

Spatiotemporal dynamics of recruitment in Aleppo pine (*Pinus halepensis* Miller)

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Abstract

Spatial and temporal aspects of recruitment play a central role in plant population and community dynamics and have important basic and applied implications. Here we summarize and discuss the results from studies of spatiotemporal dynamics of recruitment stages (seeds-seedlings-saplings) in Aleppo pine (*Pinus halepensis*) throughout the species' native range. Seed release is induced either by fire (pyriscence) or by drying atmospheric conditions (xeriscence), each generating a distinct temporal pattern. In both cases most seeds travel relatively short distances (<30 m). Pyriscence is not expected to promote long-distance seed dispersal, but xeriscence is associated with relatively strong winds that can transport seeds over 1 km and more, as predicted by a new mechanistic dispersal model. In the absence of fire, seed survival increases with distance from adults because of higher competition with adults and sibs and higher seed predation near the seed sources. New data provide further evidence for such distance-dependent seed predation and also show that predation rates vary among habitats and are lowest in times of high seed abundance. The resulting recruitment patterns in the absence of fire are characterized by rapid spread and complex spatiotemporal dynamics that are fairly unpredictable and give rise to variable age structure. In contrast, the spatial pattern of the first post-fire generation is highly predictable because it explicitly replicates the spatial pattern of the pre-fire population. Unlike fire-free regeneration in which multiple factors operating at various stages are likely to be important, post-fire regeneration is governed by a fairly specific set of factors (the chemical properties of ash) operating during a specific stage (saplings) and at a specific location (the canopy projection of large burned pines). Post-fire forests are therefore even-aged and have predictable spatiotemporal dynamics. Most studies of Aleppo pine recruitment have focused on the seedling and sapling stages and on post-fire regeneration; we call for greater attention to the seed stage and to more extensive sampling of all recruitment stages in both space and time.

Introduction

There has been a growing realization that the spatial and temporal contexts in which ecological processes occur can have profound effects on their progress and consequences (Levin 1992; Tilman and Kareiva 1997; Silvertown and Antonovics 2001). In plant populations, spatiotemporal change takes place mostly or entirely during early recruitment processes (Harper 1977; Schupp and Fuentes 1995; Nathan and Muller-Landau 2000). Here, "early recruitment" refers to the

set of successive processes leading from seed production, through dispersal and germination to seedling and sapling establishment. The vast majority of mortality events occur during these stages (Cavers 1983; Cheplick 1992); hence early recruitment processes are extremely important for plant population dynamics (Harper 1977; Schupp and Fuentes 1995; Nathan and Muller-Landau 2000).

Seed production (Herrera 1998; Herrera et al. 1998) and pre-dispersal seed loss (Ehrlén 1996; Garcia et al. 2000) typically exhibit considerable spa-

tiotemporal variation among individual plants. This generates non-random spatial structure in the annual (or seasonal) seed output within the population. Seed release is followed by seed dispersal, the major (or only) stage during which individual plants move in space. The process of dispersal is affected by multiple factors (Chambers and MacMahon 1994; Higgins et al. 2003) and is also characterized by substantial spatiotemporal variation (Schupp and Fuentes 1995; Nathan and Muller-Landau 2000). Seed predators can drastically alter the spatial structure of dispersed seeds (Hulme 1993; Verdu and Garciafayos 1996), and seed dormancy induces an additional component of temporal variation in the availability of seeds for germination (Andersson and Milberg 1998). Spatial patterns of seedlings can be significantly different from those of seeds, because of spatial heterogeneity in the distribution of suitable microsites for germination. Similarly, spatial variation in seedling survival, generated for example by differential herbivory, may further alter the pattern of seedlings. Successive stages of early recruitment may show low concordance (Schupp and Fuentes 1995); hence, studying the causes and consequences of plant population dynamics requires detailed investigation of the spatial and temporal aspects of early recruitment processes.

The Aleppo pine (*Pinus halepensis* Miller) is the most widely distributed pine of the Mediterranean Basin (Barbéro et al. 1998; Quézel 2000). It is also common in plantations within and outside its natural range, spreading rapidly from plantations to nearby natural habitats (Richardson 2000). The species, considered one of the most invasive pines (Rejmánek and Richardson 1996), threatens native biodiversity in various habitats and causes severe financial losses, especially across the Southern Hemisphere (Richardson 2000). Given the key role of early recruitment processes in determining tree spatial dynamics, the management of natural, planted and invasive Aleppo pine populations necessitates comprehensive and reliable information about the important features of early recruitment in this species.

Different aspects of early recruitment processes in Aleppo pine populations were discussed in various chapters of a recent book on Mediterranean pines edited by Ne'eman and Trabaud (2000). Some chapters explicitly account for spatiotemporal aspects. Serotiny, seed dispersal and seed predation are covered by Nathan and Ne'eman (2000), soil seed banks by Izhaki and Ne'eman (2000), and post-fire seedling regeneration by Trabaud (2000), Arianoutsou and Ne'eman

(2000), and Ne'eman (2000). These reviews reflect growing interest on recruitment processes, with some central topics that have been studied intensively. However, there are still substantial gaps in our knowledge on some major spatiotemporal aspects of recruitment. To summarize the gains and identify the gaps in our current knowledge, we collate, update and consolidate results from studies that have explicitly considered variation in time and space. In a companion review (Ne'eman et al. 2003), we compare general features of Aleppo pine recruitment in post-fire versus fire-free conditions in order to examine the evidence for fire selection. Here, we examine the common features of the spatiotemporal patterns observed at different sites across the species range, their underlying mechanisms, and consequences. The focus is on spatial scales of meters to a few hundred meters ("local scale"), and temporal scales of days to eight years, thus covering mass dispersal episodes, dispersal seasons and year-to-year fluctuations occurring within a pine population and its nearby surroundings.

Spatiotemporal aspects of early recruitment in Aleppo pine

Among many studies of Aleppo pine recruitment, we selected for this review only those that *explicitly* took into account space, time or both. The observed spatiotemporal patterns of the seed stage are summarized in Table 1 and those belong to the seedling (first two years) and sapling (third to eighth year) stages in Table 2.

