

Soil seed banks in Mediterranean Aleppo pine forests: the effect of heat, cover and ash on seedling emergence

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Summary

1 East Mediterranean Aleppo pine (*Pinus halepensis*) forests are subjected to periodic stand-replacing fires. We simulated two of the effects of fire on the germinable soil seed bank in four pine stands on Mt. Carmel, Israel, that differed in their post-fire ages. Soil samples were heated to 100 °C, or covered by pine ash. Vermiculite was used to simulate litter cover.

2 Heat exposure increased overall seedling density, richness and taxon diversity in all stands, but density of annual taxa (e.g. grasses and legumes) were not clearly affected.

3 Ash cover dramatically decreased germination of all taxa and highest germination was achieved with heating and no cover. Vermiculite cover resulted in intermediate germination levels.

4 The combined effect of heat exposure and ash cover, simulating a post-fire situation under a canopy of pine, reduced the germination level of all taxa in the soil seed bank. However, it also creates conditions that facilitate the establishment of pine seedlings from the canopy stored seed bank.

Keywords: ash cover, *Cistus*, fire, heat exposure, *Pinus halepensis*, seed bank

Journal of Ecology (2000) **88**, 667–675

Introduction

One of the major goals in ecology is to understand how environmental conditions govern community composition and population density, both of which change after vegetation fire. However, resprouting plants, which survive even after high-intensity canopy wildfires, show much less pronounced demographic changes than do obligate seed plants. We focus on environmental factors that may control seed germination in Mediterranean pine forests and which therefore play a significant role in shaping community structure.

Seed banks are important in the dynamics of many plant communities (see Leck *et al.* 1989 for a review), including those of Mediterranean type ecosystems (e.g. Ferrandis *et al.* 1996, 1999; Traubad *et al.* 1997; Ne'eman & Izhaki 1999), as they provide an immediate source of propagules for recruitment after disturbance. Fire is a frequent event in Mediterranean forests (Biswell 1974; Keeley 1994; Traubad 1994) and germination of seeds from soil and canopy-stored seed banks therefore affects the composition of the post-fire plant community

(Ne'eman *et al.* 1992; Traubad 1994; Daskalidou & Thanos 1996); although seed predation (Nathan & Ne'eman 2000) and seedling establishment and survival, which are affected by factors such as intra- and interspecific competition (Katz 1993; Ne'eman & Izhaki 1998), are also important.

Studies in Mediterranean and other fire-prone ecosystems have demonstrated that the probability that a seed from the soil seed bank will germinate depends on a number of environmental factors. These factors include heat exposure (Thanos & Georghiou 1988; Keeley 1991, 1994), light (Thanos & Skordilis 1987; Mayer & Poljakoff-Mayber 1982; Traubad & Renard 1999), smoke (Brown 1993; Keeley & Fotheringham 1997, 1998a,b), ash (Ne'eman *et al.* 1993; González-Rabanal & Casal 1995), ethylene (Ne'eman *et al.* 1999), nitrates (Thanos & Rundel 1995; Henig-Sever 1997), soil water potential, pH (Thanos & Skordilis 1987; Henig-Sever *et al.* 1996) and litter cover (Traubad & Renard 1999); some or all of which may directly and/or indirectly affect post-fire regeneration. It is difficult to determine the precise role of each factor under natural conditions because their effects may be both interrelated and space- and time-dependent.

Mediterranean pine forests comprise a heterogeneous mosaic of microhabitats and stands of differ-

ent ages. In an earlier study, we demonstrated that seed banks differed in composition between the three main microhabitats: pine-dominated areas, shrub-dominated areas and herbaceous-dominated gaps (Ne'eman & Izhaki 1999). Each microhabitat is characterized by different physical and chemical properties of the soil; understanding how these and other factors control germination at different sites is crucial for an understanding of the long-term dynamics of Mediterranean pine forests.

Our aims were to distinguish between the effects of heat exposure (simulating fire) and ash cover on the response of the germinable seed bank in pine stands of different ages. A controlled germination experiment evaluated effects on seedling density, taxon richness and taxon diversity in four stands. Cover type was investigated using treatments with and without ash and with vermiculite as a neutral covering material.

Methods

STUDY SITES

Four Aleppo pine (*Pinus halepensis* Mill.) forest stands were located within a 10 × 10 km area on Mt. Carmel, Israel. The climate is typically Mediterranean with a mean annual rainfall of 600–700 mm. These stands, whose fire history has been verified from aerial photographs, represented a chronosequence of 7, 12, 21 and 56 years since the last fire. The post-fire regeneration of the natural Aleppo pine forest in this region has been described by Schiller *et al.* (1997).

