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Int. J. Wildland Fire 7(4): 295-306, 1997

Regeneration of Natural Pine Forest - Review of Work Done After the 1989 Fire in Mount Carmel, Israel

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Abstract. In September 1989 a fire burned a large natural *Pinus halepensis* Mill. forest on Mt. Carmel, Israel. This paper summarizes the main results of five years of research, in which the effects of natural factors and management on the development of the forest and the vegetation were studied. It was found that the burned pine tree skeletons were correlated with the spatial pattern of seed germination. Fewer pine seedlings were found one year after the fire near the burned trunks, but the survival and growth rate of these young pine trees was higher in the following four years. Pine ash was found to inhibit post-fire seed germination, offering a possible explanation for the apparent effect of the old burned trees on the spatial pattern of the new pine seedlings. Both laboratory experiments and field measurements indicate that the high pH of the ash, is the main factor responsible for the inhibition of germination. We examined several management regimes designed to enhance the growth of the young post-fire pine trees and assess their influence on the recovery of the forest. The results revealed that four years after fire, and three years after treatments, forest regeneration was mainly affected by the natural process while management had only a marginal effect. Management such as cutting and leaving, or cutting and removing the burned trunks and twigs from the plots, had almost no effect on species composition and cover. However, thinning of *Pinus* and *Cistus* seedlings increased survival and growth of remaining seedlings.

Keywords. Fire, ash, *Pinus halepensis*, *Cistus*, forest management, germination, growth, species richness, vegetation cover, Israel.

Introduction

Fire is a dominant factor in the evolution and ecology of Mediterranean-type ecosystems (Biswell 1974, Naveh 1975, Trabaud 1990), as a result most of these ecosystems are resilient to fire (Keeley 1986, Westman 1986, Naveh 1989). Wildfires are an extreme disturbance in forest ecosystems, causing extensive destruction of the above-ground plant biomass, and affecting seeds and rhizomes located in the upper layers of the soil. Most minerals incorporated in plant biomass are lost as gaseous emissions to the atmosphere, or as particulate matter in the smoke. Weight loss of nutrient elements in the West Mediterranean can be high (98, 97 and 79% of N, C and P respectively), and only the remainder is left as ash (Trabaud 1994), which is still exposed to loss through erosion. None the less, the concentration of most major nutrients in the soil of oak and pine forests in Israel increases as a result of fire, and creates favorable conditions for plant growth (Kutiel and Naveh 1987).

Most perennial species of the sclerophyllous Mediterranean vegetation in Israel are post-fire resprouters, resistant to fire (Naveh 1973, Lahav 1988). *Pinus halepensis* Mill. and *Cistus* species are obligate seeders, the former with a canopy-stored seed bank, and the later with a soil-stored seed bank. In both of the species, death of mature plants, as a result of fire, is followed by a pulse of seedling recruitment (Naveh 1973, Arianoutsou and Margaris 1981, Trabaud et al. 1985, Lahav 1988, Trabaud and Oustric 1989, Moravec 1990, Saracino and Leone 1993, Thanos et al. 1996).

In September 1989, a wild fire completely burned about 300 hectares of the largest natural pine forest in the Mount Carmel National Park and Nature Reserve, Israel. The public demanded urgent actions to enhance the rehabilitation of the burned forest. This call revealed the existence of only a partial knowledge of the natural process of post-fire recovery in the Mount Carmel ecosystem, particulary with regard to rate of recovery, the natural factors controlling it and management options to enhance it. An intensive scientific research effort was launched. As a part of this effort, we studied the spatial pattern of seedling establishment after fire (Izhaki et al. 1992, Ne'eman et al. 1992), the possible role of ash in regulating post-fire germination (Ne'eman et al. 1993), the means by which the ash affects germination (Henig-Sever et al. 1996), and the effect of various management actions on species richness and abundance in the regenerating forest (Ne'eman 1994, Ne'eman et al. 1995). The scope of this paper is to review the main results of this work and present an update of our knowledge on the post-fire regeneration of the natural *Pinus halepensis* forests on Mount Carmel.

Results and discussion

Study area

Prior to the fire, the study site was a natural forest of scattered *Pinus halepensis* Mill. trees with an understorey composed mainly of *Quercus calliprinos* Webb., *Pistacia lentiscus* L., *Cistus salviifolius* L. and several other small trees and bushes. The forest was composed of multi-aged pine trees, the average age was 51±12 and the density about 200 trees per hectare. This site, that was completely burned as a result of human activity in September 1989, but was not burned before in the last 50 years. The forest is within the Mt. Carmel Nature Reserve, Israel (32°44'N 35°01'E), 320 m above sea level and 7 km from the Mediterranean sea, south-east of the city of Haifa. As typical for all natural pine forests in Israel, the bedrock is chalky marl with a shellow Rendsine soil, rich with chalk.The climate is mild Mediterranean. The rainy winter is only about three months long with mean annual rainfall of about 700 mm, and the avarage monthly minimal temperature in January is 5° C. The dry summer is about six months long with avarage monthly maximal temperature in August 27° C.

The effect of the old burned pine trees

Our first study on the effect of old burned pine trees on the germination and establishment of pine seedlings was carried out in 1991, one and a half years after the fire (Ne'eman et al. 1992). Thirty burned trees were randomly chosen, and the density of seedlings of the various species was recorded in 0.5 m x 0.5 m quadrats laid along four rectangular transects. The transects radiated out in a cross with the burned trunk in the center. Transect length varied with the diameter of the burned canopy, with about 30 quadrats counted around each burned trunk. The quadrats were classified according to whether they were beneath the burned canopy, less than 4 m from the burned trunk (NEAR), or outside of the burned canopy, more than 4 m from it (FAR) (Ne'eman et al. 1992). In 1994, five years after the fire, 38 trees were chosen in the same burned plot. Pine seedlings were counted in 1 m x 1 m quadrats laid out in the same method, with at least 16 quadrats around each burned trunk. The height and two rectangular crown diameters were recorded (±1 cm) for each of the ten tallest pine seedlings growing less than 4 m from the burned trunk near (NEAR), and for the ten tallest seedlings growing farther away than 4 m, but less than 8 m. The biomass index (BMINDEX = (height) x (diameter)^2) was calculated for each seedling. This index was found to be significantly correlated (R^2=0.94, $P<0.05$) with above ground dry mass (Ne'eman 1994).

