WIND DISPERAL OF SEEDS FROM A FOREST INTO A CLEARING

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Abstract. Although there are many studies of wind dispersal of seeds from a forest into an adjacent clearing, no physical model has yet been advanced. The model constructed here calculates the trajectories of seeds from individual trees in the area source to a line of seed traps (in the clearing) oriented perpendicular to the forest edge. The model uses a log-normal distribution of horizontal wind velocities at a nearby reference station to evaluate wind velocities at any point in the forest and clearing as a function of both height above the ground and distance from the forest edge. The model predicts that (1) the slope of the area source dispersal curve (seed density vs. leeward distance) approximates a negative exponential; and (2) the great majority of seed deposition in the clearing is contributed by source trees lying within a few tree heights of the forest edge. An evaluation of previously published empirical data shows that the area source model adequately characterizes the decline in seed density with leeward distance.

Key words: area source dispersal curve; clearcuts; micrometeorological dispersal model; seed dispersal; seed traps; small particle dispersal model; terminal velocity; wind dispersal; wind profiles.

INTRODUCTION

Seed dispersal plays an important role in both applied and theoretical problems. Decades of forestry research have shown that clearcuts with diameters exceeding \( \approx 200-400 \) m will be poorly stocked by naturally regenerating tree species because of dispersal constraints (e.g., Barrett 1966, Ronco 1970). Two empirical solutions to the problem (narrow strip-cuts or residual patches of "seed trees" in large cuts) could become landscape design solutions if we had a model relating seed deposition to distance and source strength.

There are at least two broad classes of arguments for landscape-scale persistence of tree species where seed dispersal plays a crucial role. The "shifting mosaic" model of Bormann and Likens (1979) views poor competitors (shade intolerants) as good dispersers who have therefore the advantage of early arrival in rare, ephemeral, large gaps. At the opposite extreme, metapopulation models argue that species are effectively equivalent competitors whose constituent local populations are randomly walking toward extinction or monoculture, but the rate of change is slowed by seed exchange within the metapopulation (Hanski and Gilpin 1991). More empirically, it has been demonstrated by field experiments that seed dispersal can be a serious constraint on local species distribution (e.g., Primack and Miao 1992).

Nonetheless, we know surprisingly little about the process of seed dispersal (Levin 1984). Simple analytical models for the dispersion by wind of heavy particles (such as seeds) from a point source (for example, a tall tree) have been derived and tested (e.g., Walker 1965, Stewart 1968, Greene and Johnson 1989). Such models could easily be extended to the dispersal of seeds from an area source (a collection of point sources) by computer simulation. The area source models must not assume that the horizontal wind velocity is independent of lateral distance from the source. It is well known that horizontal wind velocities at a given height change significantly with distance leeward of an obstacle such as a forest (e.g., Nageli 1953, Caborn 1957, Flemming 1968, Raynor 1971), and therefore these models cannot be applied to the dispersal of seeds across a forest/clearing edge. Instead, these models are limited to cases such as (1) an isolated tree in a field, and (2) a tree dispersing seeds solely within a forest. This is unfortunate as it has become clear that many plant species require a canopy gap for successful recruitment into the canopy (Pickett and White 1985), that is, the more significant dispersal events involve flight trajectories across forest/clearing edges.

The objective of this paper is to construct a micrometeorological model of the dispersal of seeds from a forest to an adjacent clearing. The model will be tested using forestry studies of dispersal into clearcuts as well as our own studies of dispersal into burns and clearcuts.

One might wonder: why rely on models when seed deposition can be measured directly in the field? There are two reasons. First, accurate characterization of a dispersal curve requires a dense network of seed traps and we may have to wait as much as 5 yr to obtain an adequate seed production year. In addition, this time-
consuming enterprise will not permit us to generalize to other species or other sites where, for example, forest height may be different.

**The Model**

The dispersal model is for an array (forest) of point sources (single trees) with each point source idealized as abscising all seeds from a point in three-dimensional space. Model derivation requires four steps. First, we assume a log-normal distribution of horizontal wind speeds at a standard meteorological reporting station. We then modify this distribution to account for the nonrandom nature of seed abscission. Third, we link the reference station wind speed to the speed at the top of a forest, and subsequently down through the forest to the ground. Fourth, we relate the reference station wind speed to the speeds within the clearing. At this point, the wind structure in both forest and clearing has been established and therefore the seed disposition from any tree to any Cartesian coordinate in the clearing can be estimated. A list of symbols and recommended model default values can be found in the Appendix.

**Distribution of wind speeds at a reference station**

Assume a log-normal distribution of wind speeds at height $z$, (the standard height is 10 m) at a reference station (typically an airport) where air flow is unobstructed by the fetch (drag) of trees or buildings (Greene and Johnson 1989). Although we will modify this shortly, assume further that abscission is random with respect to wind speed. Then, the number of seeds abscising from a source at any wind speed $u$ is

$$dQ/du = Q(\sqrt{2\pi} \sigma_u)^{-1} \times \exp(-1/2\sigma_u^2 [\ln(u/u_0)^2]),$$

(1)

where $Q$ is the number of seeds on the tree, $u_0$ is the median horizontal wind speed, and $\sigma_u$ is the standard deviation of the natural logarithms of the horizontal wind speeds. At 10 m height, North American airports give a long-term average $u_0$ of 4.3 m/s (range of 2.0–6.5 m/s: Hare and Thomas 1974, Luna and Church 1974) and average $\sigma_u$ of 0.55 (Luna and Church 1974).

**The effect of nonrandom abscission**

Thus far, we have attempted to model the flow regime as measured by anemometers rather than by abscising seeds. But as stressed by Greene and Johnson (1989), wind-dispersed diaspores preferentially abscise at higher wind speeds. The recent study by Greene and Johnson (1992a) for *Acer saccharinum* L. is the only quantitative study of the probability of abscission in relation to horizontal wind speed and we will assume that the relationship identified there is similar for other species.

Greene and Johnson (1992a) found that the probability of abscission was roughly proportional to drag (that is, to the square of the horizontal wind speed), and thus the joint probability ($j$) of abscission and the frequency of a given wind speed ($u_f = dQ/du$: see Eq. 1) is:

$$j = (u^p u_f) \int_{u=0}^{u_{\infty}} u^p u_f \, du,$$

(2)

where $p \approx 2.0$. The integral in Eq. 2 is equal to the moment-generating function for a log-normal distribution (the $p$th moment):

$$\int_{u=0}^{u_{\infty}} u^p u_f \, du = \sigma_u^p \exp(p^2 \sigma_u^2/2).$$

With some manipulation it can be shown that the effect of nonrandom abscission is to increase the median speed of Eq. 1 such that

$$u_{vr} = [\exp(\sigma_u^2)] u_{vr},$$

(3)

where $u_{vr}$ indicates the median speed given abscission, and $u_{vr}$ is the median speed measured by anemometers at the reference station. Assuming that $p \approx 2.0$ and that $\sigma_u = 0.55$, then $u_{vr} = 1.83 u_{vr}$. Thus, our default value of the median speed (airport) is increased from 4.3 to 7.87 m/s. In what follows we will assume $u_{vr} = 7.87$. This is reasonable because $\sigma_u$ is an inverse function of $u_{vr}$ (Luna and Church 1974), such that over the range 2.0 < $u_{vr}$ < 6.5 m/s we expect $u_{vr}$ to be within 25% of 7.87 m/s. That is, geographic differences in median speed are rendered relatively unimportant by nonrandom abscission.

