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A THEORETICAL FRAMEWORK FOR DATA ANALYSIS OF WIND DISPERSAL OF SEEDS AND POLLEN[1]

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Abstract. We compared a variety of models for the analysis of data on the wind dispersal of seeds and pollen. Dispersal distances from a source depend upon such factors as settling velocity, height of release, wind speed and turbulence, and specific morphological adaptations for dispersal. The dispersal curve, which describes the frequency distribution of dispersal distances, usually shows its peak at some distance from a source and falls off with distance. We used the location of that peak as a measure of dispersal, and organized data in terms of the predictions of two models for the dynamics of advection and diffusion. These data are summarized in a seed dispersal diagram in which the modal distance normalized by the height of seed release is plotted against the mean wind speed normalized by the falling speed of seeds. Data from 15 studies were used to compare actual dispersal relationships with our model predictions.

Key words: diffusion of seeds; Gaussian plume; modal dispersal distance; pollen; seed dispersal; seed dispersal diagram; spores; tilted plume.

INTRODUCTION

The dispersal of seeds and pollen is fundamental to the ecology and evolutionary biology of plants, and in the response of plants to environmental variability and local environmental deterioration. Thus, an explication of the mechanisms of dispersal is central to an understanding of the population biology of plants, and of the community dynamics of interacting species (Werner 1975, Harper 1977). Clearly, as Harper (1977) says, "any attempt to discuss the dynamics of plant populations must concern itself with the parameters of [dispersal]."

The shape of the curve relating the number of dispersed seeds to distance from source will vary depending upon such factors as speed of descent (the settling velocity), height of release, wind speed and turbulence, and specific morphological adaptations for dispersal (Augspurger and Franson 1987). Typically, this dispersal curve will fall off with distance, but it may achieve its apex at some distance away from a point source. (Some care must be taken in the interpretation of data regarding this effect, since even a two-dimensional normal distribution would have a displaced peak when expressed in radial coordinates.) In the case of a distributed source, in contrast, the peak usually will occur at or close to the boundary of the source region. Our interest is in understanding what factors control the forms of such dispersal curves. Explicitly, we will consider diffusive and advective forces in relation to properties of the propagules and height of release. We will not take into account the shape of the parent plant, although this has the potential to affect the near-field flow dynamics substantially (Niklas 1984).

The most widely used forms for the dispersal curve, the inverse power law (Gregory 1968) and the negative exponential (Frampton et al. 1942, Kiyosawa and Shiyomi 1972), are phenomenological in derivation. These describe the asymptotic distribution of seeds, spores, or pollen from point releases (or the time-averaged solutions for continuous point sources); they do not deal with the transients. General reviews can be found in Gregory and Read (1949) and Minogue (1986).

The inverse power law (Fig. 1) is described by

$$y = as^{-b}, \tag{1}$$

where s is distance from source, y is the probability density associated with dispersal, and a and b are constants. It owes its popularity in part to the fact that it transforms to a straight line on a log–log plot, facilitating parameter estimation. Note further that b is di-

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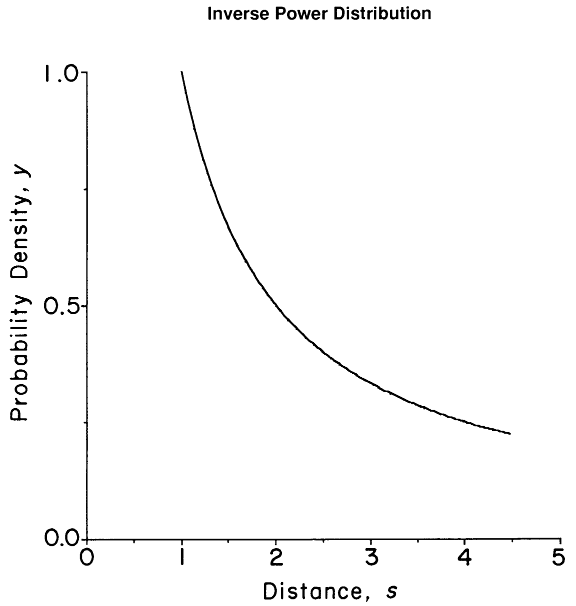

FIG. 1. The inverse power law of dispersal. Here s denotes distance from source, y denotes probability density.

mensionless, which is an advantage in dealing with studies on different scales.

The negative exponential (log-linear, Fig. 2) model has the shape

$$y = ae^{-bs}, \quad (2)$$

which transforms to linear on a semilog plot. One significant advantage over the inverse power model is that y remains finite as s tends to zero. On mathematical grounds, this may make the log-linear model preferable (Minogue 1986), but comparison of the success of the two models in fitting data does not indicate a clear preference for either model. For example, Gregory (1968) measured 124 dispersal gradients for dry airborne spores or pollen, and found that 59 were fitted better by the power law, and 65 by the exponential model (Fitt and McCartney 1986). Similar conclusions emerged from the studies of McCartney and Bainbridge (1984), who simulated dispersal of spores by using 20 μm droplets.

The advantages of the above models are that they are simple, have only two parameters, and can be fit to data reasonably well. Their principal disadvantage is that, while parameters can be fit for particular situations, such models provide no way to extrapolate from one situation to another based on independently measured physical parameters, and no understanding of the underlying mechanisms. Thus, if interest is in such parameters as height of release, settling velocity, or wind, one must determine relationships empirically by conducting a wide range of studies. Note also that neither model allows for distributional peaks to be displaced from the source, as is observed in most data sets.

