



The effect of stand age and microhabitat on soil seed banks in Mediterranean Aleppo pine forests after fire

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Abstract

Soil samples from three microhabitats (gaps, beneath shrubs and beneath trees) in five stands of various post-fire ages (6–55 years) were collected in an east Mediterranean Aleppo pine *Pinus halepensis* forest. Total germinable seed bank densities varied between 300 and 1300 seeds per m². Herbaceous taxa were the major constituents of the germinable seed bank in gaps, regardless of stand age. Perennials were the major components beneath shrubs in all stands except the youngest stand where herbaceous species were the major components in all microhabitats. Important tree and shrub species (e.g., *Pinus halepensis*, *Quercus calliprinos*, *Pistacia lentiscus*, *Phillyrea latifolia*) of the mature pine forest were not an important component of the soil seed bank and therefore, little resemblance was observed between the above-ground plant species composition and soil seed bank composition. This is consistent with the fact that these species regenerate by resprouting rather than by germination from the seed bank. Both microhabitats and forest-stands, which were of different ages, contributed to the variation in taxa richness, germinable seed density and diversity among samples. The effect of small-scale spatial heterogeneity (among microhabitats) was much more pronounced. In contrast to other studies, species richness, species diversity, and density of seed banks did not decrease with post-fire age. Moreover, stand age was a poor predictor for these attributes of the soil seed bank in an Aleppo pine forest. The heterogeneity plays an important role in conservation and management of this ecosystem.

Introduction

Fire is the major natural disturbance in coniferous forests, but because these plants are well adapted to fire, the recovery starts rapidly (Clark & Wilson 1994). Recruitment of seedlings after fire is dependent upon factors relating to the soil seed bank, such as size and composition of the dormant seed bank, longevity of the dormant seeds and their mortality due to fire (Whelan 1995; Bond & van Wilgen 1996). Therefore, there is great interest in the environmental factors and mechanisms that control seed bank size and composition.

Several spatial and temporal factors have been found to affect soil seed bank under secondary succession. The size and composition of a seed bank is often correlated with the density and composition of

the above ground vegetation (Trabaud et al. 1997; but see Looney & Gibson 1995). The number of seeds in the seed bank usually decreases with soil depth (Hill & Stevens 1981; Putz & Appanah 1987), but the protection of the seeds from fire's heat increases (Bond & van Wilgen 1996). Density and diversity of seed banks are usually high early in succession and decline with time (Garwood 1989; Pickett & McDonnell 1989; Roberts & Vankat 1991; but see Milberg 1995). The largest seed banks do not always appear in the youngest successional communities (Zammit & Zedler 1988). In addition, the number of herbaceous species in the seed bank decreases with time (Roberts & Vankat 1991; but see Looney & Gibson 1995).

Although numerous studies have investigated seed density and species composition of soil seed banks (Leck et al. 1989), relatively few studies have in-

vestigated either the among-stand effects, known as β -diversity (Sweeney 1956) or the effect of within-stand patchiness, α -diversity, on seed bank density and composition. None of these studies was carried out in east Mediterranean pine forests. The role of seed banks may be more important in this ecosystem with its seasonal climate than in ecosystems where seedling recruitment is not limited to one season (Jimenez & Armesto 1992).

The Aleppo pine forest on Mt. Carmel is a mosaic of many stands that differ in many environmental characteristics such as elevation, distance from the seashore, bedrock, soil, and fire history (Schiller et al. 1997). Furthermore, each of these forest stands is composed of a mosaic of various microhabitats, associated with the above-ground vegetation: gaps (clearings), beneath dwarf shrubs and beneath pine trees.

The purpose of this study is to explore patterns in soil seed bank within an Aleppo pine (*Pinus halepensis* Mill.) community in relation to the heterogeneity between and within stands on Mt. Carmel, Israel. Soil samples were collected from these three microhabitats in five pine forest stands of various post-fire ages. The importance of stand heterogeneity in shaping the soil seed bank in such pine forests was studied by comparing seedling richness, density, composition and diversity among these microhabitats across stands in different post-fire stages.

Methods

Study sites

The study sites were located within a 10×10 km area on Mt. Carmel, in the Israeli Mediterranean region. Each site is part of a forest stand of 1–10 ha. The climate is typical Mediterranean with a mean annual rainfall of 600–700 mm. Five sites of natural *Pinus halepensis* forests with known fire history, based on aerial photographs, were selected in the summer (June–July) of 1994. Stand age, altitude and rock formations of the various sites are presented in Table 1. The rocks in all sites are various formations of chalky marls with typical yellow Rendzina soils. The slope in all sites was $<10^\circ$. These five forest stands represented a time sequence ranging from 6 to 55 years since fire. No record of fire was documented for the oldest forest stand (Sanatorium) in the last 55 years, hence we used this value as an estimation for stand age. More data on

Table 1. Characteristics of the five Aleppo pine stands on Mount Carmel, Israel, in which soil seed bank was studied.

| Stand age | Location | Last fire | Altitude m above sea | Rock formation |
|-----------|------------|-----------|-------------------------|-------------------|
| 6 | Hai-bar | 1989 | 370 | Shair |
| 11 | Mitla | 1983 | 340 | Shamir |
| 20 | Etzba | 1974 | 180 | Dalia |
| 38 | Arkan | 1956 | 420 | Hreibe |
| >55 | Sanatorium | unknown | 340 | Dalia |

the post-fire regeneration of the natural Aleppo pine forest can be found in Ne'eman (1997).

The understorey of the natural pine forests on Mt. Carmel is composed mainly of small trees such as *Quercus calliprinos* and *Pistacia palaestina*, shrubs such as *Pistacia lentiscus*, *Phillyrea latifolia*, and climbers such as *Smilax aspera* and *Clematis cirrhosa* (Schiller et al. 1997). Among the pine trees there are shrubby patches dominated mainly by *Cistus salvifolius* and *C. creticus*, and gaps with mainly herbaceous vegetation. The area of the shrubby patches and the herbaceous gaps is from 10–100 m².

