SPATIOTEMPORAL VARIATION IN SEED DISPERSAL AND RECRUITMENT NEAR AND FAR FROM *PINUS HALEPENSIS* TREES

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Abstract. Spatiotemporal variation in the wind-generated dispersion pattern of Aleppo pine (*Pinus halepensis*) seeds was examined by placing seed traps up to 110 m away from a small, isolated stand in Israel during six successive dispersal seasons. Subsequent recruitment was surveyed two years later. Of the 5487 seeds, 97% were trapped ≤ 20 m from the nearest adult tree. Seasonal dispersal curves were consistently right-skewed and leptokurtic. The inverse power law and the negative exponential model accounted for a similar fraction of the variation in the number of dispersed seeds at different distances (79–86% and 76–88%, respectively). Seed dispersal rates varied significantly among seasons. Eighty saplings (3–5 yr old) became established during the three years of the study, most within 15 m of the nearest canopy, some farther away, and none directly under the tree canopies. The estimated probability of seed survival to sapling stage increased significantly with increasing distance from adults, as predicted by the escape hypothesis.

Winds varied significantly between seasons, generating significant interseasonal variation in seed deposition patterns far from, but not near to, adult trees. Coefficients of variation of seed dispersal rates were lower near adult trees than farther away. Both Moran's *I* correlograms and partial Mantel tests revealed interseasonal consistency in seed deposition patterns for the total study area and for the area near adult trees but showed considerable variation farther away. We suggest that the low spatiotemporal variation near adults and the high variation far away act to intensify the effects of predation (by increasing the efficiency of predators near adults and reducing it far away) and competition (by increasing the intensity of seedling competition near adults and reducing it far away) in structuring the observed survivorship curve predicted by the escape hypothesis.

Key words: dispersal distance; dispersal seasons; escape hypothesis; Pinus halepensis; *recruitment; saplings; seed deposition pattern; seed dispersal; spatial analysis; spatiotemporal variation; survival, function of dispersal distance; wind dispersal.*

INTRODUCTION

Seed dispersal is the main process linking the spatial pattern of parent plants with that of their offspring (Harper 1977, Howe and Smallwood 1982, Willson 1992, Venable and Brown 1993, Chambers and MacMahon 1994, Schupp and Fuentes 1995). The spatial pattern of dispersed seeds serves as a template for subsequent processes such as predation, germination, competition, and growth that ultimately shape the spatial pattern of adult plants. The basic component of this spatial pattern is usually described by the "dispersal curve," showing the change, typically a rapid decline, in the density of dispersed seeds with increasing distance from the parent plant (Harper 1977, Okubo and

Levin 1989, Willson 1993). In investigating the spatial pattern of tree regeneration in tropical forests, Janzen (1970) combined this dispersal curve with two other functions describing the change with distance in the per capita probability of seed survival to maturity (the "survivorship curve"), and in the density of recruits (the population "recruitment curve"). Janzen (1970) and Connell (1971) proposed the escape hypothesis (Howe and Smallwood 1982), suggesting a positive slope of the survivorship curve, determined by the high mortality of progeny (seeds and seedlings) in the vicinity of adult plants, due to seed predators, parasites, pathogens, and seedling herbivores. They predicted that recruitment should occur mostly at some distance away from parent plants, whereas Hubbell (1980) argued that, with realistic dispersal and survivorship curves, recruitment should always be higher near adults because of the disproportionately high seed densities there. McCanny (1985) demonstrated how different slopes of the survivorship curve can produce, out of the same dispersal curve, positive (Janzen-Connell model), zero, and negative (Hubbell's model) slopes of the recruitment curves.

Studies testing the escape hypothesis (Augspurger 1983, Clark and Clark 1984, Schupp 1988, Augspurger and Kitajima 1992, Condit et al. 1992) have examined the fate of seeds (or seedlings) at different densities and distances from adult plants. Clark and Clark (1984) suggested that because of significant, but usually unknown, interannual variation in fecundity and dispersal, a single-time approach comparing the distance of progeny of different cohorts from adults would produce less conclusive results than an approach comparing that distance for the same cohort at different times (see also Augspurger 1983). Yet, none of the studies of the escape hypothesis has explicitly dealt with the effect of spatiotemporal variation in seed densities on seed survival and recruitment. Spatiotemporal variation in seed densities can affect seed survival and recruitment indirectly, through its effects on seed predators, the major component of the escape hypothesis (Janzen 1970). Given the significance of risk sensitivity in foraging, predators may be more sensitive to the variance, rather than the average, in the availability of their resources (Real and Caraco 1986, Kacelnik and Bateson 1996). Spatiotemporal variation in seed densities can also affect seedling survival through intraspecific seedling competition. Competition is expected to be intense if seedlings germinate in the same sites each year, but is negligible if germination varies considerably in space and time. Therefore, differences in the magnitude of spatiotemporal variation near and far from adult plants can influence the pattern of survivorship and recruitment predicted by the escape hypothesis. However, no data pertaining to the role of this variation in determining plant population dynamics are currently available. The spatiotemporal variation in seed dispersion near and far from adult plants has never been described; moreover, the role of spatiotemporal variation in juvenile dispersion has largely been ignored (Gaines and Bertness 1993, Schupp and Fuentes 1995). Recently, Houle (1998) found interannual inconsistency in the spatial pattern of wind-dispersed seeds in a North American tree species, but the potential effect of distance from the adult trees was not addressed.

Wind is typically variable and unpredictable in time and space; hence, considerable spatiotemporal variation is expected in the dispersion pattern of wind-dispersed seeds. The dispersal of seeds to relatively large distances by wind is typically a rare event (Silvertown 1991, Portnoy and Willson 1993), in which multiple factors may be involved (Greene and Johnson 1995). Therefore, spatiotemporal variation in densities of wind-dispersed seeds at relatively long distances from their source seems inevitable. The magnitude of spatiotemporal variation expected near adult plants is less obvious: is the variation in wind conditions strong enough to generate significant spatiotemporal variation in densities of seeds falling only a few meters from their source?

In this paper, we describe the spatiotemporal patterns in dispersal and recruitment in an isolated stand of Aleppo pine (*Pinus halepensis* Miller), a Mediterranean wind-dispersed tree, during six successive dispersal seasons. First, we use field data to determine dispersal, survivorship, and recruitment curves, and examine these results in light of the predictions of the escape hypothesis. Then we employ spatial analyses to investigate the magnitude of spatiotemporal variation in seed deposition near and far from adult trees. We suggest that the general support for the escape hypothesis shown by our data is related to the finding of low spatiotemporal variation in seed densities near adult trees, and the high variation farther away.

METHODS

Study species

Pinus halepensis is the most widely distributed pine of the Mediterranean region (Mirov 1967, Barbéro et al. 1998), and the most common naturally growing and planted conifer in Israel. Indigenous trees occur in stands of various sizes or as scattered individuals (Zohary 1962). Cone crops are relatively large and are produced annually (Krugman and Jenkinson 1974). Pollination takes place in spring, fertilization a year later, and seed dispersal begins in the third year after pollination (Panetsos 1981). Mature seeds are retained in persistent cones, and seed release is often delayed, building up a canopy-stored seed bank (i.e., serotiny). Many authors have emphasized the role of fire as a primary generator of seed release and recruitment in this species (e.g., Naveh 1975, Panetsos 1981, Trabaud et al. 1985, Daskalakou and Thanos 1996, Izhaki and Ne'eman 1996, Thanos et al. 1996, Ne'eman and Izhaki 1998). However, extensive seed release (of ~60% of the annual seed crop; Nathan et al. 1999) and recruitment (Acherar et al. 1984, Lepart and Debussche 1991, Trabaud 1991, Sadot 1992) occur also independently of fire. In Israel, seed release without fire is induced by dry and hot weather spells (locally called Sharav) during spring and fall (Schiller 1979, Nathan et al. 1999).