Seed release

Patterns: Serotiny – the delay of seed release by storing seeds in the canopy – can determine the timing and magnitude of seed release and hence is a key topic in studying temporal dynamics of early recruitment. The Aleppo pine is a partially serotinous species, and mass seed release is induced either by fire (pyriscence sensu Lamont et al. 1991) or by drying atmospheric conditions (xeriscentence sensu Nathan et al. 1999). The two types exhibit very different temporal patterns. Because Aleppo pine trees typically do not survive a fire, pyriscence occurs only once in a tree's lifetime. Although most seeds are released shortly after the fire, this is not a boom-and-bust phenomenon. The typical temporal pattern of pyriscence in Aleppo pine exhibits its low levels of seed release during the fire event

itself, increasing rapidly to a maximum within the first day, followed by a gradual decrease that lasts months (Table 1) or even years (R. Nathan, *personal observations*). The typical temporal pattern of xeriscence reflects the temporal occurrence of dry weather events. In Israel, such conditions (locally called Sharav) occur seasonally, during spring and fall (Nathan et al. 1999), but in many other parts of the Mediterranean, seed release occurs mostly during summer and fall (Thanos et al. 1996; Leone et al. 2000; Tapias et al. 2001).

Mechanisms: The physiological mechanism of xeriscence involves differential shrinkage of different scale tissues in response to water loss induced by drying conditions (Allen and Wardrop 1964; Harlow et al. 1964). This general reflex mechanism known from several pine species has recently been demonstrated in Aleppo pine in particular (Doussi and Thanos 2002). However, the physiological basis for the dichotomy between pyriscence and xeriscence observed among cones of the same individual tree is still unclear. Doussi and Thanos (2002) reported that Aleppo pine cones are sealed with a resin band at the apophysis edge of the cone scale. However, Leone et al. (2000) found that xeriscent cones have significantly larger resin ducts than pyriscent cones and explained this unexpected finding by earlier tracheid occlusion in xeriscent cones, perhaps associated with intrusion by resin. They suggested another explanation for the pyriscence / xeriscence dichotomy: among five anatomical features examined, pyriscent cones differentiated most markedly from xeriscent ones by having a significantly thicker sclereid wall. In addition, the wall thickness in pyriscent cones was rather uniform along the adaxial – abaxial dissection, whereas the abaxial face was significantly thicker than the adaxial in xeriscent cones. These findings can explain the more sensitive response of xeriscent cones to gradients in air moisture; they do not provide, however, an explanation for the mechanisms that generate pyriscence.

Seed dispersal

Patterns: The basic description of the spatial pattern of dispersed seeds is the seed dispersal curve, which summarizes the frequency distribution of the distances traveled by seeds in a population. Similar to nearly all other wind-dispersed tree species, seed dispersal curves estimated for Aleppo pine show a peak at, or very close to, the source, followed by a rapid decline, and a long tail (Table 1). The mean

(\pm SE) seed dispersal distance estimated by sampling dispersed seeds in a radius of 110 m around an isolated Aleppo pine Israeli population during six successive dispersal seasons was 12.1 ± 0.1 m (Nathan et al. 2000). No quantitative estimates of the distances traveled by seeds after a fire are available (such estimates are also rare for any other plant species). Indirect estimates, however, inferred from germination of soil samples taken from a recently burned stand, suggest a general tendency of seed densities to decline with increasing distance from burned trees (Eshel et al. 2000). Thus, the spatial patterns of post-fire and fire-free seed dispersal show the same general trend.

Most data on seed dispersal are obtained from the vicinity of the adult trees, where most seeds are deposited. Yet, the few seeds that travel long distances can have a tremendous impact on the tree population spread, maintenance of fragmented populations, and other important large-scale processes. Because rare long-distance dispersal events are inherently difficult to quantify, data are scarce for Aleppo pine as in other plants (Cain et al. 2000; Nathan et al. 2003). Seed dispersal is usually quantified by seed traps, but this method requires huge sampling efforts to quantify rare long-distance dispersal events, simply because those rare events should be sought in an area that becomes larger with increasing distance from the seed source (Greene and Calogeropoulos 2002). We illustrate this problem using data collected by seed-traps placed in a small isolated Aleppo pine stand in Israel. Seed traps revealed intensive seed rain close to adult trees, estimated as roughly 3 million seeds released from this stand during three successive years (Nathan et al. 2000). Fifty-three traps with a total sampling area of 44 m² placed at distances of 30 to 110 m from the nearest adult tree collected only 26 seeds throughout the three years of study. The farthest were two seeds collected 87 m from the nearest adult tree. This example, which corresponds to a general observation obtained from many other seed-trap studies (Greene and Calogeropoulos 2002), implies that long-distance dispersal should be measured by more specialized methods, which are not yet available (Nathan et al. 2003). Still, in the absence of empirical data, models provide an alternative way to study long distance dispersal.

To estimate dispersal kernels of Aleppo pine seeds, and the tail of such kernels in particular, we employ here the coupled Eulerian-Lagrangian closure model of Nathan et al. (2002b). This mechanistic model accurately describes wind flow within and above a forest