One and a half years after the fire, seedling density of *Pinus halepensis* was significantly lower near the burned trunks than farther away (Figure 1A), additionaly it was lower near large burned trunks than near small ones ($F_{2,85}=4.20$, $P<0.05$), (Ne'eman et al. 1992). *Cistus salviifolius* seedling density near the burned trunks was 12±16 and 36±16 frarther away, this difference was significant ($F_{2,85}=20.38$, $P<0.001$) (Ne'eman et al. 1992). Only very few annual plant species were growing in near the burned trunks (Ne'eman et al. 1992). *Rhus coriaria* was the single species that was present almost only near

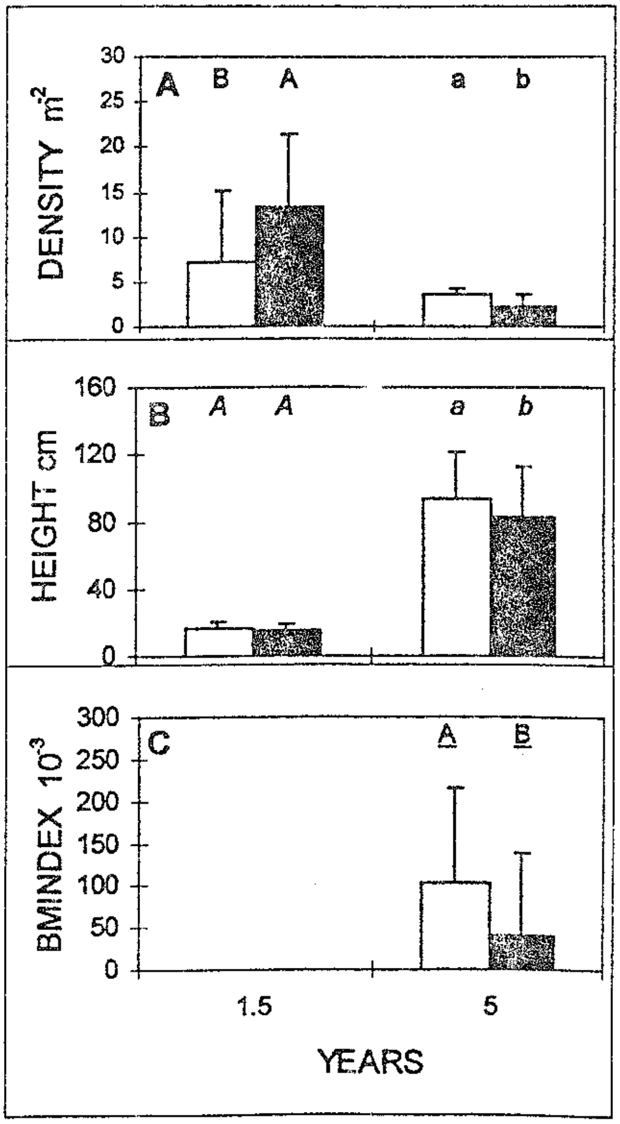

Figure 1. Density (A), height (B) and biomass index (C), of *Pinus halepensis* seedlings growing near (<4 m, empty bars) and far (>4 m, full bars) from the burned trunks, in plots 1.5 years (data from Ne'eman et al., 1992) and 5 years after fire. Columns with identical letters are not significantly different (Duncan's multiple range test, P<0.05), vertical bars represent one standard deviation.

the burned trunks and absent elsewhere, and its density was significantly higher near big burned trunks ($F_{2,85}$=9.43, P<0.001) (Izhaki et al. 1992; Ne'eman et al. 1992). There was no significant difference in the mean height of pine seedlings growing near or far from the burned trunks one and a half years after the fire (Figure 1B, $F_{2,85}$=1.39, P=0.16) (Ne'eman et al. 1992). At that time, one and a half years after the fire, all large burned trunks were surrounded by ash circles with very low seedling density. The lower pine seedling density within these ash circles, could create the impression of poor site conditions, where big pine trees grew before the fire. In other words, it seemed as if these sites, that proved their ability to support big pine trees in the previous pre-fire forest, would have been abandoned, and there seemed to be a risk that no new pine tree would grow there in the post-fire forest.

In the same plot, five years after the fire, the picture changed. Pine seedling density was significantly higher near the burned trunks (Figure 1A, $F_{1,74}$= 31.01, P<0.0001), and pines were significantly taller (Figure 1B, $F_{1,74}$= 20.60, P<0.0001). The biomass index of pine seedlings near the burned trunks was significantly higher than that of distant ones (Figure 1C, $F_{1,74}$= 10.40, P<0.01). Since pine seeds, in large burned areas with no seed immigration from unburned ones, germinate mainly in the first year after the fire, the relative change in pine seedling densities could only be the result of lower mortality of seedlings growing near the burned trunks, or higher mortality of seedlings growing farther away. The higher biomass index of the seedlings near the burned trunks, indicated that they have had overall better growing conditions.

In summary, as a result of uneven distribution of plant biomass in the pine forest, fire intensity and ash cover should be low in clearings, higher in bush-covered sites and the highest at the location of old big pine trees. During the first three years after fire, large ash-covered circles could be seen around the big burned pine trees. Fire intensity and ash cover seemed to be the cause of the described spatial pattern of seedling densities. Intraspecific competition among pine seedlings and interspecific competition between *Pinus halepensis, Cistus salviifolius* and *C. creticus* apparently have an important role in the survival and growth of pine seedlings after fire (Lahav 1988, Katz 1993). Since the density of both *Pinus* and *Cistus* spp. was lower near the burned trunks, these pine seedlings presumably experienced lower competition than other seedlings. These seedlings could also enjoy improved mineral nutrition, the result of the thicker ash layer. The improved conditions can explain our results showing that five years after the fire, pine seedlings growing near the burned trunks had higher biomass index. Since biomass is the best criterion for the predicted competitive ability of a plant (Gaudet and Keddy 1988), individual plants with high biomass may have a competitive advantage over individuals with a low biomass (Tillman 1990). Therefore, we can suppose that pine seedlings with the highest biomass, will also tend to compete better and grow bigger in the future. Preliminary observations show that bigger young pine trees, and those in other young pine forest 7, 11 and 20 years after fire, seem to be grouped around the remains of the old burned trunks also (Ne'eman and Izhaki unpublished data).

The effect of ash on germination

The effect of pine ash on the germination of *Pinus halepensis, Cistus salviifolius* and *C. creticus* was tested in pots (Ne'eman et al. 1993). Twenty seeds were sown in one liter pots with 10 replicates, the soil and seeds were covered with 1, 2, and 5 cm, of pine ash, no ash cover was present in the control. Since *Cistus* seeds are hard seeded (Thanos et al. 1992), these seeds were pre-heated at 100°C for 15 min. Ash cover of 1, 2 and 5 cm, significantly reduced the percentage of germination in *Pinus halepensis* (Figure 2, $F_{3,36}$=47.03, P<0.001) (Ne'eman et al. 1993). There was no significant effect on stem length (Figure 2, $F_{3,36}$=2.04, P>0.05), but roots were shorter with 1 and 5 cm ash covers compared to the control (Figure 2, $F_{3,36}$=3.94, P<0.05) (Ne'eman et al. 1993). Similar results were found for *Cistus salviifolius* and for *C. creticus* (Ne'eman et al. 1993). However, ash cover of 1 and 2 cm significantly increased germination of *Rhus coriaria* seeds (38.1%±10.0% and 40.9%±17.3% respectively) relative to control (7.3%±5.5%), but 5 cm ash depth decreased it (10.9%±6.4%, $F_{4,45}$=2.04, P<0.05) (Ne'eman, unpublished data). These results, of differential effect of ash on germination of different species, support our hypothesis about the role of ash in causing the differential patterns of seedling recruitment around the burned big pine trees (Izhaki et al. 1992; Ne'eman et al. 1992).

