

SEROTINY, SEED DISPERSAL AND SEED PREDATION IN *PINUS HALEPENSIS*

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Introduction

Reproduction in higher plants follows a series of consecutive phases, from flowering and pollination, through seed production, dispersal, dormancy and germination, to the successful establishment of seedlings and saplings into reproductive adults. The stages related to the seed phase represent the most critical and sensitive step with important implications for the structure and dynamics of plant populations and communities. In this chapter we focus on the patterns, underlying mechanisms, influencing factors and the potential consequences of serotiny, seed dispersal, and seed predation in Aleppo pine (*Pinus halepensis* Mill.). Because seed dispersal is the only mobile stage during a plant life cycle, it was investigated to understand the high colonisation ability (or invasive ability) of *P. halepensis* (Acherar *et al.* 1984, Trabaud 1987, 1991, Lepart and Debussche 1991, Sadot 1992, Rejmánek and Richardson 1996, Richardson 2000). Comprehensive and updated reviews of related topics in the genus *Pinus* can be found in Richardson (1998).

Serotiny and Seed Release

Serotiny and Fires

Seed release in *P. halepensis* begins only during the third year after pollination, and many mature seeds are retained in persistent serotinous cones. Serotiny, the retention of mature seeds in a canopy-stored seed bank (Le Maitre 1985, Lamont *et al.* 1991) evolved under the selective pressure of fires (Lamont *et al.* 1991), hence the term is synonymous with fire-induced seed release (pyriscence *sensu* Lamont 1991). Fire is a major factor affecting life history traits of plants in Mediterranean-type ecosystems (Naveh 1975, Trabaud 1987, Barbéro *et al.* 1998), and *P. halepensis* is frequently

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presented as a typical example of pyriscent pine (e.g., Agee 1998). In the absence of thick bark, sprouting ability or 'grass stage' (Agee 1998, Keeley and Zedler 1998), serotiny constitutes the major adaptation of this species to fires. Many studies have emphasised the role of fire as a prime generator of seed release in *P. halepensis* (e.g., Trabaud *et al.* 1985, Daskalidou and Thanos 1996, Saracino *et al.* 1997, Agee 1998, Doussi and Thanos 1999, Leone *et al.* 1999, Roitemberg and Ne'eman 1999). The adaptive value of fire in generating many new establishment opportunities, with reduced inter- and intra-specific competition, and favourable micro-scale conditions for germination is well established (Ne'eman *et al.* 1992, 1993, Ne'eman and Izhaki 1998, Ne'eman 2000). However, alternative advantages related to the seed phase, such as the reduction of post-dispersal seed predation by predator satiation (Lamont *et al.* 1991) and the favourable conditions for dispersal by wind (Whelan 1986, Lamont *et al.* 1991; but see Lanner 1998), are yet to be studied.

Pyriscence and Xeriscence

Cone opening in pyriscent pines is based on the reflex mechanism driven by a gradient in moisture content between scale tissues and the ambient air (Allen and Wardrop 1964, Harlow *et al.* 1964, Dawson *et al.* 1997). In the few closed-cone pine species considered as obligate pyriscent, a prerequisite step requires high temperatures to melt the resins binding the epiphysis of the cone scale (Lamont *et al.* 1991). In many other pines, resin bonds are weak or practically absent, and seed release is not restricted to fire (Le Maitre 1985, Keeley and Zedler 1998). Thus, cone opening depends primarily on the reflex mechanism, and drying conditions rather than necessarily high temperatures are needed to induce seed release. In fact, substantial cone opening without fire has been observed also in other (if not all!) pyriscent pines (McMaster and Zedler 1981, Keeley and Zedler 1998). In *P. halepensis*, dispersal begins in the third year after pollination when cone colour is brown, but many cones remain closed and turn grey in the following year, and are then considered serotinous. They differ from brown cones in their resin ducts and in the direction and thickness of scleroides in the cone scales, which are adhered by resin (Leone *et al.* 1999, Doussi and Thanos 1999). However, of 50 cones of this type marked in Israel in the fall of 1994, 27 (54%) had opened by the spring of 1998 without any fire (Nathan *et al.* 1999). Seed release may not always be an abrupt event, and partially open cones may contain seeds (Schiller 1979) that are shed over a prolonged period (R. Nathan, pers. observ.). Moreover, when the cones were gradually and stepwise heated from 40 to 120°C, no difference was found between brown and grey cones in the degree of opening and the number of seeds released (Roitemberg and Ne'eman 1999).

