

In: Seed Dispersal and Frugivory: Ecology, Evolution and Conservation.

D. J. Levey, W. R. Silva and M. Galetti (Eds.) CAB International Press, Oxfordshire. UK. 2001

Mechanistic models for tree seed dispersal by wind in dense forests and open landscapes

RAN NATHAN, HENRY S. HORN, JEROME CHAVE and SIMON A. LEVIN
*Department of Ecology and Evolutionary Biology, Princeton University,
Princeton, New Jersey 08544-1003, USA*

INTRODUCTION

Seed dispersal is the main process linking spatial patterns of parent plants and their descendants (Harper, 1977; Schupp and Fuentes, 1995; Nathan and Muller-Landau, 2000). To examine the consequences of seed dispersal for patterns of plant recruitment, the spatial patterns of dispersed seeds must be quantified and their determinants understood (Nathan and Muller-Landau, 2000). A powerful framework towards this end is a combination of theoretical models and fieldwork (Okubo and Levin, 1989; Nathan and Muller-Landau, 2000).

Wind is a common dispersal agent of seeds, especially of temperate and boreal trees (Howe and Smallwood, 1982; van der Pijl, 1982). Early mechanistic models of seed dispersal by wind have recently been extended to a broad array of species and systems (reviewed in Nathan *et al.*, 2001). However, while our understanding of the mechanisms of seed dispersal by wind continues to improve, fundamental issues remain largely unexplored. In particular, it is well known that the roughness structure of the ground surface strongly affects wind conditions at the 'surface layer' (the lower part of the 'atmospheric planetary boundary layer'; Oke, 1987; Stull, 1988), where seed dispersal mostly takes place. Thus, landscape structure can strongly influence deposition patterns of wind-dispersed seeds. For example, it has long been suggested that treefall gaps act as sinks for wind within and over a forest and therefore should receive a disproportionate number of wind-blown seeds (Augsburger and Franson, 1988; Schupp *et al.*, 1989). Overall, the suggested mechanisms and the predictions about spatial distributions of wind-dispersed seeds remain relatively unexplored.

Only two mechanistic wind dispersal models have explicitly incorporated landscape structure: a model of seed dispersal from a forest into a clearing (Greene and Johnson, 1996), and one of secondary dispersal on snow (Greene and Johnson, 1997). No comparison has yet been made between the predicted distributions of dispersal distance under different landscape structures. Yet, such comparisons are important to assess how dispersal may determine recruitment in different environments.

In this study we compare wind dispersal of tree seeds in two distinct landscape structures: dense forests and trees scattered in an open landscape. These two environments differ greatly in wind conditions. The characteristic wind profile, which describes mean horizontal windspeed at different heights, is typically logarithmic over low vegetation in open landscapes and exponential within dense forests (Kaimal and Finnigan, 1994; see *Methods*; Fig. 1). Winds in open landscapes are typically stronger than winds within dense forests. Moreover, the different shape of the wind profiles implies that seeds dispersed in open landscapes encounter relatively strong horizontal winds over a much wider vertical range during their flight than seeds released from similar height within dense forests. This can be illustrated by comparing the length of the arrows indicating the horizontal wind speed in the two profiles in Fig. 1. Thus, everything else being equal, the distribution of the dispersal distances is expected to be more limited in dense forest than in open landscapes. We shall examine this prediction with two mathematical models of seed dispersal by wind that differ only in the shape of the wind profile. Then, we will apply and test the model's predictions against extensive seed trap data collected in an isolated stand of Aleppo pine (*Pinus halepensis* Mill.) in Israel. In particular, we compare fits of the two models for dispersal data collected within versus outside the stand, expecting the model that incorporates the exponential profile to perform better within the stand, and the one that incorporates the logarithmic profile to perform better outside the stand.

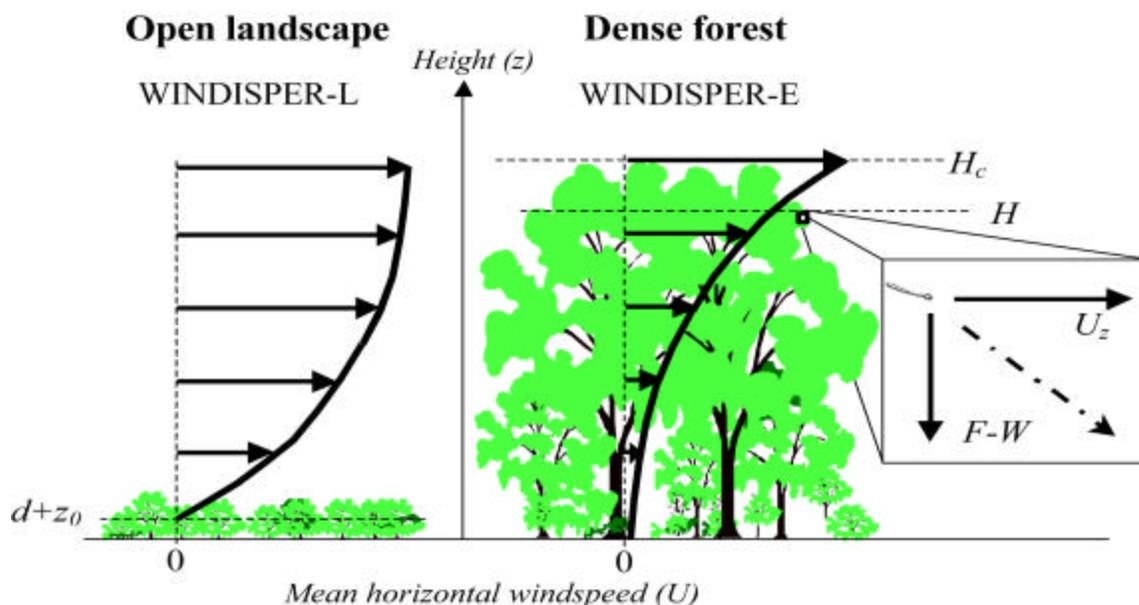


Fig. 1. Main factors influencing tree seed dispersal in open landscapes, as modeled in WINDISPER-L, and in dense forests, as modeled in WINDISPER-E. In both landscape types, the horizontal component of seed flight is determined by the horizontal windspeed (U), and the vertical component by the terminal velocity (F), *i.e.*, the constant rate of seed fall in still air, and the vertical windspeed (W). The two landscape types differ in the vertical wind profiles, describing the change in U with height (z) above the ground surface. A logarithmic profile is typically observed in open landscapes above short vegetation, characterized by the roughness length (z_0) and the displacement height (d), where $d+z_0$ is the height at which $U = 0$. An exponential profile is typically observed within a forest below the canopy height (H_c).