Ash is composed mainly of minerals released by oxidation of plant material and some remains of organic materials when fire temperature is low and oxidation incomplete. Some soluble components of charred but not ashed wood were found to induce post-fire germination mainly in Californian and South-African species (Keeley 1994). Smoke stimulated the germination of South-African species (de Lange and Boucher 1990). The effect of mineral ash on germination can be exerted through its pH value, its osmotic potential, or the action of specific ions. The pH and osmotic potential were measured in ash and soil samples one week, seven month and one year after the June 1993 *Pinus halepensis* forest fire at Amirim, Upper Galilee, Israel. In order to sample a wide range of natural occurring values, measurements were taken under pine trees at locations with medium and high fire intensities, and in a near unburned forest. Both measurements, of pH and osmotic potential were taken in a 1:2 mixture of ash/soil to distilled water. The results (Table 1) (Henig-Sever et al. 1996) present the values of pH and osmotic potential in saturated ash and soil after a fire, in

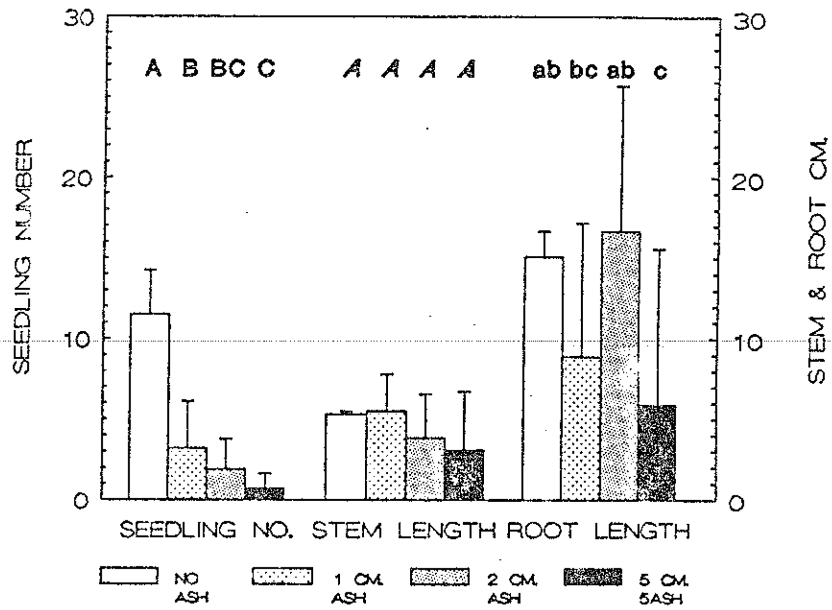

Figure 2. Seedling number (out of 20 seeds), stem length and root length of *Pinus halepensis* in pots without ash, and with 1, 2, and 5cm of ash cover. Columns with identical letters are not significantly different (Duncan's multiple range test, P<0.05), vertical bars represent one standard deviation (From Ne'eman et al., 1993).

similar conditions where post-fire seed germination occurs.

The effect of pH on germination of *Pinus halepensis, Cistus salviifolius* and *C. creticus*, was studied in 10 replicates, 10 seeds per 5 cm Petri dish. Buffer solutions with adjusted pH values in the range 6 - 11, were used to examine the effect of pH on germination. For pH 6, 7, 8 and 9 we used 0.05 M Bis-Tris propane buffer solutions, and for pH 10 and 11 0.05 M CAPS [3-(cyclohexylamino)-1 propane sulfonic acid] buffer was used. Distilled water served as a control (Henig-Sever et al. 1996). The effect of pH on the germination of all three species was significant (Figure 3, $F_{6,63}$=127.00, P<0.05, $F_{6,63}$=150.89, P<0.05 and $F_{6,63}$=182.96, P<0.05, for of *Pinus halepensis, Cistus salviifolius* and *C. creticus* respectively) (Henig-Sever et al. 1996). pH values higher than 8 caused reduction of germination in all species, until complete inhibition of germination at pH 11.

Table 1. Changes in the pH and π=osmotic potential (MPa) of *P. halepensis* ash and soil at the Amirim wildfire site (June 1993) 1 week, 7 months and 1 year after fire. Soil was collected from an unburned site (1), a medium intensity fire site (2) and a high intensity fire site (3) (From Henig-Sever et al., 1996).

	1 week		7 months		1 year	
	pH	π	pH	π	pH	π
Ash	10.0	-0.26	9.8	-0.11	no ash left	
Soil 1	7.0	-0.04	7.3	-0.05	7.4	-0.02
Soil 2	8.3	-0.01	8.8	-0.07	8.8	-0.03
Soil 3	8.5	-0.02	9.1	-0.08	9.0	-0.04

The effect of osmotic potential was also studied in Petry dishes using manitol solutions. Osmotic potential, within the range measured in ash and soil, had only a minor effect on the germination of all the tested species. At 0.3 Mpa the reduction of final germination percentage, relative to control, was 5% and not significant for *P. halepensis*, 17.3% and significant for *C. salviifolius* and 64% and significant for *C. creticus*. (Henig-Sever et al. 1996). We may conclude that extreme pH values are the main factor in inhibiting seed germination by ash.

Treatments of the burned trees

The first question, raised after the 1989 fire on Mt. Carmel, was what to do with the burned pine trees. Leaving them in the burned area may be dangerous for the public, serve as fuel for the next fire, or serve as inoculation place for bark beetles. Since logging is done mechanically, it is associated with serious disturbance to soil surface, which may have a negative effect on the post fire recovery. Removing the burned trunks may also contribute to depletion of minerals gathered by the trees during several decades. In order to estimate the effect of logging, twenty-nine uniform plots in respect of rock, soil, altitude, slope and aspect, each of about 4900 m², were randomly chosen in the burned area. The plots were randomly treated as follows (Ne'eman et al. 1995):

1. **"Burned control"** plots were not treated (plots 10, 20, 30, 40, and 50 in Figure 4).

