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Seed release without fire in *Pinus halepensis*, a Mediterranean serotinous wind-dispersed tree

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Summary

1 Although serotiny is frequently considered to have evolved under the selective pressure of fires, the drying conditions that induce cone opening are not necessarily associated with fire. We hypothesized that in *Pinus halepensis*, a Mediterranean serotinous wind-dispersed tree, xeriscence (seed release induced primarily by drying conditions not generated by fire) bears intrinsic adaptive values, independent of those of pyriscence (fire-induced seed release).

2 We used seed-traps to quantify seed release in two scrubland pine stands in Israel. Contemporary meteorological data were used to seek correlations with climatic factors affecting seed release.

3 Substantial seed release, estimated to be about 60% of the annual crop, was observed in the absence of fire. Seed release was distinctly seasonal, with high rates in spring and autumn, and was strongly correlated with short, infrequent but temporally predictable Sharav events (dry and hot weather). In the most extensive Sharav-induced seed release, seed density reached 117 seeds m^{-2} and 15% of the annual crop was released within 6 days. Stepwise multiple regression revealed that mean relative humidity (in both stands) and maximum temperature (in one stand) were significant predictors of seed release.

4 Vertical (upwards) wind velocity was significantly positively correlated with dry and hot weather. Seed counts in distant traps ($>$ 20 m from the nearest tree) were significantly greater in periods in which Sharav events occurred than in other periods. Xeriscence may therefore have an adaptive value in promoting dispersal distance by wind.

5 Both xeriscence and pyriscence appear to be involved in determining serotiny in *P. halepensis* and provide means of exploiting establishment opportunities generated either by fire or by other factors.

Keywords: dispersal distance, serotiny, Sharav, temporal pattern, xeriscence

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Introduction

Serotiny, the long-term retention of seeds in a plant canopy, occurs in various taxa, mostly in Australia, South Africa, North America and the Mediterranean (Lamont *et al.* 1991; Whelan 1995; Bond & van Wilgen 1996). In woody plants of the northern hemisphere, serotiny is restricted to conifers, occurring in about a fifth of the species in the genus *Pinus* (Lamont *et al.* 1991). As an evolutionary strategy, serotiny requires a mechanism of seed release that is guided by environmental cues associated with favourable establishment opportunities (Lamont *et al.* 1991). Fire is often regarded as the most effective cue and serotiny is therefore generally used as a synonym for fire-induced seed release (although this is defined as pyriscence by Lamont 1991). However, only six of the 22 serotinous pines are obligate pyriscents (Lamont *et al.* 1991). In obligate pyriscent pines, cone opening is a process com-

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prising two essential steps: first, the fire heat melts the resins binding the apophyses of the cone scale, and secondly, the cone scales reflex away from the cone axis. The scale–reflex mechanism is based on a greater shrinkage of the abaxial sclerenchyma cells than of the adaxial tracheid cells in response to water loss, driven by a gradient in moisture content between scale tissues and the ambient air (Allen & Wardrop 1964; Harlow *et al.* 1964).

In facultative pyriscent pines, resin bonds are weak or practically absent and seed release is not restricted to fire (Keeley & Zedler 1998). Cone opening depends primarily on the scale–reflex mechanism, and hence drying conditions that are not necessarily associated with high temperatures are needed to induce seed release. For example, Dawson *et al.* (1997) found that *P. radiata* cones opened in response to low relative humidity in a constant 'normal' temperature of 23 °C. Lamont (1991) suggested several technical terms to describe different mechanisms of seed release, but did not specify a term for induction by drying conditions. We propose the term *xeriscence* to describe seed release induced primarily by drying conditions that are not generated by fire (e.g. dry weather spells), whereas *facultative pyriscence* is regarded to be primarily induced by drying conditions that are generated by fire. The ultimate theoretical distinction between xeriscence and pyriscence is important because each term indicates a mechanism evolved to synchronize seed release with an entirely different environmental cue. However, as xeriscence and facultative pyriscence are currently believed to be driven by the same proximate morphophysiological mechanism, they are empirically indistinguishable. This complicates our understanding of serotiny in many species inhabiting environments in which both fire and dry weather may have been involved in the evolution of this trait.

The Aleppo pine (*Pinus halepensis* Miller), a Mediterranean serotinous tree (Mirov 1967; Barbéro *et al.* 1998), illustrates this complication. Its mature seeds are retained in persistent cones, and their release is often delayed, building up a canopy-stored seed bank (Panetsos 1981). Rundel (1981, p. 521), following Naveh (1974), listed *P. halepensis* as a good example of a closed-cone pine, and Whelan (1995, p. 97), also following Naveh (1974, 1975), included the species among 'fire pines' in which cones 'are sealed with resin, delaying seed release until a fire has broken the resin bonds and allowed the cone scales to open'. Recent studies have found no evidence for resin binding the cone scales in *P. halepensis* (G. Ne'eman, personal communication). In fact, Naveh did not implicitly state that *P. halepensis* scales are sealed with resin, but that the species relies 'solely on post-fire seed germination from cones that burst open from the heat of the fire' (Naveh 1975, p. 202). Many other authors also emphasized the role of fire as a prime generator of seed release in *P. halepensis* (Panetsos 1981; Trabaud *et al.* 1985; Ne'eman *et al.* 1992; Richardson *et al.* 1992; Saracino & Leone 1993; Daskalakou & Thanos 1996; Agee 1998). Indeed, fire does generate massive release of *P. halepensis* seeds (Saracino & Leone 1993; Daskalakou & Thanos 1996) but considerable release also occurs independently of fire (Schiller 1979; Acherar *et al.* 1984; Daskalakou & Thanos 1996).