Soil sampling, fire treatment and seedling emergence

In each of the five sites, soil samples (25 × 25 × 5 cm deep) were collected every 5 m along each of five parallel 60–100 m transects. An effort was made to ensure that these transects represented the intra-site variation including the different moderate slopes and various aspects. The soil samples were categorized according to three microhabitat types: beneath trees, beneath shrubs and in gaps that were covered with the remains of the herbaceous vegetation. Eleven to 29 soil samples were collected for each microhabitat in each stand, except in the 38-year stand where no gaps were found to sample.

Each soil sample was spread uniformly over a germination (20 × 30 cm) flat. The flats were placed into a pre-heated dry-oven at 150 °C for 25 min. The actual temperature at 1 cm depth reached 100 °C. A preliminary study showed that this treatment yields maximal germination (Izhaki and Ne'eman unpublished data). The flats were randomized in an open garden and watered by an automatic overhead sprinkler system to keep the soil moist.

Seedling emergence was recorded every three days. Identification of seedlings was done to the species level or to the closest possible taxa. Seedlings were removed from flats after identification. The ex-

periment ran from 15 October 1994 until 28 January 1995, when no new seedlings emerged for 10 consecutive days. The number of germinated seeds per m² (hereafter germinable seed density) for all taxa was calculated.

Statistical analysis

The main objective of this study was to reveal the source of variation in soil seed bank among microhabitats and stands of different ages. Thus, first we used two-way ANOVA (SAS 1988) to analyze the effect of both microhabitats and stands on germinable seed density per m² in the upper (5 cm) soil layer (for each taxon and for all taxa combined), taxa richness (no. of taxa per flat) and diversity using Simpson index (D) (Begon et al. 1996). Germinable seed density data was transformed to log₁₀ (number+1) prior to statistical analysis to correct the normality of the distribution and to improve homogeneity of variance.

Although the five stands selected for this study represented a post-fire chronosequence, the variation in germinable seed density among stands may originate from the variation in other environmental factors than age (Zammit & Zedler 1994). Furthermore, a robust statistical analysis of time-since-fire effects demands replicates from each post-fire age, which unfortunately are not available under natural fire regime. Thus, sampling along transects from different slopes provided a minimum level of replication over the chronosequence. In order to reveal the differences in the seed bank among the three microhabitats while controlling the possible effect of stand age, we used the years since fire as the covariate. The relationships between microhabitats and germinable seed density, taxa richness and diversity were investigated using one-way ANCOVA (SAS 1988) with years since fire as covariate.

Germinable seed taxa composition

To examine the relationships among taxa composition and the external variables such as microhabitats and stands, Canonical Correspondence Analysis (CCA) was selected from the CANOCO 3.1 program of ter Braak (1987). This technique detects the patterns of variation in the germinable seed taxa data that can be explained 'best' by the observed external variables (Palmer 1993; ter Braak 1995). CCA ordines taxa using axes that are constrained to be linear combinations of the measured external variables, so that the relationship between taxa and these variables can be

clearly seen. Thus, ordination axes (representing gradient of change in community composition) in CCA are extracted with the constraint that the axes are linear combinations of pre-defined external variables which have been scored for each sample (Prentice & Cramer 1990). The main assumption of CCA is that the response model of the taxa to the external variable is unimodal (e.g., ter Braak 1995).

The ordination diagram of the CCA method allows simultaneous plotting of species scores and external variables in a 'species-conditional biplot' scaling. The centroids (weighed average) of categorical external variables are represented in the diagram by points rather than arrows (ter Braak 1994). Each taxa point in the diagram is at the centroid (weighted average) of the sample points in which it occurs (ter Braak 1995). Taxa that are close to each other are expected to be similar in their distribution across the stands and microhabitats.

To measure the association between species and external variables we used the eigenvalue that measures how much variation in the species data is explained by each axis, hence, by the external variables (ter Braak 1995). A Monte Carlo permutation test was used to test the extent to which variation in the community composition is related to variation in external data and is significantly different from random (ter Braak 1995). The external variables were randomly re-assigned to the samples within sites (restricted permutation test). The data were then re-analyzed in this way 99 times to test the null hypothesis that seed bank composition was unrelated to the external variables (microhabitats and years since fire). Significance probabilities of the null hypothesis are given for the overall 'trace' (sum) of the eigenvalues for the constrained (canonical) axes (ter Braak 1987, 1995). Density data was transformed to log₁₀ (number+1) prior to analysis.

Results

Sources of variation in soil-seed bank on Mt. Carmel pine forest

Two-way ANOVA revealed that both microhabitats and stands were responsible for the variation among samples in total germinable seed density, taxa richness and diversity (Table 2). However, the variation due to microhabitats was much stronger as indicated by higher mean square values. The coefficient of variation

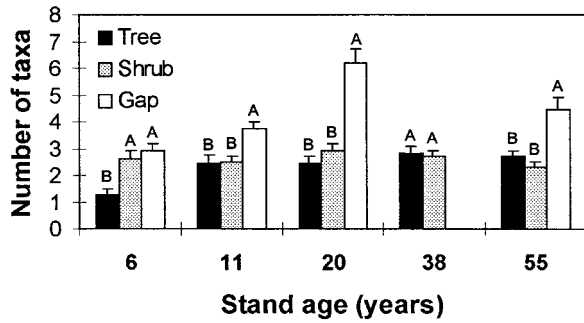


Figure 1. Taxa richness (mean \pm SE) of germinable seed bank of three microhabitats (gaps, beneath trees and beneath shrubs) from five pine-forest stands on Mt. Carmel Israel, last burned 6, 11, 20, 38 and 55 years before 1994. Different letters above bars indicate significant differences among microhabitat means within each stand (as indicated by Tukey HSD Multiple Comparison, $p < 0.05$).

(CV) of total seed density among the three microhabitats, in each of the five forest stands, ranged from 77% to 164%. These values were much higher than those found for the CV of total seed density among the five stands in each of the three microhabitats (ranged from 37% to 49%). These results suggest that the main source of variation in soil seed bank density on Mt. Carmel are the different microhabitats within each forest stand rather than different stands. Therefore, hereafter we focus mainly on the effect of the different microhabitats on soil seed bank variables.

Taxa richness

Among the 27 taxa identified in the entire seed bank (Table 3), only four were lignified perennials, the rest were herbaceous plants. The total number of germinated taxa per flat was significantly different among the three microhabitats while controlling for stand age by analysis of covariance (ANCOVA, microhabitat: $F_{2,306} = 38.86$, $p = 0.0001$; stand age: $F_{1,306} = 9.10$, $p = 0.003$).

