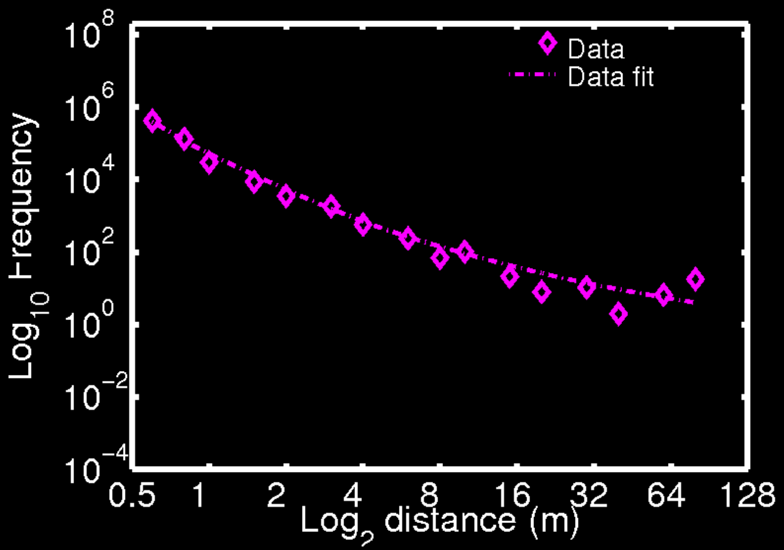
$$k(x; x_0, h, u) = \int_0^\infty \int_{-\infty}^\infty \int_{-\infty}^\infty \phi(u)\theta(x_0, h)k(x, x_0, h, u)dudx_0dh$$

where

  - $\phi = \phi(u)$ is a pdf for the horizontal wind velocity at $z = h$
  - $\theta = \theta(x_0, h)$ is a pdf for the release location
  - k is computed from the Round formula or realization of Taylors model

Field Study: Bullock and Clarke





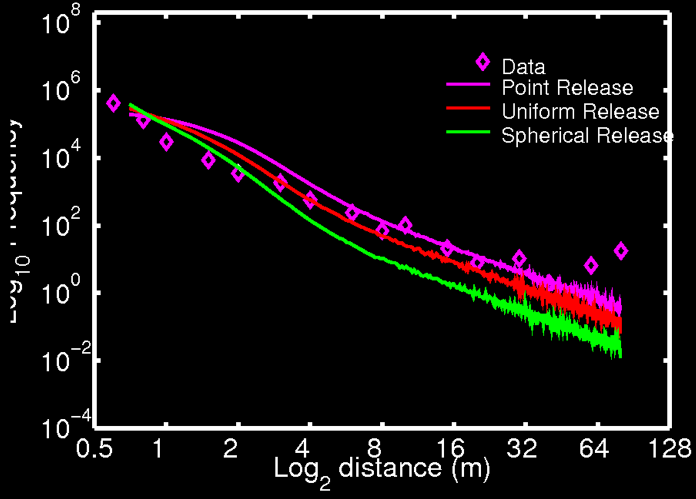
- *Calluna vulgaris* bush isolated in a field
- Seed dispersal was measured up to 80*m* from the source
  (a distance several orders of magnitude greater than the height of the plant)
- An equal area seed trap design was used to measure dispersal in four orthogonal directions from the source
- Data was collected from late July to early September, 2000
  (and hourly wind measurments)

Numerical Experiments

To test the validity of the model, we ran three numerical experiments:

- Plant Geometry:
  The *Calluna vulgaris* bush is modeled as a spherical plant, with a uniform seed density on the surface
- Autocorrelation in wind velocities:
  The Taylor model is compared to the Rounds analytic solution
- Release velocity:
  The vertical seed velocity at release is correlated with the horizontal wind speed

Plant Geometry

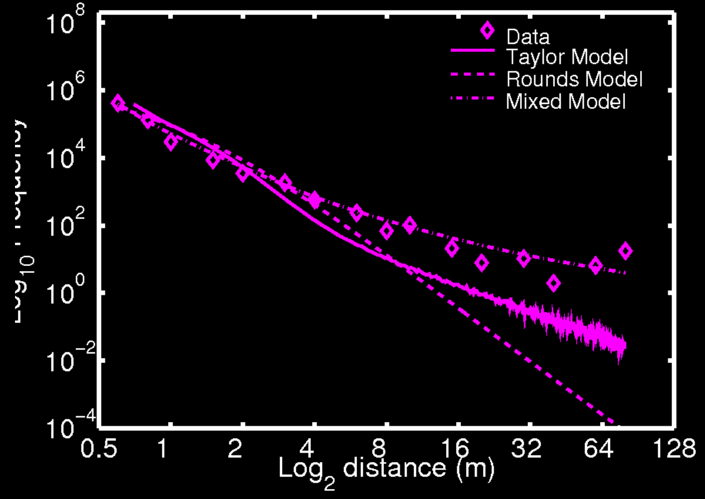


- Seed are released from a point source, uniformly from a vertical line source and as a function of surface area

Student Version of MATLAB

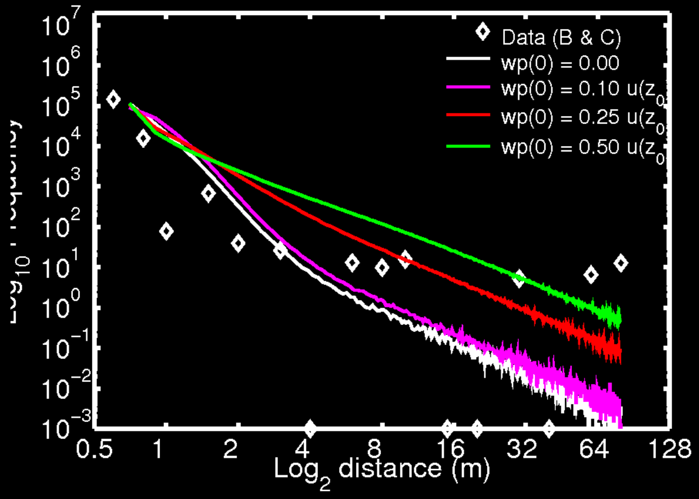
- Autocorrelated wind fluctuations
- The point source overestimates local dispersal and slightly underestimates long-distance dispersal
- The spherical release better approximates local dispersal, but also underestimates long-distance dispersal

Autocorrelated wind fluctuations



- The IBM describes local dispersal well
- The IBM has more weight in the tail then the Rounds solution
- Similar to the maximum-likelihood fit, the IBM model predicts a change in con-cavity

Release Velocity



- The seeds are release with a positive initial velocity:

$$w(h) = \gamma * u(h)$$

where $\gamma \in \{0.0, 0.1, 0.25, 0.5\}$

- For small γ, the IBM predicts local dispersal well
- For large γ, the IBM predicts more weight in the tail
- As γ increases, the shape of the kernel changes

Results

- Plant Geometry:
  Allows for seeds to be released closer to the ground, better fit for local dispersal

- Autocorrelated wind fluctuations:
  Allows for seeds to be uplifted and carried farther from the source,
  better fit of the tail (long-distance dispersal)

- Release correlated with wind speed:
  More weight associated with the tail of the dispersal kernel

- More research/data into how seeds are released?

Summary

- The model proposes mechanisms for seed dispersal
- Semi-empirical, in that statistics for the seasonal wind profile are needed
- The model requires three measured parameters
- Simple to implement, approximately 50 lines of C code,
  5 minutes to generate a dispersal kernel
- The model helps to explain previous model for seed dispersal