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אין לעשוח כל שימוש מסחרי במאמרים.
SOIL SEED BANKS IN MEDITERRANEAN PINE FORESTS

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Introduction

In most habitats a substantial number of dormant seeds can be found in the soil (Leck et al. 1989). The ultimate goal of such seed banks is to provide an immediate source of propagules for regeneration after disturbance (Thompson 1992). According to whether or not viable seeds persist for more than a year, the seed bank of any plant species is classified as ‘transient’ or ‘persistent’ (Thompson and Grime 1979). Persistent seed banks play a predominant role in habitats where disturbances, such as fire, are frequent and unpredictable. Most plant communities in the Mediterranean region are subjected to disturbances, such as uncontrolled grazing and logging, and they are susceptible to fires mainly during the long (4-7 months) dry summer (Quezel 2000). The effects of fire on Pinus halepensis and P. brutia forests are most remarkable, because like other pine species, they are highly flammable (Navah 1974, Agee 1998). Because seed banks are intimately connected with disturbance, it would be expected that seed banks of these disturbed pine forests would play a major role in their recovery after fire and other disturbances. Furthermore, the role of seed banks should be even more important under the seasonal Mediterranean climate than in ecosystems where seedling recruitment is not limited only to one short season (Jiménez and Armesto 1992).

In contrast to the enormous literature on seed banks of plant communities worldwide (e.g., Vyvsey 1988, 1989, Leck et al. 1989, Thompson 1992, Kigel and Galil 1995 and references within), only a few studies have been published on forest soil seed banks in the Mediterranean basin, and these were mainly on broadleaved forests (e.g., Trabaud 1994, Valbuena and Trabaud 1995, Ferrandis et al. 1999b). Here we review the available information on seed banks of Mediterranean pine forests. We will first describe the composition of soil seed banks and their post-fire dynamics. Then we will consider their function in an attempt to draw some general conclusions about their importance. The role of canopy-stored pine seed banks is reviewed in another chapter of this volume (Nathan and Ne’eman 2000).

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General Characteristics of Seed Banks in Mediterranean Pine Forests

Species Composition

Seed bank composition is time- and space-dependent, as we will discuss in the next sections. Here we focus on the general floristic characters of the soil seed bank in Mediterranean pine forests immediately and several years after fire, presenting the dominant taxa in the soil as determined in several different studies (Table 1). Probably the most interesting point concerning species composition of soil seed banks in pine forests is the almost total absence of pine seeds. This point will be discussed later in this chapter.

The genus Cistus (Cistaceae) is probably the most important contributor to the seed banks of pine forests around the Mediterranean basin. All Cistus species are obligate seeders that totally depend on well-furnished seed bank for their recovery after disturbance (Troumbis and Trabaud 1986, Trabaud and Oustric 1989, Thanos et al. 1992, Santiesteban et al. 1993, Troumbis 1996, Pugnaire and Lozano 1997, Ferrandis et al. 1999a, Trabaud and Renard 1999). Le Houërou (1974) defined twelve Cistus species as typical pyrolyphites. Cistus monspeliensis was the major component of the seed bank in P. pinaster forest in SE Spain immediately after fire. C. ladanifer was the major component in a 12-year-old P. halepensis - P. pinaster mixed forest in Spain. Cistus salvifolius and C. creticus were the major components of soil seed banks in 11 and 20 years post-fire P. halepensis forests in Israel and remained an important component even 38 and 55 years after fire (Ne’eman and Ishaki 1999).

Erica spp. (Ericaceae) and Rosmarinus officinalis (Lamiaceae) are the other two common woody perennials in the soil seed banks of west Mediterranean pine forests (Table 1), but are absent from its eastern part. The importance of annual plants in the soil seed bank is closely related to the successional stage of the pine forest. They are particularly abundant immediately after fire, and their density usually decreases in later stages. Trifolium spp. (Fabaceae) are among the most common species in soil seed banks immediately after fire in P. pinaster forest in Spain (Table 1). Indeed, considerable amounts of annual leguminous species germinate in recently burned Aleppo pine forests (Papavassiliou and Arianoutsou 1993, Kazanis and Arianoutsou 1996) as well as in P. brutia forests (Thanos et al. 1989). Poaceae taxa were dominant in the seed bank of P. halepensis forest 6 years after fire with decreasing densities during later successional stages (Table 1). The annual Anagallis arvensis (Primulaceae) is an important constituent of the seed banks in both young and mature P. halepensis forests in Israel (Table 1). In comparison, annual and perennial herbaceous species of Brassicaceae and Asteraceae are the most important taxa in the seed bank of unburned as well as post-fire oak forest in NW Spain (Table 1).