Nathan *et al.* (1999) hypothesised that serotiny may have evolved to synchronise seed release with drying conditions that are not necessarily associated with fires (i.e., dry spells). They introduced the term 'xeriscence', referring to the opening of cones induced by drying conditions that are not generated by fires, as distinct from 'facultative pyriscence' (Lamont 1991), in which cone opening is induced by the drying conditions that are generated by fires. The theoretical distinction between xeriscence and facultative pyriscence is important because each term indicates a mechanism that evolved to synchronise seed release with an entirely different environmental cue. It has been argued, mostly on the grounds of the abundant recruit-

ment unrelated to fire (Acherar *et al.* 1984, Lepart and Debussche 1991, Trabaud 1991, Sadot 1992), that *P. halepensis* should not be considered a fire-dependent species but rather an opportunist able to occupy newly opened establishment sites (Trabaud 1987, 1991, Lepart and Debussche 1991, Richardson 2000). In addition, fire heat negatively affects seed viability and germination (Shomer-Ilan 1964, Martínez-Sánchez *et al.* 1995, Hanley and Fenner 1998), whereas dehydration, such as that produced by dry spells, positively affects both (Shomer-Ilan 1964).

The proportion of the annual cone crop that remained closed in the absence of fire in *P. halepensis* was estimated in the forests of Attica in Greece (Daskalakou and Thanos 1996). Third-year (brown) cones were observed by binoculars and classified as closed, half-opened, and opened. In one site, the proportion of closed cones (out of 100 randomly selected cones) decreased from 100 to 60% during the nine months from May to January. In another site, the proportion decreased from 100 to <70% within five months but increased to >80% later (Daskalakou and Thanos 1996). Either re-closing of cones in response to high relative humidity or sampling artefact related to the random selection of cones may account for this unexpected increase. In two other sites, the proportion of closed cones was calculated by repeated observations of the same cones. In one of these sites, the proportion of closed cones dropped from 100% in April to <50% eight months later. In the other it dropped from 100% in May to <40% five months later, and remained virtually the same for the next ten months. Thus, in the absence of fires, about 60% of the annual cone crop opened within several months. The proportion of open cones provides a useful estimate of the degree of serotiny in *P. halepensis*. However, as in many other pines, *P. halepensis* cones open and close with successive dry and wet periods, and re-closed cones are difficult to distinguish in the field from cones that have not opened yet. Thus, closed cones, especially if observed during winter, are not necessarily serotinous.

The proportion of the annual seed crop released without fire in *P. halepensis* was estimated on Mt. Carmel in the Mediterranean region of Israel (Nathan *et al.* 1999). In this study, 94 seed-traps were placed in a small isolated stand (96 adult trees) and monitored over three years. Based on the seed-trap data, the mean annual seed release was estimated as 988,000 for the whole stand, or an average of 10,290 per tree. The number of cones per tree was (mean \pm SE) 242 \pm 63, and the number of seeds per cone was 72 \pm 1, 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 seed crop. Though the two studies in Greece and Israel used different techniques and measured different entities, they converged in a similar proportion of approximately 60% of the annual cone (or seed) crop opened (or released) each year in the absence of fire. Thus, *P. halepensis* meets the definition of partially serotinous species (i.e., most seeds released within a few years) of Lamont *et al.* (1991). The remaining proportion (40%) constitutes the potential seed pool for post-fire regeneration, which is likely to be lower due to pre-dispersal seed predation, and the reduction in seed viability with cone age (Schiller 1979, D. Roitemberg and G. Ne'eman, unpublished data). Furthermore, though fire generates the simultaneous opening of many cones, a certain proportion (that has not yet been quantified) still remains closed (R. Nathan, pers. observ.).