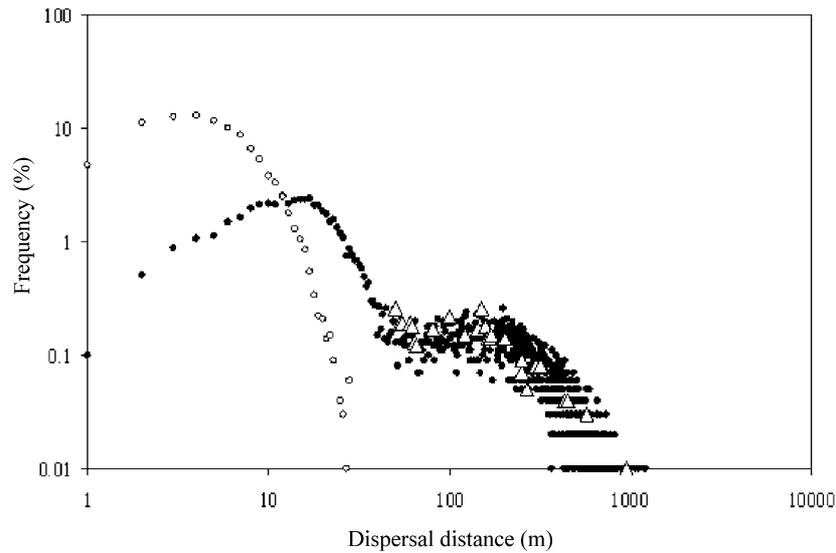


Figure 1. Simulated dispersal kernels for Aleppo pine seeds in two different wind conditions: typical wind conditions recorded during dispersal seasons (mean horizontal windspeed $\bar{u} = 5.46$ m/s, open circles) and extreme wind conditions recorded during a Sharav event ($\bar{u} = 21.2$ m/s, black circles). Each simulation is based on 10,000 randomly selected dispersal events. Seeds that have been uplifted above the top forest canopy are marked by open triangles. The kernels were calculated by a coupled Eulerian-Lagrangian closure model (Nathan et al. 2002b) (see text). Data for both wind and biological parameters are from measurements taken in an Aleppo pine stand on Mt. Carmel, Israel (Nathan et al. 2000, 2001).

and has a clear advantage over other mechanistic models applied to Aleppo pine (Nathan et al. 2001; Nathan et al. 2002a) in considering small-scale wind fluctuations and wind updrafts. This model was tested against field data collected for 5 wind-dispersed tree species in a North American temperate forest, and its predictions closely match the observed dispersal patterns (Nathan et al. 2002b). To parameterize the model we draw on field data collected in Israel (Nathan et al. 2001). We use the model to simulate dispersal in typical (average) winds observed during dispersal seasons and in extremely strong winds observed during a Sharav event (Figure 1).

The simulated dispersal kernels show that dispersal over 30 m in typical winds is extremely unlikely, whereas extreme winds can carry seeds two orders of magnitude farther. Seeds uplifted by vertical updrafts travel relatively long distances, but unlike a previous conclusion from simulations of a considerably denser and taller forest of the eastern US (Nathan et al. 2002b), some seeds that are not uplifted can also travel very large distances. The two simulations differ greatly in the dispersal properties of the simulated species, the forest structure and the wind conditions hence the difference between the two predictions cannot be easily explained; yet, the current simulation shows

that in certain circumstances long-distance dispersal of wind-dispersed seeds does not require uplifting.

To find generalizations among early recruitment characteristics, one needs to examine the consistency of the observed patterns. For example, is there a difference in the spatial pattern of recruitment among sites? Is there a difference in the spatial pattern generated by the same population at different times? An attempt to answer the latter question revealed that seed dispersion patterns in an isolated stand in Israel were similar during six successive dispersal seasons, despite significant differences among seasons in the rates of seed dispersal and wind conditions (Nathan et al. 2000). This puzzling finding has been explained by repeating the spatial analyses on two data subsets obtained by dividing the total stand area into 'near' and 'far' (>20 m from the nearest center of an adult tree) zones. Seed dispersion patterns were similar across seasons for the 'near' zone but dissimilar for the 'far' zone. Nathan et al. (2000) proposed that such spatiotemporal dynamics are expected to lead to higher survival rates of seeds far from the adult trees, because low temporal consistency implies lower levels of seed predation and seedling competition.

Mechanisms: The mechanisms of seed release (see *Seed release* above) can critically affect seed dispersal because they determine the wind conditions

experienced by seeds during flight. Sharav events, which induce mass seed release, are associated with relatively high horizontal and vertical wind speed, compared to other periods of the year (Nathan et al. 1999). Because long-distance dispersal critically depends on the occurrence of strong winds (Figure 1), the synchronization of seed release with Sharav events provides a key mechanism for Aleppo pine long-distance dispersal. Because Sharav conditions occur throughout the native distribution of Aleppo pine, either as Sirocco-type winds in North Africa and Spain, or as Foehn-type winds in Southern Europe (see Nathan and Ne'eman 2000, p. 108), we suggest that this relationship between xeriscence and long-distance dispersal is general and not restricted to the Eastern Mediterranean.

Long-distance dispersal can also be induced by fire, because it generates turbulent updrafts (Whelan 1986; Lamont et al. 1991). We are not aware of any direct evidence to support or refute this hypothesis for Aleppo pine. Yet, our preliminary observations on seed release during fire events suggest a time lag of a few hours between the fire event and the initiation of cone opening; hence fire-induced turbulent winds do not coincide with fire-induced seed release. Nevertheless, it is uncertain whether Aleppo pine seeds can survive such event because seed germination is reduced by exposure to 200 °C for 1.5 minutes (Habrouk et al. 1999), and seeds are killed by exposure to 150 °C for 5 minutes (Martínez-Sánchez et al. 1995). Moreover, if a seed is released during a fire, there is a high probability that its delicate wing will be burned. Fire-induced long-distance dispersal is thus unlikely in Aleppo pine.

Mechanistic dispersal models provide the means to explore the relative roles of various influencing factors in shaping the spatial and temporal patterns of dispersal, which are often too complex to be examined quantitatively in the field. Two models of this kind have been applied for Aleppo pine, and verified against extensive data collected in two sites in Israel during 9 dispersal seasons (Nathan et al. 2001; Nathan et al. 2002a). Both models proved reliable in predicting the observed dispersal patterns (R^2 values ranging between 84 and 94%). Sensitivity analyses for the factors affecting the predicted dispersal distance showed that the wind conditions are far more important than the major biological factors (Nathan et al. 2001). This finding is reconfirmed in the present paper by the simulations of a third, more realistic (*see above*), dispersal model: the simulations show that dif-

ferences in windspeed can drastically affect dispersal kernels (Figure 1). Seed terminal velocity (the constant rate of fall in still air) plays a relatively minor role in determining the variation in dispersal distance because of its relatively low variation within species, in wind-dispersed tree species in general (Greene and Johnson 1992) and in Aleppo pine in particular (Nathan et al. 1996). The height of seed release also has a significant but small effect on the predicted dispersal distance.