Above Ground Community versus Below Ground Seed Bank Composition

Studies in various habitats have found that the composition of the seed bank is not representative of the above ground plant community (Leck 1989, Trabaud 2000a). This contradiction has been consistent in studies of coniferous forests although the degree of divergence varies from site to site (Archibold 1989). The general pattern is that dominant species of the mature forest are sparse or absent from the soil seed
bank, whereas those from early successional stages that are absent from the mature forest community are often well represented in the soil seed bank (Harper 1997, Pickett and McDonnell 1989, Thompson 1992). The same pattern was observed in Mediterranean pine forests. As mentioned, one of the most striking examples is *P. halepensis*, which is a dominant species in pine forests but is almost absent from the soil seed banks of the forests a few years after fire (see below).

<table>
<thead>
<tr>
<th>Location</th>
<th>Forest type</th>
<th>Time since fire</th>
<th>Taxa</th>
<th>Growth form</th>
<th>Relative abundance in seed bank %</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Israel</td>
<td><em>Pinus halepensis</em></td>
<td>6 years</td>
<td>Grasses (Poaceae) Cistus spp. (Cistaceae) Anagallis arvensis (Primulaceae)</td>
<td>Dwarf shrub Annual</td>
<td>78 16</td>
<td>Ne’eman and Izhaki 1999, Izhaki et al. MS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>11 years</td>
<td>Cistus spp. (Cistaceae) Anagallis arvensis (Primulaceae) Grasses (Poaceae)</td>
<td>Dwarf shrub Annual</td>
<td>43 32</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>20 years</td>
<td>Cistus spp. (Cistaceae) Anagallis arvensis (Primulaceae) Grasses (Poaceae)</td>
<td>Grass Dwarf shrub Annual</td>
<td>12 66 25</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>38 years</td>
<td>Cistus spp. (Cistaceae) Anagallis arvensis (Primulaceae) Grasses (Poaceae)</td>
<td>Grass Annual</td>
<td>4 46</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>55 years</td>
<td>Cistus spp. (Cistaceae) Grasses (Poaceae) Anagallis arvensis (Primulaceae)</td>
<td>Dwarf shrub Grass Annual</td>
<td>40 6 60</td>
<td></td>
</tr>
<tr>
<td>SE Spain</td>
<td><em>Pinus pinaster</em></td>
<td>2 days</td>
<td>Citrus monspeliensis (Cistaceae) Trifolium glomeratum (Fabaceae) Rosmarinus officinalis (Lamiaceae)</td>
<td>Grass Dwarf shrub Shrub Annual</td>
<td>29 6 31 15</td>
<td>Ferrandis et al. 1996</td>
</tr>
<tr>
<td>Spain</td>
<td><em>P. halepensis</em></td>
<td>12 years</td>
<td>Citrus latifolius (Cistaceae) Eriogonum sp. (Ericaceae) Rosmarinus officinalis (Lamiaceae) Cardamine pratensis (Brassicaceae) Helichrysum stoechas (Brassicaceae) Sonchus oleraceus (Asteraceae) Conyza campestris (Asteraceae) Cardamine pratensis (Brassicaceae) Festuca elatius (Poaceae)</td>
<td>Shrub Dwarf shrub</td>
<td>47 40 6</td>
<td>Trabaud et al. 1997</td>
</tr>
<tr>
<td>NW Spain</td>
<td><em>Quercus pyrenaica</em></td>
<td>Unburned</td>
<td>Cardamine pratensis (Brassicaceae) Helichrysum stoechas (Brassicaceae) Sonchus oleraceus (Asteraceae) Conyza campestris (Asteraceae) Cardamine pratensis (Brassicaceae) Festuca elatius (Poaceae)</td>
<td>Perennial herbaceous Perennial herbaceous Biennial herbaceous Annual</td>
<td>45 7 6 17</td>
<td>Valbuena and Trabaud 1995</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3 days</td>
<td></td>
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</table>
More than 50% of the species in a 12-year old mixed *P. halepensis* – *P. pinaster* forest in Spain were not present in the soil seed bank (Trabaud et al. 1997). These species (e.g., *Phillyrea angustifolia*, *Pistacia lentiscus*, *Quercus cocculifera* and *Brachypodium retusum*) are resprouters that typically regenerate vegetatively after fire or cutting. About 20% of the species found in the seed bank were not found in the above ground vegetation, and most of these were seeders (e.g., *Trifolium* spp.). About 22% of the species were present both in the soil and in the plant community, and all these were perennials (e.g., *Cistus ladanifer*, *C. monspeliensis*, *Erica arborea*, *E. scoparia*, *Rosmarinus officinalis*). The resemblance observed between the above ground plant community of *P. halepensis* forests in Israel 6-55 years post-fire and the composition of its soil seed bank was low. All important understorey trees, shrubs and climbers typical of the mature pine forest (e.g., *Quercus calliprinos*, *Pistacia lentiscus*, *Phillyrea latifolia*, *Arbutus andrachne*, *Smilax aspera*), which are post-fire resprouters, were missing from the soil seed bank (Ne’eman and Izhaki 1999).