Seed release in non-serotinous pines is typically seasonal, and is frequently associated with dry, warm and windy weather (Krugman & Jenkinson 1974). Schiller (1979) reported that seed release in *P. halepensis* is associated with seasonal *Sharav* events during spring and autumn. Such periods of dry and hot weather in the eastern-Mediterranean region occur in association with Khamsin depressions, northward extensions of the Red Sea trough and prolonged anti-cyclonic conditions generating dynamic subsidence (Winstanley 1972; Levi 1978).

In this paper we describe the magnitude and temporal pattern of xeriscence in *P. halepensis* and its association with Sharav events. We quantified seed release in two pine stands within the Mediterranean scrubland ecosystem of Israel and used meteorological data to specify the climatic conditions inducing seed release in the absence of fire. Sharav events are characterized by strong winds (~~Winstanley 1972;~~ Levi 1978; Alpert & Ziv 1989), thus we hypothesize that xeriscence in *P. halepensis* has been selected as a mechanism for increasing dispersal distances. Our results, considering the current emphasis on fire in selecting for serotiny in *P. halepensis*, as well as in other pines and many other serotinous species (Whelan 1995; Bond & van Wilgen 1996), may bring new insight to the understanding of this phenomenon in fire-prone and seasonally dry and hot systems.

Materials and methods

THE SPECIES

Pinus halepensis is the most widely distributed pine throughout the Mediterranean region (Mirov 1967; Barbéro *et al.* 1998) and the most common natural and planted conifer in Israel (Zohary 1962). It has been introduced throughout the world and is considered as one of the most invasive pines (Richardson *et al.* 1992; Barbéro *et al.* 1998).

The relatively large cone crops are produced annually (Krugman & Jenkinson 1974). Pollination takes place in spring, fertilization occurs a year later, and seed dispersal begins in the third year after pollination (Panetsos 1981). Cones of the youngest age groups are distinguishable by their size, colour and position along the branch. The average mass of the asymmetric samara-like winged seeds is 22 mg and they autorotate while falling at an average terminal velocity of 0.81 ms^{-1} (Nathan 1999). Seeds are generally not dispersed farther than ~ 20 m from the canopy edge (Acherar *et al.* 1984 and see below). Adult trees are usually killed by wildfires (Agee 1998) and regeneration relies exclusively on seeds (Trabaud 1987). Seeds within closed cones may be viable for 8 years and more (Schiller 1979; Daskalakou & Thanos 1996), but dispersed seeds show no long-term dormancy (Daskalakou & Thanos 1996). An endogenous rhythm restricts germination to late autumn–early winter, resulting in recruitment early in the rainy season of the Mediterranean climate (Schiller 1979).

STUDY SITES

The two study sites were located within the Mediterranean region of Israel: the Nir-'Ezyon site (hereafter NE) on the lower western slopes of Mt. Carmel (32°41′N; 34°58′E), and the Mt. Pithulim site (hereafter MP) on the Judean hills (31°45′N; 35°04′E). Mean annual rainfall at both sites is 600 mm, the mean temperature of the hottest month (August) 24–26 °C and the mean temperature of the coldest month (January) 12 °C. NE, which is lower than MP (116 and 628 m a.s.l., respectively) and closer to the shore of the Mediterranean Sea (4 and 41 km, respectively), is less dry and has a lower frequency of Sharav events (Levi 1978).

The pine stands in both sites are presumably native populations, with neither documented nor field evidence of having been planted. The stand in NE (Fig. 1a) is smaller, holding 96 adult trees, and more isolated from neighbouring stands (no other individuals < 500 m away), than the stand in MP, with approximately 450 trees in the focal stand and 180 trees around it (Fig. 1b). Sixteen randomly selected trees cored in NE in 1994 were found to be 22–66 years old (mean ± SE; 55 ± 4 years) and up to 11.6 m high (9.1 ± 0.5 m). In MP, five trees were approximately 90 years old, while all the others were < 50 years, and tree height was similar to that recorded in NE (Nathan 1999). The undercanopy in both sites was mainly *Pistacia lentiscus*, and the surrounding vegetation a mixture of abandoned *Olea europaea* groves (NE only), dense to open maquis dominated by *Quercus calliprinos*, *Phillyrea media* (NE only), *Arbutus andrachne* (MP only), *Pistacia lentiscus* and *Ceratonia siliqua*, and dense to open shrubland (batha) dominated by *Sarcopoterium spinosum*, *Cistus* spp. and *Calycotome villosa*.

