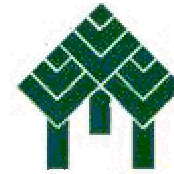


ספרית אורנים



המאמרים במערכת תדפיסים זו מוגנים על-פי

חוק זכויות יוצרים

הדפסת מאמרים תהיה לצרכי לימוד והוראה בלבד

אין לעשות כל שימוש מסחרי במאמרים.

Stability of pre- and post-fire spatial structure of pine trees in Aleppo pine forest

Gidi Ne'eman and Ido Izhaki

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The study reported here describes for the first time the similarity between pre- and post-fire spatial patterns of the trees in a Mediterranean pine forest demonstrating that the pre-fire ancestor microsite is occupied also by the next generation. Although Aleppo pine *Pinus halepensis* Mill. is an obligatory post-fire seeder, it is adapted to regenerate in its pre-fire growing microsite, thus keeping suitable growing sites from generation to generation. We studied the effect of the dead burned adult pines on the density and size of their recruited saplings 2, 5, 11 and 20 yr after fire. A comparison of pine sapling density and size was made between the 'near' zone (under the former effect of the burned canopy) and the 'far' zone (beyond the former effect of the burned canopy).

In the site 2 yr after fire, seedling density was 56% higher in the 'far' zone than in the 'near' zone, but seedling size was similar. However in the site 20 yr after fire, densities were similar in both zones, but the size was bigger by 89% in the 'near' zone. Thus, population recruitment after fire seems to peak near the burned pine trees rather than at a distance from them, in contrast to Janzen's original 'distance hypothesis' model suggested for undisturbed rainforest. Here we present a new hypothetical model for the spatial pattern of post-fire regeneration of obligate seeder tree species forming open forests. It is proposed that in such trees the microsites which were kept by the burned adult trees, which are killed by the fire, are also the favorable regeneration microsite for the post-fire generation.

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Fire is a major ecological factor affecting vegetation worldwide. The hot, dry and long summer of the Mediterranean climate is the cause of frequent fires in all Mediterranean-type vegetation all over the world (Biswell 1974, Keeley 1994, Trabaud 1994). Severe wildfires are among the most grave natural disturbance. They cause complete combustion of the above-ground plant biomass, drastically decrease the organic matter on the soil surface, affect soil seed bank (Hassan and West 1986, Zammit and Zedler 1988), seed germination (Trabaud and Oustric 1989, Moreno and Oechel 1991, Thanos et al. 1992) and cause physical and chemical changes in the upper soil layers (Raison 1979, DeBano et al. 1979).

Mediterranean-type vegetation is resilient to fire (Keeley 1986, Malanson 1987). The regeneration ability of the vegetation in these ecosystems is the result of plant life-history adaptations that allow the recovery of the pre-fire population of most plant species (Trabaud 1987, Keeley 1991, 1994). Most of the typical evergreen sclerophyllous species in the Mediterranean vegetation are classified as post-fire resprouters (Trabaud 1987, Keeley 1991, Lopez-Soria and Castell 1992). Even though their above-ground part is completely burned, the underground parts stay alive. These plant species have the ability to produce adventive buds on the basal part of the burned trunk, and they begin to resprout a couple of weeks after fire, long before the winter rains

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(Trabaud 1990). Other species, like most *Pinus* spp. and Mediterranean dwarf shrub *Cistus* spp., are classified as post-fire obligate seeders (Trabaud 1987, Keeley 1991). In these species the adult plants are killed by the fire and their regeneration is solely dependent on the soil- or canopy-stored seed banks. Massive germination, which is cued by fire-related factors (Keeley 1991, 1994), occurs after the first winter rains. During the recruitment stage, intra- and inter-specific competition for space, water and light takes place (Katz 1993, Ne'eman 1994). Seed dispersal and germination, seedling establishment and sapling growth are crucial stages affecting population ecology (Schupp and Fuentes 1996) and determining the regeneration niche and growing site of the individual plants.

Post-fire secondary succession is mostly described in terms of species richness, species composition, and vegetation structure at plant communities and landscape scales (Naveh 1989, Trabaud 1994). However, the importance of small-scale spatial patterns in Mediterranean vegetation has long been recognized and studied (Shmida and Whittaker 1981, Auerbach and Shmida 1987, Olsvig-Whittaker 1988). Although there is no doubt that the pre-fire spatial pattern affects the post-fire recovery process, very little effort has been invested to document it (Davis et al. 1989, St-Pierre et al. 1991, Ne'eman et al. 1992, Rice 1993, Filion and Morin 1996), and to understand its mechanism and ecological significance (Moreno and Oechel 1991, Ne'eman 1997).

