

Recovery of vegetation in a natural east Mediterranean pine forest on Mount Carmel, Israel as affected by management strategies

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Abstract

In September 1989 a large natural *Pinus halepensis* Mill. forest on Mt. Carmel, Israel was burned down. The aim of this research was to suggest post-fire management regimes and to assess their influence on the recovery of the forest. Three treatments were applied to the old burned trees: (1) burned trees were left untreated; (2) burned trees were cut down, the trunks were removed but smaller twigs were left in the plots; (3) burned trees were cut down, the trunks and the smaller twigs were cleared. Four treatments were applied to the new seedlings in the cleared plots: (1) no seedlings were thinned out; (2) *Pinus* seedlings were thinned out; (3) *Cistus* seedlings were thinned out; (4) both *Pinus* and *Cistus* seedlings were thinned out. Species composition, percentage of cover, the density height and biomass of *Pinus* and *Cistus* seedlings were monitored.

The results of this survey, carried out 4 years after the fire and 3 years after the treatments, revealed that cutting or removing the burned trees had less influence on species composition and cover than the natural process of recovery. The thinning of seedlings influenced their height, biomass and survival. Post-fire management recommendations, based on the results of this and other research done in the same area, are proposed.

Keywords: Fire; *Pinus halepensis*; Forest management; Seedling recruitment; Shoot biomass; Species richness

1. Introduction

Fire is a dominant factor in the evolution and ecology of Mediterranean-type ecosystems all over the world (Biswell, 1974; Trabaud, 1990). As a result, most of these ecosystems are resilient to fire (Keeley, 1986; Westman, 1986; Naveh, 1989). In Israel, the effect of fire on vegetation was previously studied by Naveh (1973, 1989), Kutiel and Naveh (1987), Lahav (1988), Izhaki et al. (1992) and Ne'eman et al. (1992, 1993). Most perennial species of the sclerophyllous Mediterranean vegetation in Israel are post-fire res-

proters, which are resistant to fire (Naveh, 1973; Lahav, 1988). *Pinus halepensis* Mill. and *Cistus* species are obligate seeders. *Pinus* germinate from soil and canopy seed banks while *Cistus* germinate only from soil seed bank. Death of the mature plants, as a result of fire, is followed by a recruitment phase (Naveh, 1973; Arianoutsou and Margaris, 1981; Trabaud et al., 1985; Lahav, 1988; Trabaud and Oustric, 1989; Thanos et al., 1989; Moravec, 1990; Thanos and Marcou, 1991; Saracino and Leone, 1993).

In September 1989, a wild fire completely burned down 300 ha of the biggest natural pine forest in the Mount Carmel nature reserve. The first post-fire management problem was what to do with the dead burned

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trees. Leaving them may provide fuel for the next fire, they may be dangerous if, or when they fall down, and they may cause difficulties in passage through the area. Cutting down and removing the burned trees is done by tractors which press and harden the soil. This may effect the germination and sprouting of plants, as well as soil dwelling animals. Removing the dead organic material may affect the biogeochemical cycles in the ecosystem and consequently also plants and animals. Big old burned pine trees have an influence on the spatial pattern of germination and seedling establishment after fire (Izhaki et al., 1992; Ne'eman et al., 1992).

The second stage of management intervention concerns the phase after the massive germination following fire. Thinning out seedlings of different species may affect the nature and time needed for the recovery of the forest.

The aim of this research was to suggest post-fire management regimes that will enhance the development of pine seedlings and to assess their influence on species composition and percentage cover of other accompanying species.

2. Materials and methods

2.1. Study site

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 salvifolius* L. and several other small trees and bushes. The forest is in the Mt. Carmel nature reserve, Israel (32°44'N, 35°01'E), 320 m above sea level and 7 km from the seashore, south-east from the city of Haifa. The climate is mild Mediterranean with a mean annual rainfall of about 700 mm. The study site was totally burned down in September 1989.