Although during a tree's lifetime most seeds are released without fire, the number of seeds released in a fire event is likely to be much higher than in any comparable

(i.e., short) fire-free period. Post-fire seed densities ranged between 135 ± 18 and 855 ± 159 seeds m^{-2} in the first month after fire, and between 61 ± 27 and 194 ± 45 seeds m^{-2} in the second month in four sites in a burned forest in southern Italy (Saracino and Leone 1993). In a nearby forest, which burned two years later, densities of 190 ± 14 and 540 ± 20 seeds m^{-2} were observed (Saracino *et al.* 1997). In Israel, post-fire seed densities ranged from 50 to 150 seeds m^{-2} (Eshel *et al.* 2000). In Greece, post-fire seed densities, estimated from samples of the soil seed bank, ranged from 63 to 405 seeds m^{-2} (Daskalakou and Thanos 1996). For comparison, densities of 25 to 105 seeds m^{-2} were measured in nearby unburned forests in Greece. The density of seeds reaching the ground during a year in the absence of fire was estimated by seed-traps as 230 seeds m^{-2} in France (Acherar *et al.* 1984) and 240 ± 15 (range 108–393) seeds m^{-2} in Israel (Nathan *et al.* 1999). The maximum local short-term (6 days) seed density in Israel was 117 seeds m^{-2} (Nathan *et al.* 1999). Although differences in tree densities and in seed production have not been ruled out, it seems clear that seed densities are considerably higher after fire than in fire-free conditions. Consequently, and due to the favourable fire-induced establishment conditions, seedling densities are substantially higher after fire than in fire-free conditions.

Dry and hot weather conditions inducing seed release without fire occurs throughout the native *circum*-Mediterranean distribution of *P. halepensis*. In the southern Mediterranean (Spain, north Africa, the Near East), this weather is usually generated by desert cyclones originating on 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 (Reiter 1975). In the northern Mediterranean (France to Greece), hot and dry winds are generated by the *Foehn* effect (Reiter 1975), in which the air gets warmer and dryer due to the adiabatic compression upon descending the mountain slopes (Reiter 1975). Both Sirocco- and Foehn-type winds are relatively strong and turbulent (Brinkmann 1971, Reiter 1975).

In the eastern Mediterranean, drying conditions occur as short and infrequent but temporally predictable events called Sharav (Winstanley 1972), restricted to spring and fall. A study of seed dispersal in two native *P. halepensis* stands in Israel found a distinct seasonal pattern, strongly correlated with the occurrence of Sharav events (Nathan *et al.* 1999; see also Schiller 1979). Correspondingly, a significant negative correlation was found between the rate of seed release and relative humidity and there was a positive correlation with temperature. Sharav events in the fall can serve as a cue for favourable establishment conditions in the following rainy season. However, Sharav events also occur in similar frequencies in spring, just before the long dry summer when establishment conditions are poor. Due to high predation pressure on *P. halepensis* seeds (see below), a long delay between the time of seed release and the time of germination significantly reduces the probability of seed survival (Bond 1984). Yet, selection for xeriscence by Sharav events in *P. halepensis* in the present climatic conditions of the eastern Mediterranean should confer an advantage favourable enough to outweigh the coupled unfavourable consequences of seed release during spring. Nathan *et al.* (1999) found that Sharav events have favourable wind conditions for dispersal, particularly in the stronger vertical (upward) component, compared with winds in other periods of the year. They suggested that Sharav-induced seed release has an intrinsic adaptive advantage in increasing dispersal distance by wind. Accordingly, seed dispersal rates to distant traps (>20 m from the nearest tree) were significantly greater in peri-

ods in which Sharav events occurred than in other periods. Further study is required to elucidate the relationships between seed release and climatic conditions across the species range. Overall, both fires and drying weather conditions are probably involved in determining serotiny in *P. halepensis*, providing the means to exploit establishment opportunities generated by fires or by other disturbances during fire-free intervals.