SEED-TRAP DATA

We placed 94 identical seed-traps within and around the focal stand in both sites, along eight compass directions (Fig. 1). In each direction, the most distant sampling station (approximately 100 m from the stand edge) and the second-most distant station (50 m), consisted of four and two traps, respectively, in order to increase the chance of sampling rare long-distance dispersal events. Seed-traps were constructed as a wooden frame of 0.99 × 0.84 × 0.15 m, with small holes for water drainage at the bottom and a cover net of 18-mm wire mesh to prevent access by birds, e.g. house sparrow (*Passer domesticus*) and goldfinch (*Carduelis carduelis*), while allowing pine seeds to pass through easily. Traps were placed at ground level and the trapped seeds were susceptible to predation by ants, especially *Messor semirufus*, and by rodents, chiefly yellow-necked mouse (*Apodemus flavicollis*) in NE. In order to prevent predation, the edges of the traps were smeared with a non-drying sticky material (Rimifoot, Jewnin-Joffe Industry, Israel, Petah-Tiqwa), which was cleaned and refreshed regularly. Despite the high predation pressure observed outside the traps, protection efficiency, evaluated by 10 spray-marked pine seeds placed within each trap, was generally high (in 81% of all traps no marked seed disappeared); instances of predation from traps had no spatial or temporal pattern.

Seed dispersal data were collected in NE between October 1993 and November 1994, approximately every 11 days, and subsequently only during dispersal seasons (spring and autumn 1995 and spring 1996). In MP, seed dispersal was measured continuously between September 1996 and June 1998, approximately every 18 days. However, the collection of meteorological data in this site began on April 1997, and as there was no meteorological station nearby seed-trap data collected before this date were excluded from analyses. Recent aerial photographs of the two study sites, scanned at a resolution of 0.25 m and corrected for terrain distortion (processed by Advanced Digital Mapping, Tel Aviv, Israel), were used to identify the location of trees and seed-traps, to the nearest 1 m.

The rate of seed release in periods between successive visits was estimated as the number of seeds counted (totalled over all stations) per day. The proportion of the annual seed crop released in a year was estimated in NE, where the seed-trap data set was larger and the stand more isolated (Fig. 1). The total number of seeds released each year from the 96 trees in NE was estimated from the seed-trap data as the summation of the estimated number of seeds that were dispersed into three sections: the area under tree canopies ($n = 7$ traps), the area in gaps within the stand defined by a 10-m buffer around the trees ($n = 12$), and the area in a radius of 100 m outside the stand ($n = 43$ stations). For the first two sections, the mean density of seeds trapped in a year was multiplied by the section area. For the third sec-