The spatial pattern of the post-fire vegetation is a result of a multi-factorial system, which can be listed in a chronological order: 1) The pre-fire spatial pattern of the vegetation affects the pattern and composition of soil seed bank (Zammit and Zedler 1988, Davis et al. 1989). 2) The spatial pattern of reproductive individuals affects the pattern of post-fire seed dispersal in canopy-stored seed bank, e.g. serotinous cones (Saracino and Leone 1993, Filion and Morin 1996). 3) Pre-fire spatial pattern affects fire intensity (Davis et al. 1989). Fire intensity causes a gradient of heat temperature and duration in the soil profile. The heat may cause differential mortality of seed species in soil seed bank and may induce differential germination of the viable seed species (Keeley 1994), thus affecting the spatial pattern of post-fire seedling composition and density (Moreno and Oechel 1991). 4) Pre-fire spatial pattern affects also ash deposition (Moreno and Oechel 1991). Ash cover inhibits the germination of seed species differentially (Thomas and Wein 1990, Ne'eman et al. 1993) by the effect of its extremely high pH (Henig-Sever et al. 1995). 5) Spatial heterogeneity of burn severity and ash deposition patterns creates a wide range of local effects and is likely to influence plant reestablishment resulting in mosaic-like landscape as demonstrated after the Yellowstone 1988 fire (Turner and Romme 1994).

Positive spatial autocorrelation between adult canopy trees and their young understory offsprings was ob-

served in several cases (Horn 1975, Frelich et al. 1993) resulting in a continuation of microsite occupation by the same species. Moreover, post-fire resprouters are not killed by fire, they keep their pre-fire growing microsites and densities. This is an advantage in the highly competitive post-fire regeneration process. However, what is the fate of obligate seeder species like the pines? What are their chances to reestablish at suitable microsites, or even at the same microsites that were occupied by big, mature and reproductive pine trees before the fire – sites that have proven ability to support mature pine trees?

To answer this question we examined the spatial pattern of post-fire Aleppo pine regeneration, in relation to the location of the dead burned trunks. We analyzed the spatial pattern of pine sapling size and density, comparing the 'near' zone, near the burned trunks, with the 'far' zone farther away from them. We selected four natural pine stands 2, 5, 11 and 20 yr after fire and compared their post-fire regeneration.

Methods

The plant species

Much of the life-history variation among pine species can be explained by a model combining site productivity and fire frequency (Keeley and Zedler 1998). The Aleppo pine *Pinus halepensis* Mill. is a west Mediterranean species with disjunct populations of unique genetic composition in Israel (Schiller et al. 1985). This species is typical to moderately productive sites with high intensity stand replacing fires (Keeley and Zedler 1998). In this partially serotinous species, each individual disperses only a part of its canopy-stored seeds in autumn, while all the rest are released from their cones only by the heat and dryness of a severe wildfire (Naveh 1975, Trabaud and Oustric 1989, Saracino and Leone 1993, Daskalakou and Thanos 1996, Thanos et al. 1996). A massive wave of seed germination occurs immediately after the onset of the rainy season (Naveh 1973, Trabaud et al. 1985, Lahav 1988, Ne'eman et al. 1992, Thanos et al. 1996), creating almost an even aged pine stand. At the same time a massive germination of many other species, cued by fire-related environmental factors, also takes place (Keeley 1994). The most important among these plants are *Cistus* spp. (Thanos and Georghiou 1988, Trabaud and Oustric 1989, Roy and Sonie 1992) forming very dense stands competing with the young pine seedlings mainly for water and light (Naveh 1973, Trabaud et al. 1985, Lahav 1988, Moravec 1990, Katz 1993, Ne'eman et al. 1995). In addition to competition, young Aleppo pine seedlings and saplings in Israel are jeopardized by lethal attacks of the pine bast scale *Matsucoccus josephi* (Mendel et al. 1997) and the Indian crested porcupine *Histrix*

indica Kerr. (Izhaki and Ne'eman 1996). The first young pine trees begin producing female cones at the age of three (unpubl.). However, it is unknown how long it takes to produce a large enough seed bank for post-fire regeneration. About 30–40 yr are estimated as needed for full recovery of the Aleppo pine forest after a fire (Moravec 1990, Schiller et al. 1997).