Post-dispersal seed predation

Patterns: Data on spatial and temporal patterns of post-dispersal seed predation (hereafter simply 'seed predation') are scarce for Aleppo pine. A study in France reported opposing distance-dependent trends for two types of seed predators, a study in Israel reported a difference in predation rates between two habitat types, and a study in Italy mentioned increasing predation with time after fire (Table 1). The scarcity of data does not imply that seed predation is not an important process in Aleppo pine recruitment; it has been postulated that seed predation is the most critical factor responsible for the near absence of Aleppo pine seeds from the soil seed bank, even in dense mature Aleppo pine forests (Izhaki et al. 2000; Izhaki and Ne'eman 2000); yet, there is no actual evidence that the species can form persistent seed banks in the absence of seed predation.

More information on predation of Aleppo pine seeds is available from a study carried out by the first author in an isolated pine stand on Mt Carmel in the Mediterranean region of Israel. In this study, seed removal from seed trays was followed during 4 successive dispersal seasons (2 years) in approximately 12-day intervals. Seed removal rate was estimated as the proportion of seeds removed from a seed tray (out of 20 seeds). Seed trays were protected from removal by wind or runoff water, but were accessible for ants and rodents, the major seed predators observed in the site (Nathan et al. 1999). Because there is no evidence to support the possibility that these predators act as secondary seed dispersers (Nathan and Ne'eman 2000), seed removal rates are interpreted as seed predation rates. The seed trays were placed in the vicinity of 61 seed trap stations. In each station, seed tray position was randomly relocated every visit, to minimize learning effects. The stations were located at different distances from adult pines and in the three main habitat types of that site: pine canopy, shrubland (batha)

Table 1. Spatiotemporal patterns of the seed stage of early Aleppo pine recruitment observed in field studies at the Mediterranean Basin.

Spatial scale*	Temporal scale	Pattern description	Fire	Country	References
<i>Seed release</i>					
	2 months	Rates decline with time after fire	Yes	Israel	Goubitz (2001)
	5 months	Rates decline with time after fire; seeds released immediately after fire were heavier and darker than those released at later stages	Yes	Italy	Saracino et al. (1997)
	9–16 months	Intensive cone opening during the first 4–8 months of observation (spring to summer), followed by lower rates in the following months, including the next spring and summer	No	Greece	Daskalidou and Thanos (1996)
	4.5 years	High rates during spring and fall, very low rates during summer and winter	No	Israel	Nathan et al. (1999)
<i>Seed dispersal</i>					
10 m		Seed densities decrease with distance from burned trees	Yes	Israel	Eshel et al. (2000)
30 m		Seed densities decrease with distance from forest edge	No	France	Acherar et al. (1984)
110 m		Seed densities decrease with distance from adult trees	No	Israel	Nathan et al. (2000)
110 m	3 years	Spatial patterns generated in different seasons are similar near adult trees but dissimilar farther away	No	Israel	Nathan et al. (2000)
110 m	5 years	Dispersal distances are higher during Sharav events	No	Israel	Nathan et al. (1999)
<i>Post-dispersal seed predation</i>					
not reported	not reported	Predation rates differ among habitat types (Grey ashes > black ashes or sands) and increase with time after fire	Yes	Italy	Saracino et al. (1997), Leone et al. (2000)
30 m		Predation rates by rodents increase with distance; predation rates by ants decrease with distance from adult trees; ants act during day, rodents during night	No	France	Acherar et al. (1984)
110 m	2 years	Predation rates decrease with distance from adult trees, differ among habitat types (Shrubland > Pine canopy > Olive grove) and are lower in periods of higher seed rain.	No	Israel	Nathan, this study
20 m	6 months	Predation rates of buried seeds differ among habitat types (Open > Shrub) and reach a maximum of 3–7% two months after sowing	No	Israel	Noy-Meir et al. (2002)

*In studies examining the variation with distance from adult trees, the spatial scale refers to the longest distance sampled. In studies examining variation among habitat types, the spatial scale refers to the distance across the sampled area.

and abandoned olive grove. Observed dispersal rates at the seed traps provide information on the ‘background’ seed densities experience by seed predators during each time interval. A detailed description of the spatial organization of seed traps, environmental conditions of the study site, and results on the patterns of seed dispersal are given in Nathan et al. (2000). Here we report some of the main findings of the seed predation experiments.

Throughout the study period, seed predation rates were consistently very high: $95.0\% \pm 0.4\%$ (mean \pm SE) of the seeds placed in trays were removed by the next census. Predation rates vary significantly among habitat types (Figure 2; Friedman’s test, $\chi^2 = 15.6$, $df = 2$, $p < 0.001$): highest in the shrubland

($97.2\% \pm 0.9\%$), intermediate beneath pine canopies ($93.5\% \pm 2.1\%$) and lowest in the abandoned olive grove ($88.1\% \pm 1.6\%$). Outside the pine canopy, seed traps stations were classified into three distance categories: ‘near’ (<20 m from the nearest tree; $n = 16$), ‘intermediate’ (20–60 m; $n = 32$), and ‘far’ (>60 m; $n = 6$). In general, predation rates progressively decline with increasing distance from the trees (Figure 2): highest ‘near’ ($98.1\% \pm 0.9\%$), slightly lower at ‘intermediate’ ($95.7\% \pm 0.7\%$), and lowest ‘far’ ($84.5\% \pm 2.7\%$), with overall highly significant difference between these three distance categories (Friedman’s test, $\chi^2 = 21.3$, $df = 2$, $p < 0.001$). This general trend is most pronounced in the olive grove, whereas the ‘near’ and ‘intermediate’ zones