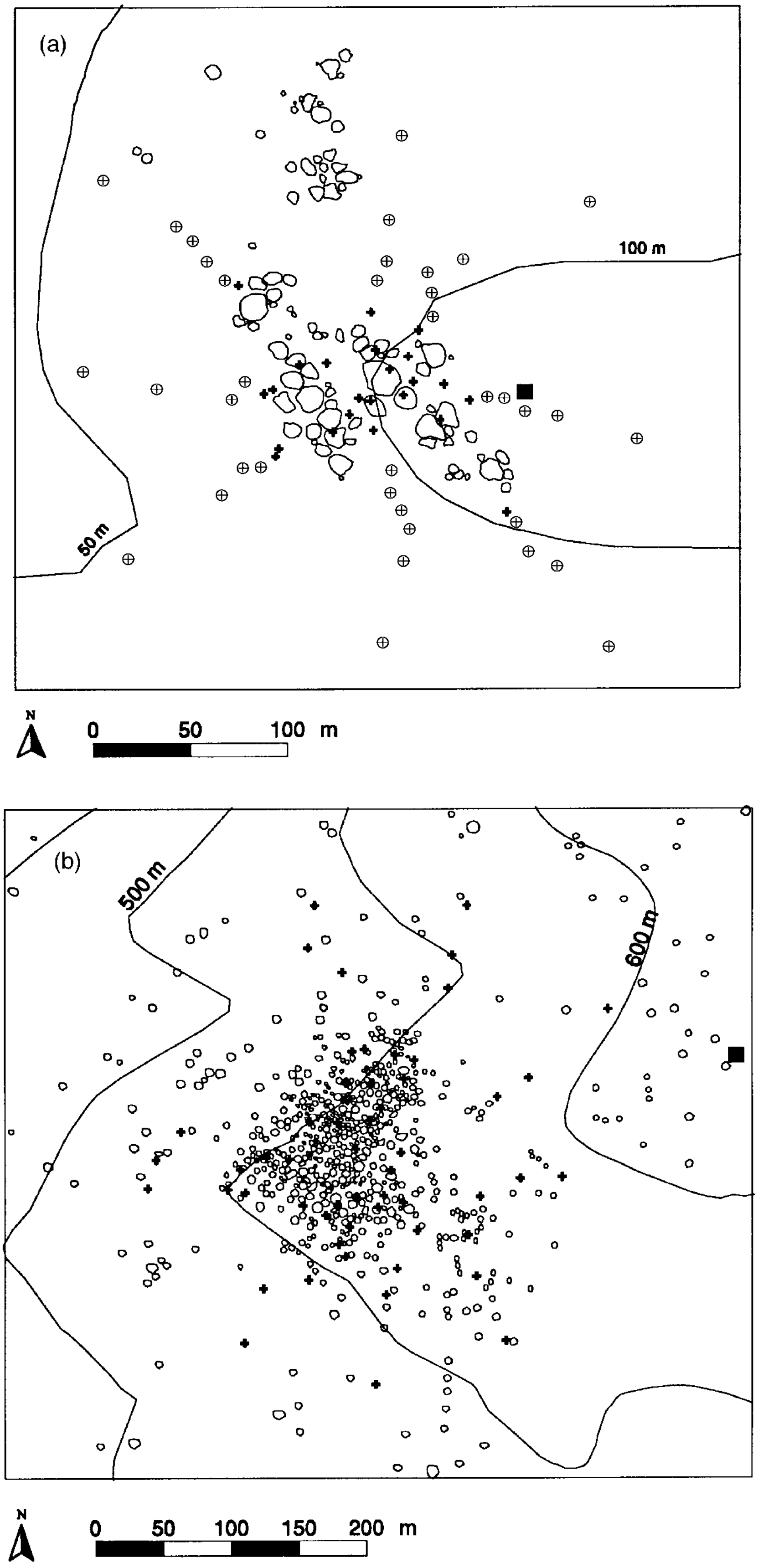

Fig. 1 The study sites: (a) south of Nir-'Ezyon at the lower western slopes of Mt. Carmel; (b) Mt. Pithulim, the Judean hills. Polygons show adult (seed-producing) trees, and crosses indicate seed-trap stations, circled (in Nir-'Ezyon map) if > 20 m from the nearest central location of an adult tree. Black squares show the location of a meteorological station active in Nir-'Ezyon during autumn 1995, and in Mt. Pithulim from spring 1997 to spring 1998.

tion, the number of seeds released was estimated by fitting an empirical negative exponential function (Nathan 1999). The annual seed crop was estimated by multiplying the mean annual cone crop (estimated by counting second- and third-year cones in nine randomly selected trees) by the mean number of seeds per cone (estimated by counting filled seeds in 324 closed cones).

METEOROLOGICAL DATA

Meteorological conditions in NE were extracted from hourly averages recorded in the Israel Meteorological Service (IMS) station at 'En-Karmel, 1.5 km south-west of the site. Horizontal wind velocity was measured 10 m above ground level by a propeller anemometer (model 05103; R. M. Young Co., Traverse City, Michigan, USA). Relative humidity (RH, in percentage) was calculated from dry- and wet-bulb temperatures (in °C) using the formulations of Pearcy *et al.* (1989, pp. 433 and 435) corrected for a typographical error, and slightly modified to fit the local instruments (I. Seter, personal communication). A comparison between the IMS data and contemporary data collected in NE during a period of 32 days in autumn 1995 revealed fairly high correlations ($r_{Spearman}$ = 0.891, 0.672 and 0.804 for air temperature, RH, and horizontal wind velocity, respectively; $n = 762$, $P < 0.001$). No significant difference was found between measurements of the horizontal wind velocity at the two sites (2.79 ± 0.07 vs. 2.82 ± 0.07 m s^{-1}; Wilcoxon signed ranks test, $Z = -1.63$, $P = 0.104$). However, small but significant differences indicated that the IMS station tended to underestimate air temperature (22.44 ± 0.12 vs. 23.18 ± 0.13 °C; $Z = -7.29$, $P < 0.001$), and to overestimate RH (75.80 ± 0.54 vs. 72.41 ± 0.69%; $Z = -6.75$, $P < 0.001$) of NE.

In MP, horizontal wind velocity (model 03002 anemometer; R.M. Young Co.) measured 10 m above ground level, vertical wind velocity (model 27005 Gill UVW anemometer; R.M. Young Co.) measured 6.4 m above ground level (this variable was not measured in the IMS station), and air temperature and RH (model HMP35C probe; Campbell Scientific, Logan, Utah, USA), were measured between April 1997 and June 1998.

The occurrence of Sharav events during the entire study period was analysed from daily synoptic maps (I. Seter, personal communication) for all days with any hourly record of < 35% RH and > 30 °C. Sharav events were identified when one or more of the three main synoptic situations involved (Khamsin depressions, Red Sea trough and anti-cyclonic conditions) occurred and were classified as strong (> 35 °C and < 30% RH) or moderate (> 30 °C and < 35% RH).

SEED RELEASE AND METEOROLOGICAL VARIABLES

Relationships between rate of seed release and meteorological variables were assessed using stepwise multiple regression. For NE, the analysis was restricted to the first 36 successive periods (October 1993–November 1994), when seed-trap counts were taken continuously, excluding four periods when insufficient (> 25% missing) meteorological data were available. MP data comprised 24 periods (April 1997–June 1998). Independent variables were the observed mean, maximum and minimum of air temperature, RH and horizontal wind velocity. $P < 0.05$ was used as a criterion for either acceptance or removal of variables. Preliminary tests found no violation of the normality and homoscedasticity assumptions.