Study sites

Study sites were located in burned natural Aleppo pine forest area in the Mt. Carmel Nature Reserve and National Park, Israel, 5–10 km south-east of the city of Haifa. The bedrock in all sites are chalky-marl formations which under the prevailing climatic conditions produced a light-brown calcareous Rendzina soil. The climate is a typical east Mediterranean one with a mean annual rainfall of ca 700 mm concentrated mainly during December–February, and a long hot and dry period May–October. Mean temperature of the coldest month (January) is 12°C and of the warmest month (August) is 26°C. Typical Carmel unburned Aleppo pine forests are the result of natural invasion into abandoned agricultural and grazing lands, as is the case in most of the Mediterranean basin (Barbero et al. 1998). They are composed of multi-aged pine trees, ca 200 ha⁻¹, with a dense evergreen understory, mainly *Quercus calliprinos* Webb., *Pistacia lentiscus* L., *Cistus salvifolius* L., and several other trees, shrubs, dwarf shrubs, geophytes and many annual species.

To examine the effect of time on the regeneration dynamics of the natural Aleppo pine forest on Mt. Carmel, we selected (in 1994), within a range of 6 km. Similar natural Aleppo pine forests in three sites with one being studied at two dates: Hai-bar89a, Hai-bar89b, Mitla83 and Etzba74, that were burned 2, 5, 11 and 20 yr earlier, respectively. The fires in these three locations were homogeneous crown stand destroying fires, leaving only main trunks. The 5-yr old post-fire stand (Hai-bar89b) was also studied earlier (Hai-bar89a), 2 yr after the fire (see also Izhaki et al. 1992, Ne'eman et al. 1992).

Sampling procedure

Remnants of old big burned trees in all study sites were identified out of which 19–41 trees were randomly

selected. Most remnants were > 15 m apart, a typical situation for the burned studied stands as well as for adjacent unburned ones. The density of young pine trees was measured in each 1 m² quadrat along four rectangular belt transects originating from a burned tree trunk up to 8 m. All quadrats were divided into two zone categories: quadrats located ≤ 4 m from the burned trunks, hereafter the 'near' zone, and quadrats located > 4 m from the burned trunks, hereafter the 'far' zone. According to our previous observations the average diameter of the burned canopies was 8 m, and therefore the 'near' quadrats were located under the projection of the burned canopy and the 'far' quadrats were located beyond the burned canopy. Furthermore, the division into these categories was also based on differences in fire intensity, ash accumulation, post-fire seed density and seedling density (Ne'eman et al. 1992, and unpubl.).

The height, mean of two perpendicular crown diameter, and distance to the burned trunk were measured for the ten tallest young pine saplings in the 'near' zone, and for the tallest ten pines in the 'far' zone. We selected the biggest saplings since biomass was found to be the best criterion for the predicted competitive ability of a plant (Gaudet and Keddy 1988, Tilman 1990).

Data analysis

Although study sites vary in their post-fire age, we did not use them as a chronosequence. The reason is that sites varied in their environmental conditions such as altitude and aspect (Table 1) and probably also by their pre-fire composition and fire intensity. Furthermore, each post-fire stage was represented by a single site; therefore, we could not establish replications for each post-fire stage. Because of these two reasons we did focus on the spatial pattern of saplings in all sites, and did not use the differences among sites as a chronosequence.

Biomass index (hereafter BMINDEX) was calculated for each measured pine sapling as a combined measure for plant size [BMINDEX = (crown diameter)² × (height)]. In an earlier study conducted in the same area (Ne'eman 1994), BMINDEX was found to be significantly correlated with actual sapling above ground dry weight ($R^2 = 0.94$, $p < 0.05$). The natural logarithm (ln) of BMINDEX and square root transformation of densities were used in all statistical analyses. Two-way

Table 1. Environmental characteristics of the study sites, Mt. Carmel, Israel.

Site	Last fire	Years since fire	Altitude m	Meridian	Latitude	Aspect	Slope %
Hai-bar89a	1989	2	370	35°01'E	32°45'N	280	5
Hai-bar89b	1989	5	370	35°01'E	32°45'N	280	5
Mitla83	1983	11	340	32°44'E	34°59'N	190	10
Etzba74	1974	20	180	32°43'E	34°58'N	100	5

Table 2. Average \pm SD pine and sapling density (m^{-2}) size (BMINDEX $\times 10^{-6}$) on sites 2, 5, 11 and 20 yr after fire, near and far from the trunk of burned pines, n = number of trees sampled, p = Probability of paired t-test.