GAUSSIAN PLUME MODELS

A step in the direction of a mechanistic approach is provided by Gaussian plume models (Fig. 3A: Pasquill 1962, Hanna et al. 1982). These models, which compute the horizontal and vertical distribution of particles under the influence of diffusion and advection, have been used most widely for describing the dispersion of air pollutants around smokestacks; however, they also have been applied to spore dispersal (e.g., Gregory et al. 1961, Fitt and McCartney 1986).

Boundary value problems for diffusion equations can be difficult to solve, as we discuss in the next section. The Gaussian plume approach (Csanady 1973, Hanna et al. 1982) finesses this problem by assuming reflection boundary conditions at the surface of the earth (thereby ignoring some of the effects of deposition). For flat terrain, this leads to an easily solved problem for the three-dimensional steady-state seed distribution $S(x, y, z)$ downwind from a continuous point source at height H above the ground (Sutton 1947). Deposition at the surface of the earth, at horizontal position (x, y), is given by

$$D = S(x, y, 0)\ V_d, \quad (3)$$

where V_d is the deposition velocity (Chamberlain 1975).

The Gaussian plume model, as just described, deals with very light particles (such as particulate pollutants), and makes no allowance for gravitational settling. For heavy particles, a modification, the tilted plume model (Fig. 3B), replaces the effective height H of the plume by $H - (xW_s/\bar{u})$, where W_s is the settling velocity of seeds and $\bar{u}$ is the mean wind speed. This extends the plume model to the case where particulates have a nontrivial settling velocity (e.g., Csanady 1963).

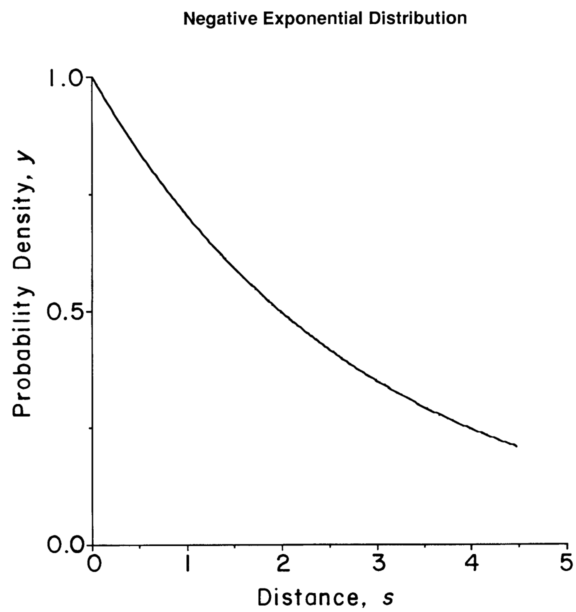

FIG. 2. The log-linear law of dispersal. Here s denotes distance from source, y denotes probability density.

In computing the deposition rate for heavy particles, we ignore bouncing or resuspension of seeds hitting the ground (but see Liddle et al. 1987), and assume that deposition due to diffusion can be ignored relative to sedimentation; thus, the rate of deposition at the ground is given by

$$D = S(x, y, 0)W_s, \quad (4)$$

where $W_s = V_d$. This leads to an expression for the concentration of seeds at the ground level,

$$D = Q(x, y) = \frac{nW_s}{2\pi\bar{u}\sigma_y\sigma_z}\exp\left\{\frac{y^2}{2\sigma_y^2} - \frac{(H - W_s x/\bar{u})^2}{2\sigma_z^2}\right\}, \quad (5)$$

in which $\bar{u}$ is the constant wind speed in the x direction at height H. In general, $n = n(x)$ (the effective source strength at distance x) and the standard deviations σ_z, σ_y are functions of x (e.g., Pasquill and Smith 1983: 333). The dependence of n on x allows for losses due to deposition (Horst 1977). However, in this paper we neglect the decay in n, and assume that n is constant.

Since our primary interest is in how far seeds move downwind, we suppress the crosswind (y) distribution, which is Gaussian, by integrating in that direction. The result, called the crosswind-integrated deposition, CWID (Fig. 4), is given by

$$\text{CWID} = \int_{-\infty}^{\infty} Q(x, y)\,dy \equiv Q(x) = \frac{nW_s}{\sqrt{2\pi}\bar{u}\sigma_z}\exp\left\{\frac{-(H - W_s x/\bar{u})^2}{2\sigma_z^2}\right\}. \quad (6)$$

We henceforth take

$$\sigma_z^2 = 2Ax/\bar{u}, \quad (7)$$

where A is the vertical diffusivity (the coefficient of diffusion in the vertical direction). The motivation for this is the assumption that particles spread diffusively about their mean height. Given a constant wind speed $\bar{u}$, the time t for particles to reach position x is $x/\bar{u}$. It is well known that for a diffusion process, the variance increases linearly with time at the rate $2A$, where A is the diffusion coefficient. Hence, Eq. 7 results. The distribution is skewed; the mode (maximum) always is less than or equal to the mean, and is given by

$$x_m = \frac{\bar{u}H}{W_s}\{[1 + (A/HW_s)^2]^{1/2} - (A/HW_s)\}, \quad (8)$$

which coincides with the mean if there is no vertical diffusivity ($A = 0$). Define

$$2A/H = W,^* \quad (9)$$

where W^* is vertical mixing velocity. W^* is a measure of how fast particles released at height H would reach the ground by diffusion alone, if gravity were ignored.

