



Canopy seed bank structure in relation to: fire, tree size and density

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Abstract

To assess the canopy seed bank structure of *Pinus halepensis*, we measured the level of serotiny and the seed bank size and density of trees in unburned stands and post-fire regenerated stands in Israel. We analysed the effects of tree size, tree density and fire history on the level of serotiny. The level of serotiny decreased with an increase in tree height. The high level of serotiny in short trees could be explained by selection to increase regeneration chances after burning at pre-mature age. Also, limitation of long-distance seed dispersal opportunities in short trees may favour high serotiny levels. The level of serotiny was higher in post-fire stands than in unburned stands, suggesting a fast selection for serotiny by fire. Unburned stands had a higher total stand seed density than post-fire regenerated stands, but the proportion of seeds in serotinous cones of the total stand seed density was higher in post-fire regenerated stands. The fact that *P. halepensis* bears simultaneously serotinous and non-serotinous cones reflects its dual strategy as both a post-fire obligate seeder, mainly from serotinous cones and an early coloniser during fire-free periods, mainly from non-serotinous cones. The relative investment in these strategies is dependent on fire history and varies with tree height. Furthermore, mature brown cones can contribute to post-fire regeneration in case of spring fires, and serotinous cones are known to open partially also in dry spell events. Thus, post-fire regeneration and invasion are strategies, which seem to complement each other.

Introduction

Canopy seed banks are formed when mature seeds are retained in the canopy due to delayed seed release (serotiny). Serotiny is considered to be an adaptation of obligate seeders to high intensity canopy fires, which completely destroy the above ground vegetation, thus relying on post-fire regeneration from soil or serotinous (canopy) seed banks (Trabaud 1987; Lamont et al. 1991; Keeley 1994). Serotiny is common among pine species growing in fire-prone ecosystems (Agee 1998; Keeley and Zedler 1998), and

also among angiosperms growing under similar conditions, mainly in Australia and South Africa (Lamont et al. 1991). Considerable variation in the level of serotiny exists among populations and species of many serotinous species. This variation is often attributed to variation in the fire frequency regime (Gauthier et al. 1996; Enright et al. 1998). Consequently, partial serotiny, the co-occurrence of serotinous and non-serotinous cones, is a common phenomenon at the individual, population and species levels. Thus, understanding how fire and other factors determine the level of serotiny is critical to the study of

reproduction and establishment of many plant species inhabiting fire-prone environments.

Pinus halepensis Mill. is a lowland West-Mediterranean species with an East-Mediterranean disjunct population in Israel (Panetsos 1981; Barbero et al. 1998; Quezel 2000) of a distinct genetic composition (Schiller et al. 1985). In this part of the Mediterranean basin natural fires occur in low frequency, but the frequency of human-induced fires can be high, depending on human population dynamics. *Pinus halepensis* is an obligate seeder (Arianoutsou and Ne'eman 2000; Trabaud 2000), whose extensive post-fire regeneration, in the absence of any other fire adaptive trait such as thick bark, sprouting ability or 'grass stage' (Keeley and Zedler 1998), depends entirely on its canopy seed bank (Daskalidou and Thanos 1996; Saracino et al. 1997). However, extensive regeneration occurs also without fire. The species is a very successful early coloniser of disturbed sites throughout its natural range (Lepart and Debussche 1991; Trabaud 1987; Trabaud 1991) and an active invader in the Southern Hemisphere (Richardson 2000). Seeds of *P. halepensis* are almost completely absent from the soil seed bank of pine forests (Ne'eman and Izhaki 1999), presumably due to heavy seed predation (Nathan and Ne'eman 2000). The probability of seed survival, which can be as low as one sapling per 500,000 dispersed seeds very close to the parent tree, increases significantly with distance, and can be three orders of magnitude higher at 50 m from the trees (Nathan et al. 2000). Therefore, long-distance seed dispersal from the canopy seed bank into open areas, with favourable germination and establishment opportunities, is an important factor in the reproductive success of this species. The dual life strategy is attributable to the species' partial serotiny: *P. halepensis* produces large annual cone crops that mature and turn from green to brown in the third year after pollination. Some brown cones open and release their seeds over spring and fall (non-serotinous cones) of that year. The remaining brown cones stay closed (serotinous cones), turn grey in the following year. All cones, whether closed serotinous or opened remain in the canopy. This seed bank structure enables post-fire regeneration by seeds stored in serotinous cones that are released by fire (i.e., pyriscence) (Lamont 1991, Keeley and Zedler 1998), and invasive regeneration during fire-free intervals by seeds from non-serotinous cones that are released by dry and hot weather (i.e., xeriscent) (Nathan et al. 1999). Thus, knowledge of the canopy seed bank structure of serotinous

and non-serotinous cones and its determinants is essential for understanding the evolutionary forces that affect the regeneration strategies of this species.