**Spatial Distribution of Seeds in Soil**

**Vertical Distribution**

A depth dependent decrease in soil seed density has been well documented in many ecosystems throughout the world including several coniferous forests (Archibold 1989). It would be expected that seed depth would be correlated with protection against predation and insulation against fire heat (De Bano et al. 1977).

The upper soil layers (0-2 cm) of burned and unburned *Quercus pyrenaica* forests in NW Spain contained more seeds with a higher diversity index than the lower layer (2-5 cm), Valbuena and Trabaud 1995). Similarly, about 70% of germinable seeds in mature Aleppo pine forest in Greece were located in the upper 2.5 cm soil layer (Thanos et al. 1999). However, the results of a study on the vertical distribution of seeds in the soil of Spanish pine forests did not agree with this pattern. Ferrandis et al. (1996) detected that seed number increased with depth in *P. pinaster* forest immediately after autumn fire. The 2-5 cm layer contained 44% more seeds than the 0-2 cm layer, but there was no significant difference in species richness between the two layers. Interestingly, more seeds of *Cistus monspeliensis* were found in the lower layer than in the upper one whereas more seeds of *C. albidus* were found in the upper layer than in the lower one. But increasing seed density with soil depth is probably not a general phenomenon in Mediterranean forests.

**Horizontal Distribution, the Effect of Microhabitats**

In general, the horizontal distribution of seeds in the soil is extremely patchy and therefore, many studies demonstrate a huge variation mean soil seed density (Kigel and Galil 1995). Patchiness may result from the aggregation of seeds around parent plants in case of poor dispersal and as an effect of microtopography on secondary dispersal of seeds (Thompson 1986). Therefore, we analysed the soil seed banks in three microhabitats in five *P. halepensis* forests of various post-fire ages in Israel. The microhabitats were characterised by the above ground vegetation: 1. Pine dom-
inated sites, 2. *Cistus* spp. dominated sites, and 3. Gaps dominated by herbaceous plants (Ne’eman and Izhaki 1999). The highest density of germinable soil seed banks was found in gaps (averages for the five forests ranged from 453 to 1288 seeds m\(^{-2}\)), the smallest was beneath pine trees (365-495 seeds m\(^{-2}\)) and intermediate sizes were found beneath shrubs (468-845 seeds m\(^{-2}\)). Herbaceous taxa were the majority constituents of the germinable seed bank in gaps (105-547 seeds m\(^{-2}\)) whereas perennials (mainly *Cistus* spp.) were the major components beneath shrubs (111-508 seeds m\(^{-2}\)). This considerable spatial heterogeneity in seed banks was detected among the three microhabitats although they were located within a range of a few meters in all pine forest stands. The coefficient of variation of seed density among the three microhabitats within the five forests (CV=77-164%) was higher than among site variations in tropical forests (8-88%, Garwood 1989).