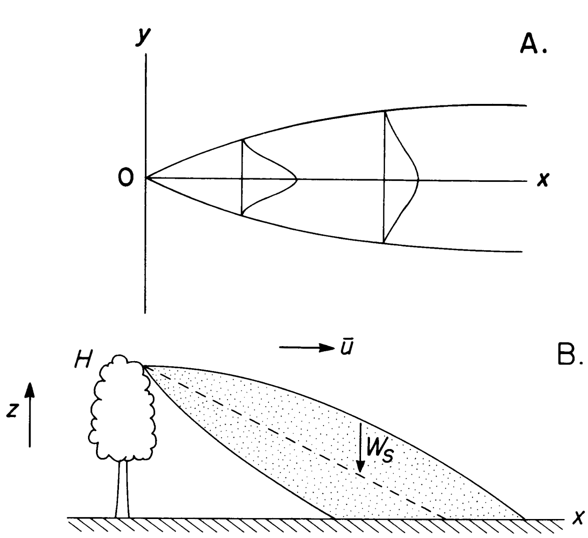

FIG. 3. (A) Schematic for Gaussian plume model, viewed from above. (B) Schematic for tilted plume model. Here H denotes height of seed source, $\bar{u}$ denotes mean wind speed, W_s denotes settling velocity of seed.

Thus W^*/W_s is a dimensionless number measuring the relative importance of turbulence and gravitation, i.e., of diffusion and settling. Eq. 8 may be rewritten as

$$\lambda\frac{x_m}{H} = \frac{\bar{u}}{W_s}, \quad (10)$$

where

$$\lambda = (1 + (W^*/2W_s)^2)^{1/2} + W^*/2W_s. \quad (11)$$

For small values of W^*/W_s (heavy seeds)

$$\lambda \approx 1 + W^*/2W_s \approx 1, \quad (12)$$

and so $x_m \sim H\bar{u}/W_s$; whereas, for large values of $W^*/2W_s$ (light seeds),

$$\lambda \approx W^*/W_s \gg 1, \quad (13)$$

and so $x_m \sim H\bar{u}/W^*$.

Thus, the Gaussian diffusion approach allows definition of a dimensionless quantity λ (analogous to a Reynolds number), measuring the relative spread about the mean for settling particles. We show that the mode of the dispersion distribution for settling particles is inversely proportional to λ and to the settling velocity of seeds, and directly proportional to the height of release and to wind velocity.

Models of Advection, Diffusion, and Settling

The Gaussian plume model makes a number of simplifications, and avoids solving the appropriate boundary value problem; instead, it assumes reflection boundary conditions, which ignore the effects of deposition. In particular, the development in this section recognizes that:

1) wind speed is not a constant, but depends upon height,
2) vertical eddy diffusivity cannot be treated as constant, but must also be allowed to depend upon height,
3) deposition at the earth's surface leads to more complicated boundary conditions than reflected in Sutton's (1947) solution.

This leads to a difficult boundary-value problem. We cannot provide an exact general solution, but do compute the mode of the distribution, for comparison with that derived in the previous section.

The most general model considers the dynamics of advective and diffusive movements in both the horizontal and the vertical directions. Horizontal advection is determined by mean wind speeds, whereas the vertical advective force is gravitational. The mean wind is variable with height, but is assumed to be stationary in time. (In the Appendix we will discuss briefly the effect of nonstationary wind on seed dispersal.) We assume here that seeds instantaneously attain their terminal falling or settling velocity.

We treat the situation in which seeds or pollen are shed (or released passively) from an isolated tree or plant. The effect of initial active release due to wind fluctuations is discussed by Augspurger and Franson (1987), among others. The ground is assumed to be level, and the seed is simply deposited without bouncing. (A situation in which seeds may still move after first hitting the ground is discussed by Liddle et al. 1987.) Under these assumptions, our basic time-dependent equation for seed dispersal is given by

$$\frac{\partial S}{\partial t} + u(z)\frac{\partial S}{\partial x} - W_s\frac{\partial S}{\partial z} = K\nabla^2 S + \frac{\partial}{\partial z}\left(A(z)\frac{\partial S}{\partial z}\right), \qquad (14)$$

where x is taken in the direction of prevailing wind, y is horizontal and orthogonal to x, and z is vertically upward. ∇^2 denotes the sum of the second derivatives in the x and y directions. S represents the airborne concentration of seeds, i.e., the number of seeds per unit volume; $u(z)$ is the height-dependent mean wind speed and W_s is the terminal falling velocity of seeds. K represents a constant horizontal eddy diffusivity (assumed to be the same in the x and y directions) and $A(z)$ is the height-dependent vertical eddy diffusivity. Closer to the ground, wind speed and vertical diffusivity both decrease due to the effects of the ground.

The initial and boundary conditions are:

1) At t = 0

$$S(x, y, z) = M^*\delta(x)\delta(y)\delta(z - H), \qquad (15)$$

where M^* is the total amount of seed released, and H is the height of the seed source. The Dirac delta functions δ indicate that all of the seeds are released from a point source located at $x = y = 0$ and $z = H$. We can extend the model to a distributed source and continuous release by the method of superposing the instantaneous point-source solutions. It is the latter solution that we present in Eq. 22.

2) At $z = 0$ (ground),

$$A(z)\frac{\partial S}{\partial z} + W_s S = V_d S, \qquad (16)$$

where V_d is the deposition velocity (Chamberlain 1953) of seeds at the ground (Calder 1961; compare with Eq. 4). In general, $A(z) \to 0$ as $z \to 0$, but $\partial S/\partial z$ may become infinite; thus, this condition must be understood in the limiting sense as $z \to 0$.