All stands are on chalky marls with typical yellow Rendzina soils. The understorey of the natural pine forests on Mt. Carmel is composed mainly of small trees (e.g. *Quercus calliprinos* and *Pistacia palaestina*), shrubs (e.g. *Pistacia lentiscus* and *Phillyrea latifolia*) and climbers (e.g. *Smilax aspera* and *Clematis cirrhosa*) (Schiller *et al.* 1997). Shrubby patches, dominated mainly by *Cistus salviifolius* and *C. creticus*, and gaps, composed mainly of herbaceous vegetation, occur among the pine trees.

SOIL SAMPLING AND TREATMENTS

Soil samples (20 × 20 × 5 cm deep) were taken beneath 24 pine trees that were randomly selected along each of five parallel 60–100 m transects in each of the four pine-stands in the summer of 1995. The transects were positioned so that they included a range of within-site variation in slope (which was always moderate) and aspect.

Each soil sample ($n = 120$ for each stand) was mixed, spread uniformly over germination flats (20 × 30 × 2 cm) and the surplus removed. Half of the flats from each stand were placed in a preheated drying oven at 150 °C for 25 min, during which time

the temperature at 1 cm depth (from both the upper and lower surface of the flat) reached 100 °C. From a preliminary study (Izhaki & Ne'eman, unpublished data) this treatment was found to result in maximum germination and was used to simulate the effect of fire.

Both heated and unheated samples from each pine stand were divided into three equal groups. One was covered by a 2-cm layer of ash, prepared by burning pine needles and fine branches, another by a 2-cm layer of vermiculite and the last was not covered. This procedure produced 20 replicates for each combination of stand × heat treatment × cover. The ash cover simulated the layer of ash (30–50 mm deep) that is present under large pine trees 3 months after a fire (Lahav 1988). Vermiculite simulated the cover provided by litter and effectively blocked out light without any chemical effect of ash. The unnatural combinations of unheated soil samples with ash cover, heated uncovered soil samples and samples with vermiculite cover were needed to separate out the effects of heat and light on seedling germination.

All flats (heated and unheated) were placed randomly in an open garden. Water availability as a limiting factor to germination was excluded by using an automatic overhead sprinkler system to keep the soil moist; surplus water drained through holes in the bottom of the flat.

Seedling emergence was recorded and seedlings were removed from flats every 3 days. Seedlings were identified to the species level or to the closest possible taxon (e.g. Poaceae and Fabaceae). It was impossible to distinguish between the seedlings of *Cistus salviifolius* and *C. creticus*, which were therefore grouped and named hereafter as *Cistus* spp. The experiment started on 24 October 1995 and finished 2 months later on 25 December when no new seedlings had emerged for 10 consecutive days. The number of germinated seeds per flat (hereafter germinable seed density) for each taxon was calculated.

STATISTICAL ANALYSIS

The main objective of this study was to explore the effect of heat exposure and the type of soil cover on the germinable soil seed bank from pine stands of various post-fire ages. Because the number of germinable seeds was not normally distributed, we used non-parametric procedures performed in Systat (1996). The Mann–Whitney *U*-test was used to compare the heated and unheated germinable seed density per flat in the upper (5 cm) soil layer (for each taxon separately and for all taxa combined). This test also enabled comparison of taxon richness (number of taxa per flat) and of diversity using the Simpson index (*D*) (Begon *et al.* 1996) within the no-cover treatment for each stand age. Kruskal–Wallis one-way ANOVAS were used to detect the

effect of cover type on these variables, considering each heat treatment \times stand combination separately.

Results

HEAT EXPOSURE

We identified 25 taxa in the entire seed bank, of which only six were lignified perennials and the rest were herbaceous plants (Table 1). Mean total germinable seed density for all stands, heat exposures and cover types was 17.0 ± 31.3 ($n=480$) seeds per flat (range 0–243). The density of germinable pine seeds was low with a mean of 0.05 ± 0.35 ($n=480$) seeds per flat (range 0–5). No seedlings of broad-leaved trees emerged (Table 1).

Comparison of the germinable seed banks of heated and unheated samples with no cover showed that heat exposure was responsible for an increase in mean total germination of 172% (from 18.5 to 50.3 seedlings per flat, $n=80$ heated and 80 unheated samples over all stands). A similar pattern was observed for each stand age when analysed separately (Mann–Whitney U -test, $P < 0.01$, $n=40$ in each case; Fig. 1). Heat exposure did not, however, affect taxa richness (number of germinated taxa per flat) (Fig. 2) or diversity of the germinable seed bank (Mann–Whitney U -test, $P > 0.05$, $n=40$ in each case).