DISPERSAL DISTANCE AND SHARAV EVENTS

To examine the hypothesis that seed release during Sharav events favours long-distance dispersal, we compared the wind components (horizontal and vertical velocities) measured in MP in times of drying conditions with those measured in other, less dry conditions. Because the strong positive (upwards) vertical component of the wind is highly dependent on a strong horizontal one (I. Seter, personal communication; and see below), we focused on the strongest horizontal winds, arbitrarily selected as > 7 m s^{-1}, to isolate the conditions most likely to promote long-distance dispersal. After testing the relationship between wind and drying conditions, we used seed-trap data to examine whether seeds were collected more frequently in distant traps (> 20 m) during periods with Sharav events compared with periods without them. This test was restricted to the seed-trap data of NE, because of its greater isolation (Fig. 1), hence the distance of a seed-trap station to the nearest tree provided a reliable estimate for the actual dispersal distance travelled by the collected seeds.

Results

MAGNITUDE OF SEED RELEASE

A total of 5811 seeds was collected in 70 visits in NE (October 1993–June 1996), and 5024 seeds in 24 visits in MP (April 1997–June 1998) (Table 1). Estimates of the annual number of seeds released from the 96 trees in NE were 1 022 000, 1 141 000 and 800 000 for the 3 years (autumn and successive spring), i.e. approximately 988 000 seeds per year for the whole stand or 10 290 seeds per tree per year. The number of cones per tree (mean ± SE) was 242.3 ± 62.9, and the number of seeds per cone

Table 1 Seed-trap data in the two study sites during strong and moderate Sharav events vs. non-Sharav periods (see text for definitions)

	Sharav			
Site	Strong	Moderate	Non-Sharav	Total
Nir-'Ezyon				
Seeds counted	2741	1003	2067	5811
Days	84	40	514	638
Rate (seeds day^{-1})	32.6	25.1	4.0	9.1
Seeds at distance (m) *				
0–20	2650	972	2033	5655
> 20	91	31	34	156
Mt. Pithulim				
Seeds counted	2990	1333	701	5024
Days	95	71	257	423
Rate (seeds day^{-1})	31.5	18.8	2.7	11.9

* Number of seeds counted in seed-traps in two categories of distance (to the nearest central location of an adult tree).

71.7 ± 1.4, giving a mean annual seed production of approximately 17 400 seeds per tree. Thus, seed release estimated from seed-traps accounted for approximately 59% of the annual crop. The annual density of dispersed seeds in seed-traps under the tree canopy was 240 ± 15 seeds m^{-2} (range 108–393). The highest rate of seed release was observed in NE during a period of 6 days (including 1 day of a strong Sharav event) in May 1996: a total of 459 seeds was counted in all the traps, the highest local density was 117 seeds m^{-2} and the estimated number of seeds released was 250 000 (2600 seeds per tree), about 15% of the average annual crop.

The claim for high serotiny levels in *P. halepensis* may have originated from the prevailing notion that closed silver-coloured cones (i.e. those at least 1 year after maturation) open exclusively in response to fire. To examine this, we marked 50 such cones in NE in autumn 1994; the cones did open in varying proportions after Sharav events but usually closed again after the winter rains. By spring 1998, 27 (54%) of these supposedly 'fire-exclusive' cones were open.

TEMPORAL PATTERN OF SHARAV EVENTS

Sharav events during the study period were rather short and infrequent but were temporally predictable in both sites (Table 2). Only 16 Sharav events of 1–6 days each (1.8 ± 0.4) occurred during the

Table 2 Frequency, duration and intensity of Sharav events of different synoptic types during the study period

	Khamsin depression		Red-Sea trough		Both	
Site	Strong	Moderate	Strong	Moderate	Strong	Moderate
Nir-'Ezyon						
Spring (Apr – Jun)						
Number of events	3	3	1	1	0	1
Duration (days) *	4,1,1	1,1,1	2	2		1
Autumn (Sep – Oct)						
Number of events	0	0	4	2	0	1
Duration (days) *			6,1,1,1	2,1		3
Mt. Pithulim						
Spring (Apr – Jun)						
Number of events	3	3	0	2	1†	0
Duration (days) *	4,2,5	2,2,3		3,2	7	
Autumn (Oct)						
Number of events	0	0	1	0	0	0
Duration (days) *			6			

* Duration of each event, separated by commas.
†This particular event began with anti-cyclonic conditions, followed by an extension of Red Sea trough active for 2–3 days and than a series of Khamsin depressions for 2–3 more days.