In all stands the average number of germinated taxa per flat in the gaps was significantly higher than beneath the trees and the shrubs, except the six-year-old stand (Figure 1). The difference between the beneath-tree and beneath-shrub was not significant except in the youngest stand (Figure 1).

Total germinable seed density

Total germinable seed density on Mt. Carmel ranged between 300 and 1300 seeds per m^2 . The average total germinable seed density was significantly different among the three microhabitats but was not signifi-

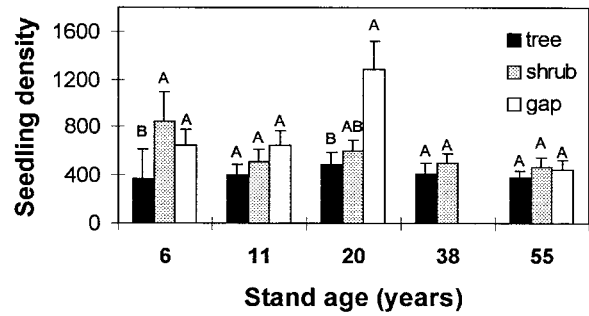


Figure 2. Total germinable seed density per m^2 (mean \pm SE) in three microhabitats (gaps, beneath trees and beneath shrubs) from five pine-forest stands on Mt. Carmel Israel, last burned 6, 11, 20, 38 and 55 years before 1994. Different letters above bars indicate significant differences among microhabitat means within each stand (as indicated by Tukey HSD Multiple Comparison, $p < 0.05$).

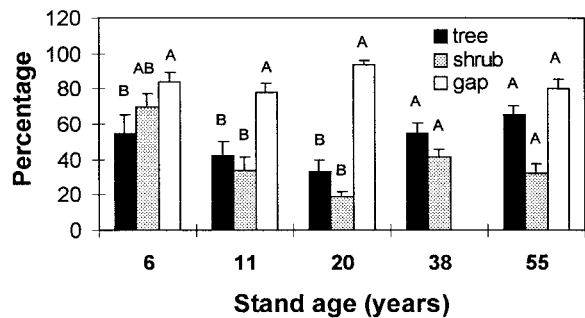


Figure 3. Percentage of seeds of herbaceous taxa (mean \pm SE) in the germinable seed bank of three microhabitats (gaps, beneath trees and beneath shrubs) from five pine-forest stands on Mt. Carmel Israel, last burned 6, 11, 20, 38 and 55 years before 1994. Different letters above bars indicate significant differences among microhabitat means within each stand (as indicated by Tukey HSD Multiple Comparison, $p < 0.05$).

cantly affected by stand age (covariant) as indicated by ANCOVA (microhabitat: $F_2 = 10.7$, $p = 0.0001$; stand age: $F_1 = 3.1$, $p = 0.08$). In two stands (ages 6 and 20 years) total germinable seed density was lower beneath trees than in gaps (Figure 2). The average (\pm STD) of total germinable seed density beneath trees across forest stands (411 ± 618 , $n = 114$) was significantly lower than beneath shrubs and in gaps (all samples from all stands pooled together, 651 ± 692 , $n = 194$, $t = 4.096$, $p < 0.0001$). Herbaceous taxa were the major constituent of the germinable seed bank in gaps, regardless of stand age (Figure 3).

Further ANCOVA analysis revealed different patterns of germinable seed densities for different taxa (Table 3). Microhabitat or stands (Table 3) did not significantly affect densities of *P. halepensis*. Significant effects of both microhabitat and stand-age on ger-

Table 2. Summary of the two-way ANOVA tables for the effect of forest stand and microhabitat on soil seed bank density, richness (number of taxa per sample) and diversity (D Simpson diversity index).

| Soil seed bank variable | Source of variation | df | MS | F |
|---------------------------|---------------------|-----|-------|--------------------|
| Germinable seed density | Microhabitat | 2 | 11.06 | 10.41*** |
| | Stand | 4 | 6.2 | 5.84*** |
| | Microhabitat × site | 7 | 2.24 | 2.11* |
| | Error | 294 | 1.06 | |
| Taxa richness | Microhabitat | 2 | 85.22 | 49.37*** |
| | Stand | 4 | 15.93 | 9.23*** |
| | Microhabitat × site | 7 | 10.05 | 5.83*** |
| | Error | 294 | 1.73 | |
| D Simpson diversity index | Microhabitat | 2 | 10.27 | 16.1*** |
| | Stand | 4 | 3.36 | 5.26*** |
| | Microhabitat × site | 7 | 1.07 | 1.68 ^{ns} |
| | Error | 294 | 0.64 | |

* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, ns = not significant.

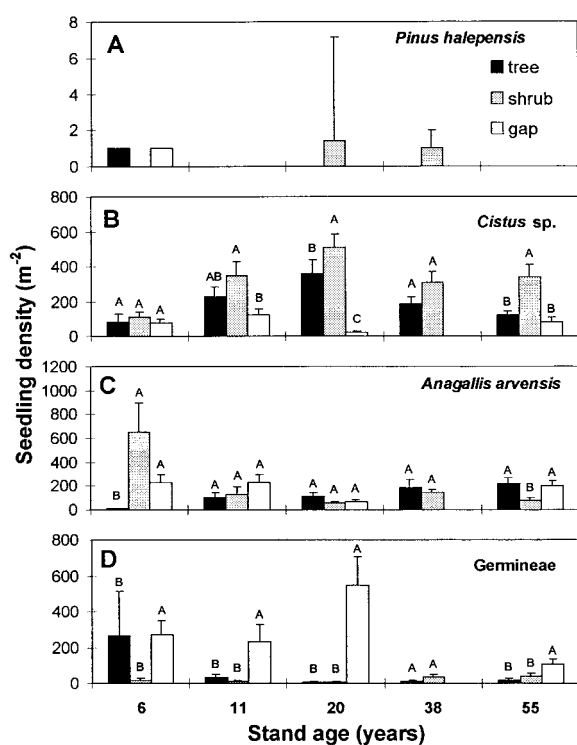


Figure 4. Germinable seed density of *Pinus halepensis* (A), *Cistus* sp. (B), *Anagallis arvensis* (C) and Gramineae taxa (D) per m² (mean \pm SE) in three microhabitats (gaps, beneath trees and beneath shrubs) from five pine-forest stands on Mt. Carmel Israel, last burned 6, 11, 20, 38 and 55 years before 1994. Different letters above bars indicate significant differences among microhabitat means within each stand (as indicated by Tukey HSD Multiple Comparison, $p < 0.05$).