Studies in Greece (Daskalidou and Thanos 1996) and Israel (Nathan et al. 1999) provided evidence for partial serotiny in *P. halepensis*, showing considerable variation among individuals and populations, with an mean xeriscent estimated as about 60% of the annual crop (see Nathan and Ne'eman 2000 for review). Partial serotiny of North American pines is considered to be a genetically-determined trait that has evolved in response to the spatio-temporal variation in fire patterns, with more frequent and more intense fires resulting in higher levels of serotiny (Perry and Lotan 1979, McMaster and Zedler 1981, Gauthier et al. 1996). However, serotiny also exhibits a more flexible character, which means the level of serotiny could be also affected by other environmental factors, such as drying conditions, seed dispersal opportunities and establishment conditions. Two main tree characteristics are known to influence fire and seed dispersal conditions: tree size and tree density. Seeds released from taller trees are more likely to disperse further, thus tree height is associated with seed dispersal (Greene and Johnson 1989; Nathan et al. 2001b). Tree density, detectable by trees by virtue of their sensitivity to red/far-red radiation ratio (Smith et al. 1990), decreases long-distance seed dispersal and seedling establishment opportunities (Lamont et al. 1991; Grace and Platt 1995; Thanos and Daskalidou 2000) and increases air humidity (Oke 1987) as well as fire risk (Bond and van Wilgen 1996). The effects of tree size and tree density on the seed bank structure of individual trees, ultimately affect the dynamics of seed dispersal and the accumulation of the canopy seed bank at the level of a whole stand, affecting its invasion and post-fire regeneration abilities.

The aim of this study is to assess if and how the relative investment in regeneration with and without fire varies with tree height, tree density and fire history. We quantify the canopy seed bank structure in unburned stands and post-fire regenerated stands *P. halepensis* stands, by measuring the level of serotiny and the seed bank size and density. The level of serotiny indicates the strength of selection for post-fire versus fire-free regeneration. The seed bank density, consisting of seeds in mature brown and serotinous cones, indicates the actual number of seeds available for fire-free and post-fire regeneration, respectively. At the individual level we examine the effects of tree

Table 1. Characteristics of the sampled *P. halepensis* stands: Stand types, location, altitude, aspect, average annual rainfall, age (various means ages from 1-80 years old) and percentage of total vegetation cover.

Stand	Stand type	Area	Altitude (m)	Aspect	Rainfall (mm.y-1)	Stand age (y)	Cover (%)
RoshHanikra	unburned	Galilee	150	SE	700	various	100
Arkan	unburned	Carmel	420	N	700	various	100
Horshat 40	unburned	Carmel	400	W	700	various	80
Nir Ezyon	unburned	Carmel	100	W	600	various	30
Etzba-old	unburned	Carmel	180	W	600	various	80
Pithulim	unburned	Judea	700	SW	500	various	80
Hamasreq	unburned	Judea	600	NW	500	various	40
Etzba-new	post-fire	Carmel	180	SW	600	25	50
Beit Oren	post-fire	Carmel	300	SE	600	15	40
Hai Bar	post-fire	Carmel	400	W	700	10	70

size and local tree density on the level of serotiny and the canopy seed bank size. At the stand level we examine the effects of stand type (unburned or post-fire regenerated) on the level of serotiny and on the canopy seed density. We hypothesize that: 1) The level of serotiny of individual trees decreases with increased tree height if increased tree height has a strong positive effect on seed dispersal chances. On the other hand, if increased tree height has a stronger positive effect on fire risk the level of serotiny is expected to increase with increased tree height. 2) The level of serotiny of individual trees is expected to increase with an increase in tree density, because of a lower probability for long range seed dispersal and increased fire risk. 3) If serotiny is a trait, which is rapidly selected by fire, the level of serotiny in burned stands is expected to be higher than the level of serotiny in post-fire regenerated stands. 4) Given the previous expectations and the fact that trees are smaller and density is higher in post-fire regenerated stands than in unburned stands, the total stand seed density is expected to be lower and the proportion of seeds in serotinous cones higher in post-fire regenerated stands than in unburned stands.