Site	Hai-bar89a		Hai-bar89b		Mitla83		Etzba74		
	Years since fire		Years since fire		Years since fire		Years since fire		
	2	2	5	5	11	11	20	20	
	Near	Far	Near	Far	Near	Far	Near	Far	
Size	Avg \pm SD	0.001 \pm 0.0006	0.001 \pm 0.001	0.10 \pm 0.11	0.06 \pm 0.10	7.72 \pm 6.50	0.45 \pm 0.53	16.96 \pm 11.2	1.94 \pm 1.70
	n	22	19	31	31	41	41	29	29
	p	0.07		0.03		0.0001		0.0001	
Density	Avg \pm SD	8.23 \pm 7.16	12.87 \pm 8.32	4.04 \pm 2.15	3.12 \pm 2.30	0.67 \pm 0.34	0.86 \pm 0.47	0.93 \pm 0.53	0.97 \pm 0.55
	n	30	30	38	38	41	41	27	26
	p	0.0001		0.002		0.02		0.69	

ANOVA was used to examine the effects of location ('near' or 'far') and sites on sapling size (BMINDEX) and density. Paired sample t-test was used for the comparisons of sapling size and density ('near' vs 'far') at each site separately. Linear regression was used to examine the effect of distance from the burned trunk on pine sapling size at each site separately.

All analyses were performed by Systat (Wilkinson et al. 1992).

Results

Sapling size

The average size (BMINDEX) of pine saplings according to their location relative to the burned trunk ('near' or 'far') and to sites differing in the number of years elapsed since last fire is presented in Table 2. Two-way ANOVA showed that sites had significant effects on sapling size ($F_3 = 663.1$, $p < 0.0001$), and the effect of location 'near' or 'far' from the burned trunk was also significant ($F_1 = 140.0$, $p < 0.0001$). The interaction between the two factors was also significant ($F_2 = 26.5$, $p < 0.0001$). Because of the significant interaction found in the two-way ANOVA, the differences between the 'near' and 'far' zones were tested by paired t-test separately for each site. In the site 2 yr after fire, there was no difference in size of saplings growing in the 'far' and 'near' zones, but the differences were significant at all other sites (Table 2). The size of saplings growing in the 'far' zone was 40% smaller than that of those growing in the 'near' zone at the site 5 yr after fire. That difference increased to 94% and 89% for sites 11 and 20 yr after fire, respectively. Because of the significant interaction found in the two-way ANOVA, the effect of the distance from the burned trunk on sapling size is presented for each site (representing years since fire) separately, excluding the site 2 yr after fire where there was no significant difference between the zones. The linear regression of ln transformed BMINDEX was significant for the three sites (Fig. 1).

Sapling density

The average density (m^{-2}) of pine saplings according to their location ('near' or 'far') relative to the burned trunk and at sites differing in the number of years elapsed since last fire is presented in Table 2. Two-way ANOVA showed that sites had significant effect on sapling density ($F_3 = 153.7$, $p < 0.0001$), while

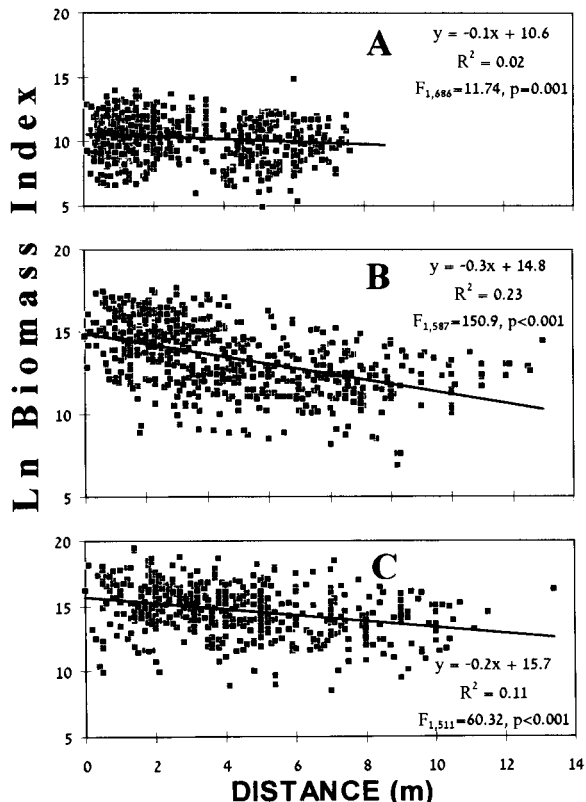


Fig. 1. Linear regression of ln biomass index [BMINDEX = (crown diameter)² \times (sapling height)] of Aleppo pine saplings vs their distance from the burned trunk (n = number of quadrats), in sites 5 yr after fire (A, n = 690), 11 yr after fire (B, n = 590), and 20 yr after fire (C, n = 514).