minable seed density were found for *Cistus* sp. as well as several herbaceous species such as Gramineae taxa, *Anagallis arvensis*, *Convolvulus pentapetaloides* and *Scabiosa palaestina*. Density patterns across microhabitats and stand age of some of these species is plotted in Figure 4. Pine germinable seeds were found in only four out of 14 combinations of stands and microhabitats, and even then in very low density, less than 2 seeds per m² (Figure 4A), relative to other major taxa. *Cistus* germinable seed bank in the 6-year-old stand showed no differences among microhabitats (Figure 4B). However, in all other stands there was a consistent pattern where the density beneath shrubs was higher than that in gaps. Germinable seed density of *A. arvensis* was higher beneath shrubs, in the 6-year stand (>600 seeds per m²) than beneath trees, but not significantly different than in gaps (>200 seeds per m²; Figure 4C). No difference in seed density among microhabitats was detected in the other stands except for the most mature forest where lowest density was detected beneath shrubs (Figure 4C).

Germinable seed density of Gramineae taxa showed a consistent and significant pattern where in all stands the highest density was in gaps, whereas no significant differences were found between shrubs and trees (Figure 4D).

Germinable seed densities of Compositae (Asteraceae) taxa, *Plantago* sp., *Medicago* sp., *Trifolium* sp., *Hymenocarpus circinnatus*, *Erodium* sp. and *Scorpiurus muricatus* were affected by microhabitat whereas no significant effect was found for stand age. In only

Table 3. The effect of microhabitat and post-fire stand age (covariate) of germinable seed density, as analyzed by ANCOVA, on each of the 4 lignified perennial and 23 herbaceous taxa identified.

| Life form | Taxa | F-statistics | | |
|-------------------|------------------------------------|------------------------|---------------------|----------------------|
| | | Microhabitat (df=2) | Stand age (df=1) | Error MS (df=307) |
| Lignified | | | | |
| | <i>Ajuga chamaepytis</i> | 2.4 | 0.01 | 0.001 |
| | <i>Cistus</i> sp. | 25.6*** | 13.4*** | 0.22 |
| | <i>Pinus halepensis</i> | 1.7 | 0.1 | 0.0006 |
| | <i>Sarcopoterium spinosum</i> | 1.8 | 0.1 | 0.004 |
| Herbaceous | | | | |
| | <i>Anagallis arvensis</i> | 4.1* | 7.2** | 0.22 |
| | <i>Anthemis pseudocotula</i> | 1.1 | 2.9 | 0.0006 |
| | <i>Carthamus tenuis</i> | 1.1 | 1.0 | 0.0003 |
| | Compositae | 5.1** | 0.1 | 0.01 |
| | <i>Convolvulus pentapetaloides</i> | 18.1*** | 9.9** | 0.04 |
| | <i>Daucus</i> sp. | 2.5 | 2.9 | 0.0003 |
| | <i>Erodium</i> sp. | 4.4* | 1.4 | 0.01 |
| | <i>Geranium robertianum</i> | 0.8 | 0.5 | 0.0003 |
| | Gramineae | 70.7*** | 6.9** | 0.14 |
| | <i>Hippocrepis</i> sp. | 0.2 | 0.8 | 0.01 |
| | <i>Hymenocarpus circinnatus</i> | 9.6*** | 0.5 | 0.007 |
| | <i>Lotus</i> sp. | 1.1 | 1.9 | 0.02 |
| | <i>Medicago</i> sp. | 8.2*** | 1.3 | 0.01 |
| | <i>Mercurialis annua</i> | 0.6 | 9.8** | 0.004 |
| | <i>Notobasis syriaca</i> | 1.0 | 0.5 | 0.0002 |
| | <i>Plantago</i> sp. | 26.8*** | 3.5 | 0.06 |
| | <i>Ranunculus asiaticus</i> | 1.5 | 0.4 | 0.004 |
| | <i>Scabiosa palaestina</i> | 5.4** | 6.3* | 0.001 |
| | <i>Scorpiurus muricatus</i> | 5.0** | 0.1 | 0.007 |
| | <i>Sedum</i> sp. | 1.9 | 1.0 | 0.001 |
| | <i>Sonchus oleraceus</i> | 0.2 | 2.2 | 0.002 |
| | <i>Trifolium</i> sp. | 8.9*** | 0.5 | 0.02 |
| | <i>Vicia peregrina</i> | 1.1 | 1.0 | 0.0002 |

* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

in species, *Mercurialis annua*, the effect of microhabitat was not significant when there was a significant effect of stand age. In all the other 14 taxa, including *P. halepensis*, no significant effect was detected for microhabitat or stand age (Table 3).

Taxa diversity

The Simpson diversity index (D) of germinable seed taxa was significantly influenced by both the microhabitat ($F_2 = 18.6$, $p = 0.0001$) and by the stand age, used as covariate ($F_1 = 8.75$, $p = 0.003$). The mean diversity index in the gaps was higher than in the other two microhabitats, except in the 11-year-old for-

est where it was not significantly higher than beneath the trees (Figure 5). In all stands, no significant differences were detected between the diversity indices beneath trees and shrubs (Figure 5).

