

FIELD VALIDATION AND SENSITIVITY ANALYSIS OF A MECHANISTIC MODEL FOR TREE SEED DISPERSAL BY WIND

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Abstract. We present a temporally and spatially explicit mechanistic model of tree seed dispersal by wind, incorporating full stochasticity based on natural variation. The model simulates the dispersal of each individual seed by integrating the temporal effects of climatic conditions on the rate of seed release, and the spatial effects of wind direction and horizontal and vertical velocities, the terminal velocity of seeds (i.e., the constant descent velocity in calm air), and the height of seed release, partitioned into tree height and the distribution of seeds with tree height. The model was tested for two *Pinus halepensis* stands within the Mediterranean region of Israel, in which seed dispersal has been extensively monitored by seed traps. The predicted dispersal curve verified expectations of a positively skewed leptokurtic distribution and of peak location at some distance from a point source and at zero distance from an area source. Long-distance dispersal events occurred with very low frequency, but given the large seed crop in *P. halepensis*, even a small fraction should result in a considerable number of seeds dispersed far from their source. The model reliably simulates the observed dispersal pattern in a spatial resolution of 1 m² (R^2 between 60% and 90%), as revealed from comparisons of the predicted and observed proportions of seed dispersed to seed traps. A sensitivity analysis using Latin hypercube sampling along with stepwise multiple rank regression showed that the effects of the horizontal and vertical wind velocities on the dispersal distance override those of the biotic factors. This suggests that the synchronization of seed release with favorable winds is the most effective plant-controlled mechanism to increase the distance of dispersal in wind-dispersed species such as *P. halepensis*.

Key words: dispersal curve; dispersal distance; height of release; long-distance dispersal; mechanistic models; model evaluation; *Pinus halepensis*; seed dispersal by wind; seed traps; stochasticity; terminal velocity; wind profile.

INTRODUCTION

Seed dispersal is the predominant stage at which plants move in space (Harper 1977, van der Pijl 1982), generating the initial spatial pattern of new individuals that not only determines the potential area of recruitment, but also serves as a template for subsequent processes such as predation and competition, which eventually shape a new spatial pattern of reproductive plants (Janzen 1970, Howe and Smallwood 1982, Schupp and Fuentes 1995, Nathan and Muller-Landau 2000). Typically, the vast majority of seeds are dispersed only short distances from parent plants (Harper 1977, Howe and Smallwood 1982, Okubo and Levin 1989, Willson 1992, 1993), thus seed dispersal can limit recruitment even on a very local scale (e.g., Eriksson and Ehrlén 1992, Primack and Miao 1992, Ribbens et al. 1994). The spatiotemporal pattern of seed dispersal also has

significant effects at the community level (Janzen 1970, Connell 1971, Shmida and Ellner 1984) and important implications for restoration and management (Bakker et al. 1996). The call for a more realistic incorporation of seed dispersal in forest dynamic models (Pacala and Hurtt 1993, Ribbens et al. 1994, Clark and Ji 1995, Malanson and Armstrong 1996, Pacala et al. 1996, Clark et al. 1998b) reflects the growing recognition that the spatiotemporal patterns generated during the seed stage are critically important to plant dynamics (Schupp and Fuentes 1995, Nathan and Muller-Landau 2000).

Phenomenological models such as the negative exponential (e.g., Malanson and Armstrong 1996, Clark 1998, Clark et al. 1998a, b, 1999, Nathan and Muller-Landau 2000, Nathan et al. 2000) and diffusion models (e.g., Pacala and Hurtt 1993, Le Corre et al. 1997) are two general types of models that are often used to describe seed dispersal. Both types have the advantages of being simple and of having few parameters, and both frequently fit the data reasonably well. On the one hand, diffusion models are more attractive as they incorporate a mechanism of multiple random individual movements (Okubo 1980), rather than just a description. On the other hand, phenomenological models have provided

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better fits to seed dispersal patterns (Clark 1998, Clark et al. 1998b, 1999). Both types, however, provide limited understanding of the underlying mechanism because their synthetic parameters do not relate directly to particular features of either plant or disperser, so they can be obtained only by fitting data, and therefore provide no basis for a priori predictions and generalization beyond studied systems. A more explanatory and realistic modeling approach would consolidate all important parameters affecting dispersal that can be directly measured and interpreted, and would incorporate the effects of their natural stochasticity to predict seed dispersion patterns of unexplored systems as well.

In this paper we describe and test a mechanistic model of tree seed dispersal by wind that fulfills the above requirements, while still providing accurate and reliable predictions. Wind is a common dispersal agent of plant seeds, especially of temperate and boreal trees (Howe and Smallwood 1982, van der Pijl 1982). We apply the model for the Aleppo pine (*Pinus halepensis* Mill.), a Mediterranean wind-dispersed tree species, and focus on the primary movement of seeds from the parent tree to a surface (phase I dispersal sensu Chambers and MacMahon 1994). Subsequent movements (phase II dispersal) by wind are unlikely in the dense habitat this species typically occupies, and, more generally, is probably negligible in forests and other rough surfaces (Greene and Johnson 1997, Vander Wall and Joyner 1998). Although the model embodies the mechanisms of both temporal and spatial components of dispersal, we focus here on the spatial component alone, and particularly on the distance of dispersal by wind, since the temporal component is analyzed and discussed elsewhere (Nathan et al. 1999). We verify and validate the model's predictions using extensive field data collected in two sites during a total of nine dispersal seasons, and evaluate the relative impact of the main factors affecting the dispersal distance through sensitivity analysis using Latin hypercube sampling and stepwise multiple rank regression.

Mechanistic models of seed dispersal by wind

This short review is intended to focus on the major components of the main wind dispersal models proposed in the literature, and, particularly, to examine to what extent they have been evaluated. Details on the underlying physical and micrometeorological theory can be found in Ward-Smith (1984), Burrows (1986), McCartney (1990) and Andersen (1991).

Dingler (1889) developed a general model for calculating the rate of fall of seeds of different morphologies, based on the opposing forces that gravitation and drag exert on a particle during vertical fall. The vertical movement, or more generally the aerodynamics, of wind-dispersed seeds has been extensively studied ever since, especially that of asymmetric samaras (winged seeds) (Norberg 1973, McCutchen 1977,

Green 1980, Guries and Nordheim 1984, Seter and Rosen 1992, Nathan et al. 1996). Samaras, like many other wind-dispersed diaspores (Augspurger 1986), reach a constant falling velocity, often called the "terminal velocity," shortly after release. The vertical distance traveled before reaching terminal velocity, called the "relaxation distance," is often neglected as it is assumed to be small compared to the vertical distance traveled after terminal velocity is reached, especially for tree seeds (Guries and Nordheim 1984, Nathan et al. 1996). Therefore, the horizontal distance a seed is carried by the wind (D) can be calculated as a function of the terminal velocity (F), the height of seed release (H) and the mean horizontal wind speed during seed flight (U), as given by the ballistic equation

$$D = \frac{H \times U}{F}. \quad (1)$$

This equation was first described in the context of seed dispersal by Dingler (1889) and formulated (though not recommended) by Schmidt (1918). Cremer (1971, 1977) and subsequent investigators (e.g., Augspurger 1986, Matlack 1987, Ernst et al. 1992) used it to estimate dispersal capacity of a variety of wind-dispersed plants. Schmidt (1918) proposed a model with a turbulence factor and argued that D is inversely correlated with F^2 rather than with F . Burrows (1973, 1975, 1983) developed formulas to simulate the aerial trajectories of wind-dispersed seeds in three spatial dimensions at different wind conditions, based on the forces of gravitation, lift, and drag (see Burrows 1986 for review).