### Soil Seed Bank Dynamics

#### Temporal Heterogeneity

Density and diversity of seed banks are usually high early in succession and decline with time (Garwood 1989, Pickett and McDonnell 1989, Roberts and Vankat 1991, but see Milberg 1995). Hence, the seed bank of pioneer species peaks early in succession then declines gradually, although seeds of some early successional species may persist for centuries (Thompson 1992). In mature woodlands, seeds of the trees and most shade-tolerant species are absent from soil seed banks or if present are only transient (Thompson 1992). However, the largest seed banks do not always appear in the youngest successional communities (Zammit and Zedler 1988). The available information on seed bank dynamics in Mediterranean pine forests demonstrates that time has an important impact on seed bank size, especially when comparing pre- and post-fire situations but also in various stages along post-fire succession and probably in different seasons as well. Thus, the huge variation in seed bank densities reported in these studies is at least partially due to temporal variation.

#### A Model for Seed Bank Dynamics

Harper (1977) postulated the basic model of seed bank dynamics in which the density of the soil seed bank is regulated by input from seed rain and output by seed predation, mortality and germination. Here we will describe the role of these components in the soil seed banks of *Pinus halepensis*, *Cistus* spp. and annuals in Mediterranean pine forests. Because most of the studies on seed bank dynamics in Mediterranean pine forests are related to fire, we will also focus on post-fire dynamics.

#### Pinus halepensis

**Seed Rain**

Aleppo pines older than 10 years disperse their seeds during the summer independently of fire. One tree releases on average 10,290 seeds per year during fire-free periods resulting in an annual seed rain density of 240 seeds m\(^{-2}\) (Nathan et al.
1999). Similar densities were obtained in France but lower values in Greece (Fig. 1a). Seed rain is expected to be much higher immediately after fire as heat induces cone opening. The quantitative data gathered from various locations around the Mediterranean basin, except in Israel, support this hypothesis (Fig. 1b). *Pinus brutia* seems to produce much smaller seed rain as only 22-68 seeds m⁻² were collected on the ground two months after fire in five sites in Samos island, Greece (Thanos et al. 1989). Indeed, seed density two months after fire does not necessarily reflect the actual seed rain because of seed predation and other mortality causes.

Regeneration in many species depends on seed influx from adjacent undisturbed individuals. There are some contradictory findings with regard to the ability of *P. halepensis* to disperse its seeds far away from the parent tree (see also Trabaud 2000a). A short seed dispersal distance (<30 m) was reported in western Europe (Acherat et al. 1984, Papio 1988). However, Nathan (1999) claimed that although only 0.2% of seeds can reach a distance of 1 km from the parent tree, 2000 seeds per year are expected to reach such a distance from a population of 100 pine trees (see also Nathan and Ne’eman 2000). The invasive ability of *P. halepensis* in Mediterranean type climates (Richardson 2000) is apparently the result of such long-range dispersal. Yet, the contribution of such seed influx to the soil seed bank is unclear, therefore we regarded it as null in our model (Fig. 1a).

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**Fig. 1.** Quantitative model of the main factors shaping the size of the soil seed bank of *Pinus halepensis* in the Mediterranean basin in (a) fire-free pine forests and (b) one year post-fire forests. Each line presents one study site based on data from Trabaud et al. 1985, 1997, Ne’eman et al. 1992, Saracino and Leone 1994, Thanos et al. 1996, Heming-Seyer 1997, Saracino et al. 1997, Nathan et al. 1999, Ne’eman and Izhaki 1999, Izhaki et al. (2000), Eshel et al. (2000).
Soil Seed Bank Size

Short-term changes in soil seed banks of *P. halepensis* were studied in four forests in Greece that burned in the summer (Daskalakou and Thanos 1996). Seed bank densities were measured just before the first rainy season (ca. 3 months after the fire) and at the end of the rainy season (ca. 9 months after the fire). Seed densities in the upper 1 cm before the rainy season varied considerably among the four forests (63-405 seeds m\(^{-2}\)) and dramatically decreased at the end of the rainy season (0-4 seeds m\(^{-2}\)). Furthermore, a similar poor pine soil seed bank was observed in three neighbouring unburned pine stands at the end of the rainy season (1.4-2.1 seeds m\(^{-2}\), Fig. 1a). Pine seeds were also rare (0-1.4 seeds m\(^{-2}\)) in the soil seed banks of 6-55 year old post-fire *P. halepensis* forests in Israel (Ne’eman and Izhaki 1999, Izhaki *et al.* 2000) and in 12-year old forest in Spain (Trabaud *et al.* 1997). The remarkable difference between seed input as seed rain and the density of buried seeds, both in post-fire and in fire-free periods, suggest that: (a) Most of the seeds do not reach the below ground seed bank and therefore disappear in various ways; (b) Aleppo pine forms a transient soil seed bank.