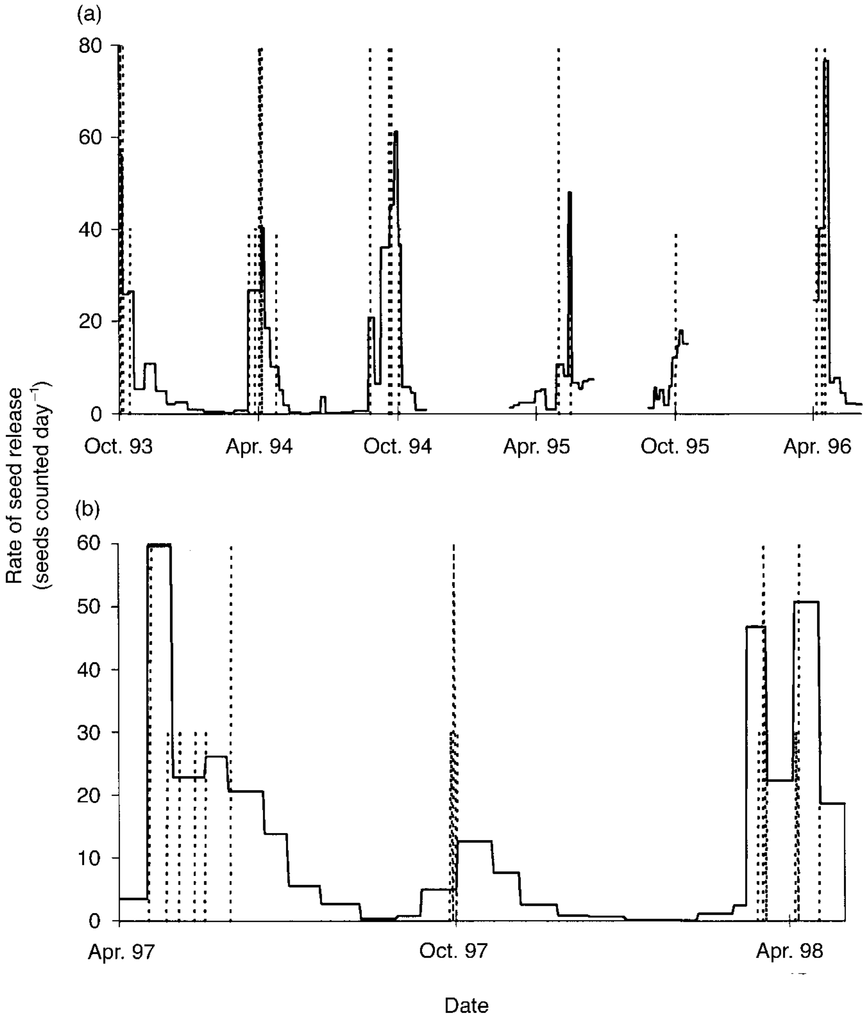

Fig. 2 Dynamics of seed release observed in (a) Nir-'Ezyon, October 1993–June 1996, and (b) Mt. Pithulim, April 1997–June 1998. Solid lines indicate the periodic rate of seed release (between successive visits) estimated as the total number of seeds counted in all seed-traps per day. Vertical dashed lines indicate Sharav events: taller lines are strong events ($<$ 30% RH, $>$ 35 °C); shorter lines, moderate ($<$ 35% RH, $>$ 30 °C).

33 months of study in NE, comprising 3.0% of the total period. Although still fairly infrequent, Sharav events were both more common and prolonged in MP: 10 events of 2–7 days (3.6 ± 0.6) occurred during 15 months, comprising 6.1% of the total period. In both sites, Sharav events were seasonal, restricted to spring (April–June) and autumn (September–October) (Table 2). Khamsin depressions occurred almost exclusively during spring; extensions of the Red Sea trough were more frequent in autumn; anti-cyclonic events were recorded only once (Table 2). Strong drying conditions ($<$ 30% RH, $>$ 35 °C) were evenly distributed between events associated with Khamsin depressions or the Red Sea trough and between spring and autumn. These findings coincide with the general reported patterns of Sharavs (Winstanley 1972; Levi 1978).

TEMPORAL PATTERN AND METEOROLOGICAL CORRELATES OF SEED RELEASE

Rates of seed release corresponded to the seasonality of Sharav events, with high rates observed in the two sites in spring and autumn, and low rates during summer and winter (Fig. 2). Not only were seed release rates much higher in periods in which Sharav events (especially extreme ones) occurred (Table 1; Mann–Whitney test $U = 23$, $N_1 = 16$, $N_2 = 51$, $P < 0.001$), but also the total number of seeds released during these relatively short periods was considerably higher (64% of all seeds in NE, 86% in MP).

The rate of seed release was negatively and significantly correlated with mean RH (Table 3). In both sites, mean RH accounted for approximately half of

Table 3 Stepwise multiple regressions for the rate of seed release (estimated as the total number of seeds counted in all seed-traps per day) by nine meteorological variables: mean, minimum and maximum of hourly records of relative humidity (RH, in percentage), air temperature (T, in °C) and horizontal wind velocity (in m s^{-1}), in the two study sites

Site	Step	Variables in model	Step-adjusted R^2 *	β†	P-value
Nir-'Ezyon‡	1	Mean RH	0.480	–0.705	< 0.001
	2	Mean RH		–0.505	< 0.001
	2	Maximum T	0.674	0.488	< 0.001
Mt. Pithulim§	1	Mean RH	0.485	–0.712	< 0.001

*The fraction of the variance accounted for by the model, adjusted for the number of independent variables.
†Standardized regression coefficient.
‡Thirty-two periods, October 1993–November 1994.
§Twenty-four periods, April 1997–June 1998.

the variation in the rate of seed release, more than any other variable (Table 3). In NE, maximum air temperature explained an additional significant proportion (19%) of the variation, being positively and significantly correlated with seed release (Table 3). The regression models accounted for a moderate proportion of the variation (67% in NE and 48% in MP, Table 3), presumably because the intervals between successive counts of seed-traps were larger than the average duration of a Sharav event.