Diaspores are (approximately) 22-mg and 22 mm long samara-like winged seeds that autorotate while falling at an average terminal velocity of 0.81 ± 0.01 m/s, mean $\pm$ 1 SE (Nathan et al. 1996). In this study, we focus on the initial wind-driven movement of seeds from the canopy to a surface (Phase I dispersal; sensu Chambers and MacMahon 1994). Subsequent movements (Phase II) by wind are unlikely to be significant because *P. halepensis* seeds generally lose their wings immediately upon hitting the ground (Acherar et al. 1984, Nathan et al. 1996), and because of the dense vegetation in the habitats of this species. Phase II dispersal by animals is not supported by any evidence from the field or literature. The species is considered to be a very successful colonizer (Acherar et al. 1984, Lepart and Debussche 1991), and is one of the most

invasive pines (Rejmánek and Richardson 1996, Barbéro et al. 1998). Isolated individuals have been found as far as several kilometers from any 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). It is an obligate seeder, i.e., regeneration relies exclusively on seeds (Naveh 1975, Trabaud 1987). Although seeds within closed cones may be viable for ≥ 8 yr (Schiller 1979, Daskalakou and Thanos 1996), dispersed seeds show no long-term dormancy (Skordilis and Thanos 1995, Daskalakou and Thanos 1996). An endogenous rhythm regulates germination to the period of late autumn–early winter, resulting in recruitment early in the rainy season of the Mediterranean climate (Schiller 1979).

Study site

The study site was an indigenous *P. halepensis* stand located near Kibbutz Nir-Ezyon on chalk and limestone formations at the lower western slopes of Mt. Carmel (32°41′ N, 34°58′ E; 116 m a.s.l), within a Mediterranean scrubland ecosystem in northwestern Israel. Mean annual rainfall is 600 mm, mean temperature of the hottest month (August) is 24–26°C, and mean temperature of the coldest month (January) is 12°C. The stand, comprising 96 adult trees covering a total canopy area of 3615 m², was isolated from neighboring stands by ≥ 500 m. Sixteen randomly selected trees were found to be 22–66 yr old in 1994 (55 $\pm$ 4 yr old, mean $\pm$ 1 SE) and up to 11.6 m tall (9.1 $\pm$ 0.5 m). The understory was mainly *Pistacia lentiscus,* and the surrounding vegetation was a mixture of abandoned *Olea europaea* groves, dense-to-open maquis dominated by *Quercus calliprinos, Phillyrea media, Pistacia lentiscus,* and *Ceratonia siliqua,* and dense-to-open shrubland (batha) dominated by *Sarcopoterium spinosum, Cistus* spp., and *Calicotome villosa.*

Seed deposition was measured by placing 94 seed traps (0.99 $\times$ 0.84 $\times$ 0.15 m), protected from seed predators (Nathan et al. 1999), at 62 stations within and around the focal stand (Fig. 1). We placed seven traps under tree canopies, seven traps in gaps between tree canopies, and the remaining 80 traps along transects extending in eight compass directions outside the stand (Fig. 1). In each direction, the most distant and the second-most distant station consisted of four and two traps, respectively, in order to increase the chance of sampling the relatively low rates of dispersal to these distances. Seed traps were checked 70 times between October 1993 and June 1996, during six dispersal seasons (spring and fall) in three successive years. Because dispersal was distinctly seasonal (Nathan et al. 1999), we restricted the analysis to data collected during dispersal seasons, defined as periods (between successive visits) during which at least three seeds were trapped (in all stations combined) per day, slightly modified to preserve seasonal continuity (see *Results: Seed dispersal*). For each seed trap station, the seasonal mean

dispersal rate (in number of seeds per square meter per day) is used as a measure of seed deposition. By dividing the average daily rate by the trapping area for each station, the larger trapping area of stations with more than one seed trap is standardized. A recent (January 1994) aerial photograph of the site, scanned at a resolution of 0.25 m and corrected for terrain distortion (processed by Advanced Digital Mapping Company, Tel Aviv, Israel), was used to precisely determine the location of the trees and of the seed traps.

Census of juvenile pines

We censused the total study area up to 110 m from the outer trees in the study site (77 380 m² total) on 29–31 May 1998 to map the exact location of juvenile pines (≥ 3 yr old). The ages of these juvenile pines were determined by counting the branch whorls (see Trabaud et al. 1985), as trees at this age class produce whorls annually. The accuracy of the whorl count was verified by determining the ages of 12 individuals from a nearby site by counting tree rings: the two age estimates were highly correlated ($r = 0.94$, $P < 0.001$), and were not significantly different ($t_{11} = 0.804$, NS). We mapped the location of each individual on an enlargement of the aerial photograph, and measured the distances from neighboring adults for confirmation.

Constructing dispersal, recruitment, and survivorship curves

Because seed shadows of adjacent trees overlap, dispersal distances traveled by seeds to different seed trap stations are difficult to estimate. Measures such as the distance to the nearest central location of a tree or to the nearest canopy edge necessarily underestimate actual dispersal distances, because some seeds come from more distant trees. We used a spatially explicit, mechanistic model of seed dispersal by wind that includes the potential contribution of all trees (Nathan 1999) to generate estimates of the distances traveled by seeds to the different seed trap stations. This model, called WINDISPER, simulates the movements of seeds released from each of the 3615 1-m² square cells that represent the canopy area of adult trees in the site, based on the direction, horizontal and vertical velocities of the wind, the terminal velocities of a seed in still air, and the height of seed release, all randomly selected from the measured distributions.