3) As $|x|$, $|y|$, $z \to \infty$,

$$S \to 0. \qquad (17)$$

As a standard model for atmospheric diffusion near the ground, we take (see Roberts 1923, Sutton 1953, Pasquill 1962, Huang 1979, Hanna et al. 1982):

$$u(z) = u_H(z/H)^m,$$
$$A(z) = A_H(z/H)^n, \qquad (18)$$

where u_H and A_H are the values of u and A at height H, and m and n are constants, the values of which depend on the stability of the atmosphere.

We choose the following scaling parameters:

(Horizontal diffusion parameter) $\kappa = KT/L^2$
(Vertical diffusion parameter) $a = A_H T/H^2$
(Deposition-velocity parameter) $q = V_d/W_s$. (19)

The ranges of the controlling parameters are given by (Hanna et al. 1982):

$m, n = 0$ to 1,
$a = 0.01$ (heavy seeds) to 10 (light plumed seeds or pollen),
$\kappa = 10$ (heavy seeds) to 0.01 (light plumed seeds or pollen),
$q = 1$ (seed diameter ≥ 1 μm) to 0 (seed diameter < 0.1 μm), (20)

We have not solved the initial/boundary value problem for the most general case, but do so for important special forms. Henceforth, we simplify the treatment somewhat by taking $\kappa = 0$ and considering only the steady-state dynamics. The assumption $\kappa = 0$ means simply that horizontal diffusion is negligible ($\kappa \to 0$). Vanishing horizontal diffusivity does not mean that seeds have no dispersion in the horizontal direction: the combined effect of the wind profile and vertical diffusion produces horizontal dispersion of seeds in the x direction, and this effect usually dominates horizontal diffusion (Csanady 1973). We further assume that the exponent $n = 1$, and rewrite Eq. 18 as

$$u(z) = u_o z^\alpha,$$
$$A(z) = ku^* z, \qquad (21)$$

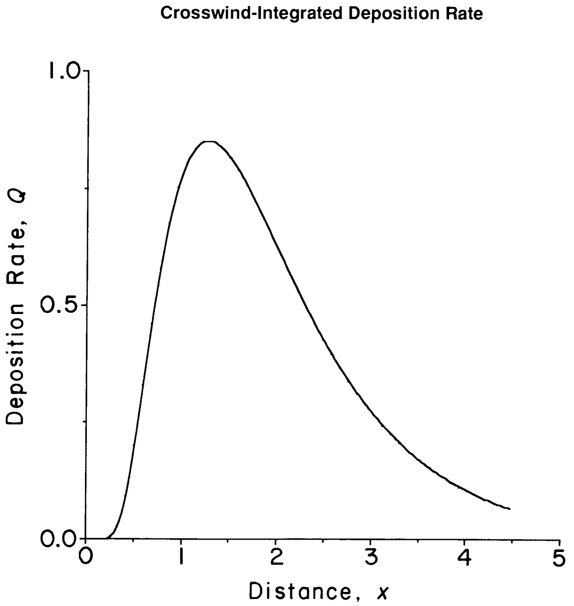

FIG. 4. Cross-wind integrated deposition at the ground for the tilted Gaussian plume model; x denotes distance from source.

where $k = 0.41$ is the von Kármán constant and u^* is the frictional velocity (Pasquill 1962).

If $W_s = V_d$, the crosswind-integrated deposition rate $Q(x)$ at the ground is calculated from the solution of the boundary-value problem (Rounds 1955, Godson 1957, Pasquill and Smith 1983:158–159):

$$Q(x) = \frac{MW_s}{H\bar{u}\Gamma(1 + \beta)} \left\{\frac{H^2\bar{u}}{2(1 + \alpha)\bar{A}}\right\}^{1+\beta} \cdot x^{-\beta-1}\exp\left\{-\frac{H^2\bar{u}}{2(1 + \alpha)\bar{A}x}\right\}. \quad (22)$$

The shape of $Q(x)$ is illustrated in Fig. 5. Here M is the rate of release of seeds per unit length of a crosswind line source placed at a height H; $\bar{u}$ and $\bar{A}$ are the mean wind speed and mean vertical diffusivity between 0 and H. The latter are defined, respectively, by

$$\bar{u} = \int_0^H u(z)\, dz/H = u_0 H^\alpha/(\alpha + 1) = u(H)/(\alpha + 1), \quad (23)$$

$$\bar{A} = \int_0^H A(z)\, dz/H = ku^*H/2 = A(H)/2. \quad (24)$$

Furthermore,

$$\beta = W_s/(ku^*(1 + \alpha)) = HW_s/2(1 + \alpha)\bar{A} \equiv W_s/W^*, \quad (25)$$

where

$$W^* \equiv 2(1 + \alpha)\bar{A}/H \text{ (vertical mixing velocity).} \quad (26)$$

We have not obtained a closed form expression for the variance, although such an estimate would be very useful. The mode (peak) of $Q(x)$, x_m, is obtained from Eq 22:

$$x_m = H^2\bar{u}/[2(1 + \alpha)(1 + \beta)\bar{A}] = H\bar{u}/(W_s + W^*) \quad (27)$$

or, as before,

$$\lambda(x_m/H) = \bar{u}/W_s, \quad (28)$$

where now

$$\lambda = 1 + \frac{W^*}{W_s}. \quad (29)$$

For small values of W^*/W_s (heavy seeds),

$$\lambda \rightarrow 1. \quad (30)$$

For large values of W^*/W_s (light seeds),

$$\lambda \rightarrow W^*/W_s \gg 1. \quad (31)$$

These asymptotic behaviors are the same as those derived from the tilted plume model, although Eq. 29 differs slightly from Eq. 11 for intermediate masses. The modifications necessary to deal with nonstationary wind and diffusivity regimes are given in the Appendix.