Materials and Methods

Study sites

Ten study sites, including all major Aleppo pine stands in Israel, were selected for this study. These include two natural unburned stands in the Judean Mountains near Jerusalem, four unburned and three post-fire regenerated stands on Mount Carmel near Haifa, and one natural unburned stand in the Western

Galilee near the Lebanese border. All stands were formed due to invasive regeneration from scattered *P. halepensis* trees after land abandonment during the late 19th and 20th century (Schiller et al. 1997). The post-fire regenerated stands were burned only once since their establishment. Unburned stands were multi-aged with a core of some older (60-80 years) trees and young ones at the edges, whereas post-fire regenerated stands were even aged. Tree size varied in all stands, but was more homogenous in the post-fire regenerated stands. For each stand, we recorded the altitude, aspect, average annual rainfall, stand age and the percentage of vegetation cover (Table 1). The bedrock in all stands was chalky marl covered by rendzine soil.

Measurements

Measurements were performed during summer 1998. In each stand, we randomly selected a minimum of 20 trees, ranging largely in tree sizes and local densities (number of surrounding trees). Tree height, trunk diameter at 130 cm height (DBH), and crown radius were recorded for each tree. Tree height was strongly related (linear regression) with the DBH ($F = 1000.095$, $df = 1$, $p < 0.001$, $R^2 = 0.683$) as well as with crown radius ($F = 200.587$, $df = 1$, $p < 0.001$, $R^2 = 0.332$) among 465 trees. We determined local tree density for each tree by counting the number of neighbouring conspecific trees within a radius of 10 m around each sampled tree and categorised them as shorter, equal or taller than the sampled one. We used only the number of equal and larger-sized neighbouring conspecific trees to calculate the local tree density. We assumed that shorter neighbours have negligible effects on the reproductive performance of

an individual, not only in terms of light competition, but also in terms of root competition, as individuals with higher biomass have the competitive advantage over smaller individuals (Gaudet and Keddy 1988). For the same reason the effects of several small woody species, that typically accompany native *P. halepensis* stands, can be neglected. We counted all cones with binoculars. On each tree we counted the number of closed cones, that were classified as green (in their second year), brown (third year) or grey (fourth year and more) and distinguished from open cones, either brown or grey. It must be noted that the group of brown cones included both closed and already opened brown cones, as this constitutes the annual mature cone crop. Consequently, we purposely omitted the open brown cones from the group of opened cones so it would include only previously opened cones and not cones that opened the current year. The term “serotinous cones” used hereafter includes only closed grey cones.

Level of serotiny

An adult *P. halepensis* tree carries several cohorts of cones simultaneously, including open cones, which remain firmly attached to the branches. This facilitates the estimation of a tree’s lifetime cone production. Serotiny in this study was defined as the proportion of cones, which remained closed after maturation of the total number of cones produced during a tree’s life-time. Immature cone cohorts, as well as mature brown cones, were intentionally disregarded because the proportions of both serotinous and non-serotinous cones in these cohorts are unknown. The level of serotiny was calculated for each tree as the percentage of serotinous cones (closed grey cones) out of open and serotinous cones (all grey cones). The influence of tree height and tree density on the level of serotiny of individual trees was analysed for all seven unburned and three post-fire regenerated stands separately.

For the comparison of the level of serotiny between unburned and post-fire regenerated stands, we focused on the stands of Mt. Carmel only to exclude potential regional-level differences. Furthermore, since post-fire regenerated stands comprised only trees up to 8 m. high, we compared only trees up to 8 m high in both stand types to exclude size effects. In a comparison between post-fire regenerated stands and unburned stands on Mt. Carmel (with tree height up to 8m high), no significant differences were found

in mean tree height ($t = 1.423$, $p = 0.272$) as well as mean tree density ($t = 0.069$, $p = 0.949$). We calculated the relative frequency distribution of 86 trees in unburned stands and 110 trees in post-fire regenerated stands, over 10 serotiny level classes. We also calculated the mean level of serotiny for both stand types.