METHODS

WIND DISPERSAL SIMULATIONS

The logarithmic wind profile has already been implemented in a mechanistic wind dispersal model (Sharpe and Fields, 1982) and in WINDISPER (Nathan *et al.*, 2001). WINDISPER simulates the temporally and spatially explicit dynamics of seed dispersal by wind by incorporating stochasticity in all operative factors. Using the same modelling approach, we introduce here a new mechanistic model to describe the dispersal of seeds by wind within dense forest canopy. We call this model 'WINDISPER-E' ('E' indicates the use of an exponential wind profile). For consistency, we refer to the original model, WINDISPER, as 'WINDISPER-L' ('L' indicates the use of a logarithmic wind profile). We emphasise that the general structure of the two models is identical; they differ only in the wind profiles used.

In the following three subsections, we first describe the general modelling approach and the main assumptions. In the second subsection, we briefly summarise the original model (WINDISPER-L); we refer readers to Nathan *et al.* (2001) for a complete description of this model. The third subsection describes the new model (WINDISPER-E) in detail. The main parameters are defined in Table 1.

General modelling approach and main assumptions

In both models, dispersal of individual seeds is simulated in a square grid with 1 m² cells representing a simulated landscape. Seeds are dispersed from source (tree canopy) cells and can be deposited in any cell depending on the dispersal direction (R) and the dispersal distance (D). The dispersal direction is randomly selected from the wind directions observed during the simulated period, and is assumed to be constant during flight. The dispersal distance, defined as the horizontal distance a seed is carried by the wind, can be calculated as

$$D = \frac{H \cdot U}{F - W} \quad (1)$$

where H is the height of seed release, U is the mean horizontal windspeed during seed flight, F is the terminal velocity of a seed falling in still air and W the mean vertical windspeed during flight, which is negative downward and positive upward.

Because wind-dispersed tree seeds typically reach terminal velocity (F) shortly after release, the vertical distance travelled before reaching F (called the relaxation distance) is typically small compared to the vertical distance travelled after F is reached (Guries and Nordheim, 1984; Nathan *et al.*, 1996). Therefore, we assume that the relaxation distance is negligible. We also assume that W is constant during flight and, to ensure finite dispersal distances, we force it to be smaller than F . Thus, events of seed uplifting are precluded, as we assume they play only a minor role in short-distance dispersal of most seeds (although they may be crucial for long-distance dispersal).

Instead of using the mean horizontal windspeed U as in Eq. 1, the two models incorporate the vertical profile of U , assumed to be logarithmic in open landscapes (WINDISPER-L) and exponential in dense forests (WINDISPER-E). In both models, the parameters that determine U (see below), as well as all the other parameters of Eq. 1, are randomly selected from their measured distribution (Table 1) for each seed dispersed. The horizontal windspeed deterministically decreases during seed fall, as dictated by the respective wind profile. Thus, the models do incorporate variation between different dispersal events, but do not incorporate random fluctuations in the horizontal windspeed during a seed's flight, assuming that these fluctuations do not have a significant effect during the typically short time most seeds remain airborne. We also assume seeds are released at random with respect to either W or U . We emphasise that these assumptions do not always hold. Rather, we assert that they generally hold for short-distance dispersal. Models of long-distance dispersal, however, will likely require that they be relaxed.

WINDISPER-L - the logarithmic wind profile model

The logarithmic wind profile describes the decline in horizontal windspeed, U , with decreasing height above the surface, due to the surface resistance, as:

$$U_z = \frac{u_*}{K} \ln \left(\frac{z - d}{z_0} \right) \quad (2)$$

where U_z is the mean U at height z above the ground, u_* is the friction velocity; K is the von Kármán constant (≈ 0.40); and z_0 and d are two roughness parameters, termed roughness length and displacement height, respectively (Stull, 1988). Eq. 2 only applies for $z \geq d + z_0$, below which $U = 0$ (Fig. 1). The roughness length scales the amount of drag the ground surface exerts on the wind and is closely related to the average height of the roughness elements, i.e., the plants.

Tightly-packed plants (e.g., those forming a dense canopy) act as though the surface is located at some height above the real surface. The height of this 'displaced surface' is called the displacement height. These two roughness parameters are not directly measurable physical quantities; they are best determined empirically by measuring U at several heights above a surface and fitting Eq. 2. Recall that WINDISPER-L describes seed dispersal from trees scattered in an open landscape of much shorter vegetation. Thus, its wind profile is assumed to be determined only by the dominant short vegetation, not by the scattered trees (Fig. 1). Numerous studies have shown that the logarithmic profile works well in describing the horizontal windspeed *above* various vegetation types (Stull, 1988; Wieringa, 1993; Kaimal and Finnigan, 1994). As detailed in Nathan *et al.* (2001), Eq. 2 can be incorporated into Eq. 1 to provide the following equation for dispersal distance (D):

$$D = \frac{u_*}{K(F-W)} \left((H-d) \ln \left(\frac{H-d}{e \cdot z_0} \right) + z_0 \right) \quad (3)$$

WINDISPER-E - the exponential wind profile model

The profile of the horizontal windspeed within plant canopies usually follows an exponential relationship (Cionco, 1965):

$$U_z = U_{H_c} \exp \left(\alpha \left(\frac{z}{H_c} - 1 \right) \right) \quad (4)$$

where H_c is the height of the canopy top; U_{H_c} is U at H_c ; and α is the attenuation coefficient (Cionco, 1965), also called the canopy flow index (Cionco, 1978). The attenuation coefficient tends to increase with increasing canopy density (Cionco, 1978; Raupach, 1988; Kaimal and Finnigan, 1994); i.e., the decline in horizontal windspeed from the canopy top (H_c) downwards is most rapid in forests of high foliage and stem density. The exponential profile generally fits observed data well (Cionco, 1978, Amiro and Davis, 1988; Amiro, 1990; Gardiner, 1994; Kaimal and Finnigan, 1994). One exception occurs when a bare-trunk layer results in a small secondary peak in windspeed at the lower half of the canopy height. This effect does not occur in stands with well-developed understory vegetation (Amiro, 1990; Gardiner, 1994).