Thus, again we have derived a dimensionless quantity, λ, measuring the relative spread about the mean for settling particles. The approximation developed in the previous section, based on the tilted Gaussian, is seen to be a good first approximation, but to require correction. Again, as in the previous section, we have

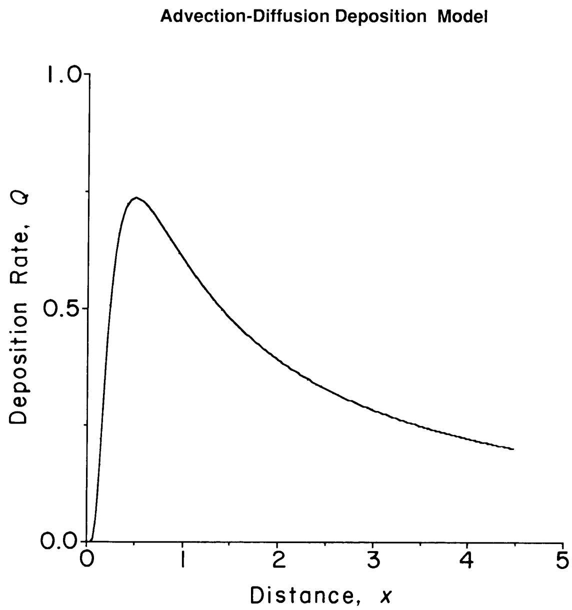

FIG. 5. Cross-wind integrated deposition curve for the advection diffusion model; x denotes distance from source.

TABLE 1. Table of dispersal data collected from a variety of studies. These data are plotted in Fig. 6. Where data are available relating x_m to measured parameters within a species or type, all data are presented; otherwise, only average figures are given. * See bottom of table for definitions of column headings.

Species and source	W (mg)	W_s (cm/s)	$\bar{u}$ (cm/s)	x_m (m)	H (m)	x_m/H	$\bar{u}/W_s$	λ
Lonchocarpus pentaphyllas[1] (fruits)	140	131	49	10	32	0.31	0.37	1.19
	225	139	49	10	32	0.31	0.35	1.13
	375	153	49	9	32	0.28	0.32	1.14
Eucalyptus deglupta[2] (seeds)	0.14	210	278	52.9	40	1.32	1.32	1.00
Eucalyptus globulus[2] (seeds)	3.03	554	278	20.1	40	0.50	0.50	1.00
Eucalyptus regnans[3] (seeds)	NA	348	145	22.9	76.3	0.30	0.42	1.40
Pseudotsuga taxifolia[4] (seeds)	NA	56	313	122	30.5	4.0	5.6	1.40
	NA	56	313	335	61	5.9	5.6	0.95
	NA	56	290	305	61	5.0	5.2	1.04
	NA	56	358	366	61	6.0	6.4	1.07
	NA	56	1028	518	61	8.5	18.3	2.15
	NA	56	156	153	45.8	3.3	2.8	0.85
Tachigalia versicolor[5] (artificial model fruits)	340	201	114	20	40	0.50	0.57	1.14
	850	368	114	12.5	40	0.31	0.31	1.00
	890	185	114	17.5	40	0.44	0.61	1.39
	1230	165	114	20	40	0.50	0.69	1.38
	1240	244	114	17.5	40	0.44	0.47	1.07
	1430	200	114	18.8	40	0.47	0.57	1.21
	1540	254	114	17.5	40	0.44	0.45	1.02
	1730	222	114	22.5	40	0.56	0.51	0.92
	1830	157	114	17.5	40	0.44	0.73	1.66
	1910	213	114	17.5	40	0.44	0.54	1.23
	2030	158	114	17.5	40	0.44	0.72	1.64
	2140	186	114	17.5	40	0.44	0.61	1.39
	2720	179	114	17.5	40	0.44	0.64	1.45
Vulpia fasciculata[6] (caryopses)	NA	NA	NA	0.05	0.03	1.67	1.3	0.78
	NA	NA	NA	0.06	0.07	0.86	1.3	1.51
	NA	NA	NA	0.11	0.11	1.00	1.3	1.30
Asclepias syriaca[7] (seeds)	4.9	25.9	139	3.8	1.0	3.8	5.4	1.42
	4.9	25.9	139	1.7	0.5	3.4	5.4	1.59
	5.1	32.6	139	6.0	1.0	6.0	4.3	0.72
	5.1	30.5	139	1.6	0.5	3.2	4.6	1.44
	5.1	42.9	264	4.0	1.0	4.0	6.1	1.53
	5.1	42.9	264	1.1	0.5	2.2	6.1	2.77
	5.3	34.9	139	4.3	1.0	4.3	4.0	0.93
	5.3	34.9	139	2.1	0.5	4.2	4.0	0.95
	5.7	36.6	139	9.9	1.0	9.9	3.8	0.38
	5.7	36.6	139	4.0	0.5	8.0	3.8	0.48
	5.9	32.6	139	4.4	1.0	4.4	4.3	0.98
	5.9	26.3	139	2.9	0.5	5.8	5.3	0.91
	6.2	33.3	139	3.8	1.0	3.8	4.2	1.11
	6.2	33.3	139	3.4	0.5	6.8	4.2	0.62
	6.5	34.9	139	1.5	1.0	1.5	4.0	2.67
	6.7	36.6	264	4.2	1.0	4.2	7.2	1.71
	7.1	34.9	264	6.2	1.0	6.2	7.6	1.23
	7.1	34.9	264	1.8	0.5	3.6	7.6	2.11
	7.6	34.9	264	11.3	1.0	11.3	7.6	0.67
	7.6	34.9	264	4.9	0.5	9.8	7.6	0.78
	7.9	36.6	264	2.5	0.5	5.0	7.2	1.44
	8.0	37.5	264	3.1	0.5	6.2	7.0	1.13
	8.2	35.7	264	5.8	1.0	5.8	7.4	1.28
Asclepias syriaca[8] (seeds)	8.8	24.9	347	10.5	1.0	10.5	13.9	1.32
Oenothera biennis[8] (seeds)	0.2	120	347	1.6	0.85	1.88	2.89	1.54
Solidago rigida[8] (seeds)	0.5	33.6	347	4.0	0.85	4.71	10.3	2.19
Verbena stricta[8] (seeds)	1.0	166	347	0.9	0.85	1.06	2.09	1.97
Apocynum sibiricum[8] (seeds)	1.2	99	347	20.5	0.85	24.1	34.7	1.44
Cirsium undulatum[8] (seeds)	6.2	30.0	347	17.0	1.0	17.0	11.5	0.68
Mirbilis hirsuta[8] (seeds)	15.7	217	347	0.40	0.85	0.47	1.6	3.40
Senecio jacobaea[9] (seeds)	NA	41	278	3.6	1.25	2.88	6.78	2.35
	NA	41	278	2.6	0.75	3.47	6.78	1.95
	NA	41	278	2.2	0.5	6.13	6.78	1.11
	NA	41	417	2.1	1.5	1.40	10.2	7.29
	NA	41	417	1.8	1.25	1.44	10.2	7.08
	NA	41	417	1.1	0.75	1.47	10.2	6.94
Tragopogon dubuis[10] (seeds)	7	13	156	2.0	0.6	3.3	12.0	3.64
Pinus ponderosa[11] (pollen)	NA	20.3	39.5	5.8	3.7	1.57	1.95	1.24
Lycopodium spp.[12] (spores)	NA	1.76	80	5	0.5	10	45.5	4.55
	NA	1.76	80	10	0.5	20	45.5	2.2