Seed Dispersal

Seed Morphology and Aerodynamics

Diaspores of *P. halepensis* are samara-like winged-seeds that fall in calm air in a constant rate as they enter autorotation. This rate, called the terminal velocity, is an important aerodynamic property frequently considered a surrogate of dispersal ability, as it reflects the time that a seed can be carried by the wind (Green 1980). The terminal velocity is primarily affected by the mass and surface area of the diaspore and is highly correlated with their ratio, called wing loading, defined as weight/area (Green 1980). Among pine species, wing loading and terminal velocity are highly positively correlated ($r=0.962$, $n=8$, $P=0.0001$, Nathan 1999). Values of wing loading of *P. halepensis* diaspores (1.49 and 1.84 $\text{N}\cdot\text{m}^{-2}$) are relatively low among pines (Nathan 1999). Correspondingly, the mean terminal velocity of 0.81 $\text{m}\cdot\text{s}^{-1}$ (Nathan *et al.* 1996) is also relatively low (Fig. 1), suggesting that *P. halepensis* has a relatively high dispersal potential among pines.

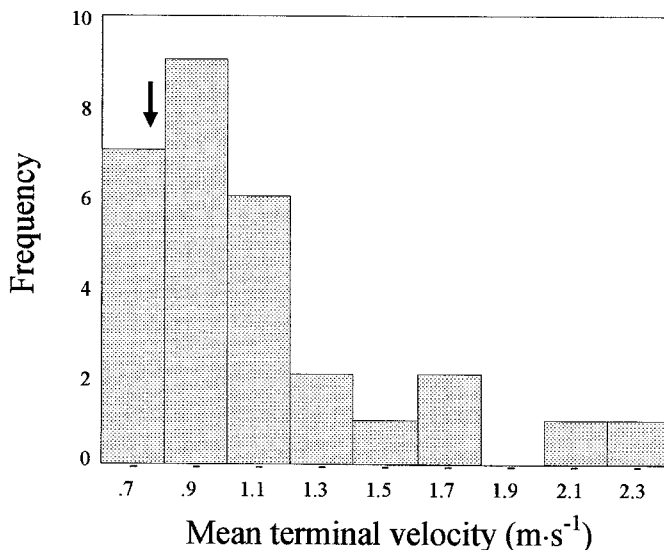


Fig. 1. Frequency distribution of mean terminal velocity measured in 20 pine species: *P. balfouriana*, *P. banksiana*, *P. caribaea*, *P. contorta* ($n=3$), *P. coulteri*, *P. echinata* ($n=2$), *P. halepensis*, *P. jeffreyi* ($n=2$), *P. lambertiana* ($n=2$), *P. palustris*, *P. pinaster*, *P. ponderosa*, *P. pungens*, *P. radiata* ($n=3$), *P. resinosa* ($n=2$), *P. strobus* ($n=2$), *P. taeda*, *P. thunbergii*, *P. virginiana* and *P. wallichiana*. The arrow indicates the mean terminal velocity of *P. halepensis* seeds. From (Nathan 1999).

Other Factors Affecting the Distance of Dispersal by Wind

Along with terminal velocity, the height of seed release is considered a major biotic determinant of the distance of seed dispersal by wind (Okubo and Levin 1989, Greene and Johnson 1989). This property can be partitioned into tree height and the distribution of seeds with tree height. In *P. halepensis*, adult trees reach heights of 10 to 20 m, and only exceptionally reaching 25 m (Richardson and Rundel 1998). This is a relatively low height among pines (Fig. 2), implying relatively low dispersal capacity as far as this property is concerned. The distribution of cones along tree height is probably age-dependent, being more homogeneous in young trees and more concentrated in the upper parts of the canopy in older ones (R. Nathan and S. Goubitz, pers. observ.). In 16 trees aged 22- 66 sampled in a native stand in Israel, cones were normally distributed along tree height, with the mean at 0.61 of tree height (Nathan 1999). For comparison, Greene and Johnson (1996) generalised that conifer cones are normally distributed along tree height between the canopy top and the middle height, with the mean at approximately 0.75 of tree height. The distribution of cones along tree height, however, may not mirror the distribution of seeds; for example, cones in the higher parts of the canopy had significantly more seeds than cones of the lower parts in *P. resinosa* (Lyons 1956). No comparable data are available for *P. halepensis*.