**Linkage to the forest top**

The vertical profile (speed at height, $z$) of the horizontal wind speeds at the reference station will be modeled as a power-law function:

$$u_r = u_{r0}(z/z_{c})^m,$$

(4)

where $u_r$ is the speed at height $z$ at the reference station, $z_c$ is the reporting height (typically 10 m), $u_{r0}$ is the speed at $z_c$, and the exponent $m$ is typically on the order of 0.14 for neutral stability (Pasquill and Smith 1983). The coupling of the reference station flow to the supracanopy flow at the nearby forest can be made at the height $2z_s$ (where $z_s$ is forest height) because at this altitude the drag of the underlying forest should be insignificant (Dumbauld and Cionco 1985). Thus, from Eq. 4

$$u_{2z_s} = u_{r0}(2z_s/z_c)^m,$$

(5)

with $u_{2z_s}$ the wind speed at double the forest height. We can relate this speed well above the canopy flow to the speed at the top of the canopy ($u_{zh}$) by employing a supracanopy flow model for neutral stability:

$$u_{zh} = \frac{u_{2z_s} \ln(z_{zh} - d + z_s/z_c)}{\ln(2z_s - d + z_s/z_c)},$$

(6)
where the displacement height, \( d \), and roughness length, \( z_0 \), are on the order of (Oke 1978):

\[
d = 0.67 z_h, \quad z_0 = 0.105 z_h.
\]

These standard values of \( d \) and \( z_0 \) are for forests with a full canopy of leaves. Data for leafless canopies are rare. Data of Allen (1968) for a leafless *Larix* canopy indicate that \( z_0 = 0.1 z_h \) and \( d = 0.15 \) smaller than the lower canopy value and we will use these as default values for leafless canopies.

**Release height in the forest**

Within the crown of a canopy tree, seeds are distributed vertically in a roughly Gaussian manner from the forest top \( (z_h) \) down to \( 0.5 z_h \). Published values for the mean height \( z_s \) of a conifer seed crop range from 0.65 \( z_h \) to 0.85 \( z_h \) (Lyons 1956, Hard 1964, Hallidin 1985), and we choose \( z_s = 0.75 z_h \) as a default value.

**Canopy flow**

Having estimated the speed at the top of the forest, we now describe the vertical profile of horizontal wind speeds from the forest top to the ground. Following Dumbauld and Cionco (1985):

\[
u_z = u_{z_h} \exp(\alpha [(z/z_h) - 1]),
\]  

where \( u_z \) is now a speed within the forest and \( z_h \) is an empirical coefficient related to the leaf area index (and, thus, to drag). Reasonable default values are \( \alpha = 4 \) for a canopy with full leaf extension, and \( \alpha = 2 \) (leafless canopy). A major problem with Eq. 7 and similar models of canopy flow (e.g., Landsberg and James 1971) is that the wind speed is greatly underestimated in the lower half of the forest \( (z < 0.5 z_h) \) where few leaves or twigs are found (Fig. 1). Indeed, wind speed is virtually independent of height in the lower half (e.g., Landsberg and James 1971). A much better approximation is made if we restrict Eq. 7 to the upper half of the forest and then assume

\[
u_z = u_{z_h} \exp(-\alpha/2),
\]

when \( z \leq 0.5 z_h \).

Let us verify that this modified canopy flow model and the coupling of the forest and airport regimes are valid. Assuming a canopy in full leaf and employing all the default values recommended thus far, we predict that the median long-term wind speed at 2 m height in the forest ought to be \( \approx 12 \% \) of the median speed at 2 m height at the reference station (airport). Nageli (1953) reported that the (coniferous) forest median speed at this height is \( \approx 11-14 \% \) of the reference value. Thus, both the coupling and the modified flow model appear to be generally consistent at least with this one study.

**Flow in the clearing**

Within the clearing, we will assume that the vertical profile is a power-law function like Eq. 4 with an exponent identical for both clearing and airport. This assumption is undoubtedly invalid near the forest edge, but we know of no useful modelling of the transition from canopy profiles to clearing profiles.

Fig. 2 depicts the relationship between horizontal wind velocities measured at equal height in a study site and a nearby reference station (Nageli 1953). The ordinate is scaled as a percentage of the reference wind speed and the ratio of leeward distance from the forest edge \( (x_f) \) and forest height \( (z_h) \). We fit the following equation to these data:

\[
u_w = u_z 0.508(x_f/z_h)^{0.186} \] (full leaf),

where \( u_w \) and \( u_z \) are measured at equivalent heights. Note that \( x_f \) refers to the distance from the forest edge to a clearing point along the direction of the wind. The equation is valid for any wind direction whether perpendicular or oblique to the forest edge (Flemming
1968). Unfortunately, the equation is for a forest in full leaf and is clearly invalid for a leafless forest. Coupling Eqs. 7 and 9 for a leafless forest would mean that the wind decreases at the clearing edge, and thus the edge becomes, relatively a sink for seed deposition. We can avoid this problem by asserting that the speed at $x_c = 0.5$ is equal to the speed inside the forest at $z = z_a$ and thus, for a leafless forest,

$$u_{gr} = u, 0.88 \left( x_c/z_a \right)^{0.186} \text{ (leafless).} \quad (10)$$

Note that Eq. 10 forces us to use the model at values of $(x_c/z_a) < 2.0$ so that the leeward wind speed does not exceed the reference wind speed.

**Turbulence within the forest**

We now examine default values for the turbulence intensities. The turbulence intensities in the horizontal ($i_u$) and vertical ($i_w$) are defined as

$$i_u = \sigma_u / \bar{u} = \sigma_{u^*},$$

$$i_w = \sigma_w / \bar{u},$$

where $\sigma_u$ and $\sigma_w$ are the standard deviations of horizontal and vertical wind speeds, respectively, at height $z_a$ and $\bar{u}$ is the mean horizontal speed at that height. Given the log-normal assumption (Eq. 1), then $i_u = \sigma_{u^*}$.

Raupe and Thom (1981) indicated that $i_u = 0.6$ is typical in the upper forest canopy and this is similar to the averaged North American airport value (10 m height) of 0.55 (Luna and Church 1974). Dumbauld and Cionco (1985) argued that $i_u$ should decline moderately with decreasing height in the canopy and average $= 0.45$ from 0.75 $z_a$ (our assumed release height) to $0.5 z_a$. Nonetheless, the modelling is simplified enormously if we assume that $i_u = 0.55$, irrespective of height or horizontal position (forest or clearing). We will adopt this simplifying fiction.