Size and density of the canopy seed bank

The size of the canopy seed bank at the individual tree level was defined as the number of viable seeds per tree and was estimated separately for seeds in mature brown and serotinous cones for unburned (on Mt. Carmel including only trees < 8m. height) and post-fire regenerated stands. It equals to the product of (a) the mean number of cones per tree; (b) the mean number of seeds per cone; and (c) the proportion of viable seeds in a cone. The number of all brown and serotinous cones on each tree where available directly from our field data. The number of seeds per cone and seed viability, examined in a preliminary study in four stands (2 unburned and 2 post-fire, $N = 40$) on Mt. Carmel, revealed means (\pm SE) of 102 ± 6.8 and 102 ± 5.1 seeds per cone and $92\% \pm 2.2$ and $69\% \pm 6.3$ of viable seeds in brown and serotinous cones, respectively, with no significant differences between stands.

The seed bank density, defined as the number of viable seeds per unit of ground area, was calculated for post-fire regenerated stands and unburned stands on Mt. Carmel only. In this case however we did include trees of all heights. Comparisons between stand types are still valid, as the difference in tree height is normalized by calculating the number of seeds per unit of ground area. The density of the canopy seed bank at the stand level, was estimated separately for seeds in mature brown and serotinous cones. This was calculated as the product of the mean number of viable seeds per tree (previous paragraph) and the density of trees. These components were estimated while taking into account the frequency distribution of tree size, by classifying all trees in a stand into three size classes based on their trunk diameter (DBH). Size class 1 ranged from 1-20 cm DBH, class 2 ranged from 21-40 cm DBH and class 3 ranged from 41-60 cm DBH. Subsequently, we selected ten circles of 10 m radius in each stand and counted the number of trees per size class in each circle. The density of trees of each size class was calculated as the mean number of trees per m^2 of the ten circles in each stand. The

Table 2. Mean (\pm S.E.) tree height, level of serotiny and total viable seed density for each stand.

Stand	n	Height (m)	Serotiny (%)	Stand seed density (# viable seeds/m ²)
RoshHanikra	59	8.8 \pm 0.4	15 \pm 2	–
Arkan	40	9.1 \pm 0.4	6 \pm 1	131
Horshat 40	60	7.8 \pm 0.3	56 \pm 7	887
Nir Ezyon	53	6.0 \pm 0.4	34 \pm 5	271
Etzba-old	20	8.6 \pm 0.7	41 \pm 3	1047
Pithulim	60	8.5 \pm 0.4	21 \pm 3	–
Hamasreq	54	7.6 \pm 0.3	6 \pm 2	–
Etba-new	40	6.0 \pm 0.2	67 \pm 11	89
Beit Oren	30	3.7 \pm 0.2	93 \pm 17	51
Hai Bar	40	2.5 \pm 0.1	94 \pm 2	9

mean number of viable seeds was calculated for each tree size class and weighted by tree density of each size class. Finally the total stand seed density was the sum of the seed densities of the three size classes. To estimate the relative contribution of the seeds in brown cones to the total viable stand seed density, we calculated the ratio between the density of seeds from brown cones and the total seed density, for unburned and post-fire regenerated stands separately.

Note that, as we included both open and closed cones for the brown cone cohort, the calculated seed density gives an estimation of the seed density of brown cones, as it would be at early spring, before the beginning of cone opening.

Statistical analyses

The relations between tree height and tree density with the level of serotiny and seed bank density were analysed by stepwise multiple regression. A t-test was used to compare the level of serotiny and the seed bank density between unburned and post-fire regenerated stands. Proportions were arcsin-square-root transformed and density estimates were Log (x) transformed before being submitted to the ANOVA as they were not normally distributed. (Zar 1984).

Results

Level of serotiny

The mean tree height varied from 2.5 to 9.1 m and the level of serotiny varied from 6 to 94% (Table 2).