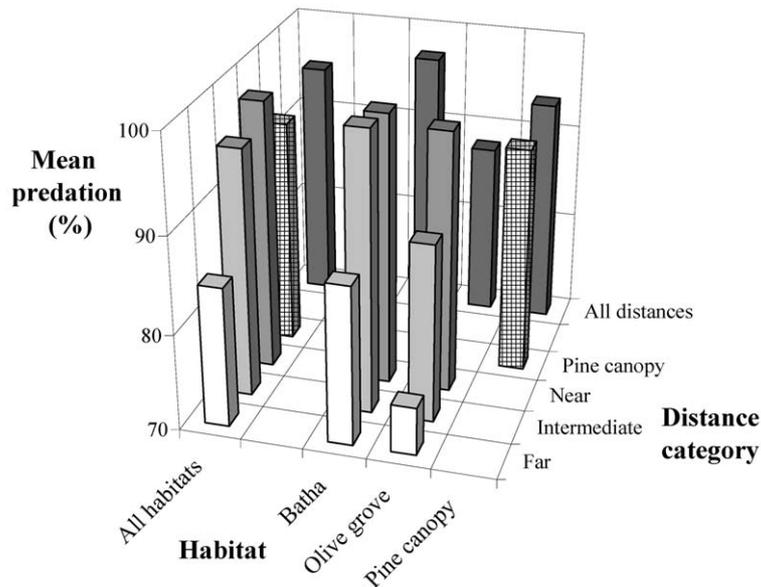


Figure 2. Predation of Aleppo pine seeds as a function of habitat and distance from the nearest center of adult pines. Data collected from 61 sites within and around an isolated Aleppo pine stand on Mt. Carmel (Israel) over a period of two years.

within the shrubland do not differ in predation rates (Figure 2).

A significant negative correlation was found between predation rates and seed rain abundance (Spearman's $\rho = -0.371$, $p = 0.010$). Correspondingly, predation rates were significantly lower in periods of high (>5 seeds m^{-2} day^{-1} , $n = 24$) versus low (≤ 5 seeds m^{-2} day^{-1} , $n = 24$) seed rain abundance ($93.3\% \pm 1.6\%$ versus $96.7\% \pm 0.7\%$, respectively; Mann–Whitney test, $p = 0.049$; Figure 3). This overall significant effect is a result of the significant difference observed in the 'far' zone ($77.4\% \pm 4.3\%$ versus $91.6\% \pm 2.7\%$, respectively; Mann–Whitney test, $p = 0.011$), whereas predation rates observed in stations at the other distance categories showed no significant difference between periods of high versus low seed rain abundance.

Mechanisms: Spatial and temporal patterns of seed predation depend on the foraging patterns of seed predators. The findings that predation rates differ among habitats (Table 1, Figure 2) can be explained by differences in habitat preference by the major seed predators, such as ants, rodents and birds. Foraging patterns of seed predators also depend on post-dispersal seed densities. Seed predators are typically attracted to high seed densities (Janzen 1970, Howe and Smallwood 1982), hence predation rates tend to be higher closer to the seed source. This pattern has been observed both in Israel (Figure 2) and – for ro-

dent predation – in France (Table 1). The preference of harvester ants for dry habitats with relatively low vegetation cover was suggested to explain the inverse trend observed in France (Acherar et al. 1984).

The finding that predation rates are generally lower during periods of high seed rain abundance (Figure 3) can be explained by predator satiation: if the numbers of seeds are higher than predators can consume, the per capita probability of seed survival should increase. However, we have no evidence that predator satiation does occur: predation rates beneath the pine canopy – where seed densities are especially high – were not significantly lower in periods of highest seed rain abundance. Yet, higher seed availability can affect seed survival by changing the way predators forage in space, even if predators are not satiated. In times of low seed availability, predators will rapidly reduce seed densities beneath the trees to the level of 'giving-up density' (in which they no longer consume seeds at a site), hence they are more likely to forage also far from the trees. In times of high seed availability, predators will lower seed densities beneath the trees to the same giving-up density more slowly; hence predators are less likely to forage far from the trees. The finding that predation rates at stations very far from pine trees were especially low during periods of high seed rain abundance supports this hypothesis. This hypothesis assumes that seed density does not affect either the giving-up density (Hulme and Hunt 1999) or the num-

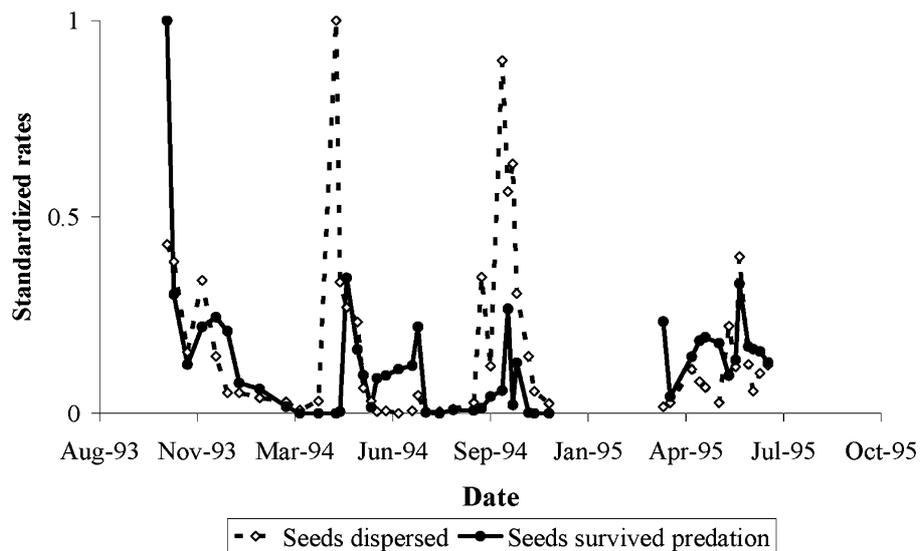


Figure 3. Standardized rates (proportion of the maximum) of predation and dispersal rates observed in an isolated Aleppo pine stand on Mt. Carmel (Israel) over a period of two years.

ber of predators (because rodents and ants, the major predators of Aleppo pine seeds, are territorial). In any case, simple experimental manipulations can help elucidate the validity of the underlying assumptions of this hypothesis and to test its predictions.