Likewise, Dumbauld and Cionco (1985) indicate some decrease in $i_w$ from $z_a$ to 0.5 $z_a$, and we will assume a typical value of 0.21. This is not much larger than reported values of vertical turbulence intensity in large clearings (0.08 $< i_w < 0.2$ for a variety of stability classes: see Pasquill and Smith 1983). As with $i_u$, we let this value of $i_w$ be independent of height or lateral position. Interestingly, the turbulence intensities are relatively insensitive to changes in $\alpha$ (Dumbauld and Cionco 1985). The values of $i_u$ and $i_w$ suggested here also will not vary markedly across the likely range of $z_a$ for forests (say, 15 $< z_a < 45$ m), and thus we will treat them as constants independent of forest height. Further, we will assume that these turbulence intensities are unaffected by our increase of $u_{gr}$ and $\bar{u}$, as we account for the abscission effect.

Given $u_{gr} = 4.3$, the default values, $\bar{u} = 5.0$ m/s, and the linkage to canopy flow, we can calculate $\sigma_u$ at any height within the forest. In the interest of simplification, however, we will average $\sigma_u$ from $z_a$ to the ground. Given the above equations and default parameters, then the mean horizontal wind speed averaged from $z_a$ to the ground (assuming $z_a = 25$ m) is $\approx 0.6$ m/s ($\alpha = 4$) or 1.4 m/s ($\alpha = 2$). Thus, roughly,

$$\sigma_u = 0.13 \text{ (full leaf),}$$

$$\sigma_u = 0.29 \text{ (leafless).}$$

The variance in fall velocities ($\sigma_r$) of a population is comprised of the variance in vertical wind speeds ($\sigma_z^2$) and terminal velocities ($\sigma_f^2$). As shown by Greene and Johnson (1992b), the standard deviation of the terminal velocities of seed populations is typically

$$\sigma_f \approx 0.13 \nu_p,$$

where $\nu_p$ is the mean terminal velocity. Given the additivity of the variances of a function, and that both the terminal velocities and vertical wind speeds have Gaussian distributions, and should be independent, then

$$\sigma_r = \sqrt{(0.13 \nu_p)^2 + \sigma_z^2}. \quad (11)$$

This equation for $\sigma_r$ will be used subsequently as our measure of the variation in fall velocities.

**Estimating the deposition from each point source**

For simplicity, imagine a landscape, as in Fig. 3, in which the conspecific seed-bearing plants are spaced uniformly within the forest at density $B$ (number per square metre) and each seed-bearing plant produces $Q$ seeds per dispersal season. The mean density of seed deposition well within the forest is given by the product $BQ$. The objective is to estimate the density of seed deposition ($N_s$) at distance $x$ along the perpendicular line of seed traps (Fig. 3).

The origin in the Cartesian coordinate system is placed at the point where the trap-line intersects the forest edge. The forest edge is labelled $Y$. To the right of the origin, the abscissa (trap-line) is labelled $x$, and to the left of the origin the abscissa is labelled $D$. Both $D$ and $x$ are positive numbers increasing in size with distance from the origin.

We now must determine the value of $u_r$ that permits the dispersal of a seed (or crop fraction) from a tree $(Y, x)$ to a point located at $x$. Unfortunately, joining Eqs. 4 and 7 through 10 results in a differential equation that can only be solved by iteration. A closed form solution can only be found by making two additional assumptions.

Within the clearing the mean horizontal speed averaged vertically and downwind ($u_{gr}$) is given by integration of Eqs. 4 and 9 or 10:

$$u_{gr} = u, 0.88 \left( x_c/z_a \right)^{0.186} \text{ (leafless),} \quad (12)$$

where $\alpha = 0.38$ (full leaf) and $\alpha = 0.65$ (leafless).

Properly, $z_c/2$ ought to be replaced by $z_a$ (the exit height of the seed at the forest edge), but this would lead to the necessity for an iterative solution. Given
that the exponent \( m \) is quite small, this assumption makes little difference quantitatively.

The second required assumption for a noniterative solution involves the mean horizontal speed \( (u_n) \) within the forest that ought to be averaged from \( z_a \) (release height) to \( z_e \) (exit height). Here we will assume that the mean speed is on the order of \( u_{m} \) and therefore,

\[
u_x = b u_n (z_e/z_a)^m, \tag{13}\]

where \( b = 0.116 \) (full leaf), and \( b = 0.21 \) (leafless). By definition (Greene and Johnson 1989)

\[
x_p = z_e u_{sp}/v_f \]

and substituting Eq. 12

\[
x_p^{0.814} = z_{m, a} (z_e/2)^m v_f^{1.0} z_a^{0.186} z_{e}^{-m}, \tag{14}\]

where the exit height \( (z_e) \) is via Eq. 13

\[
z_e = z_a - [(x_p v_f z_e)/(bu_z_e^2)],\]

and thus rearranging to solve for \( u_x \),

\[
u_x = (v_f/z_e) \times [(x_p^{0.814} z_a^{0.186} a^{-1.0} (z_e/2)^{-m}) + (x_p b^{-1.0} z_a^{-m})]. \tag{15}\]

For a single tree dispersing \( N_x \) (number per square metre) seeds at \((Y, D)\) we use Eq. 1, invoke the assumption of random or uniform azimuths during the times when seeds are abscising [and thus we must divide the expected deposit by \( 2\pi(x_p + x_D) \)], differentiate Eq. 15 with respect to \( x_p \), apply the chain rule, and arrive at the resulting dispersal equation:

\[
dN_x/dx_p = (dQ/du_x)[(2\pi(x_p + x_D))^{-1.0} \times [0.814 v_f z_a^{0.186} x_p^{0.814}a]/[z_e(z_e/2)^m x_p^{0.186}a]]. \tag{16}\]

where \( dQ/du_x \) is from Eq. 1 (with \( u_x \) substituted for \( u_n \)) and \( x_p \) is used for \( x_p \).

Before we turn to the problem of a homogeneous area source, it should be pointed out that Eq. 16 is easily used for sources contagiously distributed within the forest. Whether one is interested in the deposition from a single tree or the deposition from a number of source “patches” at estimated coordinates \((Y, D)\), one need only calculate

\[
x_p = [x^2 + y^2(D + x)^2]^{0.5}, \tag{17}\]

\[
x_D = [(D + x)^2 + y^2]^{0.5} - x_p, \tag{18}\]

and increase \( Q \) in proportion to the number of seed sources in the patch. Where the forest edge curves greatly and \( x \) is small, the investigator must resort to a spatially explicit computer simulation.

A homogenous area source

From an area source of infinite depth \((D)\) and width \((Y)\), and with a uniform spacing of point sources at density \( B \) and seed production \( Q \), then Eq. 16 becomes a double summation across \( Y \) and \( D \). In practice, the area source need not be infinite because distant sources make negligible contributions to \( N_x \), on the order of \( Y > 6 z_f v_f \) and \( D > 5 z_f v_f \).