2.2. Experimental plots and treatments of burned trees

Twenty-nine plots, uniform in 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:

(1) 'burned control' plots were not treated (plots 10, 20, 30, 40 and 50 in Fig. 1);

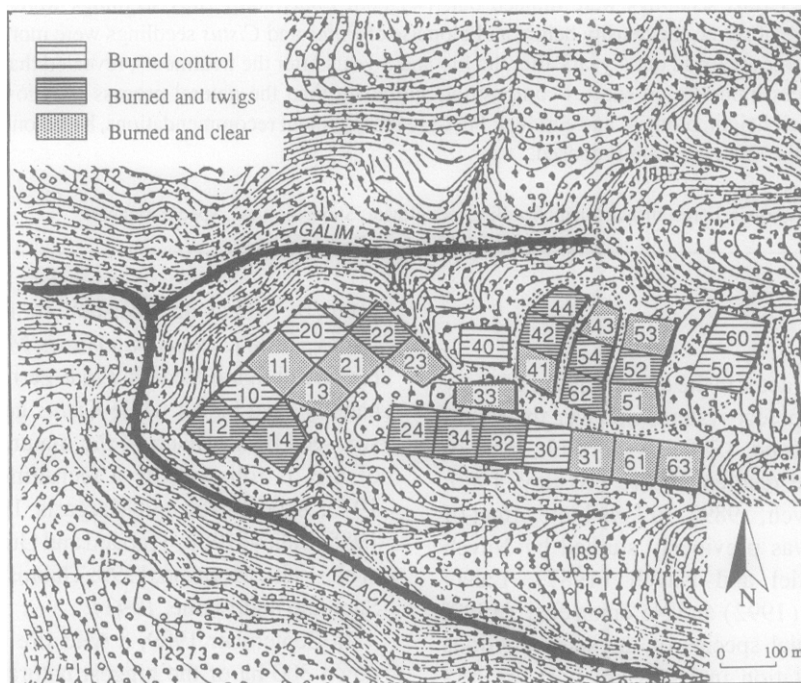


Fig. 1. The design of the experimental plots.

(2) 'burned and twigs' plots—the burned trees were cut down, the trunks were removed and the smaller twigs left in the plots (plots 11, 21, 31, 41, and 51 in Fig. 1);

(3) 'burned and clear' plots—the burned trees were cut down, the trunks and the smaller twigs were removed from the plots (plots 12, 22, 32, 42, and 52 in Fig. 1).

The rest of the plots served the zoological part of this research project (Haim, 1993; Izhaki, 1993). All treatments were carried out in September–November 1990, about 1 year after the fire. Trees were cut manually with mechanical chain saws. Small tractors removed trunks by driving on the borders between plots. The twigs from the burned and clear plots were burned outside the plots.

2.3. Thinning-out of seedlings

Each of the burned and clear plots was divided into subplots (14 m × 70 m). Subplots were treated as follows:

- (1) no seedlings were thinned out;
- (2) *Pinus* seedlings were thinned out;
- (3) *Cistus* seedlings were thinned out;
- (4) double thinning, where both *Pinus* and *Cistus* were thinned out.

Pinus seedlings were thinned out by removing all seedlings that were less than about 20–25 cm apart, leaving the tallest ones. *Cistus* seedlings were thinned out to leave the smaller ones about 20–25 cm apart. The differential approach in thinning was to favour the future development of pine trees. Thinning out was performed in February 1991, 17 months after the fire, when the seedlings were about 1 year old and after natural selection had taken its course during the dry summer.

2.4. Vegetation monitoring

(A) Two parallel permanent transects (each of 50 m) were in the middle of each plot and subplot. The presence of perennial plant species was recorded in 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 m²) in the spring.

(B) *Pinus* seedlings were counted in ten fixed (1 m × 1 m) quadrats, randomly marked along the middle transect in each subplot of the thinning-out experiments, for monitoring seedling density and calculating mortality. The height and the mean of two rectangular diameters of the crown of ten randomly chosen seedlings in each quadrat were measured at 3 month intervals. Monitoring started immediately after thinning out was completed (March 1991), and continued for three growing seasons until November 1992.

(C) *Pinus* 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 4 days for dry weight determination. The best regression equation was: $\text{dryweight} = 0.029 \times \text{height} \times \text{crown diameter} - 0.72$ ($r^2 = 94\%$, $n = 31$, $P < 0.0001$).