We shall now describe how the exponential wind profile is incorporated in the basic equation of dispersal distance (Eq. 1). As stated above, the vertical wind velocity is assumed to have a constant value, W , 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 it hits the ground. Therefore,

$$D = \int_0^{t_1} U(t) \quad (5)$$

where $U(t)$ is U at time t and, following Eq. 1, t_1 is:

$$t_1 = \frac{H}{F-W}, \quad (6)$$

i.e., the time until a seed falling at an average velocity ($F-W$) from height H reaches the ground ($z = 0$). The vertical position, $z(t)$, of a seed during flight at time t is equal to:

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

Substituting $z(t)$ from Eq. 7 into Eq. 4 results in:

$$U(t) = U_{H_c} \exp \left(\alpha \left(\frac{H - H_c - (F-W) \cdot t}{H_c} \right) \right) \quad (8)$$

and integration within the limits of Eq. 5 yields:

$$D = -\frac{U_{H_c} \cdot H_c}{\mathbf{a}(F-W)} \exp\left(\frac{\mathbf{a}(H-H_c - (F-W) \cdot t)}{H_c}\right) \Big|_0^{t_1}. \quad (9)$$

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

$$D = \frac{U_{H_c} \cdot H_c}{\mathbf{a}(F-W)} \left(\exp\left(\frac{\mathbf{a}(H-H_c)}{H_c}\right) - \exp(-\mathbf{a}) \right). \quad (10)$$

Table 1: Main variables used in WINDISPER-L and WINDISPER-E. Apart from Q, which varies only among the simulated periods, all parameters given in capital letters vary among individual dispersal events.

Symbol	Definition (units)	Formulation/Distribution [model] [†]	Standard values Mean (SD)
<i>State parameters</i>			
<i>D</i>	Horizontal dispersal distance (m)	Eq. 3 [L]; Eq. 10 [E]	
<i>R</i>	Dispersal direction (radians)	Follows meteorological data [L,E]	
<i>Species parameters</i>			
<i>Q</i>	Number of seeds released (seeds·canopy section ⁻¹ ·day ⁻¹) [‡]	Follows meteorological data [L,E]	
<i>F</i>	Terminal falling velocity (m/s)	Normal [§] [L,E]	0.81 (0.14)
<i>H</i>	Height of seed release (m)	<i>TH</i> · <i>PT</i> [L,E]	
<i>TH</i>	Tree height (m)	Normal [¶] [L,E]	9.09 (1.94)
<i>PT</i>	Proportion of <i>TH</i> from which seeds are released	Normal [§] [L,E]	0.61 (0.07)
<i>Meteorological parameters</i>			
<i>R</i>	Wind direction (radians)	Follows meteorological data [L,E]	
<i>U</i>	Horizontal windspeed (m/s)	Log-normal [§] ; Follows meteorological data [L,E]	
<i>U*</i>	Friction velocity (m/s)	Follows meteorological data [L]	
<i>d</i>	Displacement height (m)	[L]	0.36 / 0.30 ^ξ
<i>z₀</i>	Roughness length (m)	[L]	0.21 / 0.07 ^ξ
<i>a</i>	Attenuation coefficient	[E]	2.0
<i>W</i>	Vertical windspeed (m/s)	Normal [§] [L,E]	0.10 (0.35)

[†] Capital letters in square brackets indicate the factors used in the two models, incorporating logarithmic [L] or exponential [E] wind profile.

[‡] Each canopy section is 1 x 1 x *TH* m.

[§] In agreement with Greene & Johnson (1989, 1996) and with site-specific empirical data (Nathan et al. 2001).

[¶] In agreement with site-specific empirical data (Nathan et al. 2001).

^ξ The left and right values refer to the study site and its reference meteorological station, of the Israeli Meteorological Service at 'En-Karmel, respectively.

MODEL EVALUATION

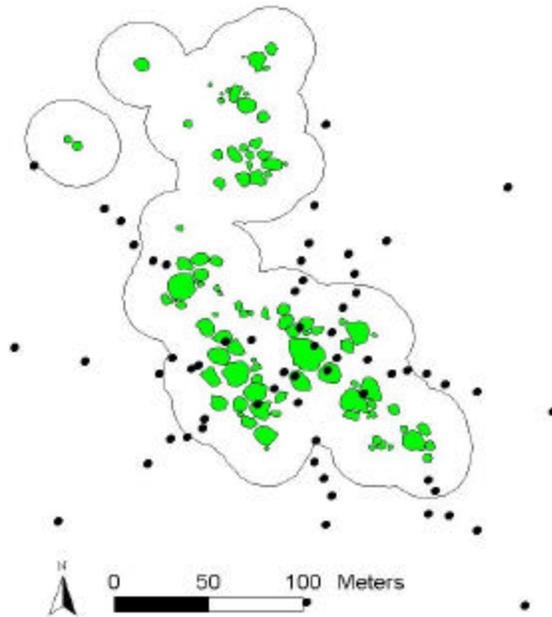
Species and site

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 (usually <15 m) for pines (Nathan and Ne'eman, 2000). Seed release is stimulated by fire and by Sharav events, which are dry and hot spells of < 1 week, characteristic of the eastern Mediterranean. These events typically occur during spring and fall and have stronger horizontal, and especially vertical, windspeeds than other periods (Nathan *et al.*, 1999). We do not deal here with fire-induced seed release.

Pinus halepensis seeds are samara-like structures typical of wind-dispersed pines, with a single asymmetric wing that generates autorotation during fall. The species is considered a very successful coloniser (Acherar *et al.*, 1984; Lepart and Debussche, 1991; Rejmánek and Richardson, 1996). Isolated individuals have been found several kilometres 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).

Of the two study sites described in Nathan *et al.* (1999; 2001), we selected the site at Nir-‘Ezyon, on the lower western slopes of Mt. Carmel (32°41’N; 34°58’E, 116 m altitude) for this analysis because of the larger database and the greater isolation of the focal stand (Fig. 2). Seed dispersal was monitored by 94 identical seed traps (0.99 x 0.84 x 0.15 m; length x width x height) placed in 62 stations within and around the stand. Fourteen stations, each with a single trap, were placed within the stand, half under tree canopies and half in the gaps between the trees. The remaining 48 stations were arranged along eight transects, radiating from the focal stand in the eight main compass directions. Each transect had six stations, at approximate distances of 5, 10, 15, 25, 50 and 100 m from the focal stand. Two traps were placed in each station at 50 m, and 4 at 100 m, to compensate for the increase in area as the distance from the source increased. This design provided 11-16 traps per 10-m annular interval up to 40 m from the nearest tree, and 4-8 traps per 10-m interval from 40 to 110 m from the nearest tree.

Fig. 2. The study site south of Nir-‘Ezyon at the lower western slopes of Mt. Carmel. Shaded blotches show adult (seed-producing) trees, and circles indicate seed-trap stations. The areas “within” and “outside” the focal stand are distinguished by a line 20 m from the nearest central location of an adult tree.