2. **"Burned and twigs"** plots were those in which the burned trees were cut down, the trunks removed and

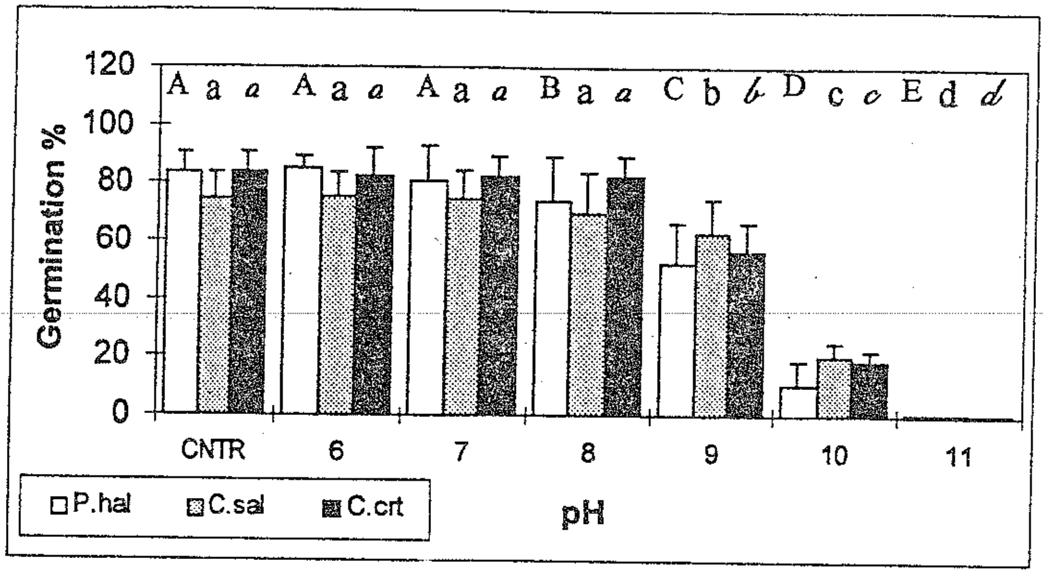

Figure 3. The effect of pH on total germination percentage of seeds of *Pinus halepensis, Cistus salviifolius* and *C. creticus*. Columns with identical letters are not significantly different (Duncan's multiple range test, P<0.05). (From Henig-Sever et al., 1996)

the smaller twigs left in the plots (plots 12, 22, 32, 42, and 52 in Figure 4).

"**Burned and clear**" plots were those in which the burned trees were cut down, and the trunks and the smaller twigs were removed from the plots (plots 11, 21, 31, 41, and 51 in Figure 4).

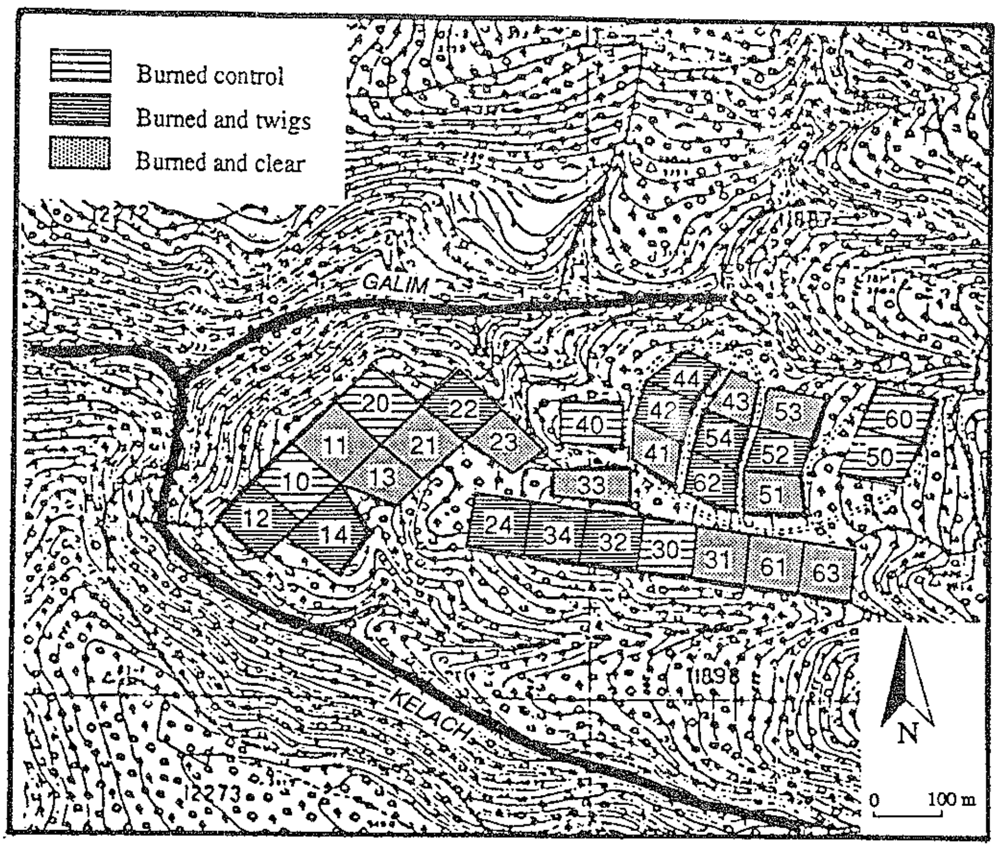

Figure 4. The design of the experimental plots (from Ne'eman et al. 1995).

The remaining plots served the zoological part of this research project. All treatments were carried out in September — November 1990, about one year after the fire. Trees were cut manually with chain saws. Light tractors driving on the borders between plots removed trunks. The twigs from the burned and clear plots were burned outside the plots in order to avoid the effects of burning and ash. Two parallel permanent transects (each of 50 m) were laid out in the middle of each plot. The presence of perennial plant species was recorded at points 10 cm apart, a total of 1000 points per plot, and percentage cover was calculated. The perennial plants were monitored in the autumn of each year. The presence of all annual species was recorded in each plot (4900 m^2) in spring (Ne'eman et al. 1995).

Species richness and composition

Since resprouting species can survive fire, and the seeds of most of these species lose their viability as a result of fire, fire is not likely to change their species richness (Keeley 1991, 1994, Trabaud 1987, 1990). Therefore we analyzed the species richness only of annual species and seeder species (regenerating from seeds after a fire). Their number per plot (4900 m^2) in the second, third and fourth springs after the fire under different treatments is presented in Table 2. The results of a two-way ANOVA, indicate statistically significant differences among the various years and treatments (F_8=15.97, P=0.0001, F_2=39.14, P=0.0001 and F_2=10.93, P=0.0003 for model, years and treatments respectively). The little higher species richness in the treated plots might be the result of new micro habitats emerging due to the disturbance caused while logging. However, the differences were already small in 1993 and are expected to disappear with time. The number of species within the plots of each treatment increased with the years elapsed since the fire. This increase in species richness during the first three years after the fire is supposed to be temporal, followed by a decline in species richness as the forest matures (Naveh 1973, Westman 1986, Moravec 1990, Trabaud 1990).