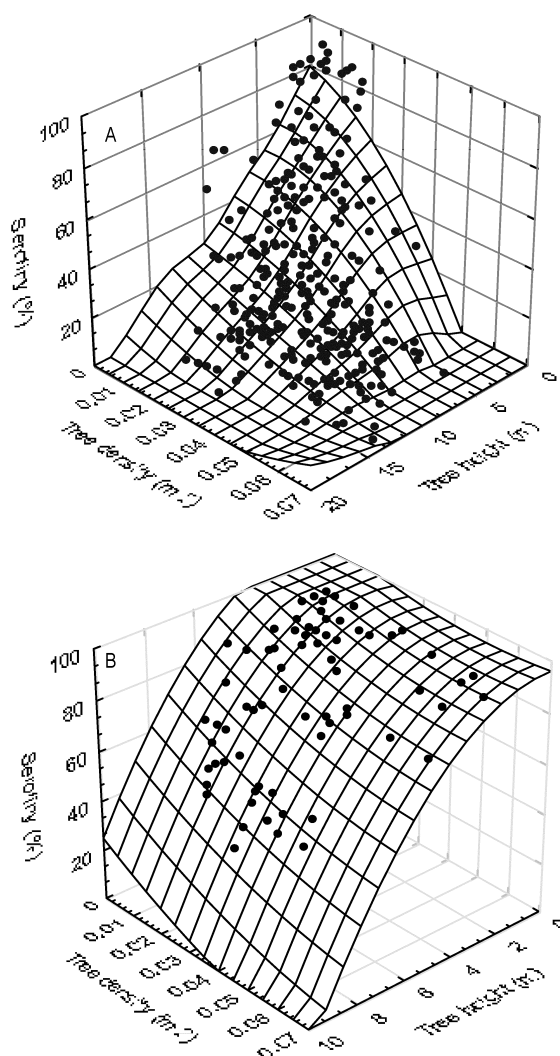


Figure 1. The 3-dimensional relationships between the level of serotiny and tree height and tree density of individual trees in seven unburned (A) and three post-fire regenerated stands (B). Note that tree height is displayed in reversed order. The displayed surfaces (least-square fit) indicate the general observed patterns

The relationships between the level of serotiny and tree height and tree density of individual trees in unburned and post-fire regenerated stands are presented in Figure 1A, Figure 1B, respectively. Due to the natural structure of the unburned stands no tall trees were found at higher densities, with few exceptions. In both unburned and post-fire regenerated stands, the overall pattern is a steep significant decrease of the level of serotiny with increasing tree height (Table 3 and Figure 1). The effect of tree density was similar to that of tree height in unburned stands, although

Table 3. Results of a stepwise multiple regression for the effect of tree height and tree density on level of serotiny for unburned stands (n= 346) and post-fire regenerated stands (n=110), (df=1). Slope “-“ indicates a negative relationship.

Stand type	Factor	Slope	F-value	p	R ²
Unburned	Tree height	-	70.636	< 0.001	0.156
	Tree density	-	6.697	0.010	0.016*
Post-fire	Tree height	-	59.535	< 0.001	0.351
	Tree density	-	8.741	0.004	0.057*

*The added value of R² in a stepwise analysis

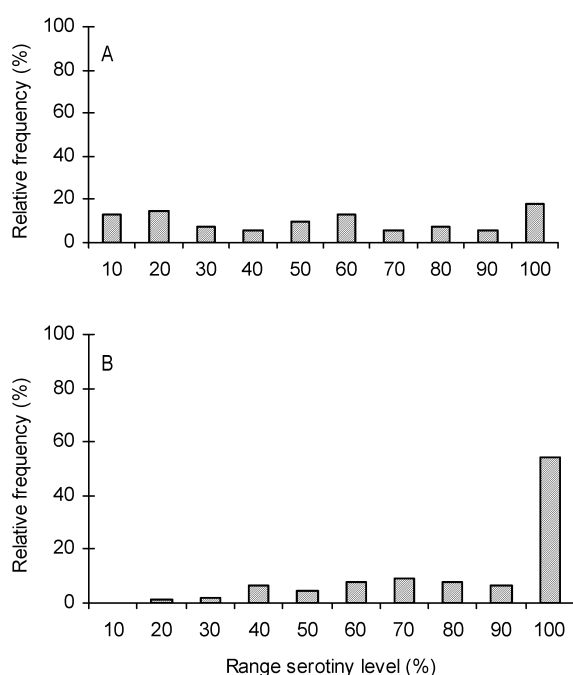


Figure 2. The distribution among the range of the level of serotiny (the x-axis indicates the upper level of serotiny classes) of 86 trees in four unburned stands, including only trees up to 8 m. high (A) and 110 trees in three post-fire regenerated stands (B) on Mt. Carmel.

much weaker and in post-fire regenerated stands the effect of tree density was not uniform and very weak as well (Table 3 and Figure 1).