Seed Viability

A seed bank can only function if its seeds retain their viability. However, it is difficult to obtain accurate information on longevity from seeds taken directly from the soil seed bank, and therefore, our knowledge is based primarily on germination trials of stored seeds (Baker 1989). As a rule, a gradual loss of seed viability is expected with seed age. *Pinus halepensis* is capable of retaining viable seeds in serotinous cones for several years. Daskalakou and Thanos (1996) found that half of the seeds in 6-9 year-old cones were still viable. Germinability of *P. halepensis* seeds from natural stands in Israel, decreased linearly from 80% in fresh seeds to 20% in seeds extracted from 8-year-old cones (Roitemberg and Ne’eman 1999). However, the duration of seed retention and viability in the cones of other *Pinus* species may last 20-30 years (Lamont *et al.* 1991). In contrast, the viability of both *P. halepensis* and *P. pinaster* seeds is only about two years when not protected by their cones (Nahal 1962, Ceballos and Ruiz de la Torre 1971). Thus, based on these figures, post-fire regeneration of *P. halepensis* depends almost exclusively upon their canopy stored seed bank rather than on their soil seed bank (e.g., Martinez-Sánchez *et al.* 1995, Daskalakou and Thanos 1996).

Seed Losses

The main causes of seed loss from soil seed banks are senescence, predation, pathogens and germination (Harper 1997). No study has evaluated the relative role of these factors in the seed bank dynamics of Mediterranean species. A substantial germination of *P. halepensis* occurring in the first rainy season after a fire was observed in east Mediterranean habitats (Fig. 1b). Germination is much lower in west Mediterranean post-fire habitats (Fig. 1b). Based on the available data (Fig. 1b), we estimated that 9-12% of the seed rain is actually germinating in the first few months following a fire. The establishment of *P. halepensis* seedlings in Spain is limited to the first two years after a fire, and no recruitment was observed later (Herranz *et al.* 1997, Trabaud 2000b). In the east Mediterranean basin post-fire germination occurs only during the first post-fire winter (Arianooutsou and Ne’eman
2000). Although this is not direct evidence for the germination rate in later years, it seems that there is no germination of pine seeds in burnt habitats later than two years after fire, and therefore, we may consider it as none (Fig. 1a). In any case, germination could not be considered the main factor causing seed depletion from the soil seed bank.

Germinable soil seed bank density and seedling recruitment were determined for *P. halepensis* in a 50-year-old *P. halepensis* forest in the Judean Mountains, Israel, during the first post-fire year (Hendig-Sever 1997, Eshel et al. 2000). In September, before the onset of germination, germinable seed density was about 150 m\(^2\) in the ash layer, only 20 in the upper 5 cm soil layer near the burned trunks, and 20 outside the projection of the burned pine canopies. Seedling density near the trunks at the end of the first winter was 3 m\(^2\), 25 m\(^2\) when ash was removed and 12 m\(^2\) outside the burned canopies. Because the post-fire seed bank is located on the soil surface, the difference between post-fire seed density and seedling density can be attributed to massive seed predation and to the inhabiting effect of ash under the burned trees (Ne’eman 1997).

Our estimates suggest that less than 1% of the post-fire seed rain is incorporated into the soil seed bank, only 9-12% of the seeds germinate and at least 87-90% of the seeds are lost (Fig. 1b). During fire-free periods germination is marginal, and therefore, seed predation and mortality are much higher (>97%, Fig. 1a). There is no quantitative information on mortality of pine seeds caused by pathogens. Nevertheless, it seems that high seed predation pressure is responsible for the disappearance of most pine seeds from the soil surface and from the soil seed bank, immediately after fire as well as in mature forests (Fig. 1a,b). Seed predators include mainly birds (Saracino et al. 1997, Nathan et al. 1999, Izhaki 2000, Nathan and Ne’eman 2000), rodents (Acherer et al. 1984, Nathan et al. 1999) and ants (Acherer et al. 1984, Schiller 1978).