Seeds were collected from traps regularly between October 1993 and November 1994 (n=36 collections, mean interval 11 days) and later only during the dispersal seasons (spring and fall 1995 and spring 1996, n = 34, mean interval 7 days). Wind measurements were taken from the Israel Meteorological Service (IMS) station at 'En-Karmel, 1.5 km southwest of the site. This station is located in an open landscape over short vegetation, in which the wind profile is typically logarithmic. A comparison between contemporaneous measurements taken at the IMS reference station and in the site (outside the stand, Fig. 2) during 32 days in fall 1995 did not reveal significant differences in wind direction and horizontal wind velocity (Nathan *et al.*, 1999). We simulate seed dispersal only during the intensive periods of seed release, thus taking into account the particular wind conditions that characterise Sharav events (there were no fires in the study site during the study period). More detailed information on the study site and the procedures for seed trapping and wind measurements are given in Nathan *et al.* (1999; 2000).

Parameter estimation

Terminal velocity (F) was estimated by analysing video photos of falling seeds (Nathan *et al.* 1996). The height of seed release (H) was calculated as the product of tree height (TH) and the proportional distribution of seeds with tree height (PT), both measured directly in the field (Nathan *et al.*, 2001). Estimates of vertical windspeed (W), displacement height (d) and roughness length (z_0) were based on wind measurements taken in the study site. The values of d and z_0 , calculated by Robinson's (1962) iterative method as modified by Haenel (1993), are typical of similar vegetation surfaces (shrubland) surrounding the stand (Wieringa, 1993). Data on wind direction (R) and horizontal windspeed (U) were taken from wind measurements taken in the IMS reference station during the dispersal seasons. As described by Nathan *et al.* (2001), u_* was assumed to be identical for the Nir-'Ezyon and IMS sites. Thus, from Eq. 2:

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

where the subscript r symbolises values of the reference station, and U_{10} is U measured 10 m above the ground. The mean horizontal windspeed at canopy height (U_{H_c}) was estimated as three times u_* . This relationship is extracted from Eq. 2, given the empirically based approximation that d and z_0 equal roughly two-thirds and one-tenth of the canopy height, respectively (Oke 1987). Because wind was not measured within the stand, we used the association with stand density (larger values characterising stands with denser canopy; see *Methods: WINDISPER-E*) to select the attenuation coefficient (\mathbf{a}). Reported values of \mathbf{a} for forest canopies range from 1.7 to 4.8 (Cionco, 1978, Pinker and Moses, 1982; Amiro and Davis, 1988; Amiro, 1990; Mursch-Radlgruber and Kovacic, 1990; Kaimal and Finnigan, 1994; Su *et al.*, 1998). We selected a relatively low value, $\mathbf{a} = 2.0$, for our site because our pine stand was relatively small and sparse.

Model validation

We use the proportions of seeds at each seed trap station relative to the total number of seeds counted in all seed traps (corrected for differences in the number of traps between sampling stations) as a descriptor of the spatial pattern of dispersal. The dispersal data collected in Nir-'Ezyon during fall 1993 and spring 1994 were used to estimate the temporal pattern of seed release, and the predictions of the two models were tested for the remaining four dispersal seasons. We also test the model's prediction for two partial sets of seed trap stations within (0-20

m from the nearest central location of a tree) and outside (20-110 m) the focal stand (Fig. 2). The areas covered by the two sectors were 28,644 and 48,736 m², with 23 and 39 stations (23 and 71 seed traps), respectively.

For statistical validation of predicted vs. observed data, we apply linear regression analysis testing for zero intercept and slope = 1. Square root transformation corrected heteroscedasticity and non-normality of both predicted and observed data. The coefficient of determination (R^2), measuring the proportion of explained variance, was calculated as the squared multiple correlation coefficient (SMCC) between the response and the predictor variables, and also by the method of Kvålseth (1985) for situations in which the variables were transformed (see Sokal and Rohlf, 1995, p. 538). We also report the mean squared error of prediction (MSE) as a measure of predictive accuracy (Wallach and Goffinet 1989).

RESULTS

Predicted distance distributions

For each model, we randomly selected 1,000,000 dispersal distances calculated during an ordinary model run. Simulations of WINDISPER-E were repeated for values of the attenuation coefficient (\mathbf{a}) other than the chosen value ($\mathbf{a} = 2.0$), covering the range reported in the literature. All distance distributions are both positively skewed and leptokurtic with the mode just a few meters away from the point of release (Fig. 3, Table 2). However, the distributions generated by the two models differ markedly in their shape at very short distances (Fig. 3). WINDISPER-L generated markedly larger dispersal distances, as indicated by all summary statistics (Table 2). Even very sparse forests ($\mathbf{a} = 1.0$) generated distance distributions that were much more shifted toward the source than those generated by isolated trees in open landscapes. Very dense forests ($\mathbf{a} = 5.0$) produced very restricted seed shadows, with 99% of the seeds travelling less than 2.7 m (Table 2). Note that the kurtosis value does not accurately reflect the fatness of the distribution's tail because it is influenced by the proportion of dispersal distances near the distribution centre and in the shoulders.

Table 2. Summary statistics of 1,000,000 randomly selected dispersal distances (in meters) calculated during simulations of the logarithmic (WINDISPER-L) and the exponential (WINDISPER-E) models. Simulations of the exponential model were repeated for values of the attenuation coefficient (\mathbf{a}) other than the chosen value ($\mathbf{a} = 2.0$), covering the range reported in the literature.

Wind profile	Mean	S.E.	Skewness	Kurtosis	Mode	Percentile		
						50	95	99
Logarithmic	32.9	1.8	460	254987	3.6	10.5	60.1	198.7
Exponential:								
$\mathbf{a} = 1.0$	7.5	0.5	382	282804	1.0	2.2	12.4	40.8
$\mathbf{a} = 2.0$	3.4	0.2	541	341870	0.5	1.1	6.1	20.2
$\mathbf{a} = 3.0$	1.8	0.1	435	224186	0.2	0.5	3.0	10.0
$\mathbf{a} = 4.0$	0.9	0.1	903	862328	0.1	0.3	1.6	5.1
$\mathbf{a} = 5.0$	0.4	0.1	978	968800	0.1	0.1	0.8	2.7