Later extensions of Eq. 1 have been generally directed at resolving the inadequacy of representing the real horizontal wind speed a seed encounters during flight with a single constant U since wind is not constant in time or space. Fields and Sharpe (1980, see also Johnson et al. 1981, Sharpe and Fields 1982) introduced the model SEDFAL, which incorporates a vertical variation in wind speed by including a logarithmic profile of U with distance above the ground (Monteith and Unsworth 1990, and see *Methods: Model algorithms: Dispersal direction and distance*). Okubo and Levin (1989) developed several mechanistic models for wind dispersal of pollen and seeds based on advection and diffusion dynamics, incorporating the effects of the turbulent mixing velocity. Greene and Johnson (1989) extended Eq. 1 by incorporating a lognormal distribution of U , the standard deviation of F and of $\ln(U)$, and the vertical wind speed (W). This model has recently been extended to account for long-distance dispersal (Greene and Johnson 1995), for dispersal from a stand to an adjacent clearing (Greene and Johnson 1996), and for secondary wind dispersal on snow (Greene and Johnson 1997). Andersen (1991) introduced two stochastic models, one basically similar to the model of Greene and Johnson (1989) but differing

in having a Weibull distribution of U , while the second incorporates stochasticity caused by turbulent winds modeled as Brownian motion.

The most fundamental problem repeatedly encountered while testing the predictive ability of these mechanistic dispersal models was the lack of data for different parameters. Sharpe and Fields (1982) compared predicted and reported (Isaac 1930) D 's and found good agreement in one case, but not in two others. The strength of this test, however, is questionable, since F was estimated from another study (Siggins 1933), while the formulation of its variation was adapted from another species. It is also unclear how the roughness parameters of the logarithmic wind profile (see *Methods: Model algorithms: Dispersal direction and distance*) were estimated. Since turbulent mixing velocity (W^*) is not measured in dispersal studies, Okubo and Levin (1989) actually examined Eq. 1 with a fairly large body of data on wind dispersal of seeds and spores. They found that the modal D is reliably estimated by Eq. 1 for seeds with $F > 1$ m/s; however, as F decreases, the modal D is underestimated since W^* becomes more influential than F . Greene and Johnson (1989, 1995, 1996) also found that their models underestimate the modal D . They also encountered difficulties in setting values for parameters not measured in their study, and the same applies to recent applications of their model for several forest trees in Japan (Sato and Hiura 1998) and Canada (Stewart et al. 1998), as well as to Andersen's (1991) tests of the models included in his review.

The principal conclusion from reviewing these models is that both the formulations and predictions of existing mechanistic models of seed dispersal by wind deserve more concrete evaluation. Mechanistic models typically require specific data in order to assign values to all parameters—data which can rarely be obtained by searching the literature. Hence, an effort should always be made to provide field estimates from the particular system studied. To facilitate this, models should include only those parameters that can be directly interpreted and measured. Greene and Johnson (1989, 1995, 1996) made large efforts to incorporate the variation of operative factors in their analytical models but that naturally required making more assumptions. For their long-distance dispersal models, they acknowledged, "Given the large number of assumptions underlying the models, it is surprising that they did not perform more badly" (Greene and Johnson 1995: 1043). Thus, purely analytical models are unlikely to accomplish the objectives of gaining better understanding and predictive ability. Given the increasing recognition of the importance of long-distance dispersal (Clark 1998, Clark et al. 1998a, 1999, Higgins and Richardson 1999), tests of predicted vs. observed modal D 's should be replaced by tests examining the entire observable frequency of D . Finally, the relative impact of parameters affecting the dispersal distance must be

examined to identify those factors that should be measured most precisely. Adherence to these recommendations should promote the acceptance of models by researchers and policy makers who doubt their credibility (Bart 1995, Aber 1997).

METHODS

Species and sites

Pinus halepensis is a native Mediterranean tree (Mirov 1967, Barbéro et al. 1998) that has been widely introduced throughout the world (Richardson and Higgins 1998). Adult trees reach relatively low heights (10–20 m) for pines (Nathan and Ne'eman 2000). Seed release is stimulated by fire and by Sharav events—dry and hot spells characteristic of the eastern Mediterranean, which occur in the spring and fall (Schiller 1979, Nathan et al. 1999). The seeds are samara-like structures typical of wind-dispersed pines, with a single asymmetric wing loosely attached to the seed, which autorotates while falling. The species is considered a very successful colonizer (Acherar et al. 1984, Lepart and Debussche 1991, Rejmánek and Richardson 1996). Isolated individuals were found as far as several kilometers from a stand (Lepart and Debussche 1991; R. Nathan, *unpublished data*). Most seeds, however, do not attain distances >20 m from the canopy edge (Acherar et al. 1984, Nathan et al. 1999, 2000).

The two study sites, within the Mediterranean region of Israel, were the Nir-Ezyon site on the lower western slopes of Mt. Carmel (32°41' N, 34°58' E; 116 m altitude) and the Mt. Pithulim site on the Judean hills (31°45' N, 35°04' E; 628 m altitude), hereafter termed NE and MP, respectively. At both sites, 94 identical seed traps (of dimension $0.99 \times 0.84 \times 0.15$ m) were placed within and around the stand. At NE, seed traps were placed in 62 stations, and measurements were taken continuously between October 1993 and November 1994 ($n = 36$; mean interval, 11 d) and later restricted to the dispersal seasons (spring and fall 1995 and spring 1996; $n = 34$; mean interval, 7 d). At MP, seed traps were placed in 54 stations, and measurements were taken continuously between April 1997 and June 1998 ($n = 24$; mean interval, 18 d). A recent aerial photograph of each site was scanned at a resolution of 0.25 m, corrected for terrain distortion (processed by Advanced Digital Mapping, Tel Aviv, Israel), and used to determine the locations of trees and of seed trap stations to the nearest 1 m. More detailed information on the seed trapping procedure and the study sites is given in Nathan et al. (1999, 2000).