We used WINDISPER to simulate dispersal during each of the six dispersal seasons. In these simulations, 297 449 seeds in total (1.4% of all seeds released) were deposited in seed trap stations. In Nathan (1999), linear regression between observed and predicted *proportions* of seeds dispersed to seed traps showed a good fit ($r^2 = 0.72$–0.87) and slopes were significantly different from zero and not significantly different from unity for all seasons, indicating that the model reliably simulates the general spatial structure of seed dispersal. In the present simulations, linear regression between ob-
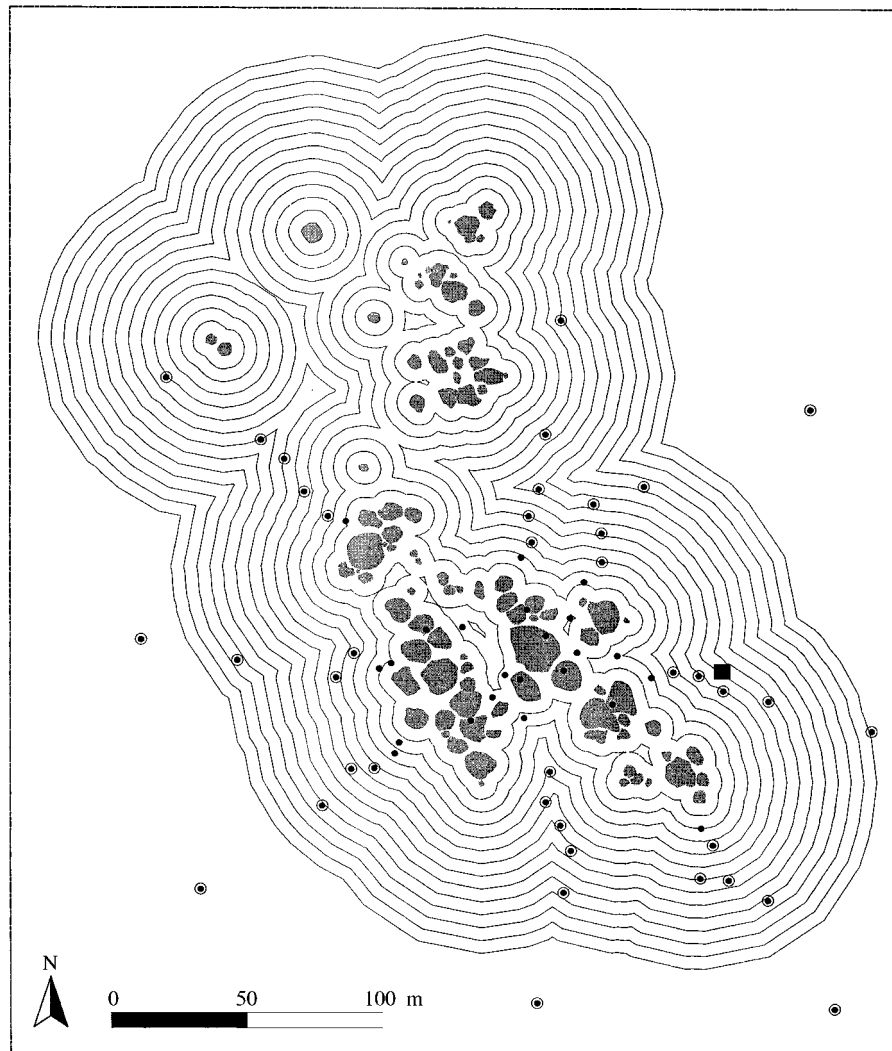
Fig. 1. The study site south of Nir-Ezyon at the lower western slopes of Mt. Carmel, northwestern Israel. Polygons show adult (seed-producing) trees, and the black square shows the location of a meteorological station active during fall 1995. Seed trap stations are circled if >20 m from the nearest central location of an adult tree. Contours show 5-m distance intervals from the nearest canopy edge.

served and predicted *rates* of dispersal to seed traps showed a similar fit ($r^2 = 0.74$–0.87) and slopes were also significantly different than zero for all seasons, but they were significantly greater than unity (1.5–3.0) for all seasons, except for fall 1995 (0.8). Thus, the model generally underestimates the actual dispersal rates. We kept track of the distances traveled by seeds in the simulations, and randomly chose a subset of those distances to characterize the dispersal curve for each dispersal season. For each seed trap station, we selected a sample of a size five times the number seeds trapped, in order to provide larger samples for those (distant) stations in which only few seeds were recorded, and to compensate for the model's tendency to underestimate the actual dispersal rates. The seasonal dispersal curves, presenting the frequency distribution

of the predicted dispersal distances grouped in 1-m intervals, were fitted with two phenomenological models: the negative exponential (linear in a semilog plot), and the inverse power law (linear in a log–log plot). The curve of the inverse power law model drops off more steeply in the vicinity of the source, but its tail drops off more gradually than that of an equivalent negative exponential curve. Ordinary least square linear regression was used to fit these dispersal curves, with 95% confidence intervals determining the significance of the differences obtained.

Recruitment and survivorship curves were calculated for each of the three years of the study, using data from saplings recorded in the 1998 field census. Those in their fifth year (i.e., from seeds germinated during winter 1993–1994) constituted the 1993 cohort, those in

their fourth year the 1994 cohort, and those in their third year the 1995 cohort. For each cohort, we pooled all individuals recorded within 5-m intervals of the nearest adult and calculated sapling density (by dividing the number of saplings by the cumulative area in each corresponding distance interval) to construct a recruitment curve. Survivorship curves were plotted for each cohort to describe the change in the proportion of viable seeds that survived in each distance interval, calculated by dividing the number of saplings recorded by an estimate of the total number of seeds that reached this interval. For each cohort and for each distance interval, seed numbers were estimated from the corresponding seed trap data collected during fall of the same year (i.e., just before germination). The number of seeds that dispersed during spring of the same year, or during previous years, but were still available for germination, was unknown; this led to underestimation of the actual number of available seeds, and thus to overestimation of the proportion of seeds surviving to saplings. To examine the effect of canopy area on dispersal and recruitment, we quantified the distances of seed trap stations and of juvenile pines from the nearest adult in two ways: (1) distance to the nearest central location of an adult tree, and (2) distance to the nearest canopy edge. All distance measurements were performed on the digitized maps of seed traps, juveniles, and adults using ARC/Info version 7.0 (ESRI 1994).

Interseasonal variation in seed deposition patterns

Two methods were used to examine the interseasonal variation in seed deposition patterns: (1) spatial autocorrelation analysis (Sokal and Oden 1978, Legendre and Fortin 1989), and (2) the partial Mantel test (Smouse et al. 1986, Legendre and Fortin 1989). Both methods were applied to the complete data set, and the partial Mantel test was also applied to two partial sets of seed trap stations ''near'' (0–20 m) and ''far'' 20–110 m from the nearest central location of a tree. The area covered by the near and far sections was 28 644 and 48 736 m^2, with 23 and 39 stations (23 and 71 seed traps), respectively.

The spatial autocorrelation analysis produces a correlogram, a spatial structure function describing the change in autocorrelation with increasing distance between stations. Spatial autocorrelation was quantified by Moran's I coefficient, which generally varies from -1, indicating negative correlation, to $+1$, indicating positive correlation between means a given distance apart. Significance tests for the departure from spatial independence ($I \approx 0$) followed Sokal and Oden (1978). The 1891 pairs of stations in the complete data set were divided into 15 equal-distance intervals; the last five intervals, corresponding to distances of 239–358 m between stations, were omitted because their sample sizes were too small (1–21 pairs each) to permit statistical credibility. Significance levels were Bonferroni-corrected for the number of distance intervals ($\alpha' = 0.5/15 = 0.0033$).

The partial Mantel statistic was calculated by the method of Smouse et al. (1986) to examine whether *differences* in dispersal rates between any two stations in any two different seasons are linearly correlated when the spatial effect is removed. For each season and for each pair of stations, we computed a seasonal matrix of relative differences (Bray and Curtis 1957) in dispersal rates, as the ratio between the absolute difference and the summation. The spatial matrix was calculated as the distance between all pairs of stations. Then, the partial Mantel test was calculated for all 15 paired comparisons between seasonal matrices, while controlling for the spatial effect expressed by the spatial matrix. Statistical significance was determined by comparison with 10 000 randomized permutations, using the Bonferroni-corrected significance level ($\alpha' = 0.0033$). Calculations of Moran's I for correlograms and of the partial Mantel tests were carried out with the R-Package (Legendre and Vaudor 1991). All other statistical analyses in this paper were carried out using SPSS 6.0 (SPSS 1993).