The germinable seed bank of Poaceae was not influenced by heat exposure (Mann–Whitney U -test, $P > 0.05$, $n=40$ for each stand age; Fig. 3). The effect on germination of Fabaceae was variable (Fig. 4), having no significant effect in two stands (the 12- and 56-year-old stands) and opposite effects in the others (inhibition in the 7-year-old stand and promotion in the 21-year-old stand; $P < 0.05$ and $P < 0.01$, respectively).

Cistus germination was strongly affected by heat exposure (Mann–Whitney U -test, $P < 0.01$, $n=40$ for each stand age; Fig. 5) with an average increase of 1215% (from 2.6 to 34.2 seedlings per flat). In contrast, the common post-fire annual *Anagallis arvensis* was not affected significantly by heat exposure (Mann–Whitney U -test, $P > 0.05$, $n=40$ for each stand age; Fig. 6).

SOIL COVER

When all taxa were combined, both heated and unheated seeds germinated in higher numbers when they were not covered compared to those covered by vermiculite or ash (Fig. 1). Furthermore, total germination density was higher in samples covered by vermiculite than those covered by ash (Fig. 1). The same patterns were observed for taxon richness (Fig. 2) and diversity, irrespective of heat treatment.

The germinable soil seed bank of Poaceae was generally higher in the absence of any cover than

with vermiculite and ash present, but the response was absent or not significant in unheated samples from the oldest stand and in heated samples of all but the youngest stand (Fig. 3). The germination of Fabaceae was significantly influenced by cover type in most cases and trended to decrease from no cover to vermiculite to ash (Fig. 4).

Cistus spp. showed the same trend as Fabaceae, with little germination in unheated samples or under ash in any flat (Fig. 5). This pattern was also seen for *A. arvensis*, except for heated samples from the 12-year-old stand (Fig. 6).

Discussion

In a previous study, Ne'eman & Izhaki (1999) sampled the soil from three microhabitats (gaps, beneath shrubs and beneath trees) in pine stands of an east Mediterranean Aleppo pine forest of various post-fire ages (6–55 years old) and measured germination after a heat treatment simulating the effect of fire. Irrespective of stand age, the major constituents of the germinable seed bank were herbaceous taxa in gap samples and perennials in samples from beneath shrubs, while the dominant tree and shrub species of the mature pine forest itself (including *P. halepensis*) were never an important component (see also Daskalidou & Thanos 1996). This lack of resemblance between the above-ground plant species composition and the soil seed bank was demonstrated again in the present study. Species richness, species diversity, and density of seed banks did not decrease with post-fire age (Ne'eman & Izhaki 1999) so that stand age could not be used as a predictor for seed bank attributes.

It should be noted that we sampled the upper 5 cm of the soil, mixed it and spread it in 2 cm deep flats, thereby disrupting the stratification of seeds in the soil. This may have caused us to underestimate germinable seed density for two reasons: (i) most seeds commonly occupy the upper 2 cm of the soil (Izhaki & Ne'eman 2000) and (ii) some species may fail to germinate at the depth that they were mixed to. However, our main purpose was not to determine absolute seed density but rather to compare the effects of heat exposure and soil cover types on germinable seed densities. Any reductions in density due to methodology would have been similar in all treatments.

Evaluation of such experimental data on the seed banks under pine trees may allow us to extrapolate to natural processes occurring at community and population levels within these forests.

HEAT EXPOSURE

In contrast with South-African fynbos and the Californian chaparral where smoke plays a major role in regulation of post-fire germination (Brown

Table 1 Number of seedlings per flat (mean \pm SE) emergent from the soil seed bank collected beneath pine trees on Mount Carmel (Israel) after heat treatment (heated and unheated) under different types of soil cover (no cover, vermiculite and ash)