Model structure

We developed a mechanistic model of wind dispersal (WINDISPER) that predicts postdispersal densities of wind-dispersed seeds within and around a simulated stand of trees. The model is conceptually similar to the SEDFAL model (Fields and Sharpe 1980) in its La-

grangian approach focusing on the movement of individual seeds (see also Andersen 1991). It calculates the postdispersal deposition of individual seeds by randomly selecting the values of all operative parameters from their empirical distributions. It is also a temporally and spatially explicit model in which the simulated landscape is a square grid whose total size, as well as the cell size, is determined by the user to correspond to the simulated system. The simulations presented in this paper were generated for a landscape of 500×500 cells for the smaller site (NE) and a landscape of 600×600 cells for the larger one (MP). In both cases, however, each cell represents a flat surface of 1 m^2 . An input file describing the distribution of adult trees of the simulated stand is used to define the "source" (seed-releasing) cells. For each individual seed dispersed, the calculated dispersal direction and distance constitute a vector originating in the center of a source cell and pointing to the deposition (recipient) cell. Seeds are "accumulated" in recipient cells (which may themselves be source cells as well), and the total number of seeds dispersed outside the simulated landscape is also recorded. The temporal component of seed dispersal is incorporated by assigning specific values for the climatic parameters that determine the number of seeds released and for wind conditions (see *Methods: Model algorithms*) for each simulated period (≥ 1 d). The model is written in C and runs on a UNIX operating system (Appendix 1). The flow diagram is outlined in Fig. 1, and the main parameters are defined in Table 1.

Model algorithms

Seed release.—As in many other tree species (Fowells 1965, Schopmeyer 1974), seed release in *P. hal-epensis* is distinctly seasonal and is highly correlated with climatic variables (Nathan et al. 1999). To estimate the number of seeds released (Q) from a source cell during a simulated period from contemporaneous climatic data we used the following equation:

$$Q = -0.195 \text{ RH} + 0.247 T_{\max} + 8.696 \quad (2)$$

where RH is the mean relative humidity and T_{\max} is the maximum temperature measured during the simulated period. This equation was calculated by a stepwise multiple regression of Q , estimated for each of the 25 periods (between successive visits) during the first two seasons measured in NE (fall 1993 and spring 1994), on contemporaneous climatic variables measured in a reference weather station ($F_{2,23} = 20.34$, $P < 0.0001$, $R^2 = 0.639$; the reference station is described in *Methods: Parameter estimation: Wind parameters*). The response variable Q was estimated from seed trap data as the estimated total number of seeds released per day during a period (Nathan et al. 1999) divided by the total canopy area (m^2) of the stand. We had previously arrived at a very similar equation using the same data but with a different definition of the response variable and a longer time span (Nathan et al. 1999). During

the model run, Q is estimated from the specific climatic parameters of the simulated period. The number of seeds dispersed from each source cell is then randomly selected from the assumed normal distribution with mean Q and standard deviation of $0.13Q$, a ratio estimated from seed-trap data.

Dispersal direction and distance.—The deposition cell of each dispersed seed is the cell pointed at by the vector of length D , originating at the center of the source cell and pointing in the direction R . A 45° sector is selected based on the wind frequencies measured during the simulated period. Assuming homogeneous distribution within each sector, R is randomly selected within the selected sector. For calculating D , Eq. 1 undergoes two modifications. First, negative (downward) and positive (upward) mean vertical wind speed (W) during flight accelerates and decelerates the rate of fall, respectively; thus,

$$D = \frac{H \times U}{F - W}. \quad (3)$$

The second modification, following SEDFAL (Fields and Sharpe 1980), copes with the inadequacy of U in describing the actual horizontal wind speed during seed flight. Within the boundary layer wind declines with decreasing height above the ground, due to the surface resistance, as described by the logarithmic wind profile:

$$U_z = \frac{u_*}{K} \ln\left(\frac{z - d}{z_0}\right) \quad (4)$$

where U_z is the mean U at height z above the ground, u_* is the friction velocity, K is von Kármán constant (≈ 0.40), and z_0 and d are the two roughness parameters, termed roughness length and displacement height, respectively (Monteith and Unsworth 1990). The roughness length is the length scale for the total magnitude of shear forces acting on the surface, and the displacement height scales the vertical distribution of those forces in the surface canopy (Wieringa 1993).

For simplicity, we assumed that F and W in Eq. 3 are constant during flight; then, D is equal to the distance a seed travels between the time of release ($t_0 = 0$) and t_1 , the time when $U = 0$ ($z = d + z_0$). Therefore,

$$D = \int_{t_0}^{t_1} U_t \quad (5)$$

where U_t is U at time t and t_1 is given by

$$t_1 = \frac{H - (d + z_0)}{F - W} \quad (6)$$

i.e., the time until a seed falling at a constant rate ($F - W$) from height H reaches a height of $d + z_0$ at which $U = 0$ (Eq. 4). The vertical position of a seed during flight in time t (z_t) is equal to