To conclude, *P. halepensis* is a serotinous obligate seeder, and its regeneration depends on a canopy stored seed bank rather than on a soil seed bank. Most of the seeds that are released either immediately after fire, or during fire-free periods are subjected to massive predation. Only a tiny fraction of the seed rain is incorporated into the soil seed bank, and the life span of the seeds there is limited to only two years. Thus, post-fire recovery depends only on the canopy-stored seed bank, and seedling recruitment occurs mainly during the first post-disturbance rainy season. Although pines also disseminate seeds during fire-free periods, recruitment is mostly in nearby open sites, is lower within the forests in France (Trabaud, pers. comm.) and rare in Israel.

*Cistus* spp.

Seed Rain *Cistus* seed production is extremely variable among species and depends on many environmental conditions, such as soil depth, rainfall, etc. (Troumbis 1996). In a >60-year-old fire-free Greek shrubland, *C. incanus* produced 30-1238 seeds m\(^2\) year\(^{-1}\) (Troumbis 1996), *C. salvifolius* produced 180-6930 seeds m\(^2\) year\(^{-1}\) and *C. villosus* 50-800 seeds m\(^2\) year\(^{-1}\) (Troumbis and Trabaud 1987).
Soil Seed Bank Size

The size of the soil seed banks of *Cistus* sp. is strongly affected by the time since fire. A dramatic depletion of 90% of the soil seeds was observed one year after fire in Spanish maquis shrubland (Ferrandis *et al.* 1999a). This continued to the point that no seeds were found two years after fire. For example, the density of *C. ladanifer* seed banks in unburned control plots was 1563 seeds m\(^{-2}\), it decreased to 633 seeds m\(^{-2}\) immediately after fire, and then to 57 seeds m\(^{-2}\) after one year and no seeds after two years (Ferrandis *et al.* 1999a). A similar trend was observed in *C. salvifolius*, although a few seeds were still present in the soil two years after fire (Ferrandis *et al.* 1999a).

A chronosequence study of *P. halepensis* forests in Israel demonstrated the long-term relations between the size of *Cistus* sp. seed banks and forest age. A gradual seed accumulation occurs between 6 and 20 years post-fire, followed by a decrease and stabilisation at 82-340 seeds m\(^{-2}\) in a 55-year-old forest (Ne’eman and Izhaki 1999). Although inter-year variation was detected in the soil seed bank of *C. incanus* in a Greek shrubland that had been fire-free for 60 years, a minimum number of seeds persisted in the soil with a range of 8.7-56 seeds m\(^{-2}\) in one site and 80-247 seeds m\(^{-2}\) in a second one. A much larger seed bank was reported in a 12-year-old *P. halepensis-P. pinaster* mixed forest in Spain where 6963 seeds m\(^{-2}\) of *C. ladanifer* were found (Trabaud *et al.* 1997). However, in the same habitat *C. monspeliensis* had only 189 seeds m\(^{-2}\).

Seed Viability

We are not aware of any direct data on the life span of soil stored *Cistus* seeds. However, because mature pine forests more than 50 years old do not include *Cistus* in significant numbers but do have significant recruitment of *Cistus* seedlings in a case of fire, this may indicate that the longevity of *Cistus* seeds in the soil is at least 2-3 decades.

Seed Losses

Very little information is available about seed predation of *Cistus* sp. Troumbis and Trabaud (1987) reported that *Cistus* seed predation by harvesting ants was negligible.

Although massive germination of *Cistus* seeds during the first post-fire year is well documented, the variation among species and habitats is huge and ranges from a few up to several thousands of seedlings m\(^{-2}\) (Trabaud 1970, Papanastassi 1977, Arianoutsou and Margaris 1981, Legrand 1993, Arianoutsou and Ne’eman 2000). However, it was only possible to estimate the proportion of germinating seeds in the total post-fire soil seed bank in a few cases. Discrepancies of 80% and 20% between seed depletion from the soil seed bank one year after fire and the final germination levels reached by seeds isolated from the soil just after fire were observed in *C. salvifolius* and *C. ladanifer*, respectively (Ferrandis *et al.* 1999a).