TABLE 1. Continued.

Species and source	W (mg)	W_s (cm/s)	$\bar{u}$ (cm/s)	x_m (m)	H (m)	x_m/H	$\bar{u}/W_s$	λ
Plantago lanceolata[13] (pollen)	NA	1.7	124	0.8	0.08	10	73	7.30
Ambrosia trifida[14] (pollen)	NA	1.56	290	20	1.5	13.3	186	14.0
Podaxis spp.[15] (spores)	NA	0.5	110	5	0.5	10	220	22.0

* W: mass of seed; W_s: falling velocity of seed; $\bar{u}$: mean wind speed; x_m: modal dispersal distance, except for *Podaxis* spores (source 15); H: height of seed release; λ: ratio of $\bar{u}_m/W_s$ and x_m/H; NA: not available.

[1] Augspurger and Hogan (1983) supplemented by *personal communication.*
[2] Cremer (1977).
[3] Cremer (1966).
[4] Isaac (1930), W_s estimated.
[5] Augspurger and Franson (1987), $\bar{u}$ estimated from $\lambda \equiv 1$ for experiment with $W = 850$ mg.
[6] Watkinson (1978), $\bar{u}/W_s$ estimated.
[7] Morse and Schmidt (1985), x_m = dispersal distance.
[8] Platt and Weis (1977) supplemented by *personal communication.*
[9] McEvoy and Cox (1987) supplemented by *personal communication.*
[10] Gross (1986, *personal communication*).
[11] Colwell (1951).
[12] Sreeramula and Ramalingam (1961), 32 μm in diameter.
[13] Tonsor (1985), 23 μm in diameter, W_s estimated from Gregory's diagram (1973).
[14] Raynor et al. (1970), 20 μm in diameter.
[15] Sreeramula and Ramalingam (1961), 14 × 11 μm spores, W_s estimated from Gregory's diagram (1973).

shown that the mode of the dispersion distribution is inversely proportional to λ and to the settling velocity of seeds, and directly proportional to height of release and to wind velocity.

DATA ANALYSIS

To compare actual dispersion relationships with our model predictions, we need information regarding the modal dispersal distance x_m, height of seed released H, mean wind speed $\bar{u}$, and falling velocity W_s of seed. Only a limited number of studies provide all of this information, but there is a growing collection. Data from 15 studies were obtained from the literature and from personal communications from colleagues (Table 1).

The choice of the mode x_m as a measure of dispersal distance has a twofold motivation. First, our mathematical results (Eqs. 8 and 27) are based on the mode rather than on the mean $\bar{x}$ or other measures. Second, the estimation of x_m from experiments is subject to less error compared with that of $\bar{x}$, simply because the calculation of $\bar{x}$ depends much more upon the tails of the spatial distribution of seeds, that is, on distances far from the source.

Fig. 6 shows the basic seed dispersal diagram, where the modal dispersal distance normalized by the height of seed released is plotted against the mean wind speed normalized by the falling speed of seed. Also shown in the figure are isolines of λ, indicating several different ratios of $\bar{u}/W_s$ and x_m/H.