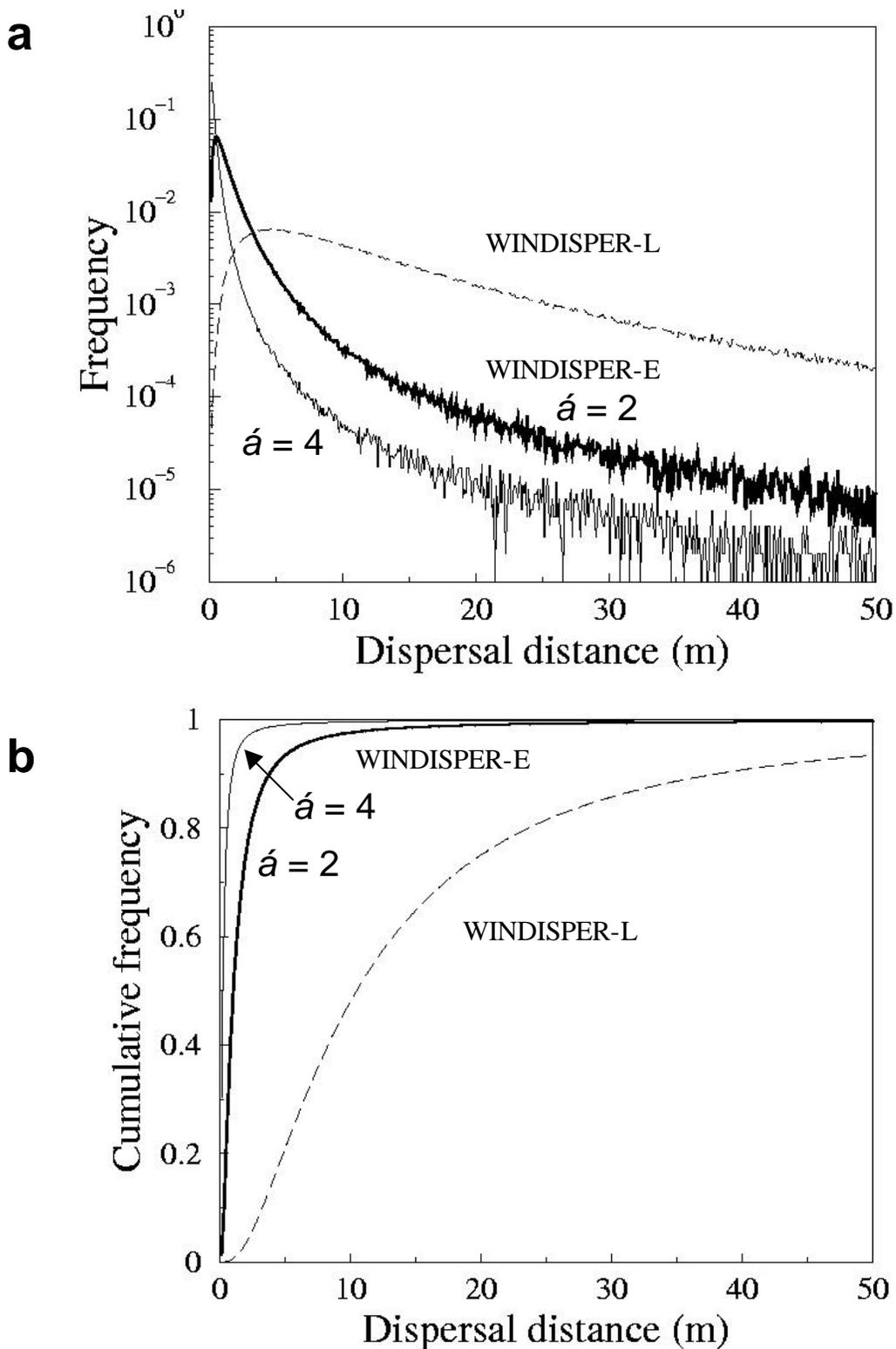


Fig. 3. Frequency (a) and cumulative frequency (b) distributions of 1,000,000 randomly-selected dispersal distances from a typical run of the logarithmic (dashed line), and the exponential (solid lines) wind profile with attenuation coefficient (\hat{a}) of 2.0 (thick line) and 4.0 (thin line).

Field validation

The model's predictions of the proportions of seeds dispersed to a seed trap station fit the empirical data sets reasonably well (Table 3). For the entire study area (all seed trap stations), the 95% confidence limits (CL) for the regression slopes are narrowly distributed around unity in all cases. The CL for the intercepts are narrowly distributed around zero (for all WINDISPER-L simulations), or are slightly larger than zero (for some of WINDISPER-E simulations). The model's predictions accounted for 83 - 90% of the variation in the observed data for WINDISPER-L, and for slightly higher percentages (87% - 94%) for WINDISPER-E. The maximum absolute error in the model's predictions for the proportions of seeds in a seed trap station was low (< 0.2%; Table 3).

The model's predictions for the area defined as 'within' the focal stand (see *Methods: model validation*) also fit the empirical data set collected between fall 1994 and spring 1996 (Table 3). As for the entire data set, WINDISPER-L exhibited better performance for the hypotheses assuming unity regression slope and zero intercept, while the predictions of WINDISPER-E accounted for a higher percentage (90% vs. 81%) of the variance in the observed data. The performance of both models is considerably lower for the area defined as 'outside' the focal stand, with WINDISPER-L explaining a slightly higher percentage (59% vs. 57%) of the variance in the observed data.

Table 3. Statistical validation of model's predictions (means of 50 independent model runs) of the proportion of seeds dispersed to a seed-trap station against observed data. Both predicted and observed data are square-root transformed.

Dispersal season(s)	MSE [†]	R^2 [‡]		Linear regression	
				Slope	Intercept (95% CL)
		SMCC	Kvålseth		
Logarithmic wind profile					
Fall 1994	0.0010	0.83	0.84	1.05 (0.92,1.17)	-0.011 (-0.031,0.008)
Spring 1995	0.0008	0.86	0.87	0.99 (0.88,1.09)	-0.001 (-0.017,0.016)
Fall 1995	0.0008	0.86	0.86	1.03 (0.92,1.14)	-0.008 (-0.025,0.009)
Spring 1996	0.0008	0.87	0.84	1.01 (0.91,1.11)	-0.005 (-0.021,0.011)
Fall 1994 - Spring 1996 [§]	0.0006	0.90	0.90	1.03 (0.94,1.12)	-0.008 (-0.023,0.007)
Within the stand [§]	0.0017	0.81	0.86	1.11 (0.87,1.35)	-0.028 (-0.082,0.026)
Outside the stand [§]	0.0002	0.59	0.61	0.82 (0.59,1.05)	0.017 (-0.007,0.041)
Exponential wind profile					
Fall 1994	0.0004	0.93	0.94	0.95 (0.88,1.02)	0.007 (-0.004,0.018)
Spring 1995	0.0008	0.87	0.87	0.88 (0.79,0.97)	0.020 (0.005,0.034)
Fall 1995	0.0008	0.87	0.90	0.90 (0.81,0.99)	0.015 (0.000,0.029)
Spring 1996	0.0006	0.90	0.87	0.91 (0.83,0.98)	0.015 (0.003,0.028)
Fall 1994 - Spring 1996 [§]	0.0004	0.94	0.94	0.93 (0.87,0.99)	0.012 (0.002,0.022)
Within the stand [§]	0.0009	0.90	0.91	0.86 (0.73,1.00)	0.031 (0.000,0.061)
Outside the stand [§]	0.0001	0.57	0.59	1.96 (1.39,2.53)	-0.097 (-0.155,-0.039)

[†] Mean squared error of prediction.