Two other intrinsic properties may affect the distance of dispersal by wind, but these have not yet been studied sufficiently in *P. halepensis*, or in other pine species. The first is the weak seed-wing attachment, causing many seeds to lose their wings after hitting the ground (Acherar *et al.* 1984, Nathan *et al.* 1996) and some to lose

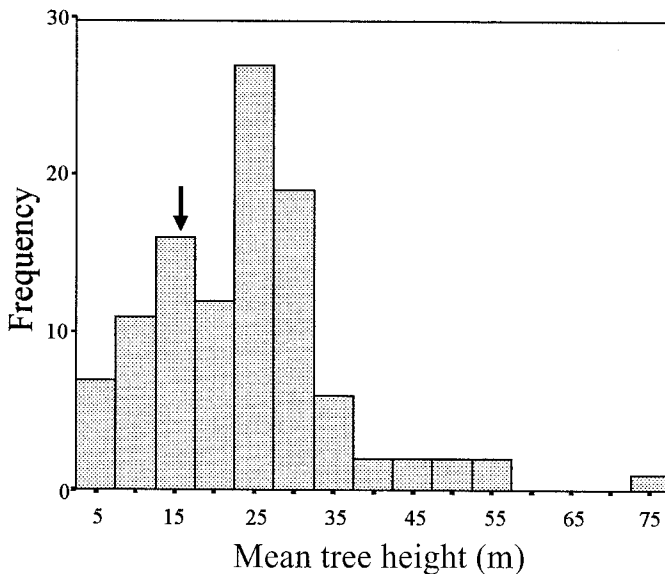


Fig. 2. Frequency distribution of mean tree height in 107 pine species, based on data compiled by Richardson and Rundel (1998). The arrow indicates the mean tree height in *P. halepensis*. From Nathan (1999).

their wings before departing the cones. Weak seed-wing attachment may be related to the high predation pressure by visual predators (Lanner 1998, and see below). Dispersal of wingless seeds should reduce the mean distance of dispersal, and may generate a bimodal distribution of dispersed seeds with one peak at zero distance generated by wingless seeds falling directly beneath the parent's canopy and a second peak at some distance away generated by winged-seeds. The second property affecting the distance of dispersal by wind is the ability to synchronise seed release with relatively strong winds (Nathan *et al.* 1999). This can be achieved by synchronising seed release with events of dry weather having relatively efficient winds for long-distance dispersal, as discussed above. Alternative mechanisms at the level of a single dispersal event, e.g., canopy vibration by strong winds drawing seeds out of partially opened cones, are discussed in Burrows (1986) and Greene and Johnson (1992b).

The relative impact of terminal velocity, height of seed release, and the horizontal and vertical components of wind velocity on the distance of dispersal of *P. halepensis* seeds were assessed by Nathan (1999), using a mechanistic model for tree seed dispersal by wind. The model was tested against independent seed-trap data collected in two *P. halepensis* stands in Israel and proved reliable in predicting the proportion of seeds dispersed in a spatial resolution of 1 m². A sensitivity analysis of the validated model showed that the effects of the horizontal and vertical velocities of the wind on the dispersal distance largely override those of the biotic factors. Among biotic factors, the height of seed release was found more influential than the terminal velocity, and tree height was more influential than the distribution of seeds with tree height. The minor impact of the terminal velocity results from its markedly low variation both within and between trees, occurring despite considerable variation in morphological properties (Nathan *et al.* 1996). This parallels the general conclusion of Greene and Johnson (1992a) for wind-dispersed seed. Dispersal capacity is not the only fitness component affecting the terminal velocity; seed predation and seedling competition are probably also involved (Nathan *et al.* 1996). Similarly, adult competition for light and resistance to windstorms are probably involved in determining tree height. Consequently, these intrinsic factors have a relatively low impact on the variation of the distances of seed dispersal by wind. The profound effect of winds on dispersal distance suggests that the most important biotic determinant of dispersal capacity in *P. halepensis* (and probably also in other wind-dispersing species) is neither the terminal velocity nor the height of seed release but the ability to synchronise seed release with relatively strong winds.