The effects of treatments on species composition of annual and seeder species were analyzed by CANOCO.

Table 2. Species richness (the mean (± std) number of annual and seeder species regenerating from seeds after a fire) per plot (about 4900 m2) in the sppring of 1991, 1992, 1993 (fire in fall 1989), in plots under various treatments: bu. co.=burned control, bu. tw.=burned and twigs, bu. cl.=burned and clear (from Ne'eman et al., 1995).

Year	bu. co.	bu. tw.	bu. cl.
1991	104.0±32	91.0±14.0	178.0±12
1992	171.0±25	181.0±13	185.0±19
1993	185.0±24	192.0±10	196.0±17

This program was developed to study the response of multiple species to environmental factors (Ter Braak 1995, Palmer 1993). Because the plots were as uniform as possible, only the treatments and years were entered as nominal environmental variables, and therefore the linear model RDA (redundancy analysis) was used. Since the distribution of species rather than samples was our interest, we used the alternative of "biplot" in plotting the species scores and the environmental variables. Only species recorded in more than three plots, of any treatment at any year, entered the presence/absence analysis. The Monte Carlo test was used to test the null hypothesis that the distribution of plant species between treatments, along the first axis of the ordination, was random. The RDA ordination (Figure 5) (Ne'eman et al. 1995), demonstrates the overall effect of years and treatments on annual and seeder species composition. Most of the species are located in the ordination plot near the axis origin, meaning that they were almost equally affected by the different treatments, and that they were only little affected by the years. The species located near the end of the arrows of each environmental variable, encircled together, were mostly affected by that specific variable. However, most of these species are known as common pine forest species and some as typical to disturbed places. The results indicate that cutting down the burned trees, removing or leaving the twigs had only a marginal effect on species richness and on their presence. This effect will probably disappear within a few more years (Ne'eman et al. 1995).

In all the studies of post-fire recovery of *Pinus halepensis* forests almost no replacement of the main species has been described, but merely of annual species or dwarf shrubs e.g. *Cistus* sp. (Naveh 1973, Lahav 1988, Rory and Some 1992, Papavassilou and Arianoutsou 1993, Arianoutsou and Thanos 1996, Kazanis and arianoutsou 1996). Most of these species grow in clearings in the forest even decades after the fire. Seedlings of *Pinus*, which is the main dominant species in the mature plant community, appear as early as the first winter after the fire. Thus, *Pinus halepensis* is both a colonizer and a late succession stage species. Although it is a short-lived tree, it has clear competitive advantages over the broad leafed local oak (*Quercus calliprinos*) on chalky marl in Israel, and is not expected to be replaced (Rabinovitch-Vin 1986).

Percentage cover

The connections among the percentage cover data (arcsin square root transformed) of main species, all climbers and all perenial grasses, the management treatments and time since fire, were analyzed by CANOCO redundancy analysis (RDA). The results (Figure 6) (Ne'eman et al. 1995), demonstrates the overall effect of the years and treatments on relative abundance (as represented by percentage cover) of the main perennial species, climbers, perennial grasses and the total percentage cover. Axis

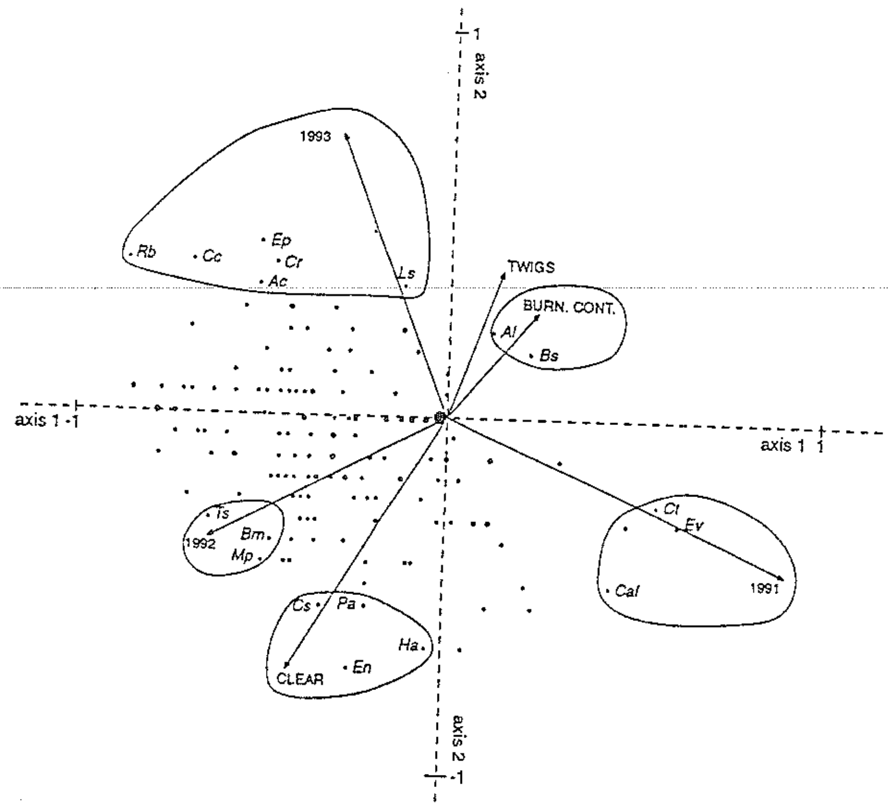

Figure 5. Ordination diagram, species-environment biplot based on redundancy analysis (RDA) for the effect of years after fire (in October 1989) and management treatments on annual and seeder species composition. The arrows represent the treatments: BURN. CONT.=burned control (with no post-fire treatment); TWIGS=the burned trees were cut, logs removed and twigs left; CLEAR=the burned trees were cut, logs and twigs removed. The encircled species are:
1991Ev=*Erophila verna*, Ct=*Chrozophora tinctor* Cal=*Chenopodium murale;*
1992Mp=Medic*ago polymorpha*,Bm=*Bromosmadritensis*, Ts=Trigo*nella spinosa;*
1993Ep=*Euphorbia peplus*,Rb=*Rostraria berythea*,Cc=*Crupina crupinastrum*, Cr=*Crepis reutriana*, Ac=*Ainswotthia cordata*, Ls=*Linum strictum;*
BURN.CONT. Al=*Asterolinon linum-stellatum*, Bs=*Bellis silvestris;*
CLEAR En=*Euphorbia natus*, Ha=*Hypocharis achyrophorus*, Cs=*Crepis saneta*, Pa=*Picris altissima* (from Ne'eman et al.1995).