Interseasonal variation in wind conditions

We used hourly average wind velocities and directions recorded in the meteorological station of the Israel Meteorological Service (IMS) at En-Karmel, 1.5 km southwest of the site, to assess interseasonal variation in wind conditions. Horizontal wind velocity was measured 10 m above the ground by a propeller anemometer (model 05103, R. M. Young, Traverse City, Michigan, USA). Because successive short-term wind records are typically not independent, we randomly selected 200 records for each dispersal season for analysis. To provide a more accurate interseasonal comparison of wind behavior during dispersal, we also selected 100 records for each season from the two periods (between successive visits) in which dispersal rate was the highest. The seasonal variation in wind velocities for the main eight compass directions was tested with one-way ANOVA, and that of wind frequencies with a chi-square test. Wind velocities were first square-root transformed to fulfill the normality and variance homogeneity assumptions. To evaluate the similarity in wind conditions between the IMS station and the study site, wind measurements were collected at the study site for a period of 32 days in autumn 1995, using similar equipment and data-logging methods, and 200 randomly selected pairs of records were compared between stations.

RESULTS

Seed dispersal

In total, 5811 seeds were collected in 70 visits to the site between October 1993 and June 1996. Forty-three periods fit the criterion of an average dispersal rate of at least three trapped seeds (in all stations combined) per day, used to define the dispersal seasons. A single

TABLE 1. Seasonal seed dispersal rates at Nir-Ezyon, Israel, during the six dispersal seasons.

Season	Months	No. days	No. visits	Traps with seeds (%)	Total no. seeds trapped	Seasonal dispersal rate (no. seeds·m^{-2}·d^{-1})
Fall 1993	Oct–Dec	63	6	29	982	0.20
Spring 1994	Apr–May	46	5	33	916	0.26
Fall 1994	Sep–Nov	62	8	44	1480	0.31
Spring 1995	Apr–Jul	78	10	28	635	0.10
Fall 1995	Sep–Nov	46	9	29	422	0.12
Spring 1996	Apr–Jun	42	6	30	1052	0.32

Note: See *Methods: Study site* and *Results: Seed dispersal* for definitions of the dispersal seasons.

period with slightly more than three trapped seeds per day in July 1994 was regarded as a temporal outlier and was omitted, whereas two periods not meeting the criterion were added because they were within well-defined sequences of periods that do meet the criterion in spring and fall 1995. Thus, the dispersal seasons comprised 44 periods (53% of the sampling time), during which 5487 seeds (94.4% of the total) were collected (Table 1). Dispersal seasons varied greatly in the number of seeds trapped, and also varied somewhat in their length (cvs of 40% and 25%, respectively; Table 1). Consequently, seasonal dispersal rates varied significantly among seasons (Friedman's nonparametric ANOVA, $\chi^2 = 68.6$, df = 5, $P < 0.0001$). In particular, seed dispersal rates during spring and fall 1995 were between two- and threefold lower than during the other dispersal seasons (Table 1).

Dispersal rates were consistently highest in the seven traps under the tree canopy, which captured 72% of the 5487 seeds collected during the dispersal seasons. Only 150 of the collected seeds (2.7%) were from the far stations. The mean daily dispersal rates in near and far sections were 0.830 ± 0.173 and 0.013 ± 0.004 seeds·m^{-2}·d^{-1}, respectively (Table 2). The mean seasonal dispersal rates were 46.72 ± 9.74 and 0.74 ± 0.21 seeds/m^{-2} per season, respectively. The largest dispersal distance was recorded in a station 87 m from the nearest canopy edge and 95 m from the nearest central location of an adult, in fall 1994 and again in spring 1995.

Dispersal curves were strongly right-skewed and leptokurtic in all six dispersal seasons (Fig. 2, Table 3).

Slopes of both the exponential and the power law functions were significantly negative in all seasons (Table 3), and the two models accounted for a similar proportion of the variation (r^2) in the number of seeds (0.82 ± 0.02 and 0.83 ± 0.01, respectively; $t_5 = 0.14$, NS). When the data were fitted with linear models (not shown), slopes were also significantly negative, but the fraction of explained variance was much lower (0.41 ± 0.01). In general, the negative exponential model consistently underestimated the number of seeds that traveled short distances (<25 m), whereas the inverse power law underestimated the numbers that traveled intermediate distances ($\sim$25–50 m; Fig. 2). Seasons with more right-skewed (higher skewness) and leptokurtic (higher kurtosis) dispersal distributions were fitted better by the inverse power law than by the negative exponential model, and vice versa (Table 3). No significant interseasonal differences were found between slopes of the inverse power law model, but several significant differences were found between those of the negative exponential model (Table 3).

Recruitment and survivorship

We located 243 juvenile pines (≥ 3 yr old) in our census of the study site in late May 1998. Of these, 80 individuals (hereafter saplings) had established during the study period: 34 belonged to the 1995 cohort, 26 to the 1994 cohort, and 20 to the 1993 cohort. Female cones of the first year after flowering (i.e., about two years before normal seed release) were found in one sapling, from the 1993 cohort. Not a single sapling was found under the canopy of any adult tree, and seedlings

TABLE 2. Seasonal seed dispersal rates (no. seeds·m^{-2}·d^{-1}) in seed trap stations ''near'' (≤ 20 m) and ''far'' (>20 m) from the nearest adult tree.