$$z_t = H - (F - W)t. \quad (7)$$

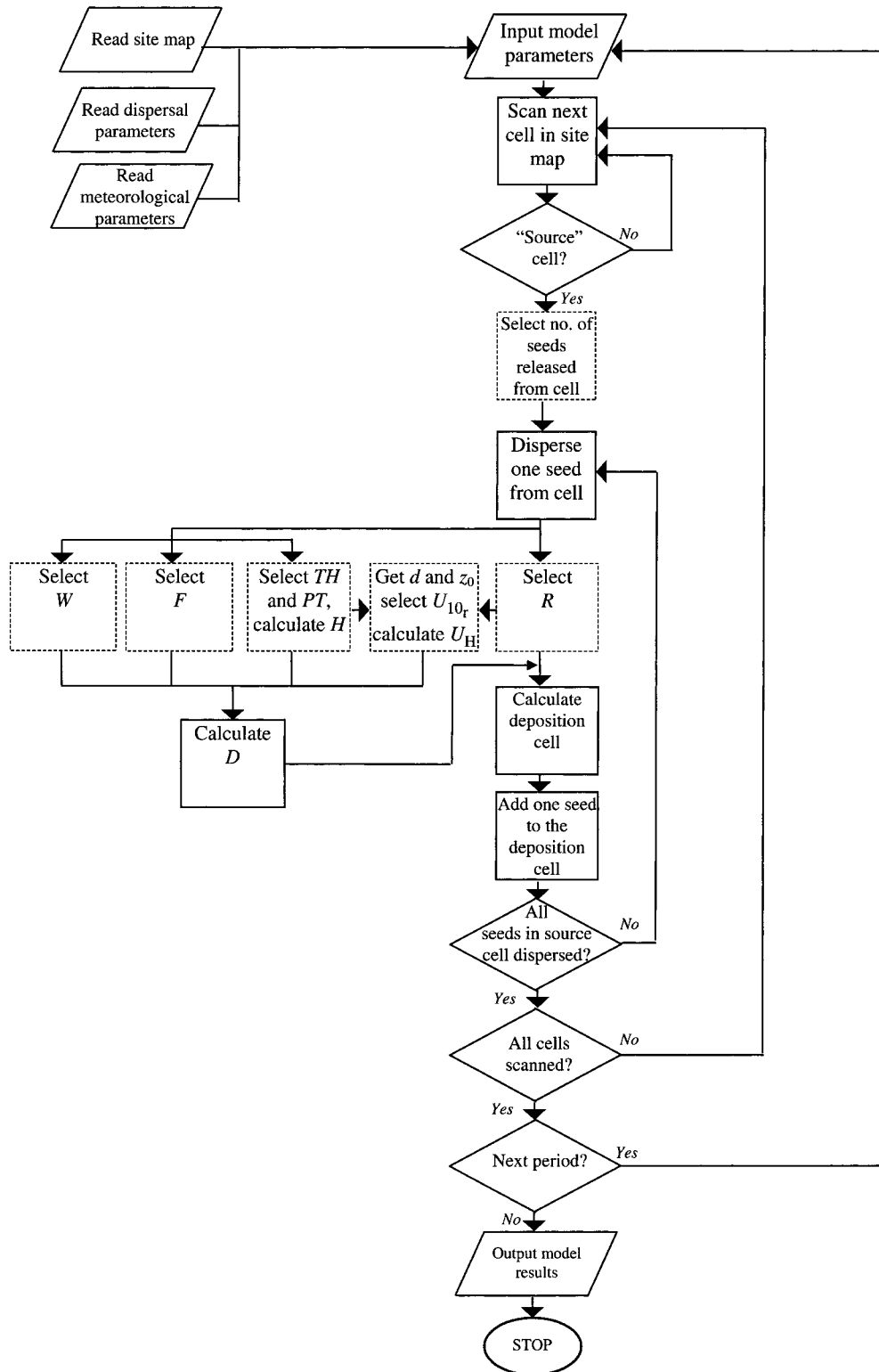


FIG. 1. Flow diagram of the simulation model WINDISPER. Parameter symbols are described in Table 1. Dashed squares indicate random selection from the empirical distribution (Table 1).

TABLE 1. Description of main variables used in WINDISPER.

Symbol	Definition (units)	Formulation	Distribution
State parameters			
D	Horizontal dispersal distance (m)	Eq. 10	
R	Dispersal direction (radians)		follows meteorological data
Species parameters			
Q	Number of seeds released (seeds·canopy section ⁻¹ ·day ⁻¹) [†]	Eq. 2	follows meteorological data
F	Terminal falling velocity (m/s)		normal [‡]
H	Height of seed release (m)	TH × PT	
TH	Tree height (m)		normal [§]
PT	Proportion of TH from which seeds are released		normal [‡]
Meteorological parameters			
R	Wind direction (radians)		follows meteorological data
U	Horizontal wind speed (m/s)	Eq. 4	log-normal [‡]
u_*	Friction velocity (m/s)	Eq. 11	follows meteorological data
W	Vertical wind speed (m/s)		normal [‡]

[†] Each canopy section is $1 \times 1 \times \text{TH}$ m.

[‡] In agreement with Greene and Johnson (1989, 1996) and with empirical data (see *Methods: Parameter estimation*).

[§] In agreement with empirical data (see *Methods: Parameter estimation*).

Substituting z in Eq. 4 with z_t in Eq. 7 results in

$$U_t = \frac{u_*}{K} \ln \left(\frac{H - (F - W)t - d}{z_0} \right) \quad (8)$$

and integration within the limits of Eq. 5 provides an equation for D :

$$D = -\frac{u_*}{K} \left(\frac{H - (F - W)t - d}{F - W} \right) \times \ln \left(\frac{H - (F - W)t - d}{z_0} + t \right) \Big|_{t_0}^{t_1} \quad (9)$$

Given $t_0 = 0$ and t_1 as in Eq. 6, Eq. 9 can be simplified to

$$D = \frac{u_*}{K(F - W)} \left((H - d) \ln \left(\frac{H - d}{ez_0} \right) + z_0 \right). \quad (10)$$

In summary, five assumptions are implicit in calculating the spatial component of seed dispersal by the model: (a) the seed flies in a straight line in the selected wind direction; (b) the seed follows the vertical and horizontal movement of the air, except for an additional downward velocity equal to F ; (c) F and W are constant during seed flight; (d) the logarithmic wind profile adequately describes the horizontal wind within the relevant heights above the ground; and (e) the roughness parameters of the logarithmic wind profile are constant in time and space. In addition, the denominator $F - W$ in Eq. 10 was forced to be larger than zero, since a nonpositive value (i.e., $W \geq F$) means infinite dispersal distance of a seed that is not sinking. This constraint is referred to below as the “ $W < F$ constraint.”

Parameter estimation

We used the Shapiro-Wilk W test (Shapiro and Wilk 1965) to examine the assumption of normal (or log-normal) distribution of the basic parameters in the model (Tables 1 and 2). This test has been shown to be the

most powerful omnibus test of normality (Pearson et al. 1977, D'Agostino 1986), but its computation when $n > 50$ is very cumbersome, and is not provided in the available statistical packages. Therefore, we randomly selected 50 observations for those variables having larger samples, using the SPSS package (SPSS 1993) to calculate the test statistic and its significance value. The reported statistics were randomly selected from several iterations of this procedure, generally showing very similar results in each repetition.

Biotic parameters.—The terminal velocity (F) was measured by analyzing video photos of descents of 2.35 m by each of 125 randomly selected seeds collected in NE (Nathan et al. 1996). The distribution of F was not significantly different from normal (Shapiro-Wilk $W = 0.969$, $df = 50$, NS). To estimate the height of seed release (H), we took the product of tree height (TH) and of the proportional distribution of seeds with tree height (PT). Assuming correlated distributions of cones and seeds with tree height, PT was estimated by counting the number of closed cones of the first and second year after pollination (easily distinguished by their color, size, and position along the branch) in five equal-sized height levels in 16 trees in NE. The distribution of PT was not significantly different from normal (Shapiro-Wilk $W = 0.914$, $df = 16$, NS), in agreement with the generalization made for North American conifers (Greene and Johnson 1996). TH was measured for the same trees in NE and for 60 trees in MP; the distributions were also not significantly different from normal (Shapiro-Wilk $W = 0.923$, $df = 16$, NS and 0.948, $df = 50$, NS, respectively). There was no significant correlation between PT and TH ($r = -0.20$, $df = 14$, NS).

Wind parameters.—In each site, wind was measured using a meteorological tower placed <100 m away from the focal stand. The tower was equipped with a Young model 27005 Gill UVW anemometer (R. M. Young, Traverse City, Michigan, USA) positioned at 6

TABLE 2. Values of species and meteorological parameters in simulations and in sensitivity analyses.

Parameter	Mean (SD)		Range in sensitivity analyses
	Nir-'Ezyon	Mt. Pithulim	
Species parameters			
F (m/s)		0.81 (0.14)	0.55–1.08
TH (m)	9.09 (1.94)	8.46 (3.26)	5.32–12.86
PT (proportion)		0.61 (0.07)	0.48–0.74
Meteorological parameters			
U (m/s)	(follows meteorological data)†		0.31–32.11 [5.43 (6.12)]‡
R (radians)	(follows meteorological data)		(not considered)
$d_{s,†}$ (m)	0.36	0.86	0.36
$d_{r,†}$ (m)	0.30	0.86	0.36
$z_{0,†}$ (m)	0.21	0.42	0.21
$z_{0,‡}$ (m)	0.07	0.42	0.21
W (m/s)	0.10 (0.35)	0.10 (0.15)	–0.58–0.76

Note: The values for Nir-'Ezyon were used in the sensitivity analyses.