Taxa composition of the germinable seed bank in relation to microhabitat and forest stands

The Monte Carlo permutation test ($F = 11.82$, $p < 0.01$) provided strong evidence that the null hypothesis of no correlation between variation in taxa composition of germinable seed bank and the external variables (microhabitats and stands) can be rejected. The ordination plot (Figure 6) illustrates the importance of

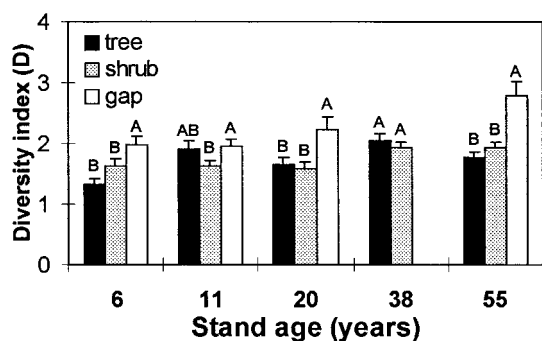


Figure 5. Simpson Diversity index (D) of germinable seeds per m^2 (mean \pm SE) in three microhabitats (gaps, beneath trees and beneath shrubs) from five pine-forest stands on Mt. Carmel Israel, last burned 6, 11, 20, 38 and 55 years before 1994. Different letters above bars indicate significant differences among microhabitat means within each stand (as indicated by Tukey HSD Multiple Comparison, $p < 0.05$).

the variation among the three microhabitats but also among forest stands. The first axis (eigenvalue=15%) mainly represents the influence of the different microhabitats on taxa composition whereas the second axis (eigenvalue=3%) mainly represents the variation among forest stands.

The 'gap' is positively correlated with the first axis whereas the 'tree' and shrub' microhabitats are negatively correlated with this axis. On the other hand, the 'tree' is separated from the other two microhabitats on the second axis. Although stand influenced taxa composition, there is no clear direction of an age influence. For example, the youngest stand (PF6) and the oldest stand (PF55) are both negatively correlated with axis 2. The composition of the germinable seed bank in the 11 and 38 year stands are similar (both located on the upper left quarter of the diagram). Thus, other factors, rather than age alone, contributed to the separation of the five forest stands along the two axes of the diagram.

Many taxa are located close to the center of the diagram, indicating an equal (or no) effect of the various external variables on seed bank composition. However, the Gramineae taxa are clearly associated with the gaps whereas *Cistus* sp. is associated with the shrub microhabitat (Figure 6). *P. halepensis* is positively correlated with the older stands and the tree and shrub microhabitat. However, because of the very low densities and number of cases in which pine seeds were recorded, we must be very careful interpreting this result.

Discussion

Seed bank composition on Mt. Carmel pine forest

The soil seed bank in a forest, is an assemblage of seed banks of the various plant species in the site. The soil seed bank of each species is a product of seed production, dispersal, predation, mortality and germination. In most of the species that recruit seedlings after fire, in the Mediterranean basin, germination occurs mainly during the first year after fire (Keeley 1994; Daskalidou & Thanos 1996). Furthermore, the main changes after fire are in vegetation structure rather than in species composition (Trabaud 1994; Schiller et al. 1997). However, the dynamics of post-fire seed banks is complex. Differences in life history traits among species are important factors during post-fire recovery. First age of reproduction, fecundity, life span and seed longevity affect community dynamics and soil seed bank size and composition (Bond & van Wilgen 1996).

Lack of correspondence between seed bank composition and the established above ground vegetation, especially in late successional stages, was described in coniferous forests (e.g. Trabaud et al. 1997, see review in Archibold 1989). Many species of late successional stages are post-fire resprouters, which have large non-refractory seeds (Keeley 1991). Therefore, predation of these seeds by insects, small mammals and birds may play a major role in reducing their presence in the seed bank (Kjellsson 1992; Maron & Simms 1997). Most of the trees and shrubs accompanying *P. halepensis* in its natural forests are resprouting species (Schiller et al. 1997). Such resprouting species have short-lived, heat sensitive seeds (Keeley 1991, 1994) and are, therefore, absent from heat treated soil seed bank samples. That is the most likely reason for the absence of *Quercus calliprinos*, *Pistacia palaestina*, *P. lentiscus*, *Phillyrea latifolia* and other prominent understorey species from the soil seed bank irrespective of stand age in our study.

P. halepensis is a post-fire obligate seeder, the adult plants do not survive a crown fire and recovery is achieved only by seed germination (Daskalidou & Thanos 1996; Ne'eman 1997). Young Aleppo pine trees begin to produce female cones at the age of 3–4 years, but massive production does not occur until the age of about 10 years, depending on tree size (Ne'eman unpublished data). Most of its cones disperse their seeds during summer but it also has serotinous cones that disperse seeds only after fire