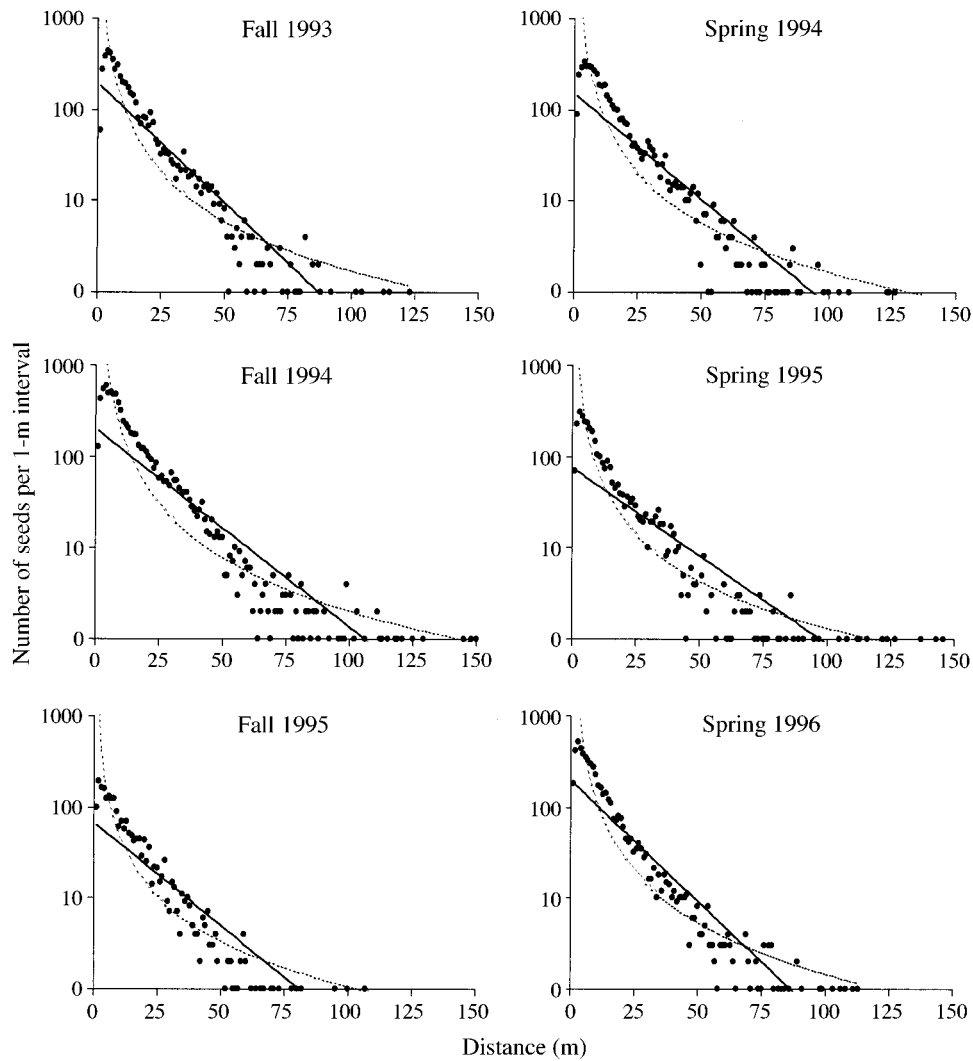| Proximity to adult trees	Fall 1993	Spring 1994	Fall 1994	Spring 1995	Fall 1995	Spring 1996
Near ($n = 23$)						
Mean	0.801	1.014	1.202	0.409	0.476	1.288
(1 SD)	(1.063)	(0.882)	(1.314)	(0.458)	(0.467)	(1.439)
CV (%)	133	87	109	112	98	112
Far ($n = 39$)						
Mean	0.008	0.017	0.027	0.010	0.002	0.014
(1 SD)	(0.022)	(0.038)	(0.044)	(0.032)	(0.007)	(0.043)
CV (%)	262	220	165	320	310	305

FIG. 2. Seasonal seed dispersal curves (note the ordinate log scale), showing the frequency distribution of predicted dispersal distances traveled by all seeds collected in seed trap stations, in 1-m intervals. Predicted dispersal distances are simulated by WINDISPER, a mechanistic model incorporating the spatially explicit distribution of adult tree canopies, the temporally explicit effects of the direction, horizontal and vertical velocities of the wind, the terminal velocities of seeds, and their height of release, all randomly selected from the measured distributions. Solid and dashed lines are the fitted negative exponential and inverse power law models, respectively.

TABLE 3. Statistics and curve fits of seasonal dispersal curves: the frequency distribution of predicted dispersal distances traveled by seeds to seed trap stations during a dispersal season (see Fig. 2).

		Distribution statistics (± 1 SE)				Negative exponential		Inverse power law	
Period	n	Mean	Skewness	Kurtosis	df	Slope†	r^2	Slope†	r^2
Fall 1993	4910	11.86 ± 0.17	2.63 ± 0.04	10.55 ± 0.07	83	-0.060_{AB}***	0.86	-1.78_A***	0.79
Spring 1994	4580	13.01 ± 0.20	2.75 ± 0.04	12.32 ± 0.07	92	-0.053_{ABC}***	0.82	-1.80_A***	0.80
Fall 1994	7400	12.82 ± 0.16	2.94 ± 0.03	13.92 ± 0.06	107	-0.051_{BC}***	0.85	-1.94_A***	0.83
Spring 1995	3175	11.95 ± 0.25	3.43 ± 0.04	18.26 ± 0.09	90	-0.044_C***	0.77	-1.70_A***	0.84
Fall 1995	2110	11.41 ± 0.26	2.98 ± 0.05	17.45 ± 0.11	70	-0.052_{ABC}***	0.76	-1.63_A***	0.83
Spring 1996	5260	10.70 ± 0.16	2.94 ± 0.03	12.80 ± 0.07	86	-0.061_A***	0.88	-1.89_A***	0.86

*** $P \le 0.001$.

† For a given parameter, similar subscript letters indicate no significant differences among seasons at $\alpha = 0.05$.
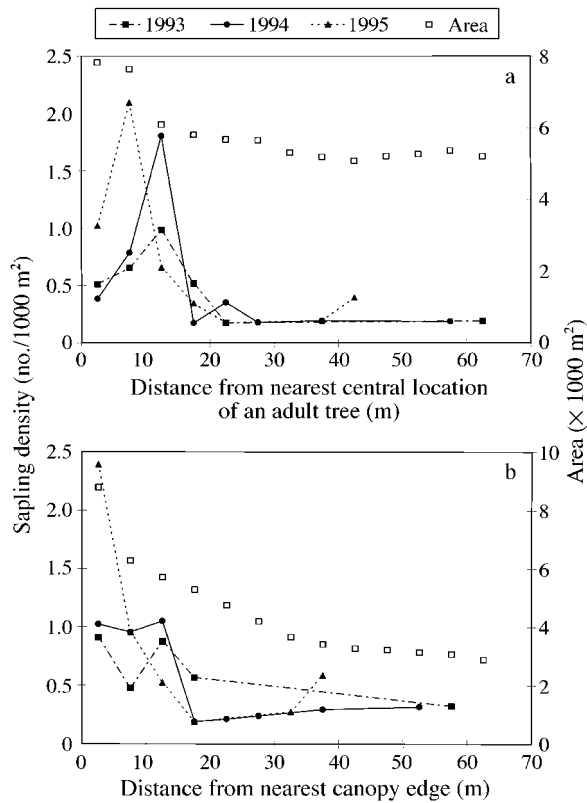
FIG. 3. Density of saplings in 5-m distance intervals as recorded in May 1998 in the Nir-Ezyon study site. Distance is measured (a) to the nearest central location of an adult tree, and (b) to the nearest canopy edge. Sapling density is the number of saplings recorded within each interval divided by the area covered by this interval shown on the right-hand ordinate. Cohort years are of the winter of germination according to the recorded age in May 1998 (e.g., 1993 is winter 1993–1994 when saplings in their fifth year [1998] have established). Data points are plotted at the middle of each distance interval.

were rarely observed there. Saplings were observed mostly in two microhabitats: cracks and crevices in limestone rock slabs, and in abandoned olive grove terraces. These microhabitats showed no particular spatial pattern with respect to the adult trees.