Germinable soil seed bank and seedling recruitment were determined for *Cistus* in a 50-year-old *P. halepensis* forest in the Judean Mountains, Israel, during the first post-fire year (Henig-Sever 1997, Eshel *et al.* 2000). In September, before the onset of germination, germinable seed density was about 450 m\(^{-2}\) in the upper 5 cm soil layer among the burned pine canopies. Seedling density at the end of the first win-
ter was 125 m². Because seed longevity is high and seed predation is assumed to be extremely low, it can be suggested that about 70% of the seeds were located in the lower part of the sampled soil. They were either protected there from the heat shock and remained dormant or, because of their minute size (mass of ca.1 mg, Thanos et al. 1992), seedlings could not reach the soil surface.

The obligate seeding strategy demonstrated by Cistus may have evolved as an adaptation to fire in areas where long fire-free periods have been an evolutionary stimulus for the development of such strategy. However, Troumbis and Trabaud (1986) suggested that fire is not the sole stress factor that is responsible for the selection of such a strategy. They claimed that competition should be an important element in the evolution of obligate seeders in unpredictable disturbance regimes. A large spectrum of disturbances in the Mediterranean landscape contributes to the unpredictability of disturbances, such as grazing, logging, climate variability, etc. Non-fire selection of the hardseededness of Cistus, which is the most apparent adaptation to fire prone environments, is supported by the fact that all the members of the Cistaceae share the same trait regardless of the fire regime in their natural habitat (Thanos et al. 1992).

**Annuals**

Annual plant life forms are typical to the flora of the Mediterranean basin, contributing to its large species diversity (Archibold 1995). Most of the annuals are heliophilous plants and their abundance decreases with forest density. Therefore, it is expected that their part in the soil seed bank of mature old growth pine forest is marginal. We are aware of only scarce quantitative data concerning the composition of the annual species in soil seed banks. Based on these data and on the composition of post-fire seedling assemblage, Poaceae, Fabaceae and Asteraeaceae are the major families (Arianoustou and Thanos 1996, Martínez-Sánchez et al. 1994, Ferrandis et al. 1996, Ferrandis et al. 1998, Thanos et al. 1999, Izhaki et al. 2000) that germinate mainly after fire. However, soft seeded fire-following species whose germination is stimulated by charred wood and smoke are generally absent from the Mediterranean flora (Keerley and Baer-Keeley 1999).

Time since fire is a major factor determining species composition and vegetation structure after fire. However, microhabitats affected the composition of soil seed banks more than time since fire. Specifically, seeds of annual species, most of them grasses, were the major component in forest gaps but were only a minor component under dwarf shrubs or pine trees (Ne’eman and Izhaki 1999).

**Conclusions**

The composition of soil seed banks in pine forests is the result of interactions among seed production by the plants, predation by animals, type of microhabitat and fire. Fig. 2 depicts a descriptive model, based mainly on Ne’eman and Izhaki (1999) and Izhaki et al. (MS), of the main factors affecting soil seed banks in gaps, under dwarf shrubs and under pine trees in unburned and burned pine forest. It includes the expected composition of the seed bank following and in the absence of fire.
Fig. 2. Descriptive model of soil seed bank and regeneration in three main microhabitats of fire-free and post-fire pine forests.
Under unburned pine trees we expect to find pine seeds and seeds of bird dispersed understory trees, shrubs and climbers. However, probably due to predation and a life span shorter than 1 year, all these taxa are almost absent from the soil seed bank of pine forests. After fire, due to cone opening, pine seeds are the major component of the seed bank on the surface of all microhabitats. As expected, Cistus and seeds of annuals are typical to gaps and under dwarf shrubs both in burned and unburned forests. In the absence of fire, seeds from the soil seed bank rarely germinate, except those of annuals in gaps. In contrast, numerous seedlings are typical to a post-fire regenerating pine forest. Under pre-fire dwarf shrubs and in pre-fire gaps there are many pine seedlings, Cistus and annual species. Nevertheless, probably due to competition and habitat quality, Cistus seedlings dominate its pre-fire microhabitat whereas annuals dominate the pre-fire gaps. Mainly because of the thick ash layer only a few pine seedlings germinate under the burned pine canopies. Because of low competition and improved growing conditions, these siblings have the best chance of replacing their mother trees. The final result is that the soil seed bank composition of pine forests contributes to the conservation of the spatial heterogeneity of the forest in the absence of fire as well as after stand replacing fire.

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References


(in Hebrew with an English abstract).