Results for an infinite area source are shown in Fig. 4 where the abscissa is scaled as the nondimensional dispersal parameter \((T)\), which was obtained by rearrangement of Eq. 14 (and substitution of \( x \) for \( x_p \), \( z_a \) for \( z_e \), and \( u_x \) for \( u_n \)):

\[
T = x^{0.814} (2z_e/z_{m, a})^{m} v_f z_a^{0.186} a/(z_{m, a}^{0.5}), \tag{19}\]

or, assuming as above that \( z_e = 10 \) m, \( z_a = 0.75 z_{m, a} \), \( m = 0.14 \), and \( u_x = 7.87 \) m/s, then

\[
T = 0.27 x^{0.814} v_f a^{0.954}. \tag{20}\]

In addition to the results for the leafless and full leaf models, Fig. 4 also depicts deposition in an imaginary situation where the forest exerts no drag, that is, wind speed is independent of horizontal position and dependent only on height via Eq. 4. Thus, the “no drag” curve depicts merely the effect of source geometry on the decline in \( N_x \). Note that in this idealization the seed
Fig. 4. Modelling results for the decline in seed density ($N_x$) vs. the nondimensional dispersal parameter ($T$). $BQ$ (the density of deposited seeds well inside the forest) with $BQ = 10$ seeds/m$^2$. The dotted line represents Eq. 21, while the dashed line is Eq. 22.

Dispersal from a leafless forest is virtually a straight line on the semi-log plot in Fig. 4. The deposit at the forest edge is half the source strength ($0.5BQ$). The data points represent examples with forest height equal to 45 m, distance ($x$) less than 90 m (we are constrained by Eq. 10 to keep $x/z_a < 2.0$), and terminal velocity ranging up to 5.0 m/s (much higher than any North American species, but we seek large $T$ values and must compensate for the limit on $x/z_a$).

By contrast, the full canopy leads to a much steeper initial decline (because horizontal wind speeds are much lower now in the immediate lee of the forest). Data points represent the ranges $15 \leq z_a \leq 45$ m, $0.3 < v_f < 1.7$ m/s, and $1 < x < 201$ m.

The effect of $\sigma_v$ (variation in settling velocities) is necessarily small at low $x$. At $x/z_a = 8$ it adds little to deposition for full canopy forests but increases deposition by $\approx 25\%$ for leafless forests when $v_f$ is as large as 1.7. Since in this paper we focus on dispersal within the first few hundred metres of a forest edge, and since for most tree species $v_f \approx 1.0$, we will ignore the effect of $\sigma_v$ (that is, variation in vertical wind speeds and seed crop terminal velocities) in what follows.

Not surprisingly, the bulk of the deposited seed in a clearing is derived from point sources near the edge. For example, at $x = 200$ m (and with $v_f = 1.0$ m/s), 90% of the deposition is due to trees within $D < 2.2z_a$ (full canopy) or $D < 3.8z_a$ (leafless). This is of some interest in arguments concerning gene flow in fire-prone (large gap) landscapes, or in the minimal size of residual strips left to disperse seeds into large strip-cuts.

In many cases ecologists or foresters are interested in area sources sufficiently large for the results in Fig. 4 to be applicable. Simple approximations (shown in Fig. 4) that can replace a summation of Eq. 16 were based on a modified negative exponential function

$$N_x = 0.5BQ \exp(-\phi T^q),$$

where the exponent $\phi$ accounts for the initially steep decline. Iteration of the simulation results to minimize the residual sums of squares yielded the parameter estimates:

$$N_x = 0.5BQ \exp(-2.647 T^{0.722}), \quad \text{(full canopy)}$$

$$N_x = 0.5BQ \exp(-2.317 T^{0.87}), \quad \text{(leafless)}$$

where $T < 2.5$.

**Problems**

The default value of each parameter is presented in the Appendix. Here we will point out four major problems with the model.

The first problem regards abscission. As shown by Greene and Johnson (1989), there is anecdotal evidence from a wide variety of taxa that the probability of abscission increases with wind speed. However, the function may not be similar to the results obtained with *Acer saccharinum* (Greene and Johnson 1992a). Until other studies become available, there seems little choice except to naively extend our result. Additionally, nonrandom abscission may significantly alter the likely values of the standard deviations of the horizontal and vertical wind speeds. But there are no data to support the contention or indicate the magnitude of the change.

A second problem involves the flow near the forest edge. Our assumption that there is an abrupt change in the vertical profile from a pseudologistic formula in the forest (Eqs. 7 and 8) to a power law argument in the clearing (coupling Eqs. 4 and 9 or 10) is both untenable and unavoidable (given the lack of a closed-form solution for the transition). The most likely effect of the assumption is that real deposition is overestimated at small $x_a$ and underestimated at large $x_a$.

A third problem involves dispersal from a leafless source. We have no empirical justification for the modification of Eq. 9, which leads to Eq. 10. We can only argue that the coefficient in Eq. 10 must be at least 0.88 to avoid a deceleration at the edge.

The final major problem is that we assume wind directions are uniform (or random). Although contagious azimuthal distributions are the norm for reporting stations, this tells us little about prevailing wind di-
rections in relation to abscission probability. Examination of the few forestry studies where seed dispersal is measured from all sides of a large clearcut and we can correct for differences in source strength (e.g., Franklin and Smith 1974) indicates that the range of differences in deposition due solely to wind direction is on the order of threefold or less. Thus, while the assumption of uniform directions is problematic, it does not make this exercise hopeless.

**FIELD TESTS OF THE MODEL**

Field tests of the model were based on studies of seed dispersal from forests into burns, clearcuts, and abandoned fields. In all cases but one, the density of deposition well within the forest (BQ) was unknown; thus, the absolute magnitude of deposited seed density could not be evaluated.

In statistical tests of the data set we will solve for the parameters in the function (a modification of Eqs. 21 and 22)

\[ N_s/N_0 = \exp(-\tau T^p), \]

where \( N_s \) is seed density at distance \( x \), \( N_0 \) is the density at the forest edge (\( x = 0 \)), and \( N_s/N_0 \) is the relative seed deposition. An iteration will produce the best estimates of the parameter values by minimizing the residual sum of squares. Confidence intervals (95% confidence) will be obtained from the covariance matrix of the partial derivatives of the function (Eq. 23):

\[ f_x = -(T^p) \exp(-\tau T^p), \]

\[ f_T = -\tau T^p \ln(T) \exp(-\tau T^p) \]

(Snedecor and Cochran 1980) using the associated \( t \) distribution values (df = \( N - 2 \)). Note that the origin value (\( T = 0, N_s/N_0 = 1.0 \)) will not be used in the maximum likelihood estimations.

In all the field tests reported below the deposition at any distance represents the mean value from a set of traps. This is unavoidable because all the forestry studies of seed dispersal give only the mean deposition per distance.

**Seed deposition at Vermilion Pass, Alberta**

A large fire occurred near Vermilion Pass, Banff National Park, Alberta in 1968. The northeast corner of this burn was used for sampling the seed deposition from an old-growth *Picea engelmannii* forest (Fig. 5). This *Picea* forest resulted from the fire dated at \( \approx 1726 \). The present canopy composition along the west and north edges of the study site was determined to be 70% *P. engelmannii*, 22% *Abies lasiocarpa*, and 8% *Pinus contorta* var. *latifolia*. The northeastern and eastern edges of the study site were composed almost entirely of *Pinus contorta* stems resulting from a fire dated at \( \approx 1897 \). According to the model, trees from the northwestern edge should contribute few seeds to the traps. As the 1968 fire extended at least 2 km to the south of the study site, *P. engelmannii* seed deposition in the clearing should be limited to trees on the western edge.