1 was correlated mainly with the years since the fire, which are located next to it in the ordination plot. Grasses and climbers are situated next to the horizontal axis, meaning they were mostly affected by the time since burnning, grasses were abundant more in 1991, the climbers in 1993. The cover of other species was affected more by the thinning treatments that will be discussed in the next chapter.

Axis 1 has an eigenvalue of 0.123 and was found to be significant by the Monte Carlo permutation test (F=36, P=0.001). The second axis was correlated with the various treatments, and its eigenvalue was only 0.02. Most of the species were located along the first axis of the ordination plot, indicating the a strong effect of the time since fire on their abundance (Ne'eman et al. 1995).

The main post-fire changes in the Mediterranean pine forest vegetation after fire are in seedling densities, their height and percentage cover. Over time the dominant species change from *Cistus* to *Pinus*, the shrubland changing into forest (Trabaud et al. 1985, Moravec 1990, Thanos and Marcou 1991).

Seedling thinning

The seedling thinning experiment was carried out in the "burned and clear" plots, described in the burned trees experiment. Each "burned and clear" plot was divided into subplots (14 m x 70 m), which were treated as follows (Ne'eman et al. 1995): (1) no seedlings were thinned, (2) *P. halepensis* seedlings were thinned, (3) *Cistus* seedlings were thinned, (4) both *P. halepensis* and *Cistus* were thinned. *Pinus* seedlings were thinned by removing all seedlings that were less than about 20-25 cm apart, leaving the tallest ones. *Cistus* seedlings were thinned to leave the smaller ones about 20-25 cm apart. The differential approach in thinning was to favor the future development of pine trees. Thinning was performed in February 1991, 17 months after fire, when the seedlings were about one year old, and after the dry summer natural selection. Percentage cover of perennial species was recorded along transects as described in the burned trees experiment. Pine seedlings were counted in ten fixed (1 m x 1 m) quadrates, randomly marked along the middle transect in each

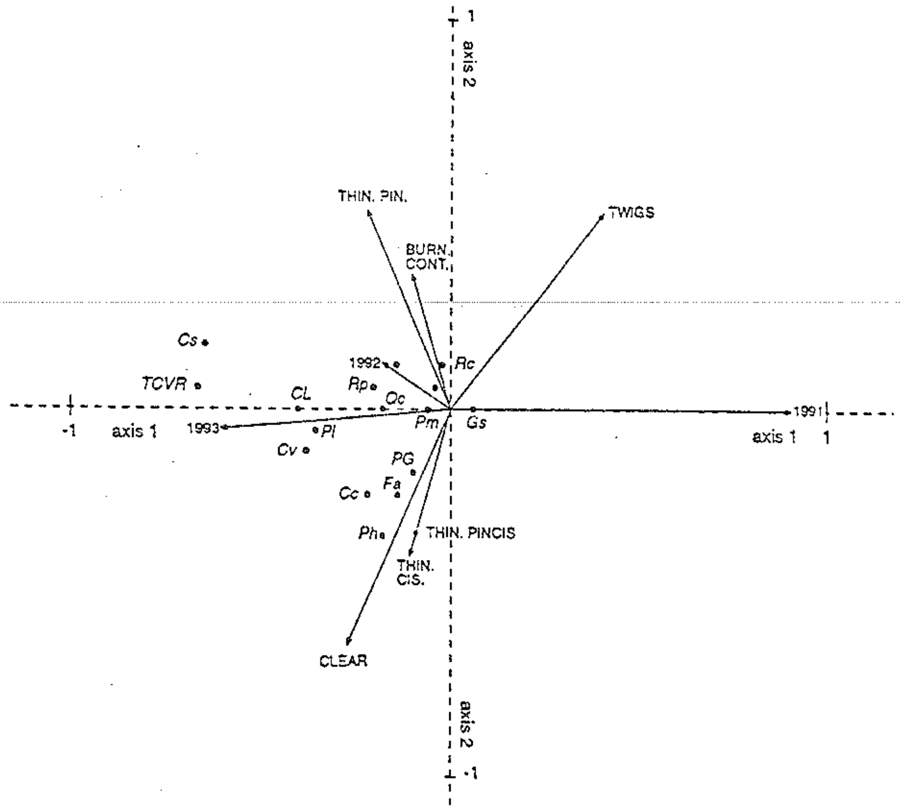

Figure 6. Ordination diagram, species-environment biplot based on redundancy analysis (RDA) for the effect of years after fire (in October 1989) and management treatments on the relative abundance (cover) of: Ph=*Pinus halepensis*, Qc=*Quercus calliprinos*, Pl=*Pistacia lentiscus*, Cs=*Cistus salviifolius*, CL=all climbers, PG=all perennial grasses, TCVR=total cover of all plants. The arrows represent the treatments: BURN. CONT.=burned control (with no post-fire treatment); TWIGS=The burned trees were cut, logs removed and twigs left; CLEAR=the burned trees were cut, logs and twigs removed. THIN. PIN.= thinning of *Pinus* seedlings; THIN. CIS.= thinning of *Cistus* seedlings; THIN. PINCIS.=thinning of both *Pinus* and *Cistus* seedlings (from Ne'eman et al. 1995).

of the thinning experiment subplots, for monitoring seedling densities and mortality. The height and mean of two rectangular diameters of the crown of ten randomly chosen seedlings in each quadrat were measured every three months. Monitoring started immediately after thinning was completed (March 1991), and continued for three growing seasons until November 1992 (Ne'eman et al. 1995). To establish a regression of size and seedlings dry weight, pine seedlings of various dimensions, growing outside but next to the experimental plots, were measured in a similar way, clipped at the base and dried at 80°C for four days for dry weight determination. The best regression equation was:

shoot dry weight=0.029 (height)x(mean crown diameter)-0.72, (r^2=94%, n=31, P<0.0001)
(Ne'eman et al. 1995).

Pine seedling densities on Mt. Carmel, in the first two post-fire years reached up to 20 seedlings per m^2 at the beginning of the second year, and decreased to about 10 seedlings two years later. These densities were higher than those recorded for another site on Mt. Carmel (Lahav 1988) and other studied locations (Trabaud et al. 1985, Moravec 1990, Thanos and Marcou 1991).