Generally speaking, the data points lie above $\lambda = 1.0$. As the falling velocity of seeds increases, the normalized modal dispersal distance decreases; very heavy seeds whose falling speed exceeds 3 m/s are dispersed almost exactly according to the predictions of the model. In practice, for heavy seeds with $W_s > 1$ m/s, we can estimate the modal dispersal distances by $H\bar{u}/W_s$ (e.g., Augspurger 1986). On the other hand, as the falling velocity decreases, the normalized modal dispersal distance increases, while the data points tend to deviate upward from the line $\lambda = 1$. This means that the normalized modal dispersal distance for light seeds (spores and pollen) is less than that given by the simple formula $H\bar{u}/W_s$. In this case, if we introduce another parameter W^*/W_s, namely the ratio of the vertical turbulent mixing velocity and the falling velocity of seed, then λ can be interpreted as a measure of W^*/W_s. Indeed, λ tends to W^*/W_s as $W^*/W_s \to \infty$.

DISCUSSION

The quantification of seed dispersal is of fundamental importance in developing an understanding of the population biology of plants, and of the dynamics of plant communities (Harper 1977). As data accumulate concerning the relationship of dispersion distances to environmental and species-specific parameters, and to such parameters as height of release, the need increases for a framework within which to organize that information. Conventional models are primarily phenomenological, and do not provide a basis for extrapolation from one environment to another, or from one species to another. Models are needed that relate dispersal distances to such measurable parameters as wind speed and settling velocity, which thereby allow comparisons among different environments.

In this paper, we discuss the standard phenomenological models of dispersal, and then consider two more specific models borrowed from the atmospheric diffusion literature. The tilted Gaussian plume model, which is the more simplistic, predicts that the mode x_m of the dispersal distribution is proportional to the wind speed u and to the height of release H, and is

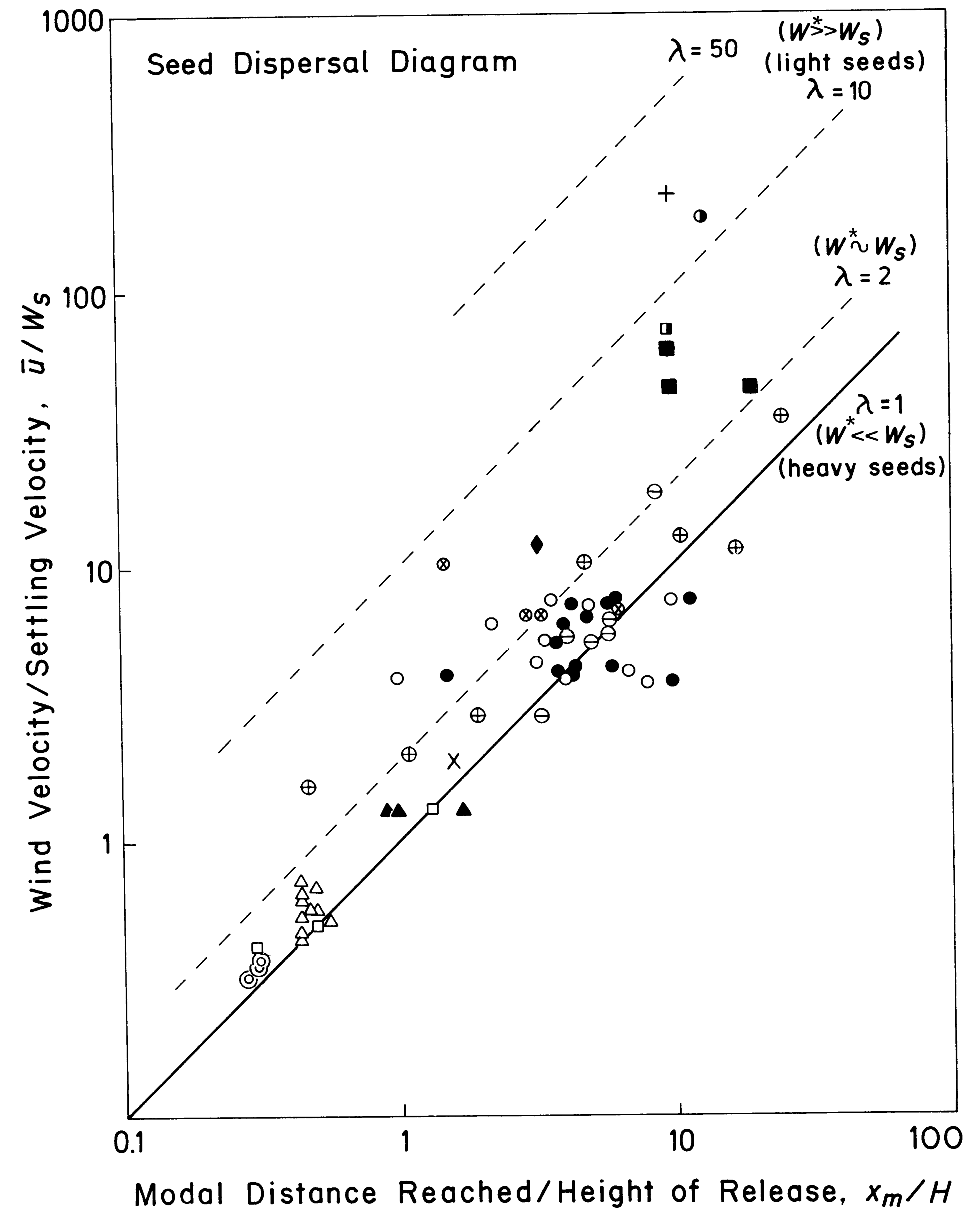

FIG. 6. Seed dispersal diagram. Relationship between the mode of dispersal distance and the mean wind speed (nondimensionalized form) for various values of λ. x_m denotes mode of seed travel distance, H denotes height of seed source, $\bar{u}$ denotes mean wind speed, W_s denotes settling velocity of seed. Here $\lambda = (\bar{u}/W_s)/(x_m/H)$. ◎ Augspurger-Hogan, △ Augspurger-Franson, ⊗ McEvoy-Cox, ◆ Gross, □ Cremer, ⊕ Platt-Weis, ▲ Watkinson, ⊖ Isaac, ●○ Morse-Schmidt, × Colwell, ■ + Sreeramula-Ramalingam, ◨ Tonsor, ◑ Raynor.