the location 'near' or 'far' from the burned trunk had no significant effect on sapling density ($F_2 = 2.6$, $p > 0.1$). The interaction between the two factors was also significant ($F_2 = 7.7$, $p < 0.0001$). Because of the significant interaction found in the two-way ANOVA, the differences between the 'near' and 'far' zones were tested by paired t-test separately for each site. The density of saplings growing in the 'far' zone was 56% higher than that of those growing in the 'near' zone, at the site 2 yr after fire (Table 2). However this difference in densities was not significant at the site 20 yr after fire (Table 2).

Discussion

The effect of distance from the burned tree

Early stage (2–5 yr)

We began our study of spatial pattern in post-fire Aleppo pine forest 2 yr after fire. At that time the most distinct spatial pattern was ash circles under the burned pine canopies, with low seedling densities, in contrast to the abundance of pine, *Cistus* and seedlings of annuals in the rest of the area not under the direct effect of the burned canopies (Lahav 1988, Kutiel and Kutiel 1989, Izhaki et al. 1992, Ne'eman et al. 1992). The results show that 2 yr after fire pine seedling density was lower near the burned pine trunks than far away from them, but there was no difference in their size. The effective seed dispersal in *P. halepensis* takes place after fire and high seed densities are found close to the mother trees (Saracino and Leone 1993, unpubl.). Therefore fire-related factors cannot explain the sparse seedling densities in the 'near' zone. We suggested earlier that inhibition of germination by ash pH is a main regulating factor of post-fire pine seed germination (Henig-Sever et al. 1995, Ne'eman 1997).

The results revealed a radical change in the spatial pattern of Aleppo pine saplings, between 2 and 5 yr after fire, indicating that the conditions that are favorable for seed germination are not optimal for seedling growth and establishment (Lamont et al. 1993, Schupp and Fuentes 1996). Seedling density, at site 5 yr after fire, was higher near the burned trunks ('near' zone) than at a greater distance ('far' zone). This difference in seedling density was due to 51% decrease in seedling density in the 'near' zone vs 75% in the 'far' zone during the period between 2 and 5 yr after fire. The lower mortality in the 'near' zone could have been the result of reduced intra- and inter-specific competition since 1) seedling densities of *P. halepensis*, *Cistus* spp. and annual species were lower (Ne'eman et al. 1992), 2) *P. halepensis* saplings could have utilized the improved mineral nutrition originating from the ash layer (Kutiel and Naveh 1987). 3) Density of resprouting evergreen

species was higher in the 'far' zone. During this period (2–5 yr after fire) the increase in seedling size in the 'near' zone was 9900%, while in the 'far' zone it was 5900%. The enhanced growth of pine saplings in the 'near' zone at this stage was apparently the result of the same factors responsible for the lower mortality rate in this zone. Density-dependent post-fire seedling mortality was documented also in Mediterranean-type ecosystem in Australia (Lamont et al. 1993).

Later stage (5–20 yr)

In a comparison between neighboring sites 20 and 5 yr after fire, the density was 77% lower in the 'near' zone and only 69% lower in the 'far' zone, resulting in no significant difference in sapling density between the zones at the site 20 yr after fire. The higher difference in density in the 'near' zone during this period can be explained by shading out of small pine saplings by higher ones, since saplings were much bigger in the 'near' zone.

The difference in size when comparing two sites 5 and 20 yr after fire was 16800% in the 'near' zone and only 3100% in the 'far' zone, indicating that differences in microsite quality might have played a major role in limiting the growth of the young pine trees in the 'far' zone. It is suggested that soil depth or soil pockets at the location of the old burned pine tree and used by the new generation of pine trees in the 'near' zone were responsible for the faster growth.

The final result was that, in an even aged pine stand 20 yr after fire, young pine trees growing at the location of their burned 'mother' tree were almost nine times bigger than same age young pines growing away from their parent's vicinity, and had thus major chances of building the next generation of the pine forest.