Pine seedling density, across different treatments, at the end of the second winter after the fire was very high and variable, between 7±3 and 20±9 seedlings per m^2 before thinning (month 3 in Figure 7A)(Ne'eman, 1994). Seedling thinning had a significant effect on the percentage of pine seedling mortality, relative to pre-thinning densities, (Figure 8A) in the first and second years ($F_{3,36}$=7.82, P=0.0004, $F_{3,36}$=5.03, P=0.0057, respectively). Percentage mortality was highest (58±33) in the subplots where no thinning was done, and the total mortality during both years was 79%. Almost no mortality was observed in the subplots where both *Pinus* and *Cistus* were thinned (Figure 8A) (Ne'eman et al. 1995).

At the end of the experiment pine seedlings were taller in both subplots where pine seedlings were thinned (48 cm ±12 cm), and shorter in the subplots where pine seedlings were not thinned (24 cm ± 7 cm) (Figure 7B) (Ne'eman 1994); the growth of seedlings was also affected in a similar way, Figure 8B). The effect of thinning on

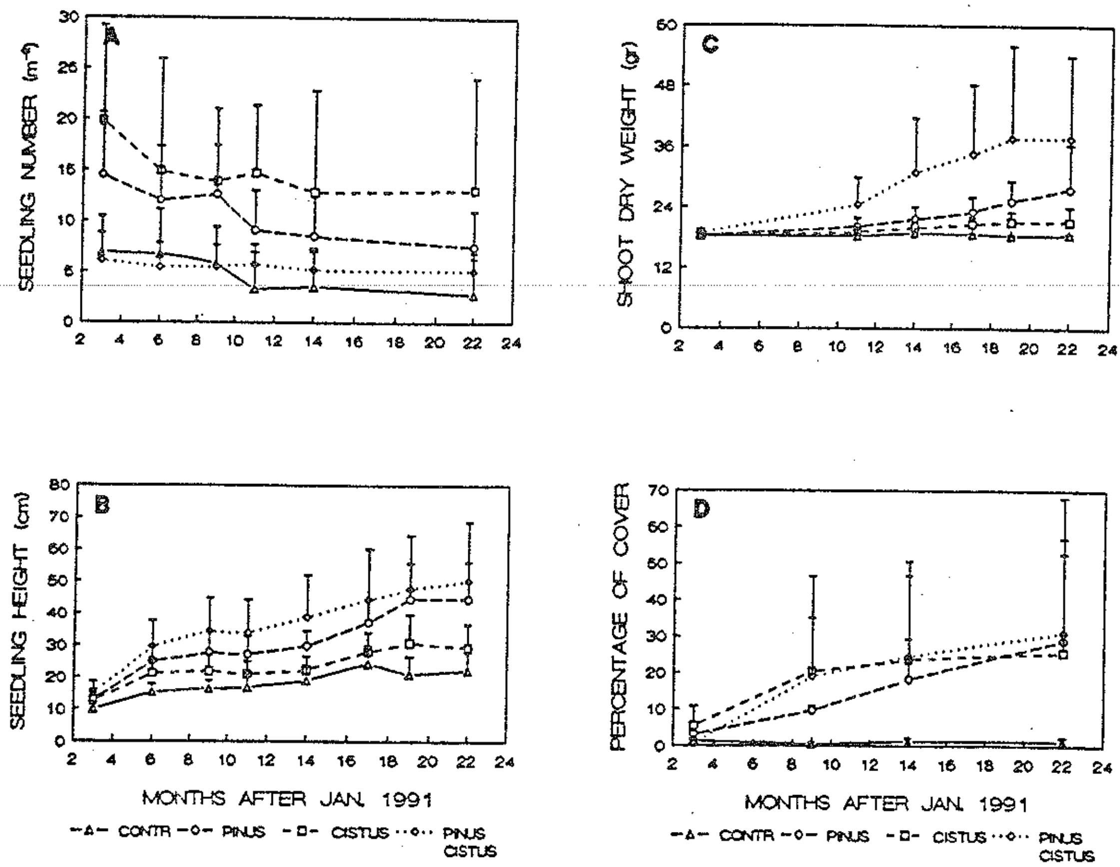

Figure 7. The effects of: CONTR= no thinning, PINUS= thinning of *Pinus* seedlings, CISTUS= thinning of *Cistus* seedlings and PINUS CISTUS=thinning of both *Pinus* and *Cistus* seedlings on the density (A), height (B), dry shoot weight (C) and percentage cover (D) of pine seedlings during 24 months after treatments (from Ne'eman 1994).

the percentage growth in height, relative to pre-thinning height, of pine seedlings (Figure 8B) was insignificant during the first year, but significant in the second ($F_{3,36}$=2.30, P=0.0959, $F_{3,36}$=5.03, P=0.0088, respectively) (Ne'eman et al. 1995).

Shoot biomass of pine seedlings at the end of the experiment, was the highest (37 g ± 20 g), and they also grew faster in the double thinning subplots; it was the lowest (20 g ± 2 g), and there was no growth in the no-thinning subplots (Figure 7C, Figure 8C) (Ne'eman 1994). The effect of thinning on the percentage of annual shoot biomass production, relative to pre-thinning biomass, was significant in first and second years ($F_{3,36}$ =7.21, P=0.0008, $F_{3,36}$=3.96, P=0.0162, respectively) (Ne'eman et al. 1995).

Cistus seedlings reacted in similar way to thinning of *Pinus* in the same experimental subplots (Ne'eman 1994).

Intraspecific competition for water (Naveh 1973) and interspecific competition with *Cistus* (Lahav 1988, Thanos et al. 1989, Moravec 1990, Thanos and Marcou 1991) was suggested to explain growth depression of pine seedlings and their mortality. Some evidence supported this hypothesis (Lahav, 1988), but other later evidence did not show that the intensity of interspecific competition differed from that of intraspesific competition (Katz 1993). Removal treatments are used to test competitive release (e.g., Keddy 1987). Thus the positive reaction of *Pinus* to the thinning of *Pinus* seedlings supported intraspecific competition, while the positive reaction of *Pinus* seedlings to the thinning of *Cistus* seedlings supported the existence of interspecific competition. The nature of the interactions among the numerous seedlings of both species is not yet completely clear (Katz 1993). However, thinning of seedlings may enhance the growth of pine seedlings (Ne'eman et al. 1995) and the natural process of pine seedlings overtopping the *Cistus* shrub layer (Trabaud et al. 1985, Moravec 1990).