The distribution of the level of serotiny among short trees of unburned stands on Mt. Carmel was even, showing similar frequencies (6-18%) over all serotiny classes (Figure 2A). The extreme serotiny values (0 and 100%) were found in 2 and 16% of the trees, respectively. The distribution pattern among all trees of post-fire regenerated stands was more biased. No trees were found in the lowest serotiny class (0-10%), intermediate serotiny classes consisted of 1-9%

of the trees and 54% of the trees were found in the highest class (91-100%) (Figure 2B). The extreme serotiny values (0 and 100%) were found in 0 and 50% of the trees, respectively. The mean level of serotiny among trees up to 8 meters high was significantly higher ($t = 3.005$, $p = 0.030$) in post-fire regenerated stands ($84.5\% \pm 7.02$, $N = 3$) than in unburned stands ($39.3\% \pm 9.31$, $N = 4$) on Mt. Carmel.

Seed bank size and stand seed density

In both unburned stands (on Mt. Carmel, including only trees < 8m height) and post-fire regenerated stands, the number of viable seeds in serotinous cones and also in brown cones increased with increasing tree height, but were not affected by tree density (Table 4).

The stand seed density varied between 131 to 1047 (mean 355) viable seeds / m² for unburned stands (on Mt. Carmel, including all trees) and between 9 to 89 (mean 50) viable seeds / m² in post-fire regenerated stands (Table 2). Thus, stand seed density is always higher in unburned stands than in post-fire regenerated stands. The proportion of seeds in brown mature cones of the total seed density was significantly higher ($t = 2.582$, $p = 0.047$) in unburned stands ($57.1\% \pm 5.2$) than in post-fire regenerated stands ($34.4\% \pm 7.5$).

Discussion

Serotiny of individual trees

The large variation in the level of serotiny in *P. halepensis* in Israel is mainly the result of the effects of fire and tree size and to a lower extent of local tree density. These findings suggest an adaptive response in the level of serotiny of *P. halepensis* trees to different environmental conditions. Considering the dual life strategy, these results can be explained from the point of view of post-fire regeneration as well as invasion strategies.

From the point of view of post-fire regeneration strategy, tree density is expected to increase fire risk, due to fuel accumulation (Bond and van Wilgen 1996; Keeley and Zedler 1998). Thus we would expect the level of serotiny to increase with higher tree density. The results showed a very weak effect of density which contradicts our hypothesis. We also found a

Table 4. Results of multiple regression tests for the effect of tree height and tree density on the number of viable seeds per tree in brown mature cones and serotinous cones for trees < 8m. in unburned stands on Mt Carmel (n= 86) and post-fire regenerated stands (n=110), (df=1). Slope “-“ indicates a negative relationship, “+” indicates a positive relationship.

Stand type	Cone type	Factor	Slope	F-value	p	R ²
Unburned	Brown	Tree height	+	26.775	< 0.001	0.181
		Tree density	-	0.098	0.754	< 0.001*
Unburned	Serotinous	Tree height	+	37.822	< 0.001	0.135
		Tree density	-	0.539	0.464	< 0.001*
Post-fire	Brown	Tree height	+	88.729	< 0.001	0.449
		Tree density	-	0.134	0.715	< 0.001*
Post-fire	Serotinous	Tree height	+	72.681	< 0.001	0.400
		Tree density	-	0.451	0.503	< 0.001*

*The added value of R² in a stepwise analysis

strong negative effect of tree height. A higher level of serotiny in shorter plants was also reported by Cowling and Lamont (1985) in a study on a *Banksia* species. However, studies of other pine species (*P. contorta* and *P. banksiana*) reported lower levels of serotiny in small pine trees than in large ones (Critchfield 1985; Lamont et al. 1991; Gauthier et al. 1993). These different patterns of the level of serotiny in relation to tree height may be explained by differences in fire regime. The trend found in *P. contorta* and *P. banksiana* is adaptive to infrequent-fire regimes, which causes trees to face “senescence risk” (Zedler 1995). In such fire regimes, the fire-free period can exceed the life span of the trees (Gauthier et al. 1993). Thus, seed accumulation in the canopy bank is expected to be increasingly favourable as a tree gets old, resulting in higher level of serotiny in older and taller trees. In *P. halepensis* we found an opposite trend, where short trees have higher levels of serotiny than tall ones. This patterns seems adaptive to frequent fire regimes, which induce “immaturity risk” (Lamont et al. 1991; Keeley et al. 1999). This is the risk of being burned before accumulating enough seeds in the canopy seed bank for post-fire recruitment (Zedler 1995). In our studied unburned stands, fire risk can be high due to a large amount of tall trees, that accumulated high fuel loads. In post-fire regenerated stands fire risk can be high due to the domination of dwarf shrubs, which rapidly increases the probability of a successive fire. Therefore, it is advantageous that *P. halepensis* trees will begin their cone production at a young age (Thanos and Daskalakou 2000; Shmida et al. 2000). However, at this early regeneration stage, dispersed seeds have a very low chance of arriving at appropriate open germination sites, that are typically saturated by the massive seed release induced by fire (Nathan and