For all cohorts, sapling density was considerably lower at greater distances from adult trees, but the pattern near adult trees varied depending on the distance measure and, to some degree, the year (Fig. 3). When distance was measured to the nearest central location of an adult, the maximum density of the 1995 cohort was in the 5–10 m interval, whereas older cohorts peaked in the 10–15 m interval (Fig. 3a). When distance was measured to the nearest canopy edge, sapling density of the 1995 cohort peaked at the 0–5 m interval (0.0024 individuals/m^2); for the older cohorts, it had two peaks in the 0–5 and 10–15 m intervals (Fig. 3b). Overall, sapling density in distance intervals within the near section (0.00083 ± 0.00017 saplings/m^2) was significantly higher than in those within the far section (0.00023 ± 0.00003 saplings/m^2; Mann-Whitney, $U =$ 12.0, $P = 0.002$). Note that the area covered by distance intervals is fairly constant (Fig. 3a), or monotonically declines (Fig. 3b) with increasing distance within the range of up to 65 m from the trees, because equal-distance intervals around the closely spaced trees at this site largely overlap (Fig. 1; see also Condit et al. 1992).

The proportion of seeds surviving to the sapling stage clearly increases with increasing distance from the trees in all cohorts, and for both methods of distance estimation (Fig. 4). In general, the probability of surviving three to five years (seed to sapling) was remarkably low, at most ~0.2%, and usually much lower. The highest estimated sapling : seed ratio within a distance interval was 1:533 (Fig. 4b: interval 30–35 m, 1995 cohort); the lowest was 1:505 035 (Fig. 4a: interval 0–5 m, 1994 cohort). Given that an average tree
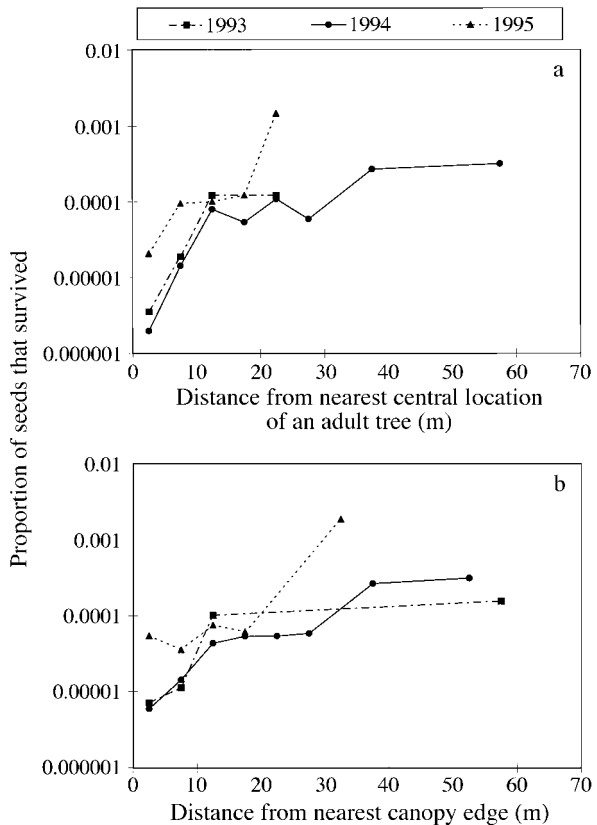

FIG. 4. Estimated proportions of seeds that survived to sapling stage until May 1998 in 5-m distance intervals in the Nir-Ezyon study site (note the ordinate log scale). Distance is measured (a) to the nearest central location of an adult tree and (b) to the nearest canopy edge. For each distance interval, the number of saplings of a certain cohort (Fig. 3) is divided by an estimate of initial size of this cohort (i.e., the number of seeds dispersed during the fall of the same year, just before germination). Data points are plotted at the middle of each distance interval.

releases an estimated 10 290 viable seeds per year (Nathan et al. 1999), almost 3×10^6 seeds were released from the 96 trees of this stand during the three years of study. The number of saplings that survived until May 1998 thus suggests an approximate sapling : seed ratio of 1:50 000 for the 1993 cohort (survival to 4.5 yr), 1:38 460 for the 1994 cohort (3.5 yr), and 1:29 410 for the 1995 cohort (2.5 yr). Note that these estimates are calculated from seed trap data, where only filled seeds were counted; hence, they do not consider empty seeds or predispersal seed loss.

Interseasonal variation in seed deposition and wind conditions

In agreement with the positive mean–variance relationship (Taylor 1961), the absolute variation in seed dispersal rates was considerably higher in near stations than in far ones (Table 2). However, the relative variation, calculated by the coefficient of variation, which controls for differences between the means, was considerably lower in the near than in the far stations (Table 2). This trend is observed in all six dispersal seasons (Table 2). The higher variation in dispersal at larger distances from the source is apparent in the triangular shape of the dispersal distances (Fig. 2). The interseasonal consistency near the source is reflected in a constant slender ''crest'' of this triangle, whereas its broader part at larger distances apparently varied between seasons.

Wind velocities and frequencies for the main eight compass directions measured at the study site during fall 1995 were not significantly different from contemporary frequencies measured at the En-Karmel IMS weather station (velocity: ANOVA, $F_{1, 398} = 0.2$, NS; frequency: $\chi^2 = 10.7$, df = 7, NS, respectively). Dispersal seasons vary considerably in wind frequencies for the eight wind sectors, when wind records were selected both from the entire season ($\chi^2 = 134.4$, df = 35, $P < 0.0001$), and from the two most intensive dispersal periods within each season ($\chi^2 = 150.9$, df = 35, $P < 0.0001$). Strong interseasonal variation was also found for wind velocities in both cases (ANOVA: $F_{5, 114} = 5.9$, $P < 0.0001$ and $F_{5, 594} = 18.4$, $P < 0.0001$, respectively).

All seasonal correlograms for the entire area are globally significant, because each has at least one value that is significant at the Bonferroni-corrected level (Fig. 5). They all share a similar general structure of a ''single bump'' pattern (Legendre and Fortin 1989: 113), significant positive correlation in the nearest distance classes (<48 m), followed by significant negative correlation at intermediate distances (72–119 m), and positive but insignificant correlation at the farthest distance classes (>191 m). Interseasonal consistency in seed dispersal rates was also found by the partial Mantel tests for the entire study (Table 4). The relative differences between stations were found to be constant also for the near section, but they were variable for the

far section (Table 5). Although all correlations for the entire area and the near section were highly significant, only seven out of the 15 pairs of seasons were significant for the far section, and only two were significant at the Bonferroni-corrected level (Table 5). Similar trends were found in the spatial correlograms for the near and far sections (Nathan 1999). Thus, both the partial Mantel test and the spatial autocorrelation analysis revealed highly significant interseasonal consistency in seed deposition pattern for the entire study area and for the area near adult trees, but interseasonal variation farther away. In both tests, the spatial patterns of the two dispersal seasons with the considerably lower dispersal rates (spring and fall 1995) were not distinctly different from those of other seasons.

DISCUSSION

The basic prediction of the escape hypothesis, that the probability of progeny survival increases with increasing distance from adult trees (Janzen 1970, Connell 1971, Howe and Smallwood 1982), is clearly supported by our findings. We also confirmed its basic assumption that seed density declines rapidly with increasing distance from adults. The prediction invokes distance- or density-responsive seed predation (Janzen 1970) and intraspecific competition with seedlings and adults (Harper 1977, Howe and Smallwood 1982) as the underlying mechanisms. Their effects upon recruitment, however, depend on the characteristics of the dispersal curve (Hubbell 1980), and, more generally, may be affected by spatiotemporal variation in the density of dispersed seeds. Yet, studies of the escape hypothesis have ignored the spatiotemporal variation in dispersal. In this paper, we analyzed the dispersal curves and the spatiotemporal variation in dispersal and recruitment in *Pinus halepensis* to investigate the effects of dispersal patterns upon recruitment. We propose that spatiotemporal variation in the density of dispersed seeds can intensify the effects of both predation and competition on recruitment patterns predicted by the escape hypothesis.