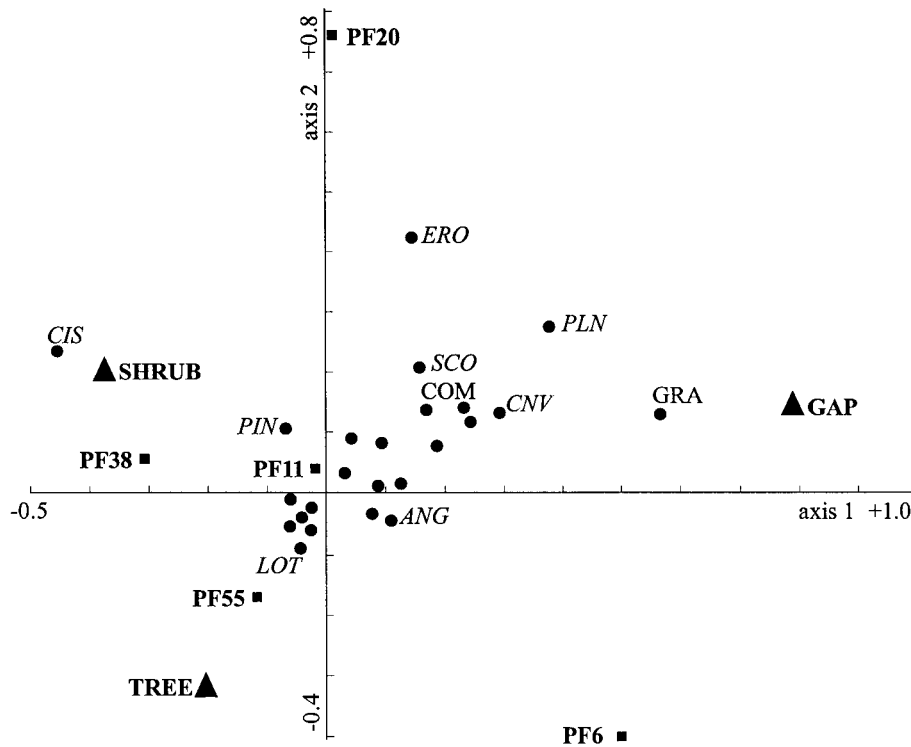


Figure 6. Ordination diagram based on a canonical correspondence analysis (CCA) showing the variation in germinable seed density of different taxa (●) on Mt. Carmel in relation to three microhabitats (TREE=beneath trees, SHRUB=beneath shrubs, GAP=clearings) and five pine-forest stands (PF6, PF11, PF20, PF38 and PF55: where the numbers are years since fire). The diagram displays 18% of the total inertia (=weighted variance) in the germinable seed density and 76% of the variance accounted for relative to the total variance in the germinable species/taxa X external variable relations. The eigenvalue of the first axis (horizontally) is 0.15 and axis 2 (vertically) is 0.03. The eigenvalues of the third and fourth axes (not displayed) are 0.014 and 0.003, respectively. Germinable species/taxa are weighted average of site scores, and external variables are centroids of sample points belonging to each category. The scale marks along the axes apply to the qualitative external variables; species/taxa scores were multiplied by 0.405 to fit in the coordinate system. Species/taxa abbreviations: ANG – *Anagallis arvensis*, CIS – *Cistus* sp., CNV – *Convolvulus pentapetaloides*, COM – Compositae, ERO – *Erodium* sp., GRA – Gramineae, LOT – *Lotus* sp., PIN – *Pinus halepensis*, PLN – *Plantago* sp., SCO – *Scorpiurus muricatus*.

(Schiller 1978; Daskalakou & Thanos 1996). Therefore, pine seeds are expected to be represented in soil seed banks of post-fire stands older than 10 years. Pine seeds are predated on the trees by rats, which inhabit mature pine forests in Israel (Haim & Izhaki 1994) and are capable of scaling the cones in order to get to the seeds (Aisner 1984). Pine seed predation by birds (Nystrand & Granstrom 1997; Saracino et al. 1997), rodents (Martinezdelgado et al. 1996; Vanderwall 1997), and probably ants continues intensively after dispersal. This high predation pressure may explain the extremely low densities of pine seeds in all habitats in all stands. As far as we know, *P. halepensis* is not a masting species, therefore the absence of pine seeds in the soil is not likely to be the result of annual fluctuations in seed production. Other studies also showed that the dominant species might not be an

important component of seed banks in mature forest (e.g. Mladenoff 1990).

Cistus salviifolius and *C. creticus*, the typical dwarf-shrub species of the Israeli pine forests, are also post-fire obligate seeders that recover by germination from their soil seed bank (Ne'eman 1997). These species, as all other members of the Cystaceae family, are hard seeded and need heat pulse to crack their seed coat before germination can begin (Thanos et al. 1992). *Cistus* germinates mainly during the first post-fire winter forming high-density stands. Plants begin to flower in their third year producing many flowers and many tiny seeds. Pronounced stand decline was observed in 15-year-old stands of *C. monspeliensis* and *C. albidus* (Roy & Sonie 1992). The growth of adjacent pine trees, which shade the *Cistus* dwarf shrubs, reduce their vigor. As a result, an increase in seed den-

sity is expected in the first post-fire period, followed by a decline as the forest matures. Our results are in agreement with this prediction, a maximum of about 500 seeds per m² was found in the 22-year-old stand. The fact that seed density was still high (about 300 seed per m²) in the 55-year-old stand and the fact that *Cistus* seeds are tiny with no special mechanism for long-distance dispersal, provide evidence for the high longevity of the seeds. *Cistus* seed densities were, in most cases, the highest under its own shrubs, indicating that the sites kept by the adult plants will probably be kept also by their own offspring after their death in case of a fire.

Seeds of some herbaceous species such as *Anagallis arvensis*, were found in all microhabitats in all stands including the mature forest. Seeds of these species may persist in a dormant but viable state in large numbers even when the pine forest has fully developed (Enright 1985). Unfortunately, little attention has been paid so far to the mechanisms determining the probability that these seeds will arrive and survive in ephemeral and unpredictable gaps or beneath trees. Other herbaceous species, and mainly grasses, were more abundant in the young stands and mainly in the gaps. This can be a result of short life span of the seeds, absence of herbaceous species under the trees and shrubs in the mature forest, or combination of both.

Spatial pattern

According to the classical succession theory, a change of species, life forms, and vegetation formation is likely to occur with time. In Israel, in the Mediterranean region, the first successional stages are dominated by pioneer herbaceous species that will be replaced by dwarf-shrubs, shrubs and a final stage of trees that dominate as the forest matures (Zohary 1973). The Aleppo pine forests on Mt. Carmel, which have developed by invasion into abandoned agricultural lands, are a mosaic-like formation with big pine trees, an understorey of small trees, patches of *Cistus* dominated dwarf shrubs and herbaceous dominated gaps (Schiller et al. 1997). This spatial structure is also present in mature forests. Notably all the dominant species of the various habitats are post-fire obligate seeders. After each fire, a new session of germination, growth, competition, mortality and establishment of survivors occurs. Such a spatial structure could theoretically evolve from an equal density of seed bank that will germinate during the first winter and will be

followed by greater mortality, during the first summer, of pine trees in the low and medium quality sites and *Cistus* mortality in the low quality sites. Competition for resources, mainly water and light, during the following seasons, can leave the pines in the best quality sites, *Cistus* in the medium and herbaceous species in the low quality sites.

However, this was not the pattern in our case, because pine seeds were almost absent from all habitats. In a study of post-fire soil seed bank, high densities of pine seeds were found under the projection of the burned canopies and low densities outside them (Ne'eman et al. 1992; Ne'eman & Izhaki 1998). Pine seedlings had the opposite pattern during the first winter (Eshel et al. unpublished data). The reason for the low germination under the burned canopies is the extreme pH of the ash layer (Henig-Sever et al. 1996). The ash also prevents germination of *Cistus* and herbaceous species (Ne'eman et al. 1993). The result is low mortality and high growth rate of the pine seedlings at the sites that were occupied by their likely mother trees. These seedlings continue to grow faster for the next 20 years and have the highest chances of replacing the burned trees (Ne'eman & Izhaki 1998). In the gaps, seeds of grass and other herbaceous species dominate. Pine and *Cistus* seedlings that do germinate there probably die during the first and second summers. Shallow soil can be the cause for this differential death of seedlings in the locations of the gap microhabitat. In the rest of the area, high competition takes place between the pine and *Cistus* seedlings (Katz 1993). The relative quick growth of *Cistus* in the first three years gives them an advantage over the pine seedlings in this microhabitat. Long term field observation on population dynamics of the various species in the different habitat with parallel monitoring of site qualities are necessary for further establishment of this proposed model.