Taxa	Heated			Unheated		
	Vermiculite <i>n</i> = 20	Ash <i>n</i> = 20	No cover <i>n</i> = 20	Vermiculite <i>n</i> = 20	Ash <i>n</i> = 20	No cover <i>n</i> = 20
Lignified						
<i>Ajuga chamaepitys</i>	0	0.111 \pm 0.099	0	0.138 \pm 0.064	0.037 \pm 0.021	0
<i>Calycotome villosa</i>	0.600 \pm 0.149	0.395 \pm 0.089	0.200 \pm 0.057	0.163 \pm 0.049	0.050 \pm 0.025	0.025 \pm 0.018
<i>Cistus</i> spp.	34.163 \pm 5.151	16.815 \pm 2.595	0.950 \pm 0.231	2.580 \pm 0.422	1.587 \pm 0.602	0.114 \pm 0.044
<i>Pinus halepensis</i>	0.025 \pm 0.018	0	0.125 \pm 0.070	0.025 \pm 0.018	0.025 \pm 0.018	0.114 \pm 0.057
<i>Sarcopoterium spinosum</i>	0	0.012 \pm 0.012	0	0.013 \pm 0.013	0	0
<i>Salvia</i> sp.	0.013 \pm 0.013	0	0	0.025 \pm 0.025	0.075 \pm 0.056	0
Herbaceous						
<i>Anagallis arvensis</i>	6.787 \pm 2.345	2.827 \pm 0.682	0.538 \pm 0.197	5.190 \pm 2.11	0.963 \pm 0.377	0.038 \pm 0.028
<i>Carthamus tenuis</i>	0	0	0	0.125 \pm 0.072	0.013 \pm 0.013	0
Asteraceae						
<i>Convolvulus pentapetaloides</i>	1.462 \pm 0.329	0.309 \pm 0.124	0.125 \pm 0.070	3.100 \pm 0.501	0.562 \pm 0.140	0.114 \pm 0.067
<i>Erodium</i> sp.	0.550 \pm 0.177	0.358 \pm 0.158	0	0.075 \pm 0.035	0.038 \pm 0.021	0
<i>Erophobia</i> sp.	0.250 \pm 0.086	0.136 \pm 0.055	0.050 \pm 0.030	0.025 \pm 0.018	0	0
<i>Euphorbia</i> sp.	0	0	0	0.025 \pm 0.025	0	0
<i>Hippocrepis</i> sp.	0.100 \pm 0.058	0.074 \pm 0.034	0	0.037 \pm 0.021	0.013 \pm 0.013	0
<i>Lotus</i> sp.	0.075 \pm 0.043	0.123 \pm 0.059	0.037 \pm 0.028	0.162 \pm 0.060	0.300 \pm 0.154	0.013 \pm 0.013
<i>Medicago</i> sp.	1.300 \pm 0.796	0.111 \pm 0.079	0	0.200 \pm 0.131	0.062 \pm 0.041	0
<i>Mercurialis annua</i>	0.025 \pm 0.018	0.062 \pm 0.027	0.013 \pm 0.013	0.075 \pm 0.053	0.025 \pm 0.018	0.013 \pm 0.013
<i>Plantago</i> sp.	0	0.012 \pm 0.012	0	0.025 \pm 0.025	0	0
Poaceae						
<i>Portulaca oleracea</i>	4.912 \pm 1.528	0.407 \pm 0.147	1.387 \pm 0.566	5.255 \pm 1.483	2.625 \pm 1.064	0.443 \pm 0.162
<i>Ranunculus asiaticus</i>	0.962 \pm 0.324	0.222 \pm 0.099	0.113 \pm 0.073	0.862 \pm 0.283	0.163 \pm 0.080	0.139 \pm 0.078
<i>Scorpiurus muricatus</i>	0.013 \pm 0.013	0	0	0.013 \pm 0.013	0	0
<i>Sedum</i> sp.	0.025 \pm 0.018	0.049 \pm 0.024	0	0.100 \pm 0.049	0.025 \pm 0.018	0.013 \pm 0.013
<i>Torilis</i> sp.	0	0	0	0.387 \pm 0.387	0	0
<i>Trifolium</i> sp.	0	0	0	0.050 \pm 0.030	0.050 \pm 0.030	0
Apiaceae						
<i>Trifolium</i> sp.	0.025 \pm 0.018	0.099 \pm 0.057	0.013 \pm 0.013	0.637 \pm 0.366	0.050 \pm 0.030	0.063 \pm 0.063
<i>Apiaceae</i>	0	0	0	0.087 \pm 0.054	0.013 \pm 0.013	0.025 \pm 0.018