† The statistics of U were estimated from wind data for each simulated period in the standard simulations and from the entire data set (all periods combined) in the sensitivity analyses.

‡ The variables d and z_0 represent the displacement height and the roughness length, respectively; the subscripts s and r refer to the study site and its reference meteorological station, respectively. The Israeli Meteorological Service (IMS) station in 'En-Karmel is the reference for Nir-'Ezyon; the meteorological station established in Mt. Pithulim is the reference station for this site.

m, and two Young model 03002 cup anemometers positioned 2 and 10 m above ground level. Measurements were taken during a period of 32 d during fall 1995 in NE and during the entire study period in MP. The UVW anemometer measured wind direction (R), and horizontal (U) and vertical (W) velocities. The distribution of $\ln(U)$ was not significantly different from normal in NE (Shapiro-Wilk $W = 0.949$, $df = 50$, NS) or in MP (Shapiro-Wilk $W = 0.970$, $df = 50$, NS). The distribution of W was not significantly different from normal in NE (Shapiro-Wilk $W = 0.981$, $df = 50$, NS), but in MP it was skewed to the right and the normality hypothesis was rejected (Shapiro-Wilk $W = 0.905$, $df = 50$, $P < 0.01$).

The displacement height (d) and the roughness length (z_0) were calculated from the measurements of U at three heights using Robinson's (1962) method as modified by Haenel (1993). The estimated values of the roughness parameters are within the range reported for similar surfaces of the shrubland outside both stands (Wieringa 1993). We assumed that the relatively short-term wind measurements in NE are sufficient to estimate W and the two roughness parameters of this site. Data on R and U during the entire study period in NE were taken from contemporaneous measurements made at the Israel Meteorological Service (IMS) station at 'En-Karmel, 1.5 km southwest of NE. Wind was measured in that IMS station 10 m above the ground by a Young model 05103 anemometer. Following SEDFAL (Fields and Sharpe 1980), u_* was assumed to be identical for the two closely located sites; thus,

$$u_* = \frac{K \times U_{10,r}}{\ln\left(\frac{10 - d_r}{z_{0,r}}\right)} \quad (11)$$

where subscript r symbolized values of the reference station, and U_{10} is U measured 10 m above the ground. A comparison between NE and the IMS reference station during the period of 32 d in fall 1995 did not reveal significant differences in contemporaneous measurements of R and U_{10} (Nathan et al. 1999). The meteorological tower in MP was placed within the study site itself, serving as a reference station for this site.

Statistical methods

We refer to "verification" as an examination of the general behavior of the model, and "validation" as a quantitative comparison of specific predictions against independent real-life data (for further discussion on stages during the model evaluation process see Oreskes et al. 1994, Rykiel 1996, and Loehle 1997).

Verification.—The term "dispersal curve" is often applied to various graphical descriptions of seed dispersal patterns (Nathan and Muller-Landau 2000); here we use this term for the frequency distribution of dispersal distances, a commonly used type of dispersal curve which is also called "distance distribution" (Nathan and Muller-Landau 2000). We constructed the dispersal curve from randomly selected 100 000 individual dispersal events during a typical run with the standard parameter values of NE (Table 2), and examined whether it is positively skewed and leptokurtic, and whether the mode is off the point of release and at zero distance from the nearest canopy (Harper 1977, Okubo and Levin 1989).

Validation.—We estimated seed dispersal to each seed trap as the mean number of seeds arriving in the nine (3×3) cells around the one identified as the seed trap location. We use the proportions of seeds at each seed trap location (out of the total number of seeds

counted in all the seed traps) as a descriptor of the spatial pattern of dispersal. To avoid using the same data for parameter estimation and for model validation, we used the dispersal data collected in NE during fall 1993 and spring 1994 to estimate the temporal pattern of seed release; the model's predictions were tested for the remaining four dispersal seasons in NE and for the three dispersal seasons in MP.

We followed the methodology of Mayer and Butler (1993) for statistical validation of predicted vs. observed data, using parametric paired t test for means, linear regression analysis testing for zero intercept and unit slope (including a simultaneous test of both conditions), and an estimate of predictive accuracy as standard methods for statistical validation. The paired t test was carried out in addition to the conventional regression analysis, to examine whether we can distinguish predictions from reality (Loehle 1997). Preliminary examination of the data revealed violation of the heteroscedasticity and normality assumptions, relaxed after square-root transformation of both predicted and observed data. We used standard methods provided by the SPSS package (SPSS 1993) to calculate the paired t test, the mean squared error of prediction (MSE) as a measure of predictive accuracy (Wallach and Goffinet 1989), and for evaluating the significance of the deviations from regression slope = 1 (and >0), and the intercept = 0. This composite hypothesis on the regression parameters was also tested simultaneously using the F test of Mayer et al. (1994). The coefficient of determination (R^2), measuring the proportion of explained variance, was calculated in the "ordinary" method, as the squared multiple correlation coefficient (SMCC) between the response and the predictor, and also by the method of Kvålseth (1985) for situations in which the variables were transformed (see Sokal and Rohlf 1995: 538).

Sensitivity analysis.—The sensitivity analysis of dispersal distance (D), the main response variable in the model, to changes in the main biotic (F , PT, TH) and wind parameters (U and W) (Tables 1 and 2), was performed in four steps. In the first step, since all input parameters were assumed to be normally (or log-normally) distributed (Table 1), we defined the range of each input parameter as between 2.5% and 97.5% of the cumulative area under the normal curve, with the means and standard deviations of NE (Table 2). This range was divided into 19 intervals, covering each 5% of the cumulative normal distribution. In the second step, a Latin hypercube sample was generated by randomly selecting 19 hypercubes, when each interval of each input parameter is sampled once and only once. A full factorial design would require sampling of all 19^5 hypercubes, a logistically impossible sample size. Since the number of samples required for a Latin hypercube sample is proportional to the number of intervals and is not a function of the number of parameters, this method enables an examination of broad

ranges of many parameters with high resolution. The Latin hypercube sampling (McKay et al. 1979) was preferred to other random sampling techniques as it has been shown to be very effective in sensitivity analyses (McKay et al. 1979, Downing et al. 1985, Seaholm et al. 1988, Helton 1993).

In the third step, the specific value of each parameter within each interval was randomly selected according to the shape of the particular normal distribution at this range. When the values of all parameters are specified, the response variable is calculated. Stages two and three were repeated 10 times to allow each interval of a parameter to be matched with more intervals of every other parameter. In the fourth step, the resulting 190 samples were subjected to stepwise multiple regression. Since the relationships between the response and the input parameters are clearly nonlinear (Eq. 10), their values were rank-transformed and then tested by ordinary regression (Iman and Conover 1979). This technique is useful when the relationships between the response and input variables are nonlinear but monotonic (Iman and Conover 1979).