Ne’eman 2000). Furthermore, even if seeds arrive, germinate and establish, young saplings can not survive any possible fire. However, if early produced cones are serotinous, they will increase the chances of regeneration after a new fire. Thus, differential adaptive response to reduce immaturity risk, as proposed in our study, or to reduce senescence risk, as proposed in other studies, could result in apparently contradicting relationships between the level of serotiny and tree size.

Based on an invasion strategy of *P. halepensis* point of view, tree height is positively associated with dispersal distances (Nathan et al. 2001b); thus, in the absence of fire, tall trees would particularly benefit from the long-distance dispersal advantage of xeriscence. The effect of tree density on serotiny can also be related to seed dispersal. More dense stands typically have more humid conditions (Oke 1987) and lower wind velocities (Greene and Johnson 1996; Nathan et al. 2001a) hence fewer cones would be expected to open and released seeds are unlikely to reach large distances. High tree density is also disadvantageous by reducing opportunities for seedling establishment (Grace and Platt 1995). These conditions act against the advantages of xeriscence for long-distance dispersal (Nathan et al. 1999), and thus may result in higher serotiny levels in more dense stands. All together, these effects are expected to result in higher level of serotiny in short trees and at higher tree densities. We found that the level of serotiny is higher in short trees than in taller trees as hypothesized, at any local tree density. This suggests a strong positive effect of the increase in tree size on dispersal opportunities, which fits our first hypothesis. The negative effect of density on the level of serotiny, contradicts our second hypothesis, but recall that this effect was weak and not always uniform. This stresses that our

understanding of the physiological mechanism of cone opening is still incomplete (Lanner 1998; Leone et al. 1999; Nathan et al. 1999).

Serotiny at the stand level

We found that in post-fire regenerated stands trees with high serotiny levels (91-100%) are much more frequent than in unburned stands. Furthermore, we found that the mean level of serotiny in young post-fire regenerating stands was twice higher than in adult unburned stands. These findings confirm our hypothesis that serotiny may be a trait which adapts rapidly to fire. This corresponds to the recent findings from Italian (Leone et al. 1999), and Greek (Thanos and Daskalakou 2000) populations of *P. halepensis*. Leone et al. (1999) found a level of serotiny within the range of 30-70% for an unburned adult stand whereas 70-100% for a young post-fire regenerated stand. Thanos and Daskalakou (2000) estimated the level of serotiny for a 5-12 years old, burned forest and a 30-50 year old, unburned forest, as 95% and 48%, respectively. This higher level of serotiny in these studies is associated with differences in fire history or with differences in stand age and tree size. It should be noted that the size effect was controlled in our study, by focusing on trees of equivalent size. In addition, all stands in this comparison were located in the same area with similar environmental characteristics. Thus, the higher level of serotiny in the post-fire stands is likely to reflect direct selection by fire, as has been proposed for other *P. halepensis* populations (Leone et al. 1999; Thanos and Daskalakou 2000) and for many North-American serotinous pines (Lotan 1975; McMaster and Zedler 1981; Gauthier et al. 1996; Keeley and Zedler 1998). The rapid one-generation response to fire selection can be explained by the proposed simple genetic control (two alleles at one locus) of this trait (Teich 1970; Perry and Lotan 1979).

Seed bank size and density

The post-fire regeneration ability of a pine tree depends on the number of viable seeds produced per tree. This canopy seed bank consists of seeds in mature brown cones and in serotinous cones. The number of viable seeds per tree from both cone types increased with tree height. The increase in the number of brown cones with tree height implies that the annual cone production increases as a tree grows. Part

of the mature brown cones stay closed, increasing the serotinous cone crop on a tree. The serotinous cone crop can suffer losses as serotinous cones are known to open also in due time in dry spell events (Nathan et al. 1999). However, in order to explain the increase in the number of serotinous cones per tree with increasing tree height, we propose that annually less serotinous cones are lost through opening than are added to the serotinous seed bank.