Dispersal Curves and Long-Distance Dispersal

Acherar *et al.* (1984) studied the wind dispersal of *P. halepensis* seeds from a 30-year-old forest, with 6-m high trees, to an adjacent open area in southern France. Seed-traps were placed at 4 m intervals from the forest edge up to a distance of 28 m. Forty-four percent of the seeds were counted at the forest edge, and 97% up to 24 m away. A similar pattern was observed in Israel, where 72% of the seeds were collected in 7% of the traps placed under tree canopies, and 97% of the seeds were trapped up to 20 m from the nearest adult (Nathan 1999). In both studies, but more profoundly in Israel, dispersal curves were right-skewed and strongly leptokurtic, i.e., having the vast majority of seeds near the source (Fig. 3). At the same time, however, the strong

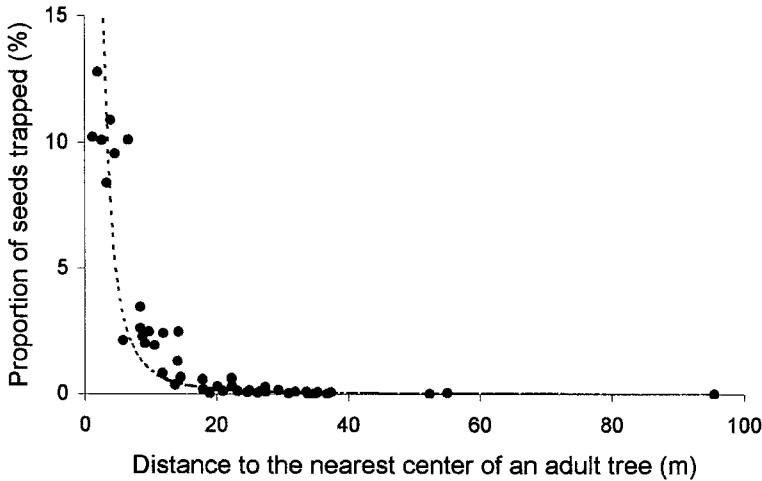


Fig. 3. Dispersal curve for *P. halepensis* seeds. Data collected by seed-traps in an isolated pine stand in Nir-Ezyon, Mt. Carmel, Israel, between October 1993 and June 1996 (Nathan 1999). Line fitted by inverse power law regression (omitting zero counts): $y = 171 x^{-2.3}$ ($R^2=0.80$).

leptokurticity suggests relatively efficient long-distance dispersal (Clark *et al.* 1998). In the last decade, the subject of long-distance seed dispersal has aroused growing interest, as its critical importance to gene flow, invasions and climatic change effects have been realized (Hengeveld 1994, Hamrick and Nason 1996, Clark *et al.* 1998). However, the ability to quantify and predict the long-distance dispersal events is still poor, due to the extreme scarcity of these events and the large stochasticity involved (Silvertown 1991, Portnoy and Willson 1993). This also applies to the study of long-distance dispersal in *P. halepensis*, though indirect evidence on the occurrence of isolated individuals at distances of several kilometers from existing trees in France (Lepart and Debussche 1991) and Israel (R. Nathan, unpublished data) implies efficient long-distance dispersal in this species.