Seed dispersal patterns

In numerous studies of seed dispersal in general, and of wind dispersal in particular, dispersal curves have been found to be strongly leptokurtic (that is, having more short-distance dispersal and more long-distance dispersal than would be expected from an equivalent normal distribution). This pattern is confirmed in the present study. The relatively fat tail is explained by the relatively strong horizontal and vertical winds during Sharav events, in which most seeds are released (Nathan et al. 1999). This dispersal curve implies that the spatial pattern of dispersed seeds should strongly resemble that of adults, as found in other wind-dispersed trees (Clark et al. 1998, Houle 1998).

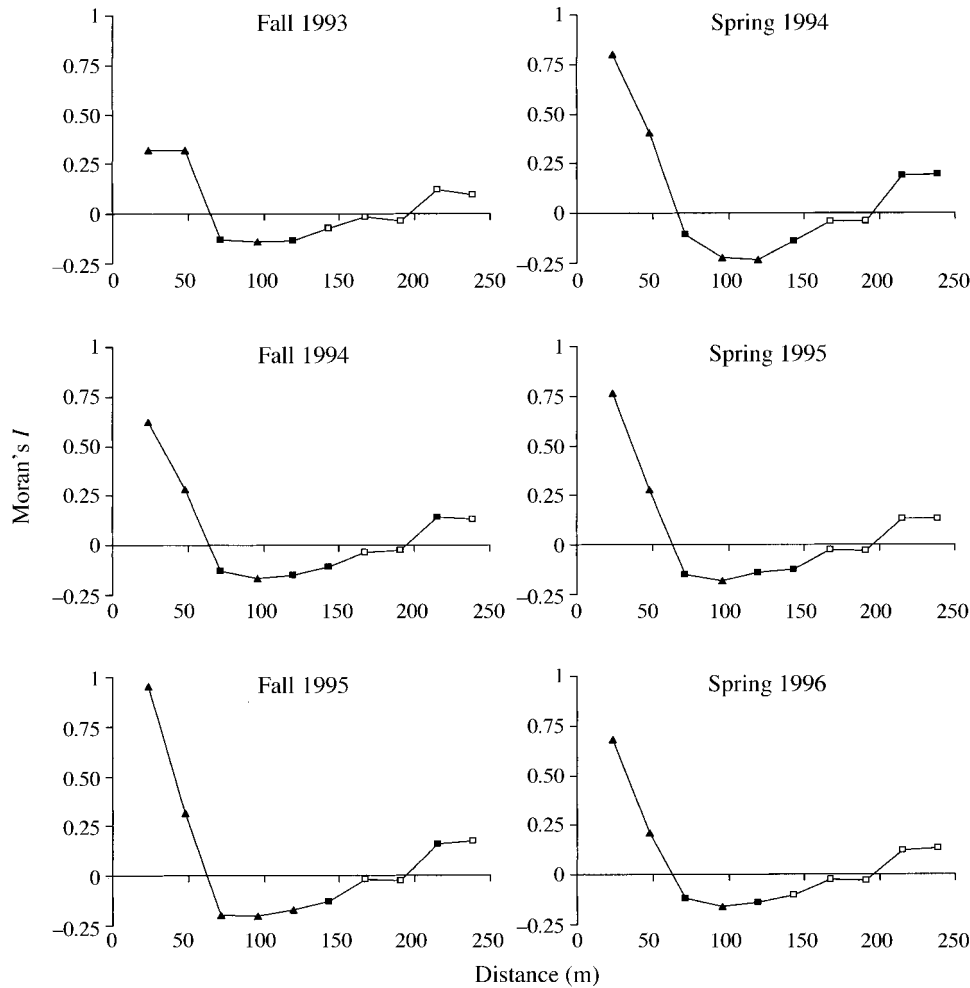The practical difficulty in tracking individual seeds during dispersal in natural settings continues to make

FIG. 5. Spatial correlograms for the six dispersal seasons at Nir-Ezyon. Solid squares represent significant ($P \leq 0.05$) correlation between seed dispersal rates (no. seeds·m^{-2}·d^{-1}) recorded a certain distance apart (given in the abscissa). Solid triangles are also significant at the Bonferroni-corrected level ($P \leq 0.0033$), and open squares are nonsignificant values. Data points are plotted at the upper limit of each distance interval.

the quantitative study of dispersal in plants a challenge. Seed traps provide a simple and reasonably reliable alternative, but because seed shadows of adjacent plants typically overlap and the exact source location of each seed is unknown, dispersal distances to seed traps cannot be estimated accurately. This problem has recently been addressed by the inverse modeling approach (Ribbens et al. 1994, Clark et al. 1998), which looks for the best fit of a certain phenomenological model against dispersal data, given the specific spatial arrangement of seed sources (trees). An alternative approach is to use a spatially explicit mechanistic model

TABLE 4. Partial Mantel correlations for the comparison of relative differences in seed dispersal rates between seed trap stations ($n = 62$).

Period	Fall 1993	Spring 1994	Fall 1994	Spring 1995	Fall 1995	Spring 1996
Fall 1993						
Spring 1994	0.297***					
Fall 1994	0.345***	0.405***				
Spring 1995	0.416***	0.505***	0.415***			
Fall 1995	0.453***	0.547***	0.376***	0.567***		
Spring 1996	0.488***	0.575***	0.505***	0.685***	0.580***	

Note: H_0: relative differences in seed dispersal rates among sites (seed trap stations) in the two seasons are *not* linearly correlated.

*** $P \leq 0.0033$ (the Bonferroni-corrected level).

TABLE 5. Partial Mantel correlations for the comparison of relative differences in seed dispersal rates between seed trap stations near and far from adult trees. Below and above the diagonal are seed traps stations near ($\leq$20 m, $n = 23$) and far ($>$20 m, $n = 39$) from the nearest central location of an adult tree, respectively.

Period	Fall 1993	Spring 1994	Fall 1994	Spring 1995	Fall 1995	Spring 1996
Fall 1993		−0.116	0.134*	0.092	0.184	0.191
Spring 1994	0.376***		0.141*	0.198	0.158	0.274*
Fall 1994	0.537***	0.605***		0.177**	0.089	0.316***
Spring 1995	0.347***	0.530***	0.553***		0.282*	0.469***
Fall 1995	0.419***	0.579***	0.688***	0.493***		0.227
Spring 1996	0.432***	0.571***	0.633***	0.529***	0.442***	

Note: H_0: relative differences in seed dispersal rates among sites (seed trap stations) in the two seasons are *not* linearly correlated.

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.0033$ (the Bonferroni-corrected level).

of wind dispersal, which has been validated for the same species and site. The validated model can be used directly to construct dispersal curves (Nathan 1999), or, as introduced in the present paper, to provide estimates of the distances traveled by seeds that are independent of seed trap data. Mechanistic models obviously embody a better understanding of the underlying mechanism and the operative factors than do phenomenological ones, but their application is usually more restricted because they typically involve too many parameters, which are often either unmeasurable or impractical to parameterize elsewhere. However, given the small number of easily measurable parameters in WINDISPER (Nathan 1999), our specific approach potentially enables wider application beyond the specific species and sites investigated.