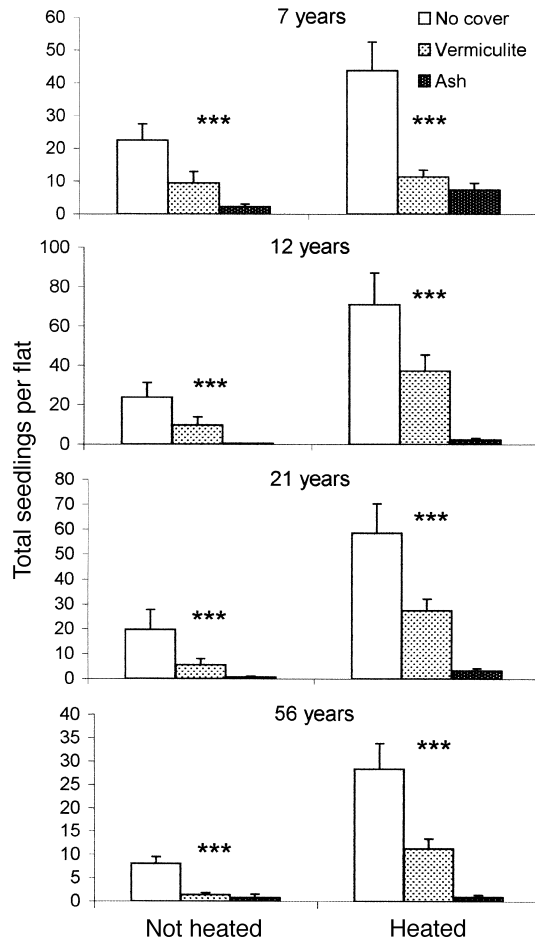


Fig. 1 Effect of soil cover (vermiculite, ash and no cover) on total germinable seed density per flat (mean \pm SE) of heated and unheated soil from beneath large pine trees from four pine forest stands on Mt. Carmel, Israel, last burned 7, 12, 21, and 56 years ago. Significant differences among means of soil cover type, analysed separately for heated and unheated seeds within each stand, are indicated above bars (Kruskal-Wallis one-way ANOVA, $n=60$); *** $P < 0.001$.

1993; Keeley & Fotheringham 1997, 1998a,b), heat is probably the major fire related factor in the Mediterranean basin (Trabaud 1987; Thanos *et al.* 1992; Keeley 1994; Keeley & Baer-Keeley 1999). Differences in the above-ground vegetation between habitats within the pine forest would lead to the soil surface and the upper level of the soil seed bank experiencing different heat regimes during fire (Davis *et al.* 1989; Moreno & Oechel 1991); this in turn would lead to differences in natural interfire conditions. More fuel is available on the forest floor under pine trees or shrubs than in gaps. In these habitats fire is therefore more intense and soil-surface temperatures are much higher during fire. In contrast, under natural fire-free conditions, higher soil surface temperatures are expected in the gaps because shading of the soil by the vegetation is limited and the sun-blocking litter layer is absent.

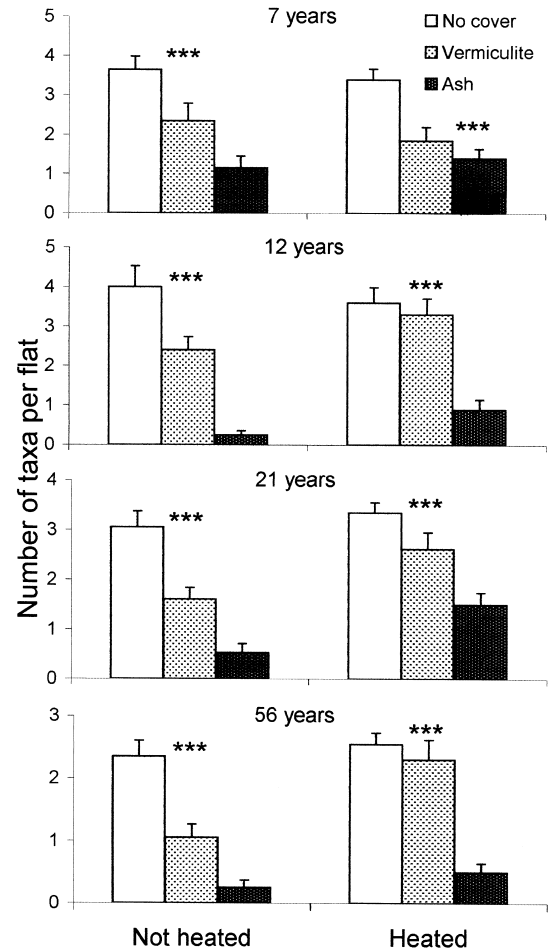


Fig. 2 Taxon richness per sample for soil from four pine forest stands. See Fig. 1 for details and significance test; *** $P < 0.001$.

Although such differences in light and temperature regimes had only minor effects on interfire germination of hard-seeded species from Mediterranean pine forest (Doussi & Thanos 1993), the mosaic of different habitats with different soil seed banks (Ne'eman & Izhaki 1999) probably experiences a variety of heat exposures during fire.

The effect of heat on germination of *P. halepensis* is well known (reviewed in Thanos 2000). Pine seeds were poorly represented in our germinable soil seed bank but even if they had been present, their germination would have been inhibited by high fire temperatures. Seeds within serotinous cones are, however, protected from the extreme heat (Hellum & Pelchat 1979) and are therefore able to germinate in large numbers in the post-fire habitat.