A mechanistic model of seed dispersal by wind applied to *P. halepensis* predicts that seeds can be dispersed as far as several hundreds of kilometers from the source; however, only a small fraction (0.2%) of seeds are expected to reach distances larger than 1 km (Nathan 1999). Given the large seed crop in *P. halepensis*, even a small fraction should result in a considerable number of seeds dispersed far from the source. Setting a minimum limit of 1 km to qualify as long-distance dispersal, about 20 long-distance dispersal events would be expected for each individual tree, out of approximately 10,000 seeds released per year (see above). The 'normal' maximum age of *P. halepensis* is approximately 120 years (Tamari 1976), excluding outliers of >200 years (Lev-Yadun *et al.* 1981). Assuming that the above estimate of the annual seed release holds for trees aged between 15 and 120 years, approximately 2,100 seeds are dispersed to long distances during a tree's life time. Even a small population of 100 individual trees is expected to disperse approximately 2,000 seeds to long distances each year. Assuming that the average ratio of 1870 seeds for one established sapling measured between 25 and 50 m from the nearest canopy edge (Nathan

1999) holds for greater distances as well, a small stand of 100 trees is expected to generate approximately one successful long-distance colonisation event each year.

Phase II Dispersal

Most studies of seed dispersal focus on the primary stage of seed dispersal (Phase I dispersal *sensu* Chambers and MacMahon 1994), the initial movement of seeds to a surface, and ignore subsequent movements (Phase II). However, Phase II dispersal by animals can substantially alter the pattern generated by Phase I dispersal by wind in several pine species (Vander Wall 1992, 1994). This has not been studied yet in *P. halepensis*. Phase II dispersal by wind is unlikely in this species because seeds generally lose their wings immediately upon hitting the ground (see above) and because of the dense vegetation in its typical habitats. Harvester ants and rodents, the main seed predators of *P. halepensis* seeds (see below), typically transport seeds to storage sites, and thus may serve as dispersal agents. There is no field or literature evidence, however, to support this possibility.

Seed Predation

Pre-Dispersal Seed Predation

Closed cones protect seeds from predation, hence it has been suggested that serotiny has evolved through predation pressure and not necessarily by fires (see Keeley and Zedler 1998). In *P. halepensis*, pre-dispersal seed predation is mostly done by insects, birds and rats. Kugler (1989) listed *Dioryctria mendacella* (Pyrilidae, Lepidoptera) and *Ernobius oertzeni* (Anobiidae, Coleoptera) as insect pests that specialise on pine cones, especially those of *P. halepensis*, and *Cadra cautella* (Pyrilidae, Lepidoptera) as a generalist pest, infecting cones of *P. halepensis* as well as fruits of many other tree species. Frankis (1991) suggested an evolving association between the closely related *P. brutia* and Krüper's nuthatch (*Sitta krueperi*). He observed that in some trees cones open only partially, and seeds can be dispersed only if extracted by birds. This intriguing suggestion certainly needs more strict investigation. Seeds of *P. brutia* are notably heavier than those of *P. halepensis* (50 vs. 20 mg, respectively), thus they are probably more attractive to birds. Nevertheless, birds were seen extracting seeds from partially opened cones also in *P. halepensis* (Acherar *et al.* 1984, Saracino and Leone 1993, R. Nathan and D. Roitemberg, pers. observ.). The observed bird species were *Carduelis spinus* and *Loxia curvirostra* in Italy (Saracino and Leone 1993) and *Passer domesticus*, *Fringilla coelebs*, *Serinus serinus*, *Carduelis chloris* and *C. carduelis* in Israel (R. Nathan and D. Roitemberg, pers. observ.). Crossbills (*L. curvirostra*) are capable of opening closed cones of *P. halepensis*, but generally prefer cones of other conifers, such as *Picea abies* (Saracino and Leone 1993), that are more easily opened (Newton 1967).

Black rats (*Rattus rattus*) developed a very specialized behavior of cone opening, by systematically stripping the scales in a spiral pattern around the shaft (Aisner and Terkel 1992). The stripping technique was found to be learned by pups

from their mothers (Aisner and Terkel 1992), whereas adults acquired it spontaneously only under particularly favourable conditions (Zohar and Terkel 1995). This suggests that pine forests inhabited by a rat tribe that has already acquired the striping technique may be subject to high pre-dispersal predation pressure, whereas this predation is unlikely to occur in forests inhabited by an inexperienced tribe. In France, red squirrels (*Sciurus vulgaris*) were observed eating seeds from both mature and pre-mature cones (Acherar *et al.* 1984). Further study is needed to quantitatively elucidate the relative role of insects, birds and mammals on pre-dispersal predation of *P. halepensis* seeds, and its consequences for seed dispersal and recruitment.