The study site was located on a valley side at \( \approx 1760 \) m altitude. From west to east, the study site is relatively flat; there was a moderate slope (on the order of 5°) from the north to the south. The valley bottom was south of the study site. The regenerating tree species in the burned area had attained a height of \( \approx 1.5 \) m (*Picea*) and 4 m (*Pinus*) by 1986.

One hundred seed traps were placed in a 10 \( \times \) 10 array near the western forest edge (Fig. 5). The lines of traps were spaced more closely near the west edge than at greater distances. Each trap consisted of a 1.0-m\(^2\) sheet of plywood with paper attached to the upper surface. The paper was covered with a viscous substance ("Tanglefoot"). Traps were set out in mid-August 1986 while the closed ovulate cones were still green. By early November the traps were covered with snow; trapped seeds were not enumerated until the following June (1987). As the great majority of seed dispersal in *P. engelmannii* occurs in early autumn (Crossley 1955, Alexander et al. 1982), the submergence of
the traps beneath the snow after early November should be relatively unimportant.

The mean descent velocity of *P. engelmannii* winged seeds was determined (by timing in still air) to be 0.61 m/s. These seeds were obtained from cones of trees at a site ≈100 km distant. Mean forest height was estimated as 29 m, and the assumption that the mean release height was 75% of this value seemed reasonable. Following a poor seed production year in 1985, the 1986 cone crop was large with at least 100 green ovulate cones for most canopy trees.

The observed and predicted dispersal curves are shown in Fig. 6 with the ordinate scaled as a percentage of deposition at the forest edge. The predicted curve is based on Eq. 21. Neither of the two model parameters (τ, φ) were significantly different from the expectations (Table 1). In summary, provided accurate values of υ₀ and zₐ, the area source model adequately characterizes the relative decline in seed density with distance.

Although the density (B) of *Picea engelmannii* canopy trees was measured at Vermilion Pass, the mean number of filled seeds per canopy tree (Q) was not known. However, the long-term average Q measured in other *Picea* stands can be used to determine whether the predicted densities of seeds in the clearing are at least within an order of magnitude of the observed densities. Alexander et al. (1982) monitored seed production by *Picea engelmannii* continuously for a decade in 13 plots in Colorado. These old-growth *Picea* stands had a canopy height and density similar to the Vermilion Pass site. The 10-yr mean annual seed production for "dominant/codominant" *Picea* trees was Q = 3669 filled seeds. At Vermilion Pass B = 0.0071, thus BQ = 26.05 seeds/m² is the rough estimate for seedfall deep within the forest. At x = 10 m, the predicted density is 7.5 seeds/m² (observed density = 2.2 seeds/m²), while at x = 190 m the predicted density is 0.59 seeds/m² (observed = 0.40 seeds/m²). Although the actual value of Q in the autumn of 1986 at Vermilion Pass is unknown, it is clear that the area source model predicts realistic magnitudes for absolute seed densities.

**Dispersal into an abandoned field**

Burton (1989) examined the dispersal of winged fruits of *Acer saccharum* and *Fraxinus americana* into an abandoned field in central Illinois. The forest, at the east edge of the field, had a mean height of 20 m.

The initial 30 m leeward of the forest edge is bordered by a road. Traps (each 0.1 m²) were placed at 10-m intervals from x = 30 to 280 m. During the period 2 October–24 November 1984, 40 filled *Acer* seeds

<table>
<thead>
<tr>
<th>Species</th>
<th>Source</th>
<th>N</th>
<th>τ</th>
<th>φ</th>
<th>σ</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. engelmannii</em></td>
<td>Present study</td>
<td>8</td>
<td>2.06 (0.99)</td>
<td>0.58 (0.41)</td>
<td>0.110</td>
</tr>
<tr>
<td><em>F. americana</em></td>
<td>Burton (1989)</td>
<td>10</td>
<td>3.75 (0.33)*</td>
<td>0.66 (0.35)*</td>
<td>0.009</td>
</tr>
<tr>
<td><em>A. saccharum</em></td>
<td>Burton (1989)</td>
<td>11</td>
<td>3.00 (0.33)*</td>
<td>0.53 (0.21)</td>
<td>0.007</td>
</tr>
<tr>
<td><em>P. engelmannii</em></td>
<td>Crossley (1955)</td>
<td>5</td>
<td>4.22 (2.04)*</td>
<td>1.17 (0.48)</td>
<td>0.030</td>
</tr>
<tr>
<td><em>P. engelmannii</em></td>
<td>Ronco (1970)</td>
<td>5</td>
<td>2.55 (1.82)</td>
<td>0.81 (0.58)</td>
<td>0.063</td>
</tr>
<tr>
<td><em>P. engelmannii</em></td>
<td>Squillance (1954)</td>
<td>9</td>
<td>2.16 (0.59)</td>
<td>1.589 (0.51)*</td>
<td>0.068</td>
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<tr>
<td><em>P. rubens</em></td>
<td>Randall (1974)</td>
<td>4</td>
<td>1.94 (0.06)</td>
<td>0.55 (0.05)</td>
<td>0.035</td>
</tr>
<tr>
<td><em>B. papyrifera</em></td>
<td>Björkborn (1971)</td>
<td>5</td>
<td>4.27 (0.91)*</td>
<td>1.30 (0.17)*</td>
<td>0.017</td>
</tr>
<tr>
<td><em>P. ponderosa</em></td>
<td>Barrett (1966)</td>
<td>3</td>
<td>2.21 (2.22)</td>
<td>0.47 (1.45)</td>
<td>0.024</td>
</tr>
<tr>
<td><em>A. magnifica</em></td>
<td>Franklin and Smith (1974)</td>
<td>3</td>
<td>2.98 (1.76)</td>
<td>0.88 (0.65)</td>
<td>0.009</td>
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<tr>
<td><em>T. mertensiana</em></td>
<td>Franklin and Smith (1973)</td>
<td>3</td>
<td>2.76 (3.53)</td>
<td>0.84 (1.59)</td>
<td>0.023</td>
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<tr>
<td><em>P. mariana</em></td>
<td>Howard (1970)</td>
<td>3</td>
<td>2.63 (4.99)</td>
<td>1.23 (2.12)</td>
<td>0.043</td>
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<tr>
<td>All (but <em>F. americana</em> and <em>A. saccharum</em>)</td>
<td>48</td>
<td>2.42 (0.46)</td>
<td>0.82 (0.18)</td>
<td>0.106</td>
<td></td>
</tr>
<tr>
<td>All (but <em>F. americana</em>)</td>
<td>59</td>
<td>2.45 (0.40)</td>
<td>0.83 (0.16)</td>
<td>0.096</td>
<td></td>
</tr>
</tbody>
</table>

* Best fit parameter does not fall within the predicted range.
were trapped, with none collected beyond \( x = 170 \) m. For *Fraxinus*, 67 filled seeds were collected between 22 August 1985 and 23 March 1986, with none found in traps at \( x > 131 \) m. Total trap area at each 10-m sampling interval was 1.9 m\(^2\) for *Acer* and 2.6 m\(^2\) for *Fraxinus*.

Mean descent velocity for the two species was measured by the authors on fruit samples (supplied by P. J. Burton, University of British Columbia) with a stopwatch in still air. For these species at this study site \( v_f = 1.27 \) m/s for *Acer* and \( v_f = 1.31 \) m/s for *Fraxinus*.