RESULTS

Model predictions

The following examples of model predictions for the distribution of dispersed seeds in NE and MP (Fig. 2) were produced during a typical program run. A typical run of all 70 periods of study in NE (3 yr) predicted dispersal of ~4 200 000 seeds from the 96 adult trees occupying this site. Though long-distance dispersal did occur (see *Verification of the dispersal curve*), the vast majority of dispersed seeds (99.3% in NE and 99.5% for MP) were deposited within the simulated landscape.

Verification of the dispersal curve

The frequency distribution of the 100 000 randomly selected dispersal distances calculated during a model run with the standard values of NE (Fig. 3) and its summary statistics (Table 3) demonstrated that the expectations of both positively skewed and leptokurtic distribution and the position of the dispersal mode some distance away from the point of release but at zero distance from the nearest canopy edge, were fully met. Despite the $W < F$ constraint, 3482 (3.5%) of the records were ≥ 100 m, 217 (0.2%) records were ≥ 1 km, and the maximum distance simulated was 216 km. The very high kurtosis (Table 3) indicates a "fat-tailed" distribution with relatively substantial long-distance dispersal (Kot et al. 1996, Clark et al. 1998a, 1999, Higgins and Richardson 1999).

Field validation

The model's predictions of the proportions of seeds dispersed to a seed trap station fit the seven empirical data sets collected at the two study sites reasonably well (Table 4). In all paired t tests, the hypothesis of

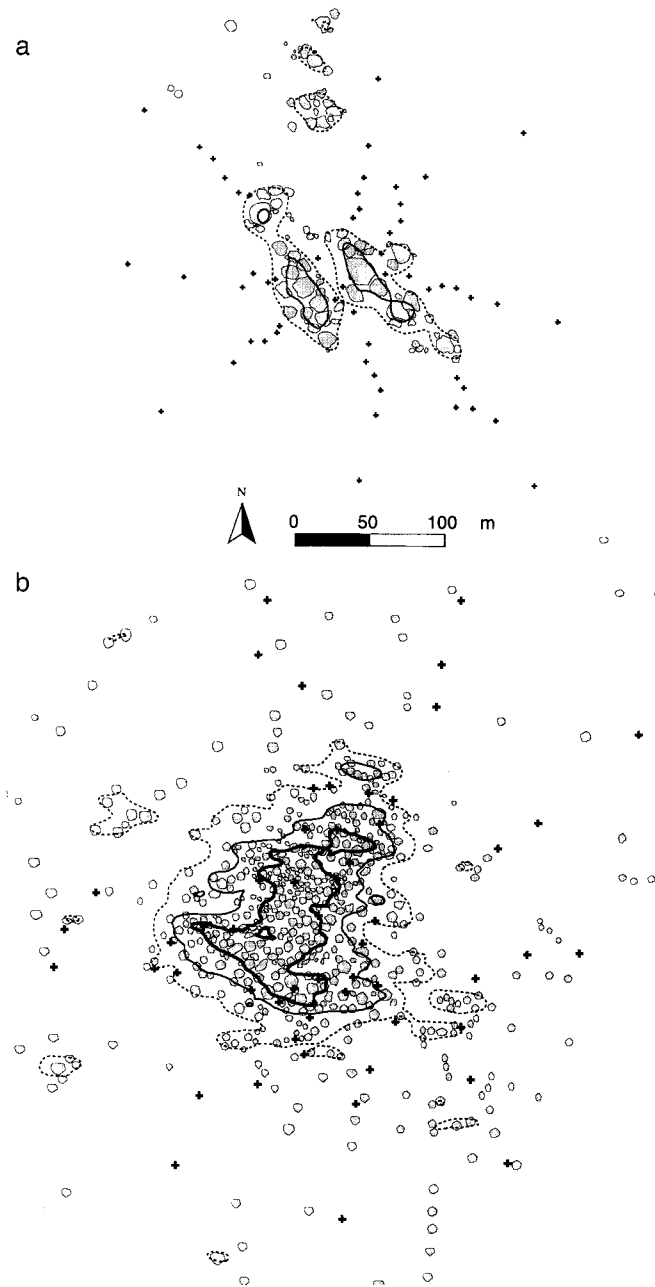


FIG. 2. Model's simulations of the proportion of seeds dispersed for (a) the period between fall 1994 and spring 1996 in NE and (b) the period between spring 1997 and spring 1998 in MP. Gray polygons show adult (seed-producing) trees, and crosses indicate seed trap stations. Contours indicate the proportion of seeds dispersed to a 1×1 -m cell out of the total number of seeds dispersed (1 811 670 seeds in NE, 9 392 501 seeds in MP) to all cells within the simulated landscape (250 000 cells in NE, 360 000 cells in MP): dashed line, 0.01%; solid line, 0.02%; bold line, 0.03%.

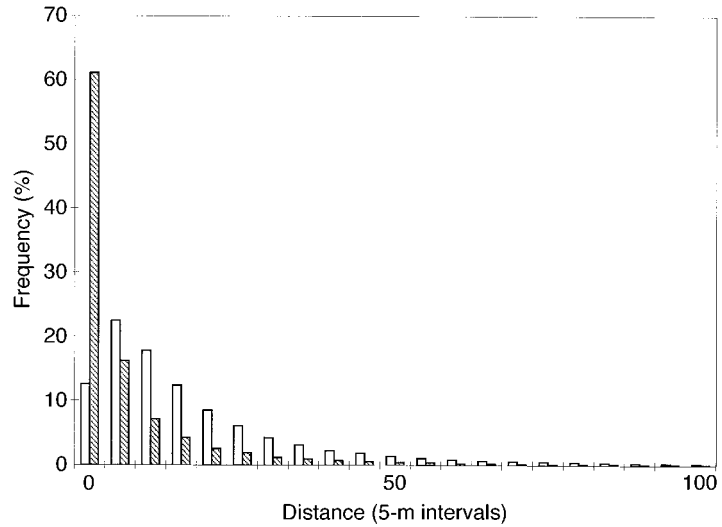
no difference between observed and predicted proportions was not rejected. All the regression slopes were significantly different from zero and not significantly different from one, and all the intercepts were not different from zero. The F test examining these two hypotheses simultaneously produced the same results. The model's predictions accounted for 83% to 90% of the variation in the observed data sets of NE, and 60%

to 78% for the data sets of MP. The maximum absolute error in the model's predictions for the proportions of seeds in a seed trap station (values range 0.0000–1.0000) was rather low (0.0012).