2.5. Data analysis

The effect of treatments on seedlings' mortality, growth and increase in shoot biomass within a certain year's growth, was assessed by one-way ANOVA followed by Duncan's multiple range test ($P < 0.05$). In all figures, bars indicated by the same letters are not significantly different. Error bars represent the standard deviation. A two-way ANOVA was used to examine the effect of the various treatments, the years passed and the interaction between treatments and years. All ANOVA analyses were performed by the GLM procedure with SAS-PC (Statistical Analysis System Institute Inc., 1988).

The effect of treatments on the relative abundance of the main perennial species (percentage cover data), and species composition of seeder species (presence absence data) were analysed by CANOCO. This program was specially developed to show how multiple species respond to environmental factors (Ter Braak and Prentice, 1990; Palmer, 1993). Because the plots were as uniform as possible, and only the treatments and years entered as nominal environmental variables, linear model redundancy analysis (RDA) was used. Since the distribution of species rather than samples was our interest, we used the alternative of 'correlation biplot' in the scaling of ordination scores. 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 zero hypothesis

Table 1

Species richness, the mean (\pm SD) number of annual and seeder species (regenerating from seeds after a fire) per plot (about 4900 m²) in the spring of 1991, 1992 and 1993 (fire in autumn 1989), and mean (\pm SD) percentage cover of *Pinus halepensis* (Pin. hal.), *Quercus calliprinos* (Q. cal.), *Pistacia lentiscus* (P. len.), *Cistus salvifolius* (C. sal.), all climbers (clim.), and all perennial grasses (Per. grs.) in the plots under various treatments

Variable	Year	Treatment ^a					
		bu.co.	bu.tw.	bu.cl.	th.cs.	th.pn.	th.p.c.
Species richness	1991	104.0 \pm 32	91.0 \pm 14.0	178.0 \pm 12			
	1992	171.0 \pm 25	181.0 \pm 13	185.0 \pm 19			
	1993	185.0 \pm 24	192.0 \pm 10	196.0 \pm 17			
Percentage cover							
P. hal.	1991	8.6 \pm 1.4	6.1 \pm 2.8	10.3 \pm 2.1			
	1992	11.1 \pm 4.0	4.8 \pm 3.9	9.1 \pm 2.7	10.4 \pm 4.3	5.0 \pm 1.6	10.6 \pm 2.2
	1993	11.5 \pm 3.9	6.8 \pm 3.3	12.1 \pm 3.2	12.8 \pm 4.0	8.7 \pm 4.0	15.4 \pm 2.0
Q. cal.	1991	2.1 \pm 1.2	0.8 \pm 1.0	2.0 \pm 2.3			
	1992	4.5 \pm 2.6	1.7 \pm 1.7	1.4 \pm 1.5	1.7 \pm 2.3	1.7 \pm 2.0	1.5 \pm 1.9
	1993	4.4 \pm 2.1	1.9 \pm 1.7	3.6 \pm 3.6	2.5 \pm 3.1	2.1 \pm 2.4	3.1 \pm 3.9
P. len.	1991	9.3 \pm 4.3	9.7 \pm 3.3	12.3 \pm 3.5			
	1992	16.1 \pm 1.1	12.5 \pm 5.2	13.8 \pm 2.7	13.5 \pm 1.5	16.2 \pm 3.7	16.2 \pm 6.6
	1993	17.8 \pm 2.9	14.4 \pm 5.1	17.7 \pm 6.2	15.6 \pm 2.2	19.6 \pm 2.6	21.1 \pm 5.3
C. Sal.	1991	23.3 \pm 3.5	23.0 \pm 6.2	23.2 \pm 4.9			
	1992	65.3 \pm 4.5	49.6 \pm 14.9	48.4 \pm 8.1	41.3 \pm 14.5	51.5 \pm 6.2	39.5 \pm 8.0
	1993	71.8 \pm 6.6	51.7 \pm 12.9	54 \pm 7.9	46.8 \pm 13.7	54.3 \pm 7.0	47.0 \pm 6.0
Clim.	1991	5.8 \pm 3.3	4.5 \pm 1.9	5.7 \pm 3.0			
	1992	12.7 \pm 6.0	10.7 \pm 4.9	11.2 \pm 4.8	10.6 \pm 3.7	10.9 \pm 2.8	10.2 \pm 4.6
	1993	15.2 \pm 3.9	10.8 \pm 5.2	16.5 \pm 5.3	15.0 \pm 3.8	15.6 \pm 6.9	12.7 \pm 6.9
Per. grs.	1991	3.6 \pm 3.6	4.2 \pm 3.0	4.2 \pm 0.8			
	1992	4.4 \pm 3.0	7.3 \pm 7.9	7.2 \pm 2.0	5.6 \pm 2.5	3.3 \pm 1.8	5.5 \pm 3.3
	1993	4.7 \pm 4.4	10.0 \pm 7.8	7.4 \pm 2.7	8.8 \pm 6.9	3.6 \pm 0.9	6.8 \pm 2.8