A considerable spatial heterogeneity in seed banks was detected among the three microhabitats although they were located within a range of a few meters in each forest stand. The coefficient of variation of seed density among the three microhabitats in the five forest stands on Mt. Carmel (CV=77–164%) was higher than those calculated for the intrasite variation in tropical forests (8–88%, Garwood 1989). In addition, a large-scale heterogeneity in seed banks was also documented among the five forest stands, all of them located within an area of 10 × 10 km. Such interstand heterogeneity was detected in other ecosystems such as Australian tropical forest stands 8–27 km

apart (Hopkins & Graham 1983) and the Californian chaparral (Sweeney 1956).

The results do not support the generalization that seed density and diversity should decrease with time since fire (Pickett & McDonnell 1989). Actually, the influence of time since fire on germinable seed density, richness and diversity in Mt. Carmel pine forest is unpredictable. Although the age of the forest stands ranged from 6 to 55 years after fire, several attributes of soil seed banks were found to be general, regardless of stand age. For example, the soil seed bank in gaps was characterized by the highest taxa richness and represented the most diverse microhabitat with the largest fraction of herbaceous species. Another generalization that emerged from this study was that in most cases, soil seed banks beneath trees contained the lowest seed density. The proportion of herbaceous species beneath trees was greater or equal to than that beneath shrubs, and species richness and diversity were similar to that beneath shrubs. These findings emphasize the role of gaps in keeping a high level of diversity and richness in late successional stages.

To conclude, this study demonstrates that the high within-stand spatial heterogeneity of Aleppo pine forests, comprised of three main microhabitats (trees, shrubs and gaps), is reflected in its germinable soil seed bank. This kind of heterogeneity is typical for stands of various post-fire ages. Hence, the result is that post-fire regeneration, via seed germination, will be similar in forests differing in their fire history. The heterogeneity has a direct effect on biodiversity, variation of genetic pools and therefore, has an important role in conservation and management of such a disturbance dependent ecosystem. For example, the common salvage harvesting practice of trees after fire by mechanical means causes destruction of the natural microhabitats and redistribution of the soil seed bank. Therefore, it is recommended to minimize interference in the vulnerable regeneration stage.

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References

- Aisner, R. 1984. Aspects of learning to open pine cones by the black rat (*Rattus rattus*) and the spread of this behaviour in Israel. M. Sc. Thesis, Tel Aviv University, Tel Aviv, Israel (in Hebrew with English abstract).
- Archibald, O. W. 1989. Seed banks and vegetation processes in coniferous forests. Pp. 107–122. In: Leck, M. A., Parker, V. T. & Simpson, R. L. (eds), *Ecology of Soil Seed Banks*. Academic Press, New York.
- Begon, M., Harper, J. L. & Townsend, C. R. 1996. *Ecology: Individuals, Populations and Communities*, 3rd Edition. Sinauer Associates, Inc. Sunderland, Massachusetts.
- Bond, W. J. & van Wilgen, B. W. 1996. *Fire and Plants*. Chapman & Hall, London, 263 pp.
- Clark, L. C. & Wilson, M. V. 1994. Heat-treatment effects on seed bank species of an old-growth Douglas-fir forest. *Northwest Sci.* 68: 1–5.
- Daskalakou, E. N. & Thanos, C. A. 1996. Aleppo pine (*Pinus halepensis*) postfire regeneration: The role of canopy and soil seed banks. *Int. J. Wildland Fire* 6: 59–66.
- Enright, N. 1985. Evidence of a soil seed bank under rain forest in New Guinea. *Aust. J. Ecol.* 10: 67–71.
- Garwood, N. C. 1989. Tropical seed banks: a review. Pp. 149–209. In: Leck, M. A., Parker, V. T. & Simpson, R. L. (eds), *Ecology of Soil Seed Banks*. Academic Press, New York.
- Haim, A. & Izhaki, I. 1994. Changes in rodent community during recovery from fire: relevance to conservation. *Biodivers. Conserv.* 3: 573–585.
- Henig-Sever, N., Eshel, A. & Ne'eman, G. 1996. pH and osmotic potential of pine ash as post-fire germination inhibitors. *Physiol. Plant.* 96: 71–76.
- Hill, M. O. & Stevens, P. A. 1981. The density of viable seed in soils of forest plantations in upland Britain. *J. Ecol.* 69: 693–709.
- Hopkins, M. S. & Graham, A. W. 1983. The species composition of soil seed banks beneath lowland tropical rainforests in North Queensland, Australia. *Biotropica* 15: 90–99.
- Jimenez, H. E. & Armesto, J. J. 1992. Importance of the soil seed bank of disturbed sites in Chilean matorral in early secondary succession. *J. Veg. Sci.* 3: 579–586.
- Katz, G. 1993. The interaction between *Pinus halepensis* and *Cistus salvifolius* in the first stages of post-fire succession on Mt. Carmel. M. Sc. Dissertation, Tel Aviv University, Tel Aviv, Israel (in Hebrew with English abstract)
- Kjellsson, G. 1992. Seed banks in Danish deciduous forests: Species composition, seed influx and distribution pattern in soil. *Ecography* 15: 86–100.
- Keeley, J. E. 1991. Seed germination and life history syndromes in the California chaparral. *Bot. Rev.* 57: 81–116.
- Keeley, J. E. 1994. Seed-germination patterns in fire-prone Mediterranean climate regions. Pp. 239–273. In: Arroyo, M. T. K. Zedler, P. H. & Fox M. D. (eds), *Ecology and Biogeography of Mediterranean Ecosystems in Chile, California, and Australia*. Springer-Verlag, New York.
- Leck, M. A., Parker, V. T. & Simpson, R. L. 1989. *Ecology of Soil Seed Banks*. Academic Press, New York. 462 pp.
- Looney, P. B. & Gibson, D. J. 1995. The relationships between the soil seed bank and above-ground vegetation of a coastal barrier island. *J. Veg. Sci.* 6: 825–836.
- Maron, J. L. & Simms, E. L. 1997. Effect of seed predation on seed bank size and seedling recruitment of bush lupine (*Lupinus arboreus*). *Oecologia* 111: 76–83.