related in a more complicated way to settling velocity W_s and turbulent mixing velocity W^*. For each, a dimensionless number λ is defined that characterizes the relative importance of turbulence and gravitation. For heavy seeds, $\lambda \approx 1$ and one obtains the simple approximation

$$x_m \sim H\bar{u}/W_s; \qquad (32)$$

whereas, for light seeds, $\lambda \gg 1$ and

$$x_m \sim H\bar{u}/W^*. \qquad (33)$$

The tilted Gaussian plume model is seen to provide a good approximation for the more explicit boundary-value problem (see Models of Advection, Diffusion, and Settling). For that problem, it is again shown that x_m, the mode of the dispersion distribution, is proportional to H and u, with proportionality constant $(W_s + W^*)^{-1}$. That is,

$$x_m = H\bar{u}/(W_s + W^*). \qquad (34)$$

This compares with the formula

$$x_m = H\bar{u}/(\sqrt{W_s^2 + (W^*/2)^2} + W^*/2), \quad (35)$$

which holds for the tilted Gaussian plume model. In the limits (W_s/W^* zero or infinite), these formulas are identical. For intermediate values, however, the tilted plume model always gives a somewhat larger value of x_m than does the more detailed model.

In Fig. 6, our calculations are used to produce a summary diagram within which to array dispersal data. These do not represent a test of Eq. 28, since in general W^* is not directly measurable. Recall, however, that λ is a measure of the relative importance of turbulent and gravitational forces, a quantity analogous to a Reynolds number. For heavy seeds, $\lambda \approx 1$, whereas, for light seeds, $\lambda \gg 1$. Thus, the placement of points in Fig. 6 can be compared with qualitative judgments concerning the values of λ, and the method provides an objective classification system. We present within that diagram a fairly large body of data on dispersal distances (accumulated in Table 1), and would welcome additional data for comparison.

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APPENDIX

Effects of nonstationarity

In both models (see Gaussian Plume Models, and Models of Advection, Diffusion, and Settling) the wind and vertical diffusivity are variable with height, but stationary in time. Thus $\bar{u}$ and W^* have been taken as time independent. However, Eq. 27 can still be applied under nonstationary wind and diffusivity regimes, if the parameters are slowly varying. We consider an ensemble average of x_m over temporal variations in $\bar{u}$ and W^*. Let $\langle R \rangle$ denote the ensemble average of R, and R' the fluctuation of R about the average:

$$R = \langle R \rangle + R', \tag{A.1}$$

where

$$\langle R' \rangle \equiv 0. \tag{A.2}$$

For small values of W^*/W_s (heavy seeds), Eq. 27 is approximated by

$$x_m = (H\bar{u}/W_s)\,(1 - W^*/W_s). \tag{A.3}$$

Expressing x_m, $\bar{u}$, and W^* in Eq. A.3 according to Eq. A.1 and taking ensemble averages, we obtain

$$\langle x_m \rangle = (H\langle \bar{u} \rangle/W_s)\{1 - (1 + \rho)\langle W^* \rangle/W_s\} \tag{A.4}$$

or

$$\langle \lambda_m \rangle(\langle x_m \rangle/H) = \langle \bar{u} \rangle/W_s, \tag{A.5}$$

with

$$\langle \lambda_m \rangle = \{1 - (1 + \rho)\,\langle W^* \rangle/W_s\}^{-1} \approx 1 + (1 + \rho)\,\langle W^* \rangle/W_s \approx 1. \tag{A.6}$$

Here ρ is defined by

$$\rho = \langle \bar{u}' W^{*\prime} \rangle/\langle \bar{u} \rangle\langle W^* \rangle. \tag{A.7}$$

In general $\bar{u}$ and W^* are positively correlated, so that $\rho \geq 0$. We assume that fluctuations are small, so that $\rho \ll 1$. In the absence of variation, Eq. A.6 collapses to Eq. 29. The relation Eq. A.5 should be compared with Eqs. 28 and 10. The environmental variability in $\bar{u}$ and W^* would not have a significant effect on the seed dispersal diagram if we were to estimate x_m and $\bar{u}$ by the ensemble averages.

For large values of W^*/W_s (light seeds), a procedure similar to that used for the case of small W^*/W_s modifies Eq. 27 to

$$\langle x_m \rangle = \{H\langle \bar{u} \rangle/\langle W^* \rangle\}\{(1 - \rho) - W_s/\langle W^* \rangle\} \approx (H\langle \bar{u} \rangle/W_s)\{(1 - \rho)\; W_s/\langle W^* \rangle\} \tag{A.8}$$

or

$$\langle \lambda_m \rangle\{\langle x_m \rangle/H\} = \langle \bar{u} \rangle/W_s. \tag{A.9}$$

Here

$$\langle \lambda_m \rangle = \langle W^* \rangle/(1 - \rho)W_s \gg 1. \tag{A.10}$$

Again the asymptotic behavior for the ensemble quantities is very similar to that of the stationary case. When there is no variation, Eq. A.10 collapses to Eq. 31.