^abu.co., burned control; bu.tw., burned and twigs; bu.cl., burned and clear; th.cs., thinning of *Cistus*; th.pn., thinning of *Pinus*; th.p.c., thinning of *Pinus* and *Cistus* (for further explanation see Fig. 4 or text).

that the distribution of plant species between the various treatments, along the first axis of the ordination, was random.

3. Results

3.1. Species richness and composition

Table 1 presents the numbers of annual and seeder species (regenerating from seeds after a fire) per plot (4900 m²) in the second, third and fourth springs after the fire, in different treatments. The results of a two-way ANOVA (Table 2) indicate statistically significant differences among the various treatments. The burned control plots had the lowest species richness, while the burned and cleared plots had the highest. The

number of species within the plots of each treatment increased with the years passed from the fire.

The results of CANOCO RDA in Fig. 2, demonstrate the overall effect of the years and treatments on species (annuals and seeders) composition. Most of the species are concentrated near the origin, indicating that they were almost equally distributed among the different

Table 2

Two-way ANOVA for the effects of time passed since the fire and the various treatments (for details see text, or Fig. 1) on the number of annual and seeder species (regenerating from seeds after a fire)

Source	d.f.	R ²	F-value	P
Model	8	0.82	15.79	0.0001
Years	2		39.14	0.0001
Treatments	2		10.93	0.0003
Years \times treatments	4		6.55	0.0008