Sensitivity analysis

Results of the stepwise multiple rank regressions show that, within their natural range of variation, wind

FIG. 3. Frequency distribution of randomly selected 100 000 dispersal distances calculated between the center of the deposition cell and the actual source cell (hatched bars) or the nearest source cell (open bars). This simulation uses the standard parameter values of NE (Table 2).



parameters, and especially U , have a large impact on dispersal distances, considerably larger than that of the biotic factors (Table 5). U accounted for ~72% of the variation in D alone, and W explained an additional 14% of the variation; i.e., ~86% of the variation was accounted for exclusively by the two wind factors. The contribution of the variation in biotic factors, though relatively low, was significant. The height of seed release (H) has more impact on D than the terminal velocity (F). When H was decomposed into its two components (PT and TH; note that these two are not significantly correlated), the latter was found to be more influential than F , while the former was the least sensitive factor. Altogether the main four (or five, if H is replaced by PT and TH) input parameters in the model account for 95% of the variation in the dispersal distance (Table 5).

DISCUSSION

There have been significant recent advances in our ability to predict seed dispersal patterns, mostly through sophisticated phenomenological models (Clark 1998, Clark et al. 1998a, b, 1999, Higgins and Richardson 1999, Nathan and Muller-Landau 2000). These models, however, cannot provide a basis for generalization beyond the studied systems, or any insight into the main features of the process (Okubo and Levin 1989, Nathan and Muller-Landau 2000). These objectives are best accomplished by mechanistic models (Nathan and Muller-Landau 2000); however, previous

mechanistic models of seed dispersal by wind rely heavily on parameters that are difficult to interpret and measure, making their validation against field data disputable, and providing no means to quantify the relative effects of the main parameters involved. We present a model of seed dispersal by wind that incorporates the full natural variation in those few basic parameters that are directly interpretable and measurable, yet provides reliable predictions at a spatial resolution of 1 m², and the means to examine the relative impact of these factors.

Factors affecting the dispersal distance

Given that most seeds fall in the vicinity of the parent plant, increasing dispersal distance should increase the probability of seed survival and of locating establishment opportunities that are unpredictable in space and time (the escape and the colonization hypotheses, Howe and Smallwood 1982). Obviously, the distance of dispersal by wind largely depends on wind conditions. However, a wind-dispersed species can influence the dispersal distance by manipulating (1) seed aerodynamics, (2) the height of seed release, and (3) the timing of seed release, with respect to the wind conditions.

Plant control of seed aerodynamics through morphological traits has been considered to be the major determinant of dispersal distance, and the terminal velocity, the most important aerodynamic property, as “a surrogate of dispersal ability” (e.g., Green 1980, Gur-

TABLE 3. Summary statistics of 100 000 randomly selected dispersal distances calculated during a simulation using the standard values of NE.

Distance	Mean	1 SEM	Median	Mode	Skewness		Kurtosis	
					Statistic	1 SE	Statistic	1 SE
To source cell	38.4	2.6	14.0	7.0	195.9	0.008	47 621.9	0.015
To nearest canopy	19.9	1.0	3.0	0.0	66.7	0.008	5 625.9	0.015

TABLE 4. Statistical validation of model predictions (means of 50 independent model runs) of the proportion of seeds dispersed to a seed-trap station against observed data.

Site and season(s)	Paired <i>t</i> -test†	MSE	$R^2‡$		Linear regression				<i>F</i>
			SMCC	Kvålseth	Lower 95% CL	Slope Mean	Upper 95% CL	Intercept§	
Nir- ² Ezyon									
Fall 1994	1.175 ^{NS}	0.0010	0.833	0.837	0.924	1.045	1.166	-0.0113 ^{NS}	0.914 ^{NS}
Spring 1995	0.625 ^{NS}	0.0008	0.861	0.868	0.883	0.985	1.087	-0.0001 ^{NS}	0.237 ^{NS}
Fall 1995	1.031 ^{NS}	0.0008	0.862	0.864	0.922	1.029	1.135	-0.0079 ^{NS}	0.652 ^{NS}
Spring 1996	0.857 ^{NS}	0.0008	0.868	0.838	0.910	1.012	1.114	-0.0048 ^{NS}	0.376 ^{NS}
Fall 1994–Spring 1996	0.996 ^{NS}	0.0006	0.897	0.898	0.943	1.034	1.124	-0.0080 ^{NS}	0.729 ^{NS}
Mt. Pithulim									
Spring 1997	0.716 ^{NS}	0.0010	0.761	0.727	0.845	1.001	1.156	-0.0031 ^{NS}	0.225 ^{NS}
Fall 1997	0.410 ^{NS}	0.0012	0.670	0.597	0.725	0.901	1.077	-0.0138 ^{NS}	0.720 ^{NS}
Spring 1998	0.699 ^{NS}	0.0008	0.781	0.721	0.861	1.010	1.159	-0.0043 ^{NS}	0.245 ^{NS}
Spring 1997–Spring 1998	0.622 ^{NS}	0.0009	0.777	0.734	0.843	0.991	1.139	0.0010 ^{NS}	0.201 ^{NS}

Note: Both predicted and observed data are square-root transformed. “NS” denotes not significant at $\alpha = 0.05$.

† H_0 : no difference between predicted and observed values.

‡ R^2 calculated as squared multiple correlation coefficient (SMCC) or by Kvålseth’s (1985) method (see *Methods: Statistical methods: Validation*).

§ H_0 : intercept = 0.

|| Simultaneous F statistic; H_0 : slope = 1 and intercept = 0.

ies and Nordheim 1984, Andersen 1991, 1993). In our results, however, the dispersal distance is far more sensitive to temporal variation in wind conditions than to intraspecific variation in the biotic factors. This is in agreement with the finding that the variation in terminal velocity is considerably smaller than the variation in vertical and horizontal wind velocities (Augsburger and Franson 1987, 1993, Greene and Johnson 1992a, Hensen and Müller 1997). The predominance of the horizontal component of wind velocity over the vertical one may be misleading, since strong positive (upward) vertical velocities were constrained to be lower than the terminal velocity (the $W < F$ constraint).

Although accounting for a relatively low proportion of the variation not explained by the wind factors, the two biotic factors did have significant independent effects on dispersal distance. The height of seed release was found to be more influential than terminal velocity, which varied little among trees, among cones within trees, and among seeds within cones (Nathan et al. 1996). Similarly, the relaxation distance was also found to be consistent among trees, among cones within trees, and among seeds within cones (Nathan et al. 1996). When the height of seed release was partitioned into its two components, tree height was found more important than the vertical distribution of seeds over the tree. Given the predominant effect of wind factors over terminal velocity and tree height on the dispersal distance, we hypothesize that the synchronization of seed release with favorable winds is the most effective plant-controlled mechanism to increase the distance of dispersal in wind-dispersed species like *P. halepensis*. This hypothesis is supported by our finding that seed release in *P. halepensis* is synchronized with predictable periods of the year having relatively effective winds for long-distance dispersal (Nathan et al. 1999). This phenomenon is only indirectly included in the

present version of the model, through the use of the regression on meteorological parameters to estimate seed release.