Birds constitute another group of seed predators that are especially important at early stages of Aleppo pine post-fire regeneration, as they have been reported to be the first to arrive at recently burned Aleppo pine forests (Saracino et al. 1997). Because birds, unlike rodents and ants, are visual predators, Saracino et al. (1997) emphasized the matching between the temporal change in the seed color and the surface color with time after a fire. The change in seed color is driven by winds that gradually remove the thin dark dust layer from the seed coat in opened cones, and the change in surface color is driven by physical and chemical processes of the exposed ash. The matching between these two processes suggests a physical mechanism over which the tree has little control yet may be effective in reducing seed predation, by providing continuous camouflage to the seeds despite changes in the background color. The predation experiments of Leone et al. (2000) revealed a finding supporting this hypothesis (gray seeds were more protected from predation on gray ashes than on black ashes), but also a countering finding (black seeds were also more protected on the background of gray ashes). The effects of seed color on seed predation should therefore be further investigated. Another untested hy-

pothesis on a potential morphological adaptation for reducing seed predation ties the weak seed-wing attachment to the fact that an undetached wing protrudes like a flag and thus attracts seed predators (Nathan et al. 1996). The phenomenon of weak seed-wing attachment – actually very common among conifers – is apparently suboptimal from the perspective of seed dispersal thus may indicate a trade-off between dispersal ability and predator avoidance (Nathan et al. 1996).

Seedling and sapling establishment

Patterns: Seedling emergence in Aleppo pine usually starts early in the rainy season (November-December) of the Mediterranean climate. After a fire, emergence is largely restricted to the first rainy season and only rarely occurs during the second year (Table 1).

Although the spatial patterns of seed dispersal provide the template for the spatial patterns of seedlings, the two patterns can be significantly different. This may occur, for example, if seeds arrive disproportionately to sites in which seed and seedling survival is disproportionately low (Schupp 1995). A strong mismatch of this kind is typically observed beneath the adult Aleppo pine canopy, where seed densities are highest (see *Seed dispersal* above), but seedling densities are very low. For example, a complete survey of seedlings and saplings in a pine stand in Israel revealed

243 individuals, but none of them was found directly beneath a pine canopy (Nathan et al. 2000).

Seedling/sapling establishment in Aleppo pine shows a strong spatial structure in both fire-free and post-fire scenarios. In the absence of fire, sapling density peaks at some (short) distance away from adult trees, with a rather long tail of low density at greater distances. Quantifying seed densities and the corresponding sapling densities permits the estimation of seed-to-sapling survival probabilities, revealing a drastic increase with distance from adult trees (Nathan et al. 2000): survival probabilities vary from 2×10^{-6} in the immediate vicinity of the pine canopy to 2×10^{-3} just 30 m away.

The spatial patterns of seedlings and saplings change with time after fire (Table 2). During the early post-fire stage (2-5 years), seedling density under the canopy of the (burned) parent tree is lower than between the trees. During later stages (5-20 years) the density of saplings in the two zones becomes roughly equal. Sapling size, however, differs markedly between the two zones, with saplings under the canopy being 11 to 17 times larger than those between the trees (Ne'eman and Izhaki 1998; Ne'eman 2000).

Mechanisms: In the absence of fire, seeds rarely germinate beneath the pine canopy because of the light regime (Thanos 2000), seed predation (Figure 2) and the thick needle layer (Arianoutsou and Ne'eman 2000). The observed spatial patterns of seedling establishment outside the adult canopy closely match the prediction of the escape hypothesis (Janzen 1970, Howe and Smallwood 1982). According to this hypothesis, survival probabilities are low close to the parent plant as a result of high rates of seed and seedling predation and strong competition with adults and sibs. The observed patterns of seed predation are in general agreement with this hypothesis (Table 1, Figure 2). Assessment of the role of adult and sib competition in determining spatial patterns of establishment in the absence of fire awaits further investigation.

A set of studies on Aleppo pine post-fire regeneration, summarized by Ne'eman (2000), revealed the mechanisms determining Aleppo pine post-fire spatial dynamics. The chemical properties of ash of burned trees play a key role in regulating post-fire germination. Although germination is inhibited by the extremely high pH (10–11) of the ash, it is stimulated by the presence of nitrate and ammonium (Henig-Sever et al. 1996, 2000). The germination of *Cistus* sp. and of some annual species was even more inhibited. In a paradoxical way, this inhibition creates an almost

competition-free space for Aleppo pine seedlings in the exact location of the burned tree. Under low competition and improved mineral nutrition, growth rate of the pine saplings under adult canopies greatly exceeds those between the trees. The final outcome is that the ash patch created by the burned large pine tree serves as the regeneration niche for the next generation (Ne'eman 2000). In the gaps between the trees, pine seedlings experience strong competition, mostly with the fast-growing *Cistus* seedlings that dominate these gaps. Overall, the explicit spatial structure of a pine forest after a fire is likely to be very similar to the spatial structure of that forest at the time the fire took place.

Discussion

Generality of observed patterns

Field studies of spatiotemporal dynamics of recruitment in Aleppo pine carried out at a variety of sites and in different times tend to reveal, in general, the same patterns (Tables 1 and 2). There is a considerable difference, however, between post-fire and fire-free recruitment processes. Seed release is induced both by fire and by drying atmospheric conditions, and in both cases most seeds travel only short distances; yet, we suggest that long-distance dispersal is much more likely to occur in the absence of fire. Spatiotemporal patterns of post-dispersal seed predation, and their underlying mechanisms, are not sufficiently known, especially in post-fire conditions. However, the major seed predators in the two cases are probably different: ants and rodents in fire-free conditions and birds in post-fire conditions. This difference can lead to variable seed dispersion patterns, but the scarcity of data on seed predation in burned sites (Table 1) precludes rigorous examination of this hypothesis. In any case, the patterns of seedling and sapling establishment are substantially different in the two cases.

In the absence of fire, Aleppo pine forests are known to spread into abandoned fields and newly unoccupied habitats generated by other disturbances (Quézel 2000; Richardson 2000). Such a remarkable colonization (or invasion) ability (Lepart and Debussche 1991; Rejmánek and Richardson 1996; Richardson 2000), which often results in a very rapid and extensive spread, requires very efficient dispersal mechanisms, as has been found in the seed dispersal studies (see *Seed dispersal* above). The spatial spread

Table 2. Spatiotemporal patterns of the seedling (1–2 years) and sapling (3–8 years) stages of early Aleppo pine recruitment observed in field studies at the Mediterranean Basin.