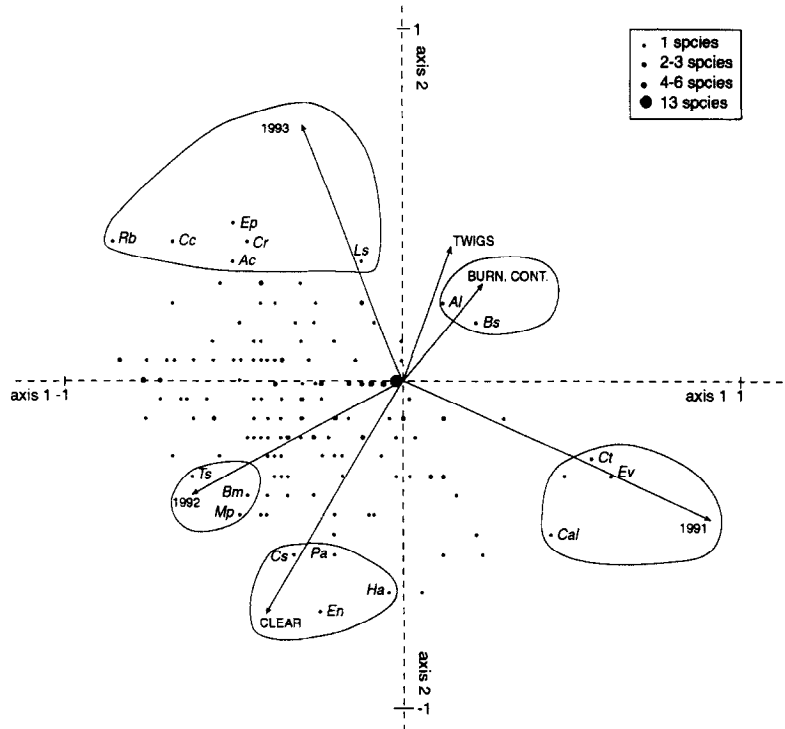


Fig. 2. Ordination diagram, species-environment biplot based on redundancy analysis (RDA) for the effect of years after fire (fire in October 1989) and management treatments on annual and seeder species composition. The arrows represent the experimental variables: BURN. CONT., burned control (with no 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 as follows. 1991: Ev, *Erophila verna*; Ct, *Chrozophora tinctoria*; Cal, *Chenopodium murale*. 1992: Mp, *Medicago polymorpha*; Bm, *Bromos madritensis*; Ts, *Trigonella spinosa*. 1993: Ep, *Euphorbia peplis*; Rb, *Rostraria berythea*; Cc, *Crupina crupinastrum*; Cr, *Crepis reutriana*; Ac, *Ainsworthia cordata*; Ls, *Linum strictum*. BURN. CONT.: Al, *Asterolinon linumstellatum*; Bs, *Bellis silvestris*. CLEAR: En, *Euphorbia natus*; Ha, *Hypochaeris achyrophorus*; Cs, *Crepis sancta*; Pa, *Picris altissima*.

treatments and that they were almost not affected by the years.

However, the species located near the end of the arrows of each environmental variable and encircled together with it, were mostly affected by that variable.

3.2. Percentage cover

The percentage cover of the main species, that of climbers and of perennial grasses in plots of the various treatments in the different years are presented in Table 1. Table 3 presents the results of a two-way ANOVA for the data. Both years and treatments affected percentage cover of *Pinus halepensis*, but there was no interaction between them (Table 3). Thinning of pine seedlings naturally reduced its cover. Thinning of *Cistus* caused a slight increase, and the thinning both of

Pinus and *Cistus* caused an overall increase, compensating for the loss of pine seedling (Table 1).

Treatments and years also affected the percentage cover of *Cistus salvifolius* (Table 3). The burned control plots had the highest cover, the plot where *Cistus* was thinned out had lower cover, but this difference decreased in the following year (Table 1).

The percentage cover of *Quercus calliprinos*, *Pistacia lentiscus*, all climbers and all perennial grasses varied a lot among treatments and years (Table 1), but only the increase with the years was significant (Table 3).

The results of the CANOCO RDA in Fig. 3, demonstrate 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 1 was

Table 3

Two-way ANOVA for the effects of time passed since the fire and the various treatments (for details see text) on the percentage cover of the main species

Variable ^a	Source	d.f.	R ²	F-value	P
P.hal.	Model	14	0.54	3.87	0.0002
	Years	2		4.74	0.0133
	Treatments	5		8.36	0.0001
	Years × treatments	7		0.43	0.8805
Q.cal.	Model	14	0.20	0.86	0.6064
	Years	2		0.86	0.4309
	Treatments	5		1.66	0.1637
	Years × treatments	7		0.29	0.9558
P.len.	Model	14	0.45	2.80	0.0042
	Years	2		14.51	0.0001
	Treatments	5		1.19	0.3273
	Years × treatments	7		0.60	0.7497
C.sal.	Model	14	0.75	10.03	0.0001
	Years	2		51.82	0.0001
	Treatments	5		6.00	0.0002
	Years × treatments	7		0.97	0.4632
Clim.	Model	14	0.48	3.15	0.0016
	Years	2		18.15	0.0001
	Treatments	5		1.06	0.3944
	Years × treatments	7		0.35	0.9238
Per.grs.	Model	14	0.25	1.15	0.3469
	Years	2		2.02	0.1181
	Treatments	5		2.10	0.2656
	Years × treatments	7		0.22	0.9801

^aP.hal., *Pinus halepensis*; Q.cal., *Quercus calliprinos*; P.len., *Pistacia lentiscus*; C.sal., *Cistus salvifolius*; Clim., climbers; Per. grs., perennial grasses.

correlated mainly with the years since the fire (that are located close to it). This axis 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 is correlated more with the various treatments, and its eigenvalue is only 0.02. Most of the species are located along the first axis, indicating the importance of the time factor. *Pinus* is located near axis 2, in the opposite direction of the thinning of *Pinus* treatment.