Cistus spp. are well represented in the germinable soil seed bank under pines although seed density is highest beneath *Cistus* shrubs (Ne'eman & Izhaki 1999). Enhancement of germination by heat exposure, due to seed-coat rupture, has been demonstrated for *Cistus* spp. as well as other genera of Cistaceae (Trabaud & Oustric 1989; Thanos *et al.*

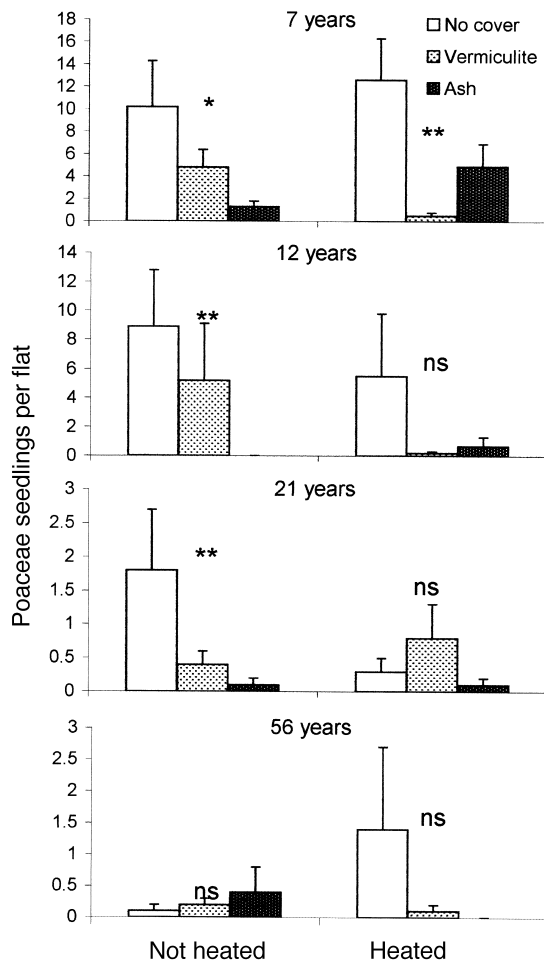


Fig. 3 Germinable seed density of Poaceae. See Fig. 1 for details and significance test; * $P < 0.05$, ** $P < 0.01$, ns = not significant.

1992) and, as expected, heat exposure dramatically increased *Cistus* spp. germination

Early post-fire vegetation of east Mediterranean pine forests is relatively rich in herbaceous taxa, and grasses and legumes are particularly abundant (Naveh 1973; Lahav 1988; Arianoutsou & Thanos 1996; Kazanis & Arianoutsou 1996; Ne'eman & Izhaki 1999; Kutiel 2000). These groups are initially widespread but become restricted to gaps once the stand exceeds about 11 years of age (Ne'eman & Izhaki 1999). The lack of a clear effect of heat on the germination of these two main herbaceous taxa was unexpected, given their prevalence in post-fire habitats. However, preliminary results suggest that dry oven heating does not enhance germination of hard seeded legumes. Other authors who used boiling water to simulate the effect of fire did find an enhancement of germination in legumes (Doussi & Thanos 1994). However, we favour the conclusion of Doussi & Thanos (1993) that legumes are opportunistic species, exploiting the post-fire open areas rather than being fire followers. Grasses and

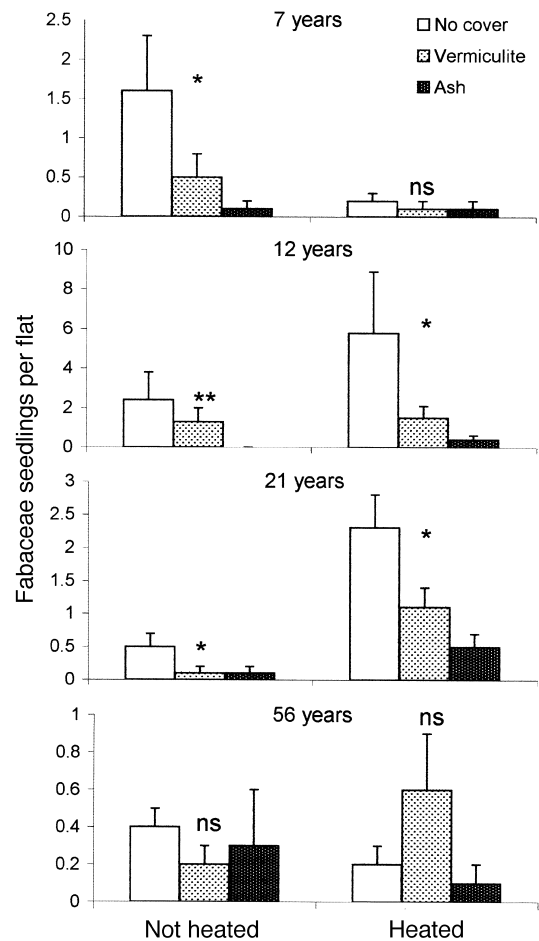


Fig. 4 Germinable seed density of Fabaceae. See Fig. 1 for details and significance test; * $P < 0.05$, ** $P < 0.01$, ns = not significant.