Spatial* scale*	Temporal scale	Pattern description	Fire	Country	References
<i>Seedling emergence</i>					
	1 year	Emergence rates associated with daily precipitation and monthly temperature; emergence starts November–December, lasting mostly 1–2 months	Yes	Greece	Daskalakou and Thanos (2003)
	2.5 years	Emergence rates decline from 72% 9 months after a fire to zero 18 months later [Study started 9 months after a fire]	Yes	Spain	Herranz et al. (1997)
20 m	6 months	Emergence rates differ among habitat types (shrub > open on terra-rossa); emergence starts December, reaching a maximum of 27% of sowed seeds after 2 months	No	Israel	Noy-Meir et al. (2002)
<i>Seedling density</i>					
30 m		Seedling densities did not change with distance from burned adult trees	Yes	France	Trabaud et al. (1985)
?		Seedling densities decrease with distance from burned adult trees	Yes	Spain	Papio (1987) cited by Trabaud (2000)
10 m		Seedling densities increase with distance from burned adult trees and differ among habitat types (beneath small burned trees > beneath big burned trees)	Yes	Israel	Ne'eman et al. (1992)
10 m		Seedling densities decrease with distance from burned adult trees [Study started 9 months after a fire]	Yes	Israel	Eshel et al. (2000)
?		Seedling densities differ among habitats (north aspect > flat > south aspect)	Yes	Spain	Ferran et al. (1991) cited by Trabaud (2000)
	1 year	Seedling densities increase to a peak a few months after the onset of the first postfire rainy season, then gradually decline	Yes	Greece	Daskalakou and Thanos (2003)
	2 years	Seedling densities increase to a peak at the end of the first germination period after a fire, then gradually decline	Yes	Greece	Daskalakou and Thanos (1997)
	2.5 years	Seedling densities decline with time after fire [Study started 9 months after a fire]	Yes	Greece	Thanos et al. (1996)
	2.5 years	Seedling densities decline with time after fire [Study started 9 months after a fire]	Yes	Spain	Herranz et al. (1997)
<i>Seed-to-sapling survival</i>					
60 m	3 years	Survival rates increase with distance from adult trees, a pattern repeated in 3 successive cohorts	No	Israel	Nathan et al. (2000)
<i>Seedling (age-specific) survival</i>					
	1 year	Survival rates lowest in the first winter after fire, with a second peak of low survival during mid summer	Yes	Greece	Daskalakou and Thanos (2003)
	2 years	Survival rates significantly higher in the first year after fire than in the following year	Yes	Israel	Ne'eman et al. (1995)
	2 years	Survival rates lowest in the first summer after fire	Yes	Spain	Papio (1987) cited by Trabaud (2000)
	2.5 years	Survival rates increase with time after fire (for some cohorts, rates from 1st to 2nd year > from 2nd to 3rd year after fire) [Study started 9 months after a fire]	Yes	Spain	Herranz et al. (1997)
	2.5 years	Survival rates lowest in the first summer after fire, then gradually increase; no mortality observed in the third year [Study started 9 months after a fire]	Yes	Greece	Thanos et al. (1996)
	3 years	Survival rates higher in the first year after fire than in the following 2 years	Yes	Greece	Thanos (1999)
20 m		Survival rates differ among habitat types (open > shrub on marl)	No	Israel	Noy-Meir et al. (2002)

Table 2. Continued.

Spatial scale*	Temporal scale	Pattern description	Fire	Country	References
<i>Sapling density</i>					
not reported		Sapling densities differ among habitat types (southern > northern aspect)	Yes	Spain	Martínez-Sánchez et al. (1996)
not reported		Sapling densities differ among habitat types (lower > upper hilltop position; shallow > steep slope)	Yes	Greece	Tsitsoni (1997)
	2 years	Sapling densities decline with time after fire [Measurements reported 2 and 4 years after a fire]	Yes	Italy	Leone et al. (2000)
	5 years	Sapling densities decline with time after a fire	Yes	France	Trabaud (1988)
	5 years	Sapling densities decline with time after fire [Study started 16 months after a fire]	Yes	Spain	De las Heras et al. (2002)
10 m	5 years	Sapling densities decline with time after fire at different rates in two spatial zones (outside burned tree > beneath burned tree after 2 years; opposite trend after 5 years)	Yes	Israel	Ne'eman and Izhaki (1998)
	5 years	Sapling densities increase with time after fire [Study started 2 years after a fire; <i>chronosequence</i>]	Yes	Algeria	Moravec (1990)
	8 years	Sapling densities increase with time after a fire [Study started 1 year after a fire; <i>chronosequence</i>]	Yes	France	Trabaud et al. (1985)
	8 years	Sapling densities decline with time after fire [Study started 1 year after a fire]	Yes	Israel	Arianoutsou and Ne'eman (2000)
?	8 years	Saplings densities increase with time after fire and differ among habitats [<i>chronosequence</i>]	Yes	Italy	Papio (1987) cited by Trabaud (2000)
100 m		Sapling densities differ among habitat and soil types (shrub > open; marl > terra-rossa)	No	Israel	Noy-Meir et al. (2002)
250 m		Sapling densities differ among habitat types (outside pine canopy > within pine canopy)	No	Israel	Nathan et al. (2000)
60 m		Sapling densities increase to a peak 10-15 m from adult trees, then decrease at longer distances	No	Israel	Nathan et al. (2000)
<i>Sapling (age-specific) survival</i>					
	5 years	Annual survival rates were lowest in the third year after fire, increasing to 98% in the 5th-7th years [Study started 16 months after a fire]	Yes	Spain	De las Heras et al. (2002)

*In studies examining the variation with distance from adult trees, the spatial scale refers to the longest distance sampled. In studies examining variation among habitat types, the spatial scale refers to the distance across the sampled area.

of Aleppo pine in the absence of fire has two different components. The small-scale component includes short-distance dispersal of most seeds, which, combined with a general increase in seed and seedling survival with distance from adult trees, generates hump-shaped recruitment curves (Nathan et al. 2000). The large-scale component relies on efficient long-distance dispersal that enables colonization of suitable sites at long distances from the population, providing the means for a very rapid spatial spread. On the top of these distance-dependent processes, Aleppo pine recruitment largely depends on the distribution of suitable habitats. The combination of short- and long-distance dispersal and habitat effects gives rise to the typical variable age structure of unburned Aleppo pine forests (Schiller et al. 1997).