The majority of the *Fraxinus* fruits dispersed during the winter from this deciduous forest and we assume \( \alpha = 2 \). For *Acer saccharum*, most fruits abscise while the majority of the leaves are still on the trees (D. F. Greene and E. A. Johnson, unpublished data for a forest in southern Ontario), and therefore for this species we will assume \( \alpha = 4 \). The meteorological default values are used. The field is large and thus we will use Eq. 21 for *Acer* and Eq. 22 for *Fraxinus*.

Predicted and observed dispersal are depicted in Fig. 7. The ordinate is scaled as a percentage of the seed density at \( x = 30 \) m. There is a tendency to underestimate deposition of *Acer* at large distances, and *Fraxinus* deposition is consistently overestimated. The *Acer* \( \tau \) is significantly higher than expected, while the \( \phi \) parameter is not significantly different from the expectation (Table 1). For *Fraxinus*, both parameter estimates are significantly different from the expectations of Eq. 22. *Fraxinus* deposition would have been estimated much better if we had used Eq. 21 (a full canopy forest).

Fig. 7. Observed and predicted seed dispersal of *Acer saccharum* and *Fraxinus americana* at an abandoned field in Illinois. The ordinate is scaled as the ratio of observed seed density \( (N_r/N_0) \) to the most windward seed traps at 30 m from the forest edge \( (N_0) \).

Fig. 8. Observed and predicted seed dispersal of *Picea* with distance for seven forestry studies. *P. rubens*: Randall 1974; *P. engelmannii*: the other six studies.

Forestry studies of *Picea* seed dispersal

Seven studies of seed dispersal into clearcuts involving *Picea engelmannii* (six of the studies) and *P. rubens* were used for further testing of the model (Fig. 8). The ordinate is scaled as the relative seed density \( (N_r/N_0) \). Three of the studies gave empirical fits but no raw data (Roe 1967, Alexander and Edminster 1983, McCaughhey et al. 1986: *Picea engelmannii*) and are presented here to underscore the great amount of intraspecific variation among studies. Ronco (1970: *P. engelmannii*) published results for five different sites but only the largest cut ("San Juan") is used in Fig. 8.

Only Randall (1974: *P. rubens*) reported the forest height (19 m), and none of these studies include estimations of \( \gamma \), \( u_\gamma \), or \( v_f \).

The area source model was used to predict the observed slopes in Fig. 8. The following assumptions were made. First, \( v_f = 0.61 \) m/s. Second, forest height \( (z_0) \) was set at 29 m (as at Vermilion Pass) for the *P. engelmannii* studies. This assumption was based on the fact that rotation age (>100 yr) *Picea* in the boreal and montane forests of North America have generally 20 < \( z_0 \) < 35 m. Thus, the assumption \( z_0 = 29 \) m was merely a midpoint for these presumed extremes. The third assumption was that mean release height was on the order of 0.75 \( z_0 \). The meteorological default values are used. We applied Eq. 21.

The parameter estimates (Table 1) are not different from the expectations except for Squillace (1954) (\( \phi \) is too large) and Randall (1974) (both parameters are too low). Note that the observed dispersal at Vermilion Pass (Fig. 6) is very similar to the *Picea* dispersal at these seven sites (Fig. 8).

Prediction of absolute magnitude can be attempted
Fig. 9. Observed and predicted seed densities of five tree species vs. the nondimensional dispersal parameter (T).

As for two of the studies in Fig. 8, Alexander et al. (1982) collected data on both seed production and canopy tree density for 13 stands for 10 consecutive years in Colorado. Mean BQ for this period was 12.75 seeds/m². The seed deposition in clearcuts averaged over an earlier 10-yr period in clearcuts near those 13 plots was provided in Alexander and Edminster (1983). Assuming the same values for \( z_a \), \( z_a \), \( \nu_r \), and \( \nu_f \) as before in this section, the area source model predicted 3.68 seeds/m² at \( x = 10 \) m (observed = 0.66 seeds/m²) and 1.52 seeds/m² at \( x = 50 \) m (observed = 0.30 seeds/m²).

The San Juan clearcut of Ronco (1970) in Colorado can also be used to predict the absolute magnitude of the seed deposition. Using the estimated BQ from the previous paragraph and the same values for the model parameters, the expected density at 10 m is 3.68 whereas Ronco (1970) observed 2.8 (west edge) and 1.93 (east edge). The prediction of absolute density is acceptable.

Forestry studies with forest height known

The following five studies of seed dispersal into clearcuts provide the forest height: Barrett (1966: Pinus ponderosa), Howard (1970: Picea mariana), Björkborn (1971: Betula papyrifera), Franklin and Smith (1973: Tsuga mertensiana), and Franklin and Smith (1974: Abies magnifica). These are the only studies where \( z_a \) was given and we were able to procure seed specimens to measure descent velocity (\( \nu_f \)). The calculated \( \nu_f \) ranged from 0.55 m/s (Betula papyrifera from southern Ontario) to 1.13 m/s (Abies magnifica from northern California).

Where these five studies reported results for \( >1 \) yr, the results were averaged. Where results were obtained for more than one edge of a single clearcut (Howard 1970, Franklin and Smith 1973, 1974), the observed deposition at equivalent leeward distances was averaged. (This is consistent with the assumption of random wind directions.) As before, it will be assumed that \( z_a = 0.75 z_a \), and we use Eq. 21 as the deciduous B. papyrifera abscises the great majority of its seeds by late October, so we assume a full canopy for this species.

Observed seed deposition for the five studies is shown in Fig. 9. The ordinate is scaled as \( N_i/N_o \) and the abscissa is the dispersal parameter \( T \). There is broad agreement between observation and theory except for B. papyrifera, where there is an initially gentle decline in deposition (high \( \phi \)) followed by a decline, which is steeper than expected (high \( \tau \)).

Pooling the data sets

We pooled the data sets (except for Acer and Fraxinus) and obtained the estimated \( \tau \) and \( \phi \) as 2.42 and 0.82, respectively. The predicted values (Eq. 21) lie within the estimated confidence intervals (Table 1).

The Acer observations are of considerable interest because they represent our largest \( T \) values. We can add them to the pooled data set by converting the \( N_i/N_{30} \) values to \( N_i/N_o \) by

\[
N_i/N_o = 0.1 N_i/N_{30}
\]

where 0.1 is the expected value (Eq. 21) for \( T = 0.825 \) (when \( x = 30 \)).

With Acer added to the other full canopy data sets (\( N = 59 \)) we obtained estimates for \( \tau \) and \( \phi \) as 2.24 and 0.83 (Table 1). Again, the expected values fall within the confidence intervals.