[‡] The coefficient of determination (R^2) calculated as squared multiple correlation coefficient (SMCC) or by Kvålseth's (1985) method.

[§] Validation of model's predictions for the total data set, and for the sectors within and outside the focal stand, separately.

DISCUSSION

How does landscape structure affect seed dispersal?

Variation in seed dispersal has critical implications for population and community dynamics of plants (Harper, 1977; Howe and Smallwood, 1982; Schupp and Fuentes, 1995; Nathan and Muller-Landau, 2000). Major sources of variation include internal (parent-controlled) factors, such as seed morphology and height of release, and external factors that influence the performance of the dispersal agent(s). The structure of the landscape affects wind flow, and thus can determine the spatial dynamics of wind-dispersed species inhabiting diverse habitats. In particular, the wind profile experienced by a tree seed during flight typically has an exponential shape within dense forests and logarithmic shape above short vegetation in open landscapes. We found a significant difference between the distributions of dispersal distances generated in the two landscape types – dispersal distances in dense forests are considerably shorter than in open landscapes. A review of seed dispersal in Dipterocarps in South-East Asia reached a similar conclusion based on empirical studies (Tamari and Jacalne, 1984).

Short- versus long-distance dispersal

In general, most seeds are dispersed over short distances; only few travel far from the source (Cain *et al.*, 2000). Although both short- and long-distance dispersal can be generated by stochastic effects, these types of dispersal often result from different mechanisms (Nathan and Muller-Landau, 2000). Moreover, the implications for recruitment after short-distance dispersal could be fundamentally different from those after long-distance dispersal. We therefore need to distinguish between the effects of landscape structure on short- and on long-distance dispersal, although the distinction between the two is not sharp. Using tree height as a qualitative criterion traditionally used by foresters (see Bullock and Clarke, 2000), one can refer to the scale of up to a few tree heights (a few tens of meters for *Pinus halepensis*), where most seeds are deposited, as short-distance dispersal, and the scale of tens of tree heights (hundreds of meters for *Pinus halepensis*), where only very few seeds are deposited, as long-distance dispersal. Our results show that such a rough criterion can be misleading since trees of the same height can generate considerably different seed shadows in different landscapes. For example, the distance travelled by 99% of the seeds can vary between almost 200 m (22 times the measured mean tree height) and less than 3 m (less than a third of the measured tree height), depending on the landscape type (Table 2).

We developed the two models to describe short-distance dispersal. Extrapolation to long-distance dispersal is inappropriate because five basic assumptions become unrealistic when larger spatial and temporal scales are considered. First, it is assumed that a seed flies in a straight line in the selected wind direction. Second, seed release is assumed to be independent of windspeed; however, seeds may typically be released in higher-than-average windspeeds (Greene and Johnson, 1992). Third, the roughness parameters of the two wind profiles are assumed to be constant in time and space. Fourth, variation in U and W (the mean vertical windspeed) during individual flights is not considered. Fifth, and most importantly, for each dispersal event, F (the seed falling velocity in still air) is constrained to be larger than W ; thus seed uplifting, a process critical for long-distance dispersal (Greene and Johnson, 1995), is not taken into account. Accordingly, our tests have shown that both models explain short-distance dispersal considerably better than long-distance dispersal.

Seed dispersal under different wind profiles: small-scale implications

Short-distance dispersal of the vast majority of the seeds generates a small-scale pattern that has critical implications for local recruitment (Janzen, 1970; Connell, 1971; Schupp and Fuentes, 1995; Nathan and Muller-Landau, 2000). A basic feature of this pattern, the rapid decline in seed densities with distance from the source (Harper 1977, Willson 1993), leads to strong sibling competition and intensive seed predation in the vicinity of adult trees (Janzen, 1970; Connell, 1971). Because dispersal distances are considerably shorter within dense forests than in open landscapes, Janzen-Connell effects are likely to be more powerful in forests. This is amplified by differences in fecundity. But, even without differences in fecundity, overlapping seed shadows in forests are likely to generate *much* higher seed densities close to adult trees than in open landscapes. Moreover, the high seed densities within forests could reach a level at which predators become satiated, hence increasing seed survival (Janzen 1971) and favouring selection for reduced dispersal distances. Strong Janzen-Connell effects, and especially predator satiation effects, are less likely in open landscapes. Overall, evaluation of the potential implications of the restricted dispersal distances within forests requires data on fecundity, dispersal and seed survival. Our models could help to estimate the effects of fecundity and dispersal, and to guide experimental studies on seed survival.

Seed dispersal under different wind profiles: large-scale implications

The critical importance of seed dispersal for various post-dispersal processes at the local (small) spatial scale has long been recognised (Harper 1977, Howe and Smallwood 1982). Recently, studies have emphasised the disproportionate importance of long-distance dispersal in determining large-scale patterns such as spatial spread, gene flow and metapopulation dynamics (Kot *et al.*, 1996; Clark *et al.*, 1998; Cain *et al.*, 2000; Nathan, 2001). Although application of our models to long-distance dispersal would require relaxation of some basic assumptions, we can still suggest which landscape type favours long-distance dispersal. Seeds dispersed by wind in open landscapes travel much farther than those dispersed within a forest due to differences in the shape of the wind profile. Accordingly, the exponential profile better fits dispersal data within a forest, while the logarithmic profile does better outside the stand. Furthermore, dense forests and open landscapes differ not only in the shape of the wind profile but also in the absolute wind velocities; winds in open landscapes are typically stronger (Stull, 1988) and produce greater dispersal distances. This difference is further amplified by the typically stronger wind updrafts above rather than within a plant canopy (Stull, 1988; Kaimal and Finnigan, 1994): stronger horizontal winds generate stronger shear-generated updrafts. Buoyancy-generated updrafts (thermals) are also more frequent in open landscapes (Stull, 1988).