Spatial model

Janzen's (1970) original 'distance hypothesis' model of tree recruitment in undisturbed rainforest assumes that seed density decreases while seed survival increases with distance from the parent. This model describes a situation in which establishment of seedlings occurs while the adult population is still extant so that the herbivores and pathogens supported by the parent act continuously and over a long period on the smaller individuals in their vicinity. The consequence is that the population recruitment curve peaks at some distance from the parent tree. However, this model of population recruitment does not fit the situation of post-fire regeneration, when the parent tree dies as described here.

Here we present a new hypothetical model for the spatial pattern of post-fire regeneration of obligate seeder species forming open forests. The model is based on the present results for the period up to 20 yr after

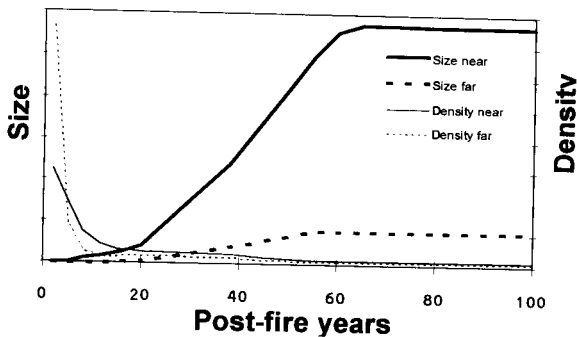


Fig. 2. A model describing the post-fire changes in sapling size and density, near and far from the burned trunks of pine trees.

fire, and on data from Mount Carmel presented by Schiller et al. (1997) for > 20 yr after fire and unburned forests. Our model describes the trends in sapling size and density 'near' and 'far' along a recovery time gradient (Fig. 2). In contrast to the 'distance hypothesis' model, the optimal conditions for recruitment occur beneath the burned canopy of the ancestors. Initial seedling density is higher in the 'far' zone, but it decreases very rapidly, due to mortality, resulting in lower densities than in the 'near' zone. The seedlings in the 'near' zone grow fast while those in the 'far' zone remain small.

The model suggests that most of the saplings in the 'far' zone are shaded out by their fast growing siblings in the 'near' zone; their density will stay lower and size smaller. This process apparently takes place during the period of 20–40 yr after fire since no differences in tree cover were found between 60-yr old unburned stands and 40-yr post-fire stands (Schiller et al. 1997). However, tree size in 40-yr post-fire stands was approximately half that in 60-yr old unburned stands (Schiller et al. 1997). Similar recovery rates were also reported from other Mediterranean countries (Trabaud et al. 1985, Moravec 1990).

We suggest that a set of adaptive life-history traits increases the probability that the microsites occupied by the former pine trees will also be the regeneration microsites of the next generation. Several of these traits were included in the life-history syndrome typical of moderate productive sites with high intensity predictable stand-replacing fires: high flammability of the pine trees, poor self-pruning and non-shedding of empty seed cones result in accumulation of dead biomass on the trees and cause high fire intensities (Keeley and Zedler 1998). The thin bark causes the death of the burned trees. However, high fire intensities probably decrease the regeneration potential of resprouting neighbors (Bond and Midgley 1995), and decrease soil seed bank densities of other seeder species.

The serotinous cones supply high seed densities at close range to mother trees after the fire, ensuring a surplus of seeds for the regeneration process. The black

color of many pine seeds on the dark burned background may reduce seed predation (Saracino and Leone 1993). Thick ash cover resulting from the burned biomass of the trees induces an extreme pH value near the burned trunks (unpubl.), reduces seed germination (Ne'eman et al. 1993), and thus seedling densities (Ne'eman et al. 1992). However, the ash improves mineral nutrition for the seedlings that did germinate in spite of the ash cover (Kutiel and Naveh 1987). The result is sparse but fast-growing seedlings at the microsite of the old burned tree, with high probability of replacing their mother trees.

Conclusions

To conclude, we note that in post-fire regeneration not only resprouting species but also obligate tree seeder species may occupy near pre-fire growing microsites. Moreover, it is suggested that in other *Pinus*, *Cupressus* and other serotinous tree species, the post-fire spatial pattern of the generation follows the pre-fire one. Another case of post-fire inhibition of herbaceous growth accompanied by massive seedling recruitment within the canopy shadow of burned tree skeletons was also described for the Californian knobcone pine *P. attenuata* (Keeley and Zedler 1998). However, more field data are needed to further support the generalization of the proposed hypothetical model.

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