Conclusions

The results summed up in this paper provide more evidence for the ability of natural *Pinus halepensis* forest vegetation to overcome severe wildfire disturbance. However, it has been described for the first time that the post-fire renewal of this natural pine forest on Mt. Carmel, Israel is not uniform or homogenous. The pre-fire forest was multi-aged with a composite structure. Large old trees grew next to young smaller ones and among them were clearings with shrubs, dwarf shrubs and annual plants. Fire intensity is correlated with fuel loads. As a result, in places

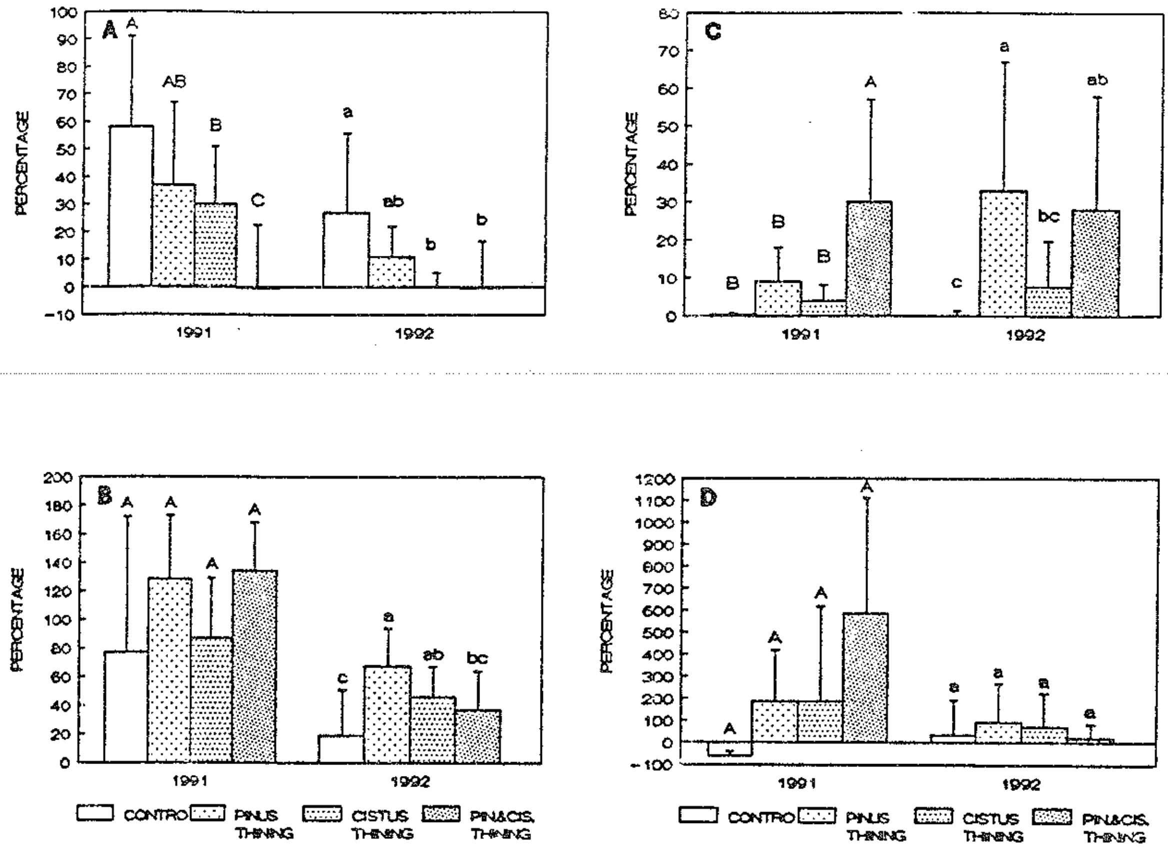

Figure 8. The effects of: CONTRO= no thinning, PINUS= thinning of *Pinus* seedlings, CISTUS= thinning of *Cistus* seedlings and PIN.&CIS.=thinning of both *Pinus* and *Cistus* seedlings on the relative annual mortality (A), relative annual growth (B), relative annual increase in dry shoot weight (C) and relative annual increase in percentage cover (D) of pine seedlings during 24 months after treatments. Columns with identical letters are not significantly different (Duncan's multiple range test, $P<0.05$), vertical bars represent one standard deviation (from Ne'eman et al. 1995).

where large pine trees grew, fire intensity was apparently higher, and a thick ash layer covered the soil. High fire temperatures at these sites, might cause mortality of a part of the soil seed bank. Morover, the germination of surviving seeds might be farther inhibited by the extremely high pH of the ash and the underlying soil. Since *P. halepensis* is only poorly represented in the soil seed bank of the pine forest (Ne'eman and Izhaki, unpublished data), and since massive seed dispersal occurs just after the fire from serotinous cones, ash seems to be the major factor regulating post-fire seed germination in *P. halepensis*. Improved mineral nutrition, and lower mortality at the sites where big pines grew before the fire, can explain why these sites were inhabited with groups of young pine trees, the biggest of all in the new forest. This unique spatial structure was documented for a post-fire, 5 years old pine forest, and seems to be true also for 11 and 20 years (Ne'eman and Izhaki, unpublished data). Thus it seems that one or some trees out of each such group, will apparently replace the old burned pine tree that grew on the same site before the fire. Such a process is not expected in dense and homogenous forests.

Cutting down the burned trees in all the above described modes did not significantly affect species composition and richness. Thinning out seedlings had a positive effect on pine seedling survival and growth.

As a result of this research, and the other above-cited works, the following preliminary management recommendations are proposed to enhance the natural development of a post-fire natural east-Mediterranean *Pinus halepensis* forests:

1. Since natural seed germination and seedling density is high, no additional planting is necessary.

2. Thinning pine seedlings, leaving the tallest ones, in the second post-fire winter will enhance their development.

3. Partial, or even drastic removal of *Cistus* seedlings will further enhance the development of pine seedlings.

4. Thinning of the pine seedlings growing at the sites of the old burned pine trees, at this time, should be done with special care, since they still are exposed to the danger of mortality in the future, mainly due to pests, drought, and competition.

5. It is recommended to treat only the young pines growing at the old pines site, and not the whole burned area which is covered mostly with *Cistus* dwarf shrubs. This practice will be less costly and may contribute to the heterogeneity of the new developing forest. It seems that it will not have a negative effect on the growth rate of the treated pines growing at their naturally favored sites.

6. The young pine trees begin to produce cones five years after the fire. Thus it is very important to prevent repeated fire during that period and longer in order to allow the production of a large enough cone stored seed bank (note that the effect of grazing, which might serve as a fire-preventing management tool, but which could also inhibit the growth of the forest, was not examined).

7. There is no reason to prevent cutting down the burned trees. However, logging should be done in autumn, before the first rains and with minimum disturbance. Special care should be taken to minimize tractor compression of the ground.

8. It is recommended that the twigs of the burned trees be burned to prevent the danger of repeated fire. This should be done in a minimal number of sites, but never at the sites of the old burned pine trees.

Acknowledgments. This research was supported by the Carmel Foundation under the Israel Ministry for Environmental Affairs, The Society for Protection of the Nature in Israel, the Israel Ministry of Arts and Science and GSF - Forschungszentrum fur Umwelt und Gesuntheit GmbH, Neuhrberg.

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