Because of the predominance of better wind conditions for long-distance dispersal in open landscapes, isolated trees or trees at the forest edge could be important for tree spatial spread, gene flow and metapopulation dynamics. This supports the notion that long-distance dispersal events can generate 'great leaps forward' that determine population spread (Mollison, 1972; Kot *et al.*, 1996; Clark *et al.*, 1998). However, the effect of landscape structure on population spread depends on multiple factors, including the relative fecundity of isolated versus forest trees, on the transition between the logarithmic and exponential models, and on the relative probability of seed survival to adulthood in different landscapes.

Prospects for future research

We show that mechanistic understanding of the physical and biological conditions affecting seed dispersal by wind at small scales can be translated to simple tools that reliably predict the dispersal of most seeds at a spatial resolution of 1 m². However, questions on how landscape structure affects dispersal will require consideration of wind dispersal mechanisms acting at large scales, too. In the absence of field data on long-distance dispersal (Cain *et al.*, 2000), models are even more important for speculating about large-scale processes. Indeed, models may help in the design of experiments, which may increase the likelihood of observing intrinsically rare events. Mechanistic models of long-distance dispersal can enhance the recent progress in predicting seed dispersal patterns over large scales through phenomenological models (Kot *et al.*, 1996; Clark, 1998; Clark *et al.*, 1998; 1999; Higgins and Richardson, 1999). This is because only mechanistic models provide the means for generalisation beyond the studied systems, and yield insights into the main operative factors (Okubo and Levin, 1989; Nathan and Muller-Landau, 2000). Thus, they allow examination of other puzzles; for example, how winds behave (and carry seeds) in the transition between the forest and open fields, and whether the biological parameters of dispersal (e.g., height of release and seed terminal velocity) also vary with landscape type. Answering these questions will necessitate integration of models and empirical studies, and will require creative solutions to challenges imposed by the complicated yet important aspects of long-distance dispersal (see Greene and Johnson, 1995; Bullock and Clarke, 2000). Further, given the success of mechanistic models in predicting wind dispersal (Nathan and Muller-Landau, 2000), we need to develop a comprehensive mechanistic approach for seed dispersal by animals and by other agents.

ACKNOWLEDGEMENTS

We gratefully acknowledge the support by the National Science Foundation (IBN-9981620) the Andrew Mellon Foundation, the Desertification and Restoration Ecology Research Centre of the Keren Kayemeth Leisrael (Jewish National Fund), and the Israel National Parks and Nature Reserve Authority. For their help with wind measurements, we thank E. Zachs (Minerva Arid Ecosystems Research Centre, the Hebrew University of Jerusalem) and I. Seter (Israel Meteorological Service). We also thank D. Roitemberg for his intensive help with fieldwork, and I. Gilderman and J. Ma for their help in C programming. Finally, we are grateful for M. Cain, D. Levey, R. Avissar, G. Katul, H. Muller-Landau, J. Dushoff and K. Kitajima for their helpful comments and discussions.

REFERENCES

- Acherar, M., Lepart, J. and Debussche, M. (1984) La colonisation des friches par le pin d'Alep (*Pinus halepensis* Miller) en Languedoc méditerranéen. *Acta Oecologica* 5, 179-189.
- Amiro, B.D. (1990) Comparison of turbulence statistics within three boreal forest canopies. *Boundary-Layer Meteorology* 51, 99-121.
- Amiro, B.D. and Davis, P.A. (1988) Statistics of atmospheric turbulence within a natural black spruce forest canopy. *Boundary-Layer Meteorology* 44, 267-283.
- Augspurger, C.K. and Franson, S.E. (1988) Input of wind-dispersed seeds into light-gaps and forests sites in a neotropical forest. *Journal of Tropical Ecology* 4, 239-252.
- Barbéro, M., Loisel, R., Quézel, P., Richardson, D.M. and Romane, F. (1998) Pines of the Mediterranean basin. In: Richardson, D.M. (ed.). *Ecology and biogeography of Pinus*. Cambridge University Press, Cambridge, pp. 153-170.
- Bullock, J.M. and Clarke, R.T. (2000) Long distance seed dispersal by wind: measuring and modelling the tail of the curve. *Oecologia* 124, 506-521.

- Cain, M.L., Milligan, B.G. and Strand, A.E. (2000) Long-distance seed dispersal in plant populations. *American Journal of Botany* 87, 1217-1227.
- Cionco, R.M. (1965) A mathematical model for air flow in a vegetative canopy. *Journal of Applied Meteorology* 4, 517-522.
- Cionco, R.M. (1978) Analysis of canopy index value for various canopy densities. *Boundary-Layer Meteorology* 15, 81-93.
- Clark, J.S. (1998) Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. *American Naturalist* 152, 204-224.
- Clark, J.S., Fastie, C., Hurtt, G., Jackson, S.T., Johnson, C., King, G.A., Lewis, M., Lynch, J., Pacala, S., Prentice, C., Schupp, E.W., Webb, T., III and Wyckoff, P. (1998) Reid's paradox of rapid plant migration: dispersal theory and interpretation of paleoecological records. *BioScience* 48, 13-24.
- Clark, J.S., Silman, M., Kern, R., Macklin, E. and HilleRisLambers, J. (1999) Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology* 80, 1475-1494.
- Connell, J.H. (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in forest trees. In: den Boer, P.J. and Gradwell, G.R. (eds.). *Dynamics of populations*. Centre for Agricultural Publishing and Documentation, Wageningen, pp. 298-312.
- Gardiner, B.A. (1994) Wind and wind forces in a plantation spruce forest. *Boundary-Layer Meteorology* 67, 161-186.
- Greene, D.F. and Johnson, E.A. (1992) Fruit abscission in *Acer saccharinum* with reference to seed dispersal. *Canadian Journal of Botany* 70, 2277-2283.
- Greene, D.F. and Johnson, E.A. (1995) Long-distance wind dispersal of tree seeds. *Canadian Journal of Botany* 73, 1036-1045.
- Greene, D.F. and Johnson, E.A. (1996) Wind dispersal of seeds from a forest into a clearing. *Ecology* 77, 595-609.
- Greene, D.F. and Johnson, E.A. (1997) Secondary dispersal of tree seeds on snow. *Journal of Ecology* 85, (Jun (3)) 329-340.
- Guries, R.P. and Nordheim, E.V. (1984) Flight characteristics and dispersal potential of maple samaras. *Forest Science* 30, 434-440.
- Haanel, H.D. (1993) Surface-layer profile evaluation using a generalization of Robinson's method for the determination of d and z_0 . *Boundary-Layer Meteorology* 65, 55-67.
- Harper, J.L. (1977) *Population biology of plants*. Academic Press, London.
- Higgins, S.I. and Richardson, D.M. (1999) Predicting plant migration rates in a changing world: the role of long-distance dispersal. *American Naturalist* 153, 464-475.
- Howe, H.F. and Smallwood, J. (1982) Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13, 201-228.
- Janzen, D.H. (1970) Herbivores and the number of tree species in tropical forests. *American Naturalist* 104, 501-528.
- Janzen, D.H. (1971) Seed predation by animals. *Annual Review of Ecology and Systematics* 2, 465-492.
- Kaimal, J.C. and Finnigan, J.J. (1994) *Atmospheric boundary layer flows: their structure and measurement*. Oxford University Press, New York.
- Kot, M., Lewis, M.A. and Van Den Driessche, P. (1996) Dispersal data and the spread of invading organisms. *Ecology* 77, 2027-2042.
- Kvålseth, T.O. (1985) Cautionary note about R^2 . *The American Statistician* 39, 279-285.
- Lepart, J. and Debussche, M. (1991) Invasion processes as related to succession and disturbance. In: Groves, R.H. and di Castri, F. (eds.). *Biogeography of Mediterranean invasions*. Cambridge University Press, Cambridge, pp. 159-177.
- Mirov, N.T. (1967) *The genus Pinus*. Ronald Press, New York.
- Mollison, D. (1972) The rate of spatial propagation of simple epidemics. *Proceedings of the Six Berkeley Symposium on mathematics, Statistics, and probability* 3, 579-614.
- Mursch-Radlgruber, E. and Kovacic, T. (1990) Mean canopy flow in an oak forest and estimation of the foliage profile by a numerical-model. *Theoretical and Applied Climatology* 41, 129-136.