Survivorship and recruitment patterns

We found that the probability of progeny survival increased with increasing distance from adult trees, as predicted by the escape hypothesis. Peak recruitment occurred at some distance from the nearest central location of a tree, as predicted by the Janzen-Connell model, but in the closest interval when the distance was measured to the nearest canopy edge, more closely resembling the pattern predicted by Hubbell's model (see *Introduction*). The reason for this difference is that not a single sapling was found under the canopy of an adult. Thus, the method with which the distance from the adults is measured can affect the description of patterns of recruitment and may even lead to contrasting conclusions.

Assuming that no tangible seed dormancy exists in *P. halepensis* (Skordilis and Thanos 1995, Daskalakou and Thanos 1996), the ''real-life'' estimates of sapling : seed ratios (between 1:29 410 and 1:50 000 for the 2.5- and the 4.5-yr-old cohorts, respectively) represent an extremely low survival probability. Seed supply is unlikely to be a limiting factor for recruitment in the near section of our study site, with a mean annual dispersal rate of 93 seeds·m^{-2}·yr^{-1}. However, mean annual dispersal rate in the far section was only 0.86 seeds·m^{-2}·yr^{-1}. Thus, despite the large seed crops, *P. halepensis* recruitment is likely to be limited by seed

supply already at distances of 20–110 m from adult trees.

The probability of progeny survival (seed to sapling) at 5-m distance intervals from adult trees was calculated in the present study by dividing the number of saplings found in each interval by an estimate, based on extensive seed trap data, of the corresponding number of seeds available for germination. This approach has the advantage of providing estimates of survival probabilities in natural settings with no interference, summing up the cumulative effects of dispersal, seed viability, mortality agents, and other environmental conditions. However, it does not allow us to differentiate between factors affecting the emerging pattern.

The clear finding that, despite intensive dispersal, no recruitment has occurred directly under tree canopies can be attributed to either seed predation or competition with adults. Extensive seed predation observed in this site (Nathan et al. 1999), as well as in other *P. halepensis* forests in Israel (Schiller 1979) and in France (Acherar et al. 1984), suggests that predation might have a strong effect. Schiller (1979) found that *P. halepensis* seedlings did not survive more than two years in a forest with dense canopy cover, and demonstrated that light conditions (intensity and spectral range) under the tree canopy were unfavorable to both seed germination and seedling growth. Acherar et al. (1984) also observed that the shading effects of adults (and of fast-growing annual herbs; see also Schiller 1979) have a significant effect on the recruitment pattern. The importance of light availability to tree regeneration is well established in temperate (e.g., Canham 1989) and tropical (e.g., Denslow 1987) forests. Seedling competition is unlikely, because the observed seedling densities under adult canopies were consistently very low.

Extensive recruitment of *P. halepensis* has been observed frequently in newly opened old fields or after fire (see *Methods: Study species*). In the absence of any substantial disturbance, sapling densities observed in this study, up to 0.0024 individuals/m^2, were considerably lower than postfire densities; for example, four years after a wildfire 8 km northeast of the study site, sapling density was 1.9 individuals/m^2 (Izhaki and Ne'eman 1996). Given that during a tree's lifetime most

of its seeds are released by dry and hot weather, and not by fire (Nathan et al. 1999), the mechanism of seed release in *P. halepensis* seems rather ineffective. However, when disturbances other than fires are more frequent and widespread than observed in the present study, non-fire-induced seed release is beneficial in locating establishment opportunities, resulting in rapid population expansion (Acherar et al. 1984, Lepart and Debussche 1991, Trabaud 1991, Sadot 1992).

Spatiotemporal variation in seed deposition as a function of the distance from adults

Houle's (1998) study was the first quantitative, empirical examination of the temporal variation in the spatial patterns of dispersed seeds. Using seed traps to quantify seed dispersal and similar spatial tests (spatial correlograms and partial Mantel tests), he found significant interannual inconsistency in the spatial pattern of dispersed seeds. However, the effect of the distance between the seed traps and the adult trees on these results was not addressed. The partitioning of our study area into near and far sections has proved instrumental in evaluating the degree of the spatial and temporal (interseasonal) variation in the seed dispersion patterns. The two tests jointly revealed significant interseasonal consistency in spatiotemporal variation for the entire area. This finding could have led us to the erroneous conclusion that spatial patterns of seed dispersal are consistent among seasons. In fact, within the far section, constituting the larger part of the study area, seed dispersion patterns varied significantly among seasons.

The pattern of low spatiotemporal variation in seed dispersal rates near adult trees and high variation farther way is probably a common pattern in wind-dispersed trees. The interseasonal variation in wind conditions, although significant, was apparently not strong enough to generate significant interseasonal variation in the dispersion pattern of (most) seeds dispersed near adults. High spatiotemporal variation at relatively long distances is inevitable, given the rarity and the complexity of long-distance dispersal events (Silvertown 1991, Portnoy and Willson 1993, Greene and Johnson 1995). This high variation can determine the probability of seed survival if seed predators are sensitive to variation in the spatial distribution and/or the temporal availability of seeds (Real and Caraco 1986, Kacelnik and Bateson 1996). Getty and Pulliam (1993) found that White-throated Sparrows (*Zonotrichia albicollis*) search where seeds are more detectable rather than where they are most abundant. If low detectability and high variation pose comparable difficulties to seed predators, that can contribute to the higher probability of seed survival in the highly variable deposition pattern far from adult trees. Spatiotemporal variation in seed densities can also affect patterns of survivorship and recruitment through its effects on intraspecific seedling competition (see *Introduction*). Furthermore, high variation should be advantageous not only in increasing the probability of seed survival (the escape hypothesis), but also in locating establishment opportunities that are unpredictable in space and time (the colonization hypothesis; Howe and Smallwood 1982).

Seed aerodynamics, and particularly the terminal velocity during fall, is often considered as the principal determinant of dispersal distance in wind-dispersed species (e.g., Green 1980). However, seed aerodynamics in *P. halepensis* were found to be consistent among trees, among cones within trees, and among seeds within cones (Nathan et al. 1996); hence, seed aerodynamics is unlikely to be a key factor in producing spatiotemporal variation in seed dispersion patterns. Variation in fecundity can also lead to variation is deposition patterns, but our study, as well as that of Houle (1998), found that the variation in seed rain abundance was not correlated with the variation in seed deposition patterns. Wind behavior has been found to be more important in determining postdispersal seed dispersion than are factors under plant control (Augspurger and Franson 1987, 1993, Greene and Johnson 1992, Nathan 1999). Seed release in *P. halepensis* was found to be synchronized with predictable periods of the year in which winds were effective for long-distance dispersal (Nathan et al. 1999). We suggest that the most effective plant-controlled mechanism increasing the variation in seed densities in wind-dispersed species like *P. halepensis* is simply the synchronization of seed release with periods of relatively strong winds. A more detailed theoretical, observational, and experimental investigation of the role of the spatiotemporal variation in seed dispersal on recruitment patterns, through, e.g., predator response and intraspecific competition, should prove instrumental in gaining better understanding of plant population dynamics.

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