Extensions and limitations

Although the model was developed and implemented for one tree species, the modeling approach presented here could be used for other wind-dispersed species of any life form with two precautions. The first relates to adequacy of the logarithmic wind profile (Eq. 4) in describing the horizontal wind a seed encounters during its flight. Numerous studies have shown that this profile works well in describing the horizontal wind speed above various vegetation types (Monteith and Unsworth 1990, Wieringa 1993). Our findings suggest that it may also work well for a landscape with relatively short trees that are rather sparsely distributed among shrubs; other wind profile equations, however, may be required to describe wind in dense forests.

The second precaution relates to the vertical movement of a seed during flight. The $W < F$ constraint in Eq. 10 is important if the distributions of F (terminal velocity) and W (vertical wind speed) largely coincide. In our data, the two distributions diverge: according to the standard values of the normally distributed F and W (Table 2), $W \geq F$ in $\sim 3\%$ of the cases in a simulation for NE and $\sim 0.03\%$ of the cases in a simulation for MP. Greene and Johnson (1995) evaluated the typical frequency in which $W \geq F$ to be in order of ~ 0.1 – 10% of the overall seed dispersal events for North American wind-dispersed tree species. Since (a) the values of the statistics of W reported in this study (Table 2) are close to those reported elsewhere (e.g., Baldocchi and Hutchison 1987, Amiro and Davis 1988), (b) these values are considerably lower than the mean F estimated for seeds of most wind-dispersed tree species (Guries and Nordheim 1984, Greene and Johnson 1995), and (c) the

TABLE 5. Stepwise multiple regressions of the dispersal distance against main input parameters in the model (see Table 1 for symbols).

Step	Variable entered	Adjusted R^2 †	β ‡	P	Variable entered	Adjusted R^2 †	β ‡	P
1	U	0.717	0.848	<0.001	U	0.717	0.848	<0.001
2	W	0.860	0.378	<0.001	W	0.860	0.378	<0.001
3	H	0.922	0.249	<0.001	TH	0.905	0.213	<0.001
4	F	0.950	-0.168	<0.001	F	0.934	-0.171	<0.001
5					PT	0.949	0.123	<0.001

Notes: The values of all parameters, selected by random Latin hypercube sampling of 19 equal-probability (0.05) intervals of the assumed distribution defined by the standard values of NE, were ranked-transformed. The parameter H on the left-hand side of the table is replaced by PT and TH on the right, since $H = PT \times TH$.

† The fraction of the variance accounted for by the model, adjusted for the number of independent variables.

‡ Standardized regression coefficient.

standard deviation of F is usually rather low, about one-eighth of the mean (Greene and Johnson 1992a); the $W < F$ constraint is probably negligible for the short-distance dispersal of (most) seeds of wind-dispersed tree species. However, it should be taken into account for simulating dispersal of very light seeds or pollen, and, indeed, when long-distance dispersal is considered (Greene and Johnson 1995). Simulations of long-distance dispersal should also relax the assumption of constant W during seed flight, since W is likely to vary during long flights.

The temporal component in the model assumes that seed release is significantly correlated with measurable climatic factors; a multiple regression equation calculated from a fraction of the available data was used to predict the rate of seed release in other periods. When the assumption of climatic correlation does not hold, there are two alternative approaches. First, when dispersal occurs randomly during the year, it is sufficient to estimate the mean and variation in the rate of seed release during a certain portion of the year. Second, if dispersal is not random during the year, the periodic rate of seed release can be estimated directly from dispersal data. This option is likely to reflect the temporal pattern of seed release more closely than the regression method, but it does not simulate any mechanism of seed release and depends on the availability of dispersal data.

In addition to the processes and factors explicitly included in our model, other processes and factors may affect seed dispersal by wind. For example, it is likely that topography and vegetation (the pine trees themselves, other trees, undercanopy, and surrounding vegetation) affect the direction, horizontal, and vertical velocities of the wind (Coultts and Grace 1995). In particular, there should be an important change in wind conditions in the transition between a stand and an opening (Greene and Johnson 1996). These factors should shorten dispersal distances within a stand, compared to dispersal from an isolated tree, and hence may explain why dispersal curves generated by an area source peaked closer to the source than those generated

by a point source. However, these patterns were predicted by our model without considering any of these factors (Fig. 3); it appears that the most parsimonious explanation of overlapping seed shadows (which is irrelevant for isolated trees) is sufficient to generate this difference.

An important feature of *P. halepensis* seeds not considered in our model is that due to the weak attachment of the wing a certain proportion of seeds lose the wing before abscission (Nathan and Ne'eman 2000). The incorporation of a "wing-loss" factor into the model should result in more right-skewed, possibly bimodal, and more leptokurtic dispersal curves, as wingless seeds fall beneath the point of release. On the other hand, the incorporation of the "threshold wind speed" factor for seed release, i.e., the differential seed release in relatively high wind speeds (Burrows 1983, Greene and Johnson 1989, 1992b, Van Dorp et al. 1996), should have the opposite effect, shifting the dispersal curve toward the tail due to higher average wind speed during dispersal.

These modifications are difficult to implement in analytical models such as those developed by Greene and Johnson (1989, 1995, 1996; see *Introduction*), since complicated differential equations soon become insoluble. In comparison, a stochastic simulation approach such as the one employed in this study has a decisive advantage of flexibility and could be modified to include any or all of these other factors that were initially left out of the model. Furthermore, any of the five principal assumptions in the calculation of the spatial component of the model (see *Model algorithms: Dispersal direction and distance*) may be relaxed by more elaborate calculations. For example, it is possible to classify the surface types of the simulated landscape according to aerial photographs of the sites, and to relate specific values of roughness parameters for each cell, to be considered in the calculation of the dispersal distance. This may not increase the predictive value of the model which has been formulated to be as simple as possible, yet it captures the critical factors governing seed dispersal dynamics. Useful models are not nec-

essarily those that retain great detail of the process being investigated (Ludwig 1989), and separating signal from noise is best accomplished by suppressing unnecessary details.

There is a growing interest in the study of long-distance dispersal because of its implications for the fields of climate change (Clark et al. 1998a), invasions (Hengeveld 1994), and gene flow (Hamrick and Nason 1996). The approach of comparing actual and predicted values at many distances along the dispersal curve, rather than just the modal or other central statistic, is clearly preferred in this context. The finding that very large dispersal distances indeed occur in our simulations despite the $W < F$ constraint, indicates a potential for simulating long-distance dispersal, and provides a null model to evaluate the role of wind updrafts ($W > F$) in promoting long-distance dispersal. However, we did not place seed traps farther than 110 m from the nearest adult tree, thus the goodness of fit of the model's predictions for larger distances is unknown. Furthermore, effective application of any dispersal model necessitates the incorporation of the recruitment that follows dispersal (Nathan and Muller-Landau 2000). Mechanistic simulation models can potentially be used for more detailed examination of the process leading from seed dispersal to recruitment in which different factors have been found to produce different patterns (Schupp and Fuentes 1995, Nathan and Muller-Landau 2000).

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APPENDIX

WINDISPER: a spatiotemporal mechanistic model of seed dispersal by wind, version 1.0.10.1999, is available in ESA's Electronic Data Archive: *Ecological Archives* E082–004.