All in all, we cannot point today to a single key factor that dictates Aleppo pine recruitment patterns in the absence of fire. Although this may reflect insufficient data, it seems more likely to reflect reality. We know that multiple processes, including seed dispersal, post-dispersal seed predation and seedling establishment, play an important role in Aleppo pine recruitment; yet, we have no evidence that any one of them is significantly more important than the others. Different processes may lead to different, possibly opposing, outcomes. Consequently, Aleppo pine recruitment in fire-free conditions is fairly unpredictable.

The spatiotemporal dynamics of post-fire recruitment are notably different. Fire could kill all individuals in a population, and despite the inability of pines to resprout, the next generation is likely to exhibit

Table 3. Summary of the numbers of studies addressing spatiotemporal aspects of early recruitment in Aleppo pine (based on Tables 1 and 2).

Fire	Spatial/Temporal	Seeds			Seedlings	Saplings	Total
		Pre-dispersal	Dispersal	Post-dispersal			
Post-fire	Spatial		1		5	2	8
	Temporal	2			4	7	13
	Both			1		1	2
Fire-free	Spatial		2			2	4
	Temporal	2					2
	Both		2	3	1	1	7
	Total	4	5	4	10	13	36

the same explicit spatial pattern. As explained above, the most crucial recruitment stage in determining the spatial pattern of the first post-fire generation is that of saplings, and specifically their higher growth rates in the canopy projection of large burned pines. Thus, unlike fire-free regeneration where multiple factors operating at various stages are likely to be important, post-fire regeneration is governed by a fairly specific set of factors operating during a specific stage and at a specific location. Consequently, the post-fire spatial dynamics in Aleppo pine are, to a large extent, predictable. Synchronized germination explains the typical even-aged post-fire forests (Schiller et al. 1997; Arianoutsou and Ne'eman 2000).

Temporal patterns of seed release

From an evolutionary perspective, pyriscence and xeriscence are two complementary mechanisms to track favorable establishment conditions in time and space. Pyriscence provides the means to exploit favorable post-fire establishment conditions, while xeriscence provides the means to exploit other kinds of disturbances (Ne'eman et al. 2003). The mass seed release shortly after a fire not only places many more seeds on the ground, but those seeds also tend to be less damaged and more likely to germinate than seeds released from cones on the burned trees at later stages (Saracino et al. 1997). Furthermore, because most fires occur during summer, delayed post-fire seed release shortens the period in which the dispersed seeds are exposed to predation. This suggests that the somewhat unexpected prolonged seed release after a fire has no adaptive value, being merely a by-product of an imperfect mechanism primarily functioning to release all seeds shortly after a fire.

Examination of the temporal pattern of xeriscence observed in Israel (Nathan et al. 1999) provides another example of such side effects. Sharav events during fall provide a cue for establishment in the following rainy season. A temporal matching between xeriscence and germination period was reported from Southern Italy as well (Leone et al. 2000). However, Sharav events in the Eastern Mediterranean are also common during spring, exposing seeds to poor establishment conditions and a long delay until the rainy season, thus considerably reducing their probability of survival. Such detrimental consequences must be outweighed by strong selective pressure for xeriscence to evolve.

Prognosis and prospective for future research

To assess the state of our current knowledge on recruitment processes in Aleppo pine populations, Table 3 summarizes the allocation of research efforts in relation to recruitment stages, post-fire versus fire-free conditions, and spatial and/or temporal perspectives. Research efforts have been mainly dedicated to studying the post-fire regeneration of seedlings and saplings throughout the species' native range. Studies of the processes belonging to the seed stage are less common and have been carried out only in a few sites in Israel and France. Only a few studies have simultaneously examined the spatial and temporal aspects of recruitment for the same population. More specific research topics, such as long-distance seed dispersal and the relative contribution of xeriscence versus pyriscence for future generation, constitute major challenges for future research.

Better understanding of recruitment processes also calls for a reassessment of the research methodologies.

Models provide the means to formalize concepts, to identify the major driving forces, to facilitate the study of patterns when and where field data are difficult to get, and to generate predictions and testable hypotheses. The use of models to study plant recruitment is currently growing in general (Nathan and Muller-Landau 2000) and should be applied more broadly to study Aleppo pine recruitment. Genetic methods provide an alternative approach that can greatly improve our understanding of recruitment processes (Ouborg et al. 1999; Cain et al. 2000; Nathan et al. 2003). Genetics constitute more than just promising methodological tools; genetics of early recruitment should be developed as a leading research topic. Potential key questions include, for example, how the genetic structure of Aleppo pine populations changes during early recruitment in post-fire versus fire-free conditions, and how much of it is attributed to seed versus pollen dispersal and to short- versus long-distance dispersal. It is also imperative to examine the field methodologies currently being applied to study Aleppo pine recruitment dynamics. For example, temporal changes have frequently been studied by diachronic monitoring of permanent plots after fire, but these are more difficult to follow over long time scales. The long-term perspective has been studied mostly, though not exclusively, by examining different sites varying in their post-fire age. Yet, the degree of similarity among different sites in key environmental conditions and population history is unknown; if high dissimilarity exists, it might obscure existing patterns or generate superficial patterns. Thus, studying recruitment dynamics at the same site for longer durations is crucially important to reduce year-specific variation and to reach more solid generalizations on Aleppo pine recruitment.

In fact, the few studies of Aleppo pine recruitment that have been carried out at the same site during 3-8 years (Tables 1 and 2) are exceptionally long in comparison with studies of recruitment of other tree species (Clark et al. 1999). We therefore have a relatively sound basis for examining the consistency of temporal dynamics of recruitment in this species. The spatial scale of some studies is also relatively large (Tables 1 and 2), but the number of sites studied concurrently is usually small, only one or rarely two. Thus, the challenge still remains to study early recruitment stages more extensively in both time and space in order to advance our understanding of the role of recruitment in Aleppo pine population dynamics.

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