Anagallis arvensis (Primulaceae, a common annual), which exhibit similar patterns to legumes, should also be regarded as opportunistic plants.

It should be emphasized that a hard seed coat should not be regarded as an exclusive adaptation selected by fire (Trabaud 1987; Thanos *et al.* 1992). Therefore, such plants, unlike smoke induced species (Keeley & Fotheringham 1997, 1998a, b), cannot be regarded as obligate fire followers.

SOIL COVER

The effect on successional plant communities of the soil cover may be mediated by factors such as physical obstruction, light interception and allelopathy, as well as by changes in soil temperature, biotic interactions and chemical properties (e.g. Facelli & Pickett 1991a, b; González-Rabanal & Casal 1995; Henig-Sever *et al.* 1996; Herr & Duchesne 1996).

The effects of ash on germination and establishment are a complex combination of direct and indirect influences. Our experiments enabled an evaluation of the effects of ash on the germinable

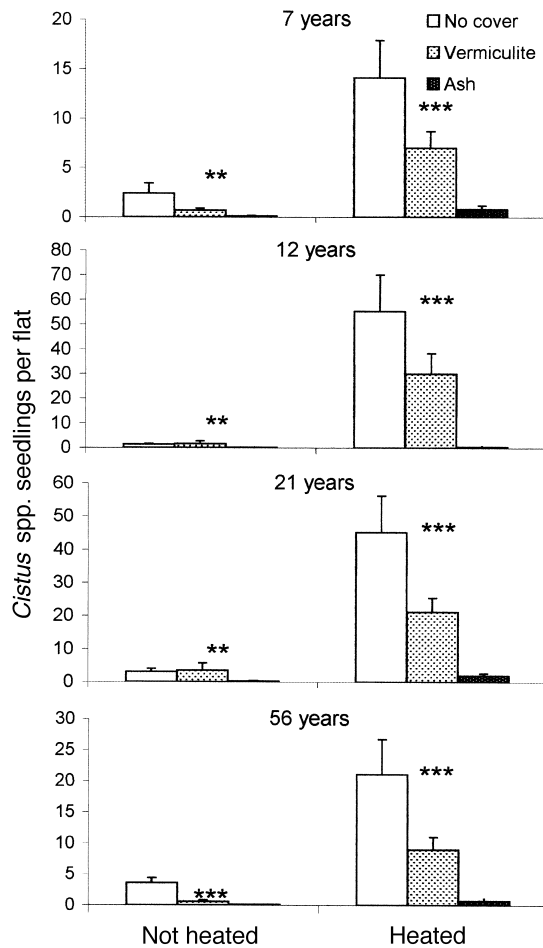


Fig. 5 Germinable seed density of *Cistus* spp. (Cistaceae). See Fig. 1 for details and significance test; ** $P < 0.01$, *** $P < 0.001$, ns = not significant.

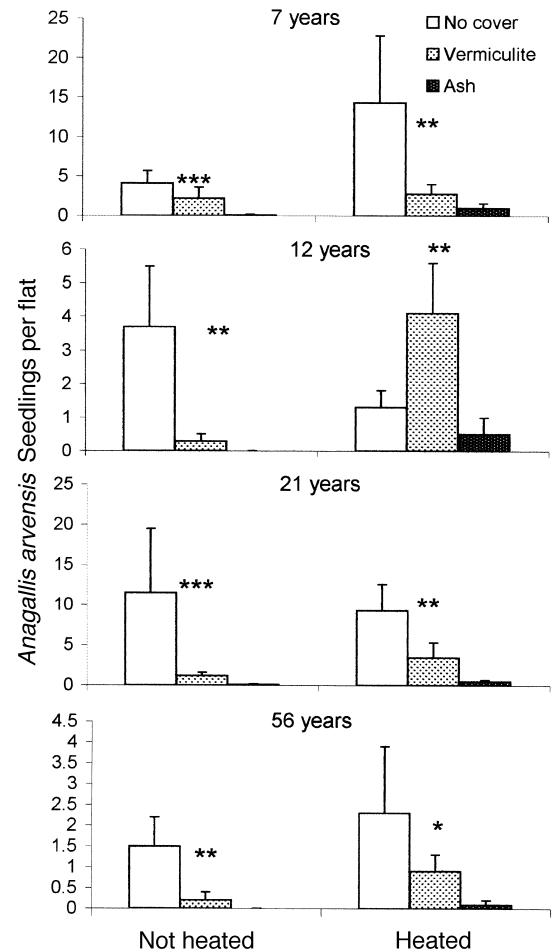


Fig. 6 Germinable seed density of *Anagallis arvensis* (Primulaceae). See Fig. 1 for details and significance test; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