- Nathan, R. (2001) Dispersal biogeography. In: Levin, S.A. (ed.). *Encyclopedia of Biodiversity*. Volume II. Academic Press, San Diego, pp. 127-152.
- Nathan, R. and Muller-Landau, H.C. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution* 15, 278-285.
- Nathan, R. and Ne'eman, G. (2000) Serotiny, seed dispersal and seed predation in *Pinus halepensis*. In: Ne'eman, G. and Trabaud, L. (eds.). *Ecology, biogeography and management of Pinus halepensis and P. brutia forest ecosystems in the Mediterranean Basin*. Backhuys, Leiden, The Netherlands, pp. 105-118.
- Nathan, R., Safriel, U.N., Noy-Meir, I. and Schiller, G. (1996) Samara's aerodynamic properties in *Pinus halepensis* Mill., a colonizing tree species, remain constant despite considerable variation in morphology. In: Steinberger, Y. (ed.). *Preservation of our world in the wake of change*. Israel Society for Ecology & Environmental Quality Sciences, Jerusalem, pp. 553-556.
- Nathan, R., Safriel, U.N., Noy-Meir, I. and Schiller, G. (1999) Seed release without fire in *Pinus halepensis*, a Mediterranean serotinous wind-dispersed tree. *Journal of Ecology* 87, 659-669.
- Nathan, R., Safriel, U.N., Noy-Meir, I. and Schiller, G. (2000) Spatiotemporal variation in seed dispersal and recruitment near and far from adult *Pinus halepensis* trees. *Ecology* 81, 2156-2169.
- Nathan, R., Safriel, U.N. and Noy-Meir, I. (2001) Field validation and sensitivity analysis of a mechanistic model for tree seed dispersal by wind. *Ecology* 82, 374-388.
- Oke, T.R. (1987) *Boundary layer climates*, 2nd edn. Rotledge, London.
- Okubo, A. and Levin, S.A. (1989) A theoretical framework for data analysis of wind dispersal of seeds and pollen. *Ecology* 70, 329-338.
- van der Pijl, L. (1982) *Principles of dispersal in higher plants*, 3rd edn. Springer, Berlin, 162pp.
- Pinker, R.T. and Moses, J.F. (1982) On the canopy flow index of a tropical forest. *Boundary-Layer Meteorology* 22, 313-324.
- Raupach, M.R. (1988) Canopy transport process. In: Steffan, W.L. and Denmead, O.T. (eds.). *Flow and transport in the natural environment: advances and applications*. Springer-Verlag, Berlin, pp. 95-127.
- Rejmánek, M. and Richardson, D.M. (1996) What attributes make some plant species more invasive? *Ecology* 77, 1655-1661.
- Richardson, D.M. and Higgins, S.I. (1998) Pines as invaders in the southern hemisphere. In: Richardson, D.M. (ed.). *Ecology and biogeography of Pinus*. Cambridge University Press, Cambridge, pp. 450-473.
- Robinson, S.M. (1962) Computing wind profile parameters. *Journal of the Atmospheric Sciences* 19, 189-190.
- Schupp, E.W., Howe, H.F., Augspurger, C.K. and Levey, D.J. (1989) Arrival and survival in tropical treefall gaps. *Ecology* 70, 562-564.
- Schupp, E.W. and Fuentes, M. (1995) Spatial patterns of seed dispersal and the unification of plant population ecology. *Ecoscience* 2, 267-275.
- Sharpe, D.M. and Fields, D.E. (1982) Integrating the effects of climate and seed fall velocities on seed dispersal by wind: a model and application. *Ecological Modelling* 17, 297-310.
- Sokal, R.R. and Rohlf, F.J. (1995) *Biometry*, 3rd edn. Freeman, New York.
- Stull, R.B. (1988) *An introduction to boundary-layer meteorology*. Kluwer Academic Publishers, Dordrecht.
- Su, H.B., Shaw, R.H., U, K.T.P., Moeng, C.H. and Sullivan, P.P. (1998) Turbulent statistics of neutrally stratified flow within and above a sparse forest from large-eddy simulation and field observations. *Boundary-Layer Meteorology* 88, 363-397.
- Tamari, C. and Jacalne, D.V. (1984) Fruit dispersal of dipterocarps. *Bull. For. & For. Prod. Res. Inst.* 325, 127-140.
- Wallach, D. and Goffinet, B. (1989) Mean squared error of prediction as a criterion for evaluating and comparing system models. *Ecological Modelling* 44, 299-306.
- Wieringa, J. (1993) Representative roughness parameters for homogeneous terrain. *Boundary-Layer Meteorology* 63, 323-363.
- Willson, M.F. (1993) Dispersal mode, seed shadows, and colonization patterns. *Vegetatio* 107/108, 261-280.