The total mean canopy seed density in unburned stands was 355 viable seeds / m² and in post-fire regenerated stands 50 viable seeds / m². In comparison, canopy seed densities in the range of 115 – 790 seeds / m² were reported for 40-50 years old forests in Greece (Thanos and Daskalakou 2000). Furthermore, Roittemberg and Ne'eman (1999) estimated that the stand canopy seed bank of a post-fire *P. halepensis* forest was about reach a density of ca. 300 seeds / m² after 30 years. The mean age of the post-fire regenerated stands in this study was 16 years. Thus, our results on the seed bank density correspond to values found in other populations in the Mediterranean basin. The results also showed that the contribution of seeds in brown mature cones to the total stand seed density was relatively large, especially in unburned stands. These results confirm our fourth hypothesis that stand seed density is higher in unburned stands, but that the proportion of seeds in serotinous cones is higher in post-fire regenerated stands. Although part of these cones will open soon after maturation, they are a part of the post-fire regeneration seed pool as long as they are closed. The extent of the role of these cones in post-fire regeneration depends on the timing of a fire event, which is therefore also important for post-fire regeneration ability. As a result of the massive seed release induced by dry spell events during spring and fall (Nathan et al. 1999), the relative contribution of seeds from brown mature cones, and subsequently the number of seeds released by fire, are expected to decrease from early spring to early winter. Therefore it seems that role of brown cones would be the largest in case of a spring fire, however, fires in the eastern-Mediterranean occur mostly during fall when fuel availability is high, humidity is low and dry spell conditions promote flammability (Naveh 1974). In addition, even when spring fires occur, survival and establishment probabilities are likely to be low, since germination does not occur before early winter (Schiller 1979), and because post-dispersal seed predation is typically heavy in this species (Nathan and Ne'eman 2000). Based on these assumptions the role

of seeds in brown cones, that open soon after maturation, play the biggest role in post-fire regeneration when a fall fire occurs before the fall seed dispersal period.

Conclusions

If indeed serotiny is advantageous for post-fire regeneration and its genetic control in *P. halepensis* is as proposed for *P. contorta*, one may raise the question of why it is only partial serotinous (overall mean was 34%)? Some of the answers are probably similar to those proposed for the case of *P. contorta*, which even under a fire return interval of 17-200 years since the end of the Pleistocene still has high frequencies of open cones (Perry and Lotan 1979). Several reasons for a low selection against non-serotinous genotypes can be proposed: (1) Brown closed cones, which open soon after maturation may also contribute to the post-fire canopy seed bank. (2) Fire patterns are highly variable in time and space with alternating high and low fire frequencies. Serotiny should be favoured under frequent fire regime, whereas non-serotiny should be favoured in long fire-free intervals when invasion to disturbed habitats is an advantage. Such a situation is typical for *P. halepensis* in Israel whose population-increase during historical times was coupled with abandonment of agricultural lands (Weinstein-Evron and Lev-Yadun 2000). (3) Long-distance dispersal of seeds released from non-serotinous and some serotinous cones occurs during hot and dry 'Sharav' events when seeds encounter favourable winds (Nathan et al. 1999).

To conclude, this study supports the notion that *P. halepensis* has a dual life-strategy of a post-fire obligate seeder as well as an invading species in the absence of fire (Nathan et al. 1999). The patchy, mosaic-like, pattern of the Mediterranean man-affected landscape creates a situation in which at the same time some populations experience forest fires while others may invade into habitats opened by other disturbances. Trees in an unburned stand may out cross with trees in a neighbouring post-fire stand and be burned later by a fire. Consequently, serotiny is a highly variable trait and kept at a relatively low level in *P. halepensis* trees in Israel. The changes in level of serotiny during tree growth, as well as the effect of the environment, result in a dynamic equilibrium between serotiny and non-serotiny. Trees increase seed sources for both post-fire regeneration and for inva-

sion without fire. Furthermore, serotinous cones may have an advantage when prospects for long-distance seed dispersal are weak, and closed brown cones also may serve as a seed source for post-fire regeneration. Thus, trees invest both in post-fire regeneration and invasion strategies, which seem to complement each other.

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