- Martinezdelgado, E., Mellink, E., Aguirrerivera, J. R. & Garciamoya, E. 1996. Removal of pinon seeds by birds and rodents in San Luis Potosi, Mexico. *Southwest. Naturalist* 41: 270–274.
- Milberg, P. 1995. Soil seed bank after eighteen years of succession from grassland to forest. *Oikos* 72: 3–13.
- Mladenoff, D. J. 1990. The relationship of the soil seed bank and understorey vegetation in old-growth northern hardwood-hemlock treefall gaps. *Can. J. Bot.* 68: 2714–2721.
- Ne'eman, G. 1997. Regeneration of natural pine forest – a review of work done after the 1989 fire in Mount Carmel, Israel. *Int. J. Wildland Fire* 7: 295–306.
- Ne'eman, G., Lahav, H. & Izhaki, I. 1992. Spatial pattern of seedlings one year after fire in a Mediterranean pine forest. *Oecologia* 91: 365–370.
- Ne'eman, G., Meir, I. & Ne'eman, R. 1993. The effect of ash on germination and early growth of shoots and roots of *Pinus*, *Cistus* and annuals. *Seed Sci. Technol.* 21: 339–349.
- Ne'eman, G. & Izhaki, I. 1998. Stability of pre- and post-fire spatial structure of pine trees in Aleppo pine forests. *Ecography* 21: 535–542.
- Nystrand, O. & Granstrom, A. 1997. Post-dispersal predation on *Pinus sylvestris* seeds by *Fringilla* spp – ground substrate affects selection for seed color. *Oecologia* 110: 353–359.
- Palmer, M. W. 1993. Testing the performance of canonical correspondence analysis. *Ecology* 74: 2215–2230.
- Pickett, S. T. A. & McDonnell, M. J. 1989. Seed bank dynamics in temperate deciduous forest. Pp. 123–147. In: Leck, M. A., Parker, V. T. & Simpson, R. L. (eds), *Ecology of Soil Seed Banks*. Academic Press, New York.
- Prentice, H. C. & Cramer, W. C. 1990. The plant-community as a niche bioassay: environmental correlates of local variation in *Gypsophila fastigiata*. *J. Ecol.* 78: 313–325.
- Putz, F. E. & Appanah, B. 1987. Buried seeds, newly dispersed seeds, and the dynamics of a lowland forest in Malaysia. *Biotropica* 19: 326–339.
- Roberts, T. L. & Vankat, J. L. 1991. Floristics of a chronosequence corresponding to old field-deciduous forest succession in southwestern Ohio. II. Seed Banks. *Bull. Torrey Bot. Club* 118: 377–384.
- Roy, J. & Sonie, L. 1992. Germination and population dynamics of *Cistus* species in relation to fire. *J. App. Ecol.* 29: 647–655.
- Saracino, A., Pacella, R., Leone, V. & Borghetti, M. 1997. Seed dispersal and changing seed characteristics in a *Pinus halepensis* Mill. forest after fire. *Plant Ecol.* 130: 13–19.
- SAS Institute, 1988. *SAS/STAT User's guide*, Cary, NC, USA.
- Schiller, G. 1978. Factors involved in natural regeneration of Aleppo pine. Ph. D. Thesis, Tel Aviv University, Tel Aviv, Israel (in Hebrew with English abstract).
- Schiller, G., Ne'eman, G. & Korol, L. 1997. Post-fire vegetation dynamics in native *Pinus halepensis* Mill. Forest on Mt. Carmel, Israel. *Isr. J. Plant Sci.* 145: 297–308.
- Sweeney, J. R. 1956. Responses of vegetation to fire: A study of the herbaceous vegetation following chaparral fires. *Publ. Bot.* 28: 143–249.
- ter Braak, C. J. F. 1987. a FORTRAN Program for Canonical Community Ordination by [Partial] [Detrended] [Canonical] Correspondence Analysis, Principal Components Analysis and Redundancy Analysis (Version 2.1). Agriculture Mathematics Group, Wageningen.
- ter Braak, C. F. J. 1994. Canonical community ordination. Part I: Basic theory and linear methods. *Ecoscience* 1: 127–140.
- ter Braak, C. F. G. 1995. Ordination. Pp. 91–173. In: Jongman, R. H. G., ter Braak, C. J. F. & van Tongeren, O. F. R. (eds), *Data Analysis in Community and Landscape Ecology*. Cambridge University Press, Cambridge.
- Thanos, C. A., Georghiou, K., Kadis, C. & Pantazi, C. 1992. *Cistaceae* – a plant family with hard seeds. *Isr. J. Bot.* 41: 251–263.
- Trabaud, L. 1994. Post fire community dynamics in the Mediterranean basin. Pp. 1–15. In: Moreno, J. N. and Ochel, W. C. (eds), *The Role of Fire in Mediterranean ecosystems*. Springer, Berlin.
- Trabaud, L., Martinezsanchez, J. J., Ferrandis, P., Gonzalezchocha, A. I. & Herranz, J. M. 1997. Above-ground vegetation and soil seed bank- The contribution to the cyclical stability of a mixed pine forest of *Pinus halepensis* and *P. Pinaster*. *Can. J. Bot.* 75: 1012–1021.
- Vanderwall, S. B. 1997. Dispersal of singleleaf pinon pine (*Pinus monophylla*) by seed-caching rodents. *J. Mammal.* 78: 181–191.
- Whelan, R. J. 1995. *The Ecology of Fire*. Cambridge University Press, New York, 346 pp.
- Zammit, C & Zedler, P. H. 1988. The influence of dominant shrubs, fire and time since fire on soil seed in mixed chaparral. *Vegetatio* 75: 175–187.
- Zammit, C & Zedler, P. H. 1994. Organisation of the soil seed bank in mixed chaparral. *Vegetatio* 111: 1–16.
- Zohary, M. 1973. *Geobotanical Foundations of the Middle East*. Gustav Fischer, Stuttgart-Swets et Zeitlinger, Amsterdam.