WIND CONDITIONS, DISPERSAL DISTANCE AND SHARAV EVENTS

Based on 10 150 hourly averages recorded in MP, horizontal and vertical wind velocities were significantly positively correlated ($r_{Spearman} = 0.797$, $P < 0.001$). The correlation, however, was not symmetrical: strong horizontal winds were associated with a variety of vertical velocities, while strong positive (upwards) vertical winds were restricted to strong horizontal ones. Vertical wind velocities were significantly higher during hours with drying conditions (< 30% RH, > 35 °C) than with others (0.60 ± 0.03 m s^{-1} and 0.43 ± 0.01 m s^{-1}, respectively; Mann–Whitney test $U = 6921.5$, $P < 0.001$) but horizontal wind velocities were independent of drying conditions (9.04 ± 0.29 m s^{-1} and 9.06 ± 0.06 m s^{-1}; Mann–Whitney test, NS).

Only 2.68% of the seeds were collected in seed-traps located > 20 m from the nearest central location of an adult tree (Table 1). This proportion was 1.64% in periods with no Sharav events, and twice that (3.26%) in periods in which Sharav events occurred ($\chi^2 = 13.27$, d.f. = 1, $P < 0.001$; Table 1).

Discussion

Fire is a major factor affecting life-history traits of plants such as *P. halepensis* in Mediterranean-type ecosystems (Naveh 1975; Vogl *et al.* 1977; Trabaud 1987; Barbéro *et al.* 1998). The high post-fire seed densities, reaching 855 seeds m^{-2} (Saracino & Leone 1993), may account for the prevailing notion that seed release in this species is restricted to fires. This notion had already been questioned (Trabaud 1987; Lepart & Debussche 1991), mostly on the grounds of the abundant recruitment unrelated to fire (Acherar *et al.* 1984; Trabaud 1987; Sadot 1992) but also since the temperatures during a fire have a negative effect on both seed viability and germination (Shomer-Ilan 1964; Martínez-Sánchez *et al.* 1995), while dehydration, which is not uniquely generated by fires, affects both positively (Shomer-Ilan 1964). In this study we found that most (60%) of the annual seed crop is released during Sharavs, a proportion that is likely to be an underestimate because of the progressive loss from a cohort of canopy-stored seeds, e.g. by predation. Thus, during a tree's lifetime, more of its seeds are likely to be released by the conditions prevailing during a Sharav than by fire. This is further supported by the observation that closed silver cones, which are supposed to be opened exclusively by fires, opened and closed during successive dry and wet periods in the absence of fire.

The adaptive value of pyriscence and xeriscence will depend on the relative contribution of fire- vs. Sharav-induced seed release to future generations. For long-lived species, this information is difficult to obtain and is currently unavailable for *P. halepensis*. Fires generate new establishment opportunities for *P. halepensis* seedlings, by reducing interspecific competition and generating favourable microscale conditions for germination and growth (Ne'eman *et al.* 1992). Additional adaptive advantages of fires, e.g. predator satiation and favourable conditions for wind dispersal (Lamont *et al.* 1991), are yet to be examined in this species. In the eastern-Mediterranean, fires, which occur mostly during autumn when fuel availability is high and Sharav conditions promote flammability (Naveh 1974), are efficient cues for the favourable establishment conditions of the following rainy season. The Sharav events themselves could function in the same manner in the autumn, but their occurrence at similar frequencies during spring, just before the dry summer with poor establishment conditions, makes them less efficient cues than fires. However, Sharavs are also associated with a relatively strong upward wind component that is critically important for long-distance dispersal (Greene & Johnson 1995). Seed dispersal rates to distant traps (> 20 m from the nearest tree) were therefore significantly greater in periods in which Sharav events occurred than in other periods.

The role of long-distance dispersal in plant dynamics is currently being emphasized (Clark 1998), but it is extremely difficult to quantify because it occurs in very low frequencies (Greene & Johnson 1995), as observed in the present study. Therefore, the significant but rather small absolute difference between 3.3% (during Sharavs) and 1.6% (during other periods) of the seeds dispersed to distances of 20–110 m is in fact relatively large, and indicates an important selective advantage. Efficient long-distance dispersal explains the high colonization capacity of *P. halepensis*, which is frequently unrelated to fire (Acherar *et al.* 1984; Lepart & Debussche 1991; Sadot 1992). The relatively strong winds during Sharavs are not the most powerful ones available, but the adaptive value of using these events as a cue is promoted by their temporal predictability, especially when they are associated with subsequently favourable establishment conditions (i.e. in autumn). We therefore propose that xeriscence in *P. halepensis* is adaptive because it promotes long-distance dispersal.