Dispersal of Larix into a clearcut

Our final test of the deposition prediction involves dispersal of seed into a clearcut, which is approximately square and \( >150 \) m on a side. This is the only test where we have an estimate of the source strength (\( BQ = 7.8 \) seeds/m²) well within the forest. This clearing at the Petawawa National Forestry Institute (northem Ontario) has Larix plantations (of L. decidua and L. laricina primarily, but also a number of Larix hybrids) on three sides, and a hardwood forest on the south side. In August 1990, traps were arrayed in the west and east plantations at \( D = 10, 25, \) and 75 m from the clearing edge. Within the clearing, five clusters of seed traps (10 m² of total trap area per cluster) were positioned every 30 m along a west–east axis that was 75 m from the northern edge. Seedfall was not enumerated until the following May. Qualitative examination of the trees in late October of 1990 indicated that most of the cones had scales flexed open across most of their long axes, while about half of the Larix leaves were still on the trees, and thus we will set \( \alpha = 4 \). Since the three area sources (sides) have \( Y < 75 \) m and \( D < 150 \) m, we will use Eq. 16 and sum the results.
We measured still-air descent of seeds taken from the traps in 1991. The mean terminal velocity was 1.19 m/s. The forest height was estimated to be 18 m, and qualitative examination of cone heights indicated that our default value of release height (\(z_a = 0.75 z_h\)) was reasonable.

Observations on dispersal are presented in Fig. 10 with BQ set equal to the observed deposition at \(D = 75\) m in the western plantation. For the statistical test we regressed observed \(N_e\) against predicted \(N_e\) for both halves of the clearing. The slopes were not significantly different from 1.0, and the intercepts were not significantly different from 0 (t-test; probability of 0.05). We should point out, however, that probably a large fraction of the seeds abscised when few leaves were on the trees and thus the predicted deposition in the middle of the cut would have been substantially larger if we could have included this.

**Fall velocities and turbulence intensities**

We predicted that the fall velocities of a population of seeds from release point to ground should have a mean equal to the still-air measure of mean terminal velocity (\(v_f\)) and a standard deviation (\(\sigma_v\)) given by Eq. 11. Zasada and Lorig (1983) observed the flight of seeds from a *Picea glauca* canopy tree at the edge of a clearing, and measured the total fall time for each seed. The tree was 18.5 m tall, and they report that cones were only found in (approximately) the highest 3.1 m (thus, we will assume \(z_a = 16.95\) m). Still air measurement of filled *P. glauca* seeds (from Ontario) indicate \(v_f = 0.61\) m/s. In what follows, we only deal with the 78% of the observations where the seeds were filled.

The mean observed fall velocity was 0.57 m/s. As we predicted \(v_f = 0.61\); this could support the contention that vertical wind speeds are roughly symmetrically distributed with a mean value of 0 at the time of abscission and during the subsequent descent.

From Eq. 11, the standard deviation of fall velocities should be \(\approx 0.15\). The observed value was 0.23. Thus, the predicted magnitude of \(\sigma_v\) appears to be generally correct, at least in the vicinity of the forest edge.

Finally, we can make a rough test of the relative contributions of \(\sigma_{v_p}, \sigma_{x_p}\), and \(\sigma_m\) to the variation in dispersal distances (\(\sigma_{d_p}\)). Here, we ignore the fact that horizontal wind speeds are a function of \(x_p\), and thus we underestimate the role of horizontal wind speed variation. Given the additivity of variances of a function, then

\[
\sigma_{d_p}^2 = \sigma_{x_p}^2 \left( \frac{\sigma_v^2}{v_f^2} + \sigma_m^2 \right)
\]

for a tree at the forest edge. (Stewart [1968] gives an analogous equation but with horizontal speeds assumed to be Gaussian rather than log-normal.) Assuming \(\sigma_m = 0.55\) and using the observed mean and variance of the fall velocities, we predict that the variance in fall velocities accounts for 35% of the variance in \(x_p\) (observed dispersal distances); Zasada and Lorig's (1983) data show that it contributes 38%.

This study by Zasada and Lorig (1983) (there are no others like it) indicates that our assumptions regarding the symmetry of vertical speeds, the applicability of still-air measures of \(v_f\), and the relative magnitudes of the contributions of the variances of vertical winds, horizontal winds, and terminal velocities are generally correct.

**Discussion**

We have presented a model for the dispersal of winged or plumed seeds from the side of a clearing (an area source). By summation of the contributions of seeds from each clearing side, the model permits estimation of deposition at a 1-m² quadrat in the Cartesian space. Alternatively, one can model the deposition from a single point source or single patch of point sources.

**Appraisal of the model**

As predicted, observed deposited seed density exhibits a roughly negative exponential decline with distance from the edge of an area source. At about five forest heights into the clearing, the deposition is on the order of 3% of the edge deposition.

In 3 of the 11 data sets both expected parameter values (\(\tau\) and \(\phi\)) were rejected. In two more data sets, one of the two values was rejected. But for the pooled data set (excluding *Fraxinus*), the full canopy model provided an acceptable estimate of the relative deposition (Table 1). In addition, the model performed well in the case (*Larix*) where we could deal with absolute rather than relative deposition.

The default values employed here are unlikely to be greatly in error. For example, the mean release height for seeds is undoubtedly within 20% of our estimate of 0.75\(z_h\) (except perhaps for trees at a forest edge),
is defined with respect to the side of immediate interest). Note, however, that this procedure will overestimate (by about twofold) deposition in the “corners” of the clearing where, for the two adjacent sides, only half the source can contribute seeds. Better accuracy in estimating deposition in the corners would require a laborious summing of the individual point source contributions (Eq. 16) across the source space \((D, Y)\). Because of this problem, Eqs. 21 and 22 are not a trustworthy guide to small clearings. Additionally, Eq. 16 is a poor approach to a very small clearing because it is based on Eq. 9 or 10, which do not account for the reduction in horizontal wind speed as a windward forest edge is approached. This problem can be dealt with (Flemming 1968) via a more complex approach than adopted here.

If one is interested in a contagiously distributed source or a single tree, then Eq. 16 should be used. This equation for a single tree can be extended to a patch by estimating the deposition from a single tree in the center of the patch and then multiplying the result by the number of conspecific canopy trees in the patch.

There are four parameters in the model (see Appendix) that must be measured directly. Two of these parameters, \(B\) (source density of the species of interest) and \(Q\) (mean seed production of a tree), could be measured as the product \(BQ\) (source strength = seed density well within the forest). But since the point of the exercise is to avoid dealing with seed traps, it would be preferable to make estimates of the individual quantities. Source density can be measured by standard methods with the proviso that we are only concerned with canopy trees (dominant, co-dominant) as they virtually monopolize seed production within a stand (Fowells 1965).

Mean seed production per tree \((Q)\) can be estimated in a number of ways. For example, one might use the mean annual seed production based on long-term forestry studies. Alternatively, there is a power-law argument developed by Greene and Johnson (1994) where \(Q\) (mean annual seed production) is a function of tree basal area and (inversely) seed mass. If one is interested in production in the near future one can estimate, for example, ovulate cone number with binoculars and then measure seed number per cone for a subsample. Estimation of \(Q\) for a particular year in the past could only be had if there are local (say, within 100 km) production studies on the species of interest.

The third parameter to be measured is forest height \((z)\). This can be done with a clinometer. The final parameter to be measured is mean terminal velocity \((v_o)\). This can be done directly with a stopwatch in still air, by reliance on published values, or by use of a regression equation involving seed mass/area ratios (see Greene and Johnson 1992b for references).