seed bank by separating them into effects that were solely due to the blocking of light (and which were mimicked by a cover of vermiculite) and those that were due to a combination of mechanisms. Total density and taxon richness of the germinable seed bank beneath pine trees were highest with no cover, lowest with ash cover, and intermediate with vermiculite cover, suggesting that some species do require light but that ash has an additional effect as a germination inhibitor.

The germination of *P. halepensis* is known to be controlled by light and water potential as well as by heat (reviewed by Thanos & Skordilis 1987; Thanos 2000). The extremely high pH of ash is also inhibitory and determines the post-fire patterns of germination (Henig-Sever *et al.* 1996) and establishment (Ne'eman & Izhaki 1998). Pine seeds were too scarce in our samples to allow further analysis, but it is known that their germination is inhibited by shade and needle cover beneath pine trees. Their seeds are not dormant and germinate readily in open sites, as is typical for early successional and pioneer species.

In contrast to its positive reaction to heat exposure, *Cistus* spp. germination was partially inhibited by vermiculite cover and almost totally by ash. Because *Cistus* spp. has been shown to germinate under all light regimes (Thanos & Georghiou 1988), it can be concluded that the effect of vermiculite was due to it forming a mechanical barrier, while the sensitivity of *Cistus* spp. to the high pH of ash (Henig-Sever *et al.* 1996) explains its absence from the ash treatments. This, in addition to their heliophilous, which determines *Cistus* spp. growth in open sites, may explain why they do not germinate under trees after a fire, despite high seed densities and exposure of the soil to direct radiation.

Grasses, legumes, and *Anagallis arvensis* responded in a similar way to the cover treatments. Highest germination occurred with no cover while ash drastically reduced germination; germination under vermiculite cover was in most cases intermediate. The gaps where these opportunistic plants grow usually lack a covering of ash even after fire and continuous occupation is therefore ensured.

Conclusion

We tested the effects of heat exposure and soil cover on the germinable seed bank in Aleppo pine forests of various post-fire ages, and confirmed previous reports that patterns and effects varied little with stand age (Ne'eman & Izhaki 1999). Cover (either as ash or vermiculite) and heat exposure act as almost independent factors in the regulation of soil seed bank germination. As a general rule, ash, and to a lesser degree vermiculite, decreased germination, whereas heat increased it.

Unheated samples may be considered to resemble the conditions during fire-free periods of forest growth, whereas vermiculite cover simulates some of the effects of litter cover that is found mainly under trees. Heat exposure creates conditions needed for the regeneration of post-fire seeders, and ash cover simulates the conditions under large burned pine trees. In the absence of fire, herbaceous annuals failed to germinate under pine trees in spite of their presence in the soil seed bank, presumably because of a covering of pine needles. In the case of fire their germination is almost completely inhibited by the layer of ash (Henig-Sever *et al.* 1996).

Our results confirm previous studies that show *Cistus* spp. germination to be generally heat dependent (Thanos & Georghiou 1988; Corral *et al.* 1990; Roy & Sonié 1992). Vermiculite cover reduced germination, mainly of heated seeds, and it therefore seems that light enhances germination. Although Thanos & Georghiou (1988) and Trabaud & Renard (1999) provide evidence for the lack of a light effect on *Cistus* spp., an effect was reported by Roy & Sonié (1992) and the contradicting results may be due to species-specific responses. Removal of the litter layer, the shrub layer, or both, had no effect on the germination of *C. monspeliensis* and *C. albidus*, which remained low (Trabaud & Renard 1999). *Cistus* spp. have a life span of about 15 years, after which their populations decline (Roy & Sonié 1992). Therefore, in the absence of fire or other disturbances their populations are subject to local extinctions (Trabaud & Renard 1999).

The soil beneath large pine trees is completely covered by needle litter. In this study, its effects were stimulated by a covering of vermiculite, which was found to decreased germination of the existing seed bank relative to uncovered soil. As a result, as long as the pine tree lives, there is little opportunity for vegetation to develop beneath it. However, if the tree dies and the needle litter is removed, *Cistus* spp. or pine seedlings would be expected to fill the gap. After a fire, the thick layer of ash covering the soil under a pine canopy will allow only a few pine seedlings to recruit there, one of which has a high probability of replacing its burned parent tree (Ne'eman 2000).

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