Sharav conditions occur throughout the native circum-Mediterranean range of *P. halepensis*. In the south (Spain, north Africa, the Near East), hot and dry weather is usually generated by desert cyclones originating in the lee side of the Atlas mountains, giving rise to Sirocco-type winds, called *Khamsin* in the eastern-Mediterranean, *Chili* or *Ghibli* in north Africa and *Leveche* in south-east Spain (Air Ministry Meteorological Office 1962; Reiter 1975; Alpert & Ziv 1989). However, when these winds pass over the Mediterranean Sea (e.g. *Marin* on the French coast) they pick up moisture and thus are typically moist and not dry (Air Ministry Meteorological Office 1962). In the north (France to Greece), hot and dry winds are generated by the *Foehn* effect, in which the air gets warmer and dryer due to the adiabatic compression upon descending the mountain slopes (Brinkmann 1971; Reiter 1975; Ahrens 1994).

Dry and hot weather is frequently associated with relatively strong winds; both Sirocco- and Foehn-type winds are relatively strong and turbulent (Air Ministry Meteorological Office 1962; Brinkmann 1971; Reiter 1975). Therefore, our hypothesis suggesting an adaptive advantage of xeriscence in promoting long-distance dispersal in *P. halepensis* can be extended to other species and regions. Greene & Johnson (1992) found that *Acer sacccharinum* samaras were released at higher than average wind velocities, and emphasized the low relative humidity associated with strong winds as an important factor involved. In fact, this particular association has previously been reported for a serotinous pine, *P. attenuata*, which surprisingly is an obligate pyriscent. In southern California, cone opening in *P. attenuata* begins several hours after fire has broken resin bonds, and then continues for up to 4 years (Vogl 1973). The post-fire seed release was positively correlated with drying conditions, which were usually accompanied by high winds. The typical Foehn-type episodes observed (the Santa Ana winds) resemble Sharav events not only in being dry, hot and windy, but also in their infrequent occurrence, short duration, predictable seasonal timing (autumn) and association with fires (Ahrens 1994). The exceptional concentration of serotinous pines in southern California (Vogl *et al.* 1977) is yet to be explained, but the similar weather events suggest that xeriscence could be involved. Richardson *et al.* (1992) similarly proposed that strong winds during dry and hot weather facilitated the rapid invasion of *P. pinaster* and *P. radiata* into the Fynbos.

Substantial cone opening in the absence of fires has been observed in most (if not all) pyriscent pines (McCune 1988; Keeley & Zedler 1998), e.g. *P. banksiana* (Gauthier *et al.* 1993), *P. radiata* (Vogl *et al.* 1977), *P. rigida* (Givnish 1981) and *P. torreyana* (McMaster & Zedler 1981), as well in many other serotinous plants in Australia and South Africa (Whelan 1995; Bond & van Wilgen 1996). This so-called ‘partial’ or ‘weak’ serotiny has been frequently attributed to the relaxation from fire selection (Perry & Lotan 1979; Givnish 1981; McMaster & Zedler 1981), because serotiny is expected to be disadvantageous where the frequency, extent or intensity of fires is too low (McMaster & Zedler 1981). A model investigating life-history strategies in fire-prone environments and parameterized for *Banksia hookeriana* in Australia, found that the value of serotiny is considerably reduced when the probability of interfire recruitment is increased (Enright *et al.* 1998). Whelan *et al.* (1998) proposed that a ‘double strategy’ of fire- and non-fire induced seed release in the serotinous *Banksia serrata* was favoured in habitats having many establishment opportunities between fires. In that sense, the partially serotinous pines also exhibit a double strategy, shedding their seeds sporadically or continuously in fire-free intervals. In *P. halepensis*, however, seed release is distinctly seasonal, as in most non-serotinous wind-dispersed pines (Krugman & Jenkinson

1974). Thus, *P. halepensis* exhibits a genuine double strategy, resembling serotinous pines by having some cones remaining closed after maturation, and non-serotinous ones by the seasonal opening of the others.

Recently, Lev-Yadun (1995) suggested a similar double strategy for *Cupressus sempervirens* in Israel. Lower proportions of serotinous cones were found in hotter and less rainy regions and, although not explicitly stated, the level of serotiny matches the regional pattern of Sharav intensity (Levi 1978). Unlike the dead serotinous cones typical of the genus *Pinus*, serotinous cones in *C. sempervirens* are alive and kept closed by an internal supply of water, while non-serotinous cones are dead. In *P. halepensis*, the physiological explanation of the double strategy, i.e. why certain cones open during Sharav conditions while others do not, still needs to be explored. In *P. banksiana*, non-fire induced seed release is mainly from small (young) trees or from old cones on large trees (Gauthier *et al.* 1993). The suggested simple genetic control of cone polymorphism in some pines (Perry & Lotan 1979) is not fully understood, neither at the genetic nor at the physiological level. As Lanner (1998) has recently pointed out, the mechanism of cone opening in the genus *Pinus* is overdue for a second look.

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