Significance of the model

An obvious applied ecology problem is the regeneration of clearcuts. The cost of hand-planting seed-
lings in large cuts makes natural regeneration an attractive option, but dependence on natural regeneration limits cut size (i.e., a dispersal constraint). Given that harvesting cost per hectare declines with cut size, and that natural regeneration is the cheapest reforestation technique, the model can be coupled with seed production and survivorship arguments to determine the largest possible cut size and shape that permits adequate natural stocking of the desired species.

Likewise, the model may be of some use in the management of weed infestations of crops. As pointed out by Ghersa and Rosh (1993), constraining weed dispersal may be a more profitable approach to mitigation than improving crop competitive ability. Although the model default values are based on studies of forests, there is no reason why they could not be suitably modified for wind-dispersed herbaceous stands dispersing or receiving seeds across heterogeneous terrain.

Another use of the model is to estimate juvenile survivorship of seedlings as a function of site characteristics given expected seed density ($N_e$ from the model multiplied by the time interval of interest) and an expectation of $Q$ (the mean annual seed production that can be had from long-term forestry production studies or by a function relating $Q$ to seed mass and tree size [Greene and Johnson 1994]). If we assume the great majority of mortality in a clearing occurs in the germination year of a cohort, and if this age-specific mortality does not markedly change over the first few years since the creation of the clearing, then we can estimate the mean 1st-yr survivorship. This approach then permits evaluation of survivorship without long-term censusing of individuals in plots, although it must be limited to a period longer than the onset of thinning, and survivorship becomes a value averaged across cohorts during the time span of interest. Additionally, since seed production in trees shows marked temporal variation, the time period would have to be long enough (say, 5 yr) for the real mean production value to approach the expected value. The validity of the approach is easily tested with seed traps in permanent plots.

Metapopulation arguments related to coexistence of species in a landscape or to the optimal arrangement of nature reserves (Hanski and Gilpin 1991) would be a good deal more quantitative if they were reformulated around a physically dimensioned dispersal argument such as that advanced here. Likewise, algebraic models such as Shmida and Ellner (1984) where dispersal figures prominently but only as a dichotomized parameter (fraction of $Q$ dispersed within a patch vs. fraction dispersed beyond the patch in an even seed rain ("bath")), could be more firmly embedded in the three-dimensional space that real plants inhabit.

In the preceding paragraphs we have been stressing the utility of this (or some similar) model, and of course we refer only to the wind-dispersed fraction of the tree flora. A similar quantification for seed dispersal by animals is unlikely and we may have to be satisfied with, eventually, merely empirical relationships among dispersal curve parameters and biotic characters such as seed size, animal size, and animal locomotory mode.

More generally, we stress here that plant community dynamics arguments seldom include physical dimensions other than time and, rarely, mass. But plant populations and metapopulations have a spatial structure, and seed dispersal is one of the processes that knits these individuals and populations into an interacting ensemble that expands or contracts in real landscapes.

ACKNOWLEDGMENTS

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## APPENDIX

List of symbols and recommended default values.

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Definition</th>
<th>Default value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\alpha$</td>
<td>coefficient related to drag of the forest</td>
<td>4.0 (leafy) 2.0 (leafless)</td>
</tr>
<tr>
<td>$\sigma_u$</td>
<td>standard deviation of vertical wind speeds (m/s)</td>
<td>0.13 (leafy) 0.29 (leafless)</td>
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<td>$B$</td>
<td>density (no./m$^2$) of seed-bearing trees of species of interest</td>
<td>To be measured</td>
</tr>
<tr>
<td>$d$</td>
<td>zero plane displacement height (m)</td>
<td>0.67 $z_a$ (leafy) 0.57 $z_a$ (leafless)</td>
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<td>$i_e = \sigma_u$</td>
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<td>vertical turbulent intensity</td>
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<td>$m$</td>
<td>power law exponent for vertical profile in clearing</td>
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<tr>
<td>$N_0$</td>
<td>density of deposited seeds at leeward forest edge</td>
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</tr>
<tr>
<td>$N_s$</td>
<td>density (no./m$^2$) of deposited seeds on the ground at $x$</td>
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<tr>
<td>$p$</td>
<td>exponent for abscission probability</td>
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<tr>
<td>$Q$</td>
<td>number of filled seeds on a tree</td>
<td>To be measured</td>
</tr>
<tr>
<td>$u$</td>
<td>a horizontal wind velocity (m/s)</td>
<td></td>
</tr>
<tr>
<td>$u_{50}$</td>
<td>50th percentile of the seasonal distribution of $u$, (m/s)</td>
<td>4.3</td>
</tr>
<tr>
<td>$u_{med}$</td>
<td>median speed modified by abscission effect (m/s)</td>
<td>7.87</td>
</tr>
<tr>
<td>$u_{ave}$</td>
<td>a horizontal wind velocity at the reference station (m/s)</td>
<td></td>
</tr>
<tr>
<td>$u_{ave}$</td>
<td>mean value of $u_e$ (m/s)</td>
<td></td>
</tr>
<tr>
<td>$u_{z0}$</td>
<td>a horizontal wind velocity at height $z$ at the reference station (m/s)</td>
<td></td>
</tr>
<tr>
<td>$u_{z=10}$</td>
<td>the horizontal wind velocity at the anemometer height (10 m) at the reference station (m/s)</td>
<td></td>
</tr>
<tr>
<td>$u_e$</td>
<td>a horizontal wind velocity in the forest stand (m/s)</td>
<td></td>
</tr>
<tr>
<td>$u_e$</td>
<td>a horizontal wind velocity in the clearing at leeward distance $x_f$ (m/s)</td>
<td></td>
</tr>
<tr>
<td>$u_h$</td>
<td>a horizontal wind velocity at height $z$ (m/s)</td>
<td></td>
</tr>
<tr>
<td>$v_f$</td>
<td>mean equilibrium descent velocity of a winged or plumed seed (m/s)</td>
<td>To be measured</td>
</tr>
<tr>
<td>$w$</td>
<td>a vertical wind velocity (m/s)</td>
<td></td>
</tr>
<tr>
<td>$x$</td>
<td>distance (in the clearing) perpendicular to the forest edge (m)</td>
<td></td>
</tr>
<tr>
<td>$x_{10}$</td>
<td>leeward distance from a source tree to forest edge (m)</td>
<td></td>
</tr>
<tr>
<td>$x_f$</td>
<td>leeward distance from the forest edge to a trap (m)</td>
<td></td>
</tr>
<tr>
<td>$z$</td>
<td>height above the ground (m)</td>
<td></td>
</tr>
<tr>
<td>$z_e$</td>
<td>height at which a seed abscise (m)</td>
<td>0.75 $z_a$</td>
</tr>
<tr>
<td>$z_s$</td>
<td>height at which a seed exits the forest (m)</td>
<td></td>
</tr>
<tr>
<td>$z_{sh}$</td>
<td>mean forest height (m)</td>
<td>To be measured</td>
</tr>
<tr>
<td>$z_0$</td>
<td>roughness length (m)</td>
<td>0.105 $z_a$</td>
</tr>
<tr>
<td>$z_r$</td>
<td>anemometer height at a reference station (m)</td>
<td>10</td>
</tr>
</tbody>
</table>