Post-Dispersal Seed Predation

Acherar *et al.* (1984) studied the post-dispersal predation of *P. halepensis* in relation to the distance from the forest edge. Predation by birds was much less extensive than predation by the diurnal ants (*Messor* sp.) and the nocturnal rodents (*Apodemus sylvaticus*). Predation was intensive and fast, as ants removed 67% of the seeds each day, and rodents removed 24% of the seeds each night. In general, the proportion of seeds removed by rodents significantly increased with increasing distance from the forest edge, while predation by ants significantly declined. Thus, rodents and ants have partitioned their activity in space and in time, substantially reducing seed densities but without altering the spatial pattern. Schiller (1979) also observed extensive seed predation by ants (*Messor* sp.) in Israel in a planted stand. In native stands in Israel, extensive predation by ants, mostly *Messor semirufus*, and by rodents, mostly *Apodemus flavicollis*, was observed, whereas birds, such as *P. domesticus*, were less important predators (Nathan *et al.* 1999).

The main predators of *P. halepensis* seeds in the absence of fire are ants and rodents, whereas the main predators in the early stages of post-fire succession are birds. Birds recolonized a burned forest in southern Italy about 15 days after fire (Saracino and Leone 1993). Passerine species observed, ranked by their relative abundance, were *P. domesticus*, *S. serinus*, *P. montanus*, *C. carduelis*, *F. coelebs*, *Parus major*, and intensive predation by *Columba palumbus* was also observed. In a nearby forest burned two years later, birds (*S. serinus*, *P. domesticus* and *F. coelebs*) were the main predators, no rodents were evident, and the activity of ants (*Messor* sp.) was restricted to a period of a few days after fire (Saracino *et al.* 1997). Seeds damaged by predators accounted for 43% of the seeds collected during five months after fire in one site and 23% in another. The colour of released seeds has changed with time from dark grey-brown to light yellowish colour, similar to the change that has occurred in the colour of the ground surface. Saracino *et al.* (1997) proposed that this matching implies an adaptive role of changing seed colour, allowing seeds to match the surface colour hence reducing the risk of predation by visual predators, such as birds. Selection by visual predators may also have led to the weak seed-wing attachment (see above), because the wing protrudes like a flag, making the seed more easily detectable (Nathan *et al.* 1996).

Conclusions

The study of serotiny, seed dispersal and seed predation in *P. halepensis* is an example of the complexity involved in these processes among pines. Pyriscence (fire-induced seed release) is extensive and widespread in this species and leads to remarkable post-fire recruitment. However, xeriscent (seed release induced by drying conditions that are not associated with fires) constitutes the major portion during a tree's lifetime, and may also result in widespread recruitment. Thus, *P. halepensis* is adapted to invading open disturbed sites, generated either by fire or by other factors.

The winged-seeds of *P. halepensis* have superior aerodynamic properties compared with seeds of most other pines, but due to very low variation in these traits both within and between trees, they have a relatively low impact on the variation in the distance of dispersal by wind. The height of seed release, mostly affected by tree height, is more variable among trees and likely to have a larger impact on the variation in dispersal distances, despite being relatively low among pines. Dispersal curves of *P. halepensis* are similar to those of many other wind-dispersed species, exhibiting rapid decline with increasing distance from the source. However, the strong leptokurticity of these curves may indicate relatively efficient long-distance dispersal. The study of long-distance dispersal is probably the most difficult yet the most promising research frontier of seed dispersal in this species. The weak seed-wing attachment giving rise to dispersal of wingless seeds and the relationships between seed release and wind conditions are two important factors that have not yet been investigated. Predation of *P. halepensis* seeds is usually extensive and rapid. The main seed predators in the absence of fire are ants and rodents, whereas birds are more influential shortly after fire. Ants and rodents may also act as Phase II dispersal agents but no evidence is currently available. Overall, we still have only a limited understanding on the role of seed predators in structuring the patterns of recruitment in this species.

Acknowledgements

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