In a forward selection of environmental variables, burned control and burned and twigs treatments entered first explaining 2% and 1% of the variance, respectively. All other thinning treatments entered later, each explaining an additional 1% of the variance.

3.3. Pine seedlings

Pine seedling density, at the end of the second winter after the fire was very high and variable, being between 7 ± 3.6 and 20 ± 9.4 seedlings m^{-2} before thinning.

Seedling thinning-out had a significant effect on the percentage of pine seedling mortality (Table 4) during 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 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 out. In the subplots where only *Pinus* or only *Cistus* were removed, the total mortality during both years was 52% and 49% respectively.

Pine seedlings were taller in both subplots where pine seedlings were thinned and lower in the subplots where pine seedlings were not thinned. The growth of seedlings was affected in a similar way (Table 4). The effect of thinning-out on the percentage growth in height of pine seedlings (Table 4) 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).

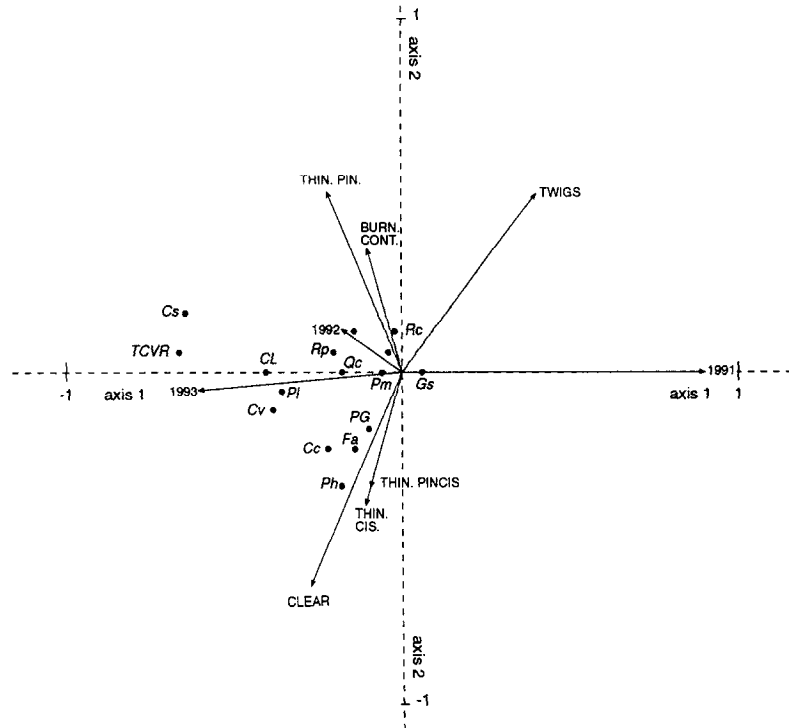


Fig. 3. Ordination diagram, species-environment biplot based on redundancy analysis (RDA) for the effect of years after fire (fire in October 1989) and management treatments on the relative abundance (cover) of: Ph, *Pinus halepensis*; Qc, *Quercus calliprinos*; Pl, *Pistacia lentiscus*; Cs, *Cistus salvifolius*; CL, all climbers; PG, all perennial grasses; TCVR, total cover of all plants. 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 were removed; THIN. PIN., *Pinus* seedlings were thinned out; THIN. CIS., *Cistus* seedlings were thinned out; THIN. PINCIS., both *Pinus* and *Cistus* seedlings were thinned out.

Table 4

Pine seedling mortality, percentage growth and percentage of annual shoot dry weight production in subplots subjected to various thinning treatments, during the first 2 years after thinning

Variable	Year	Treatment ^a			
		no th.	th.pn.	th.cs.	th.p.c.
Mortality	1991	58.0 ± 33	37.0 ± 30	30.0 ± 21	-0.5 ± 23
	1992	27.0 ± 29	11.0 ± 11	0.3 ± 5	-0.2 ± 17
Growth	1991	77.0 ± 95	128.0 ± 45	87.0 ± 42	134.0 ± 34
	1992	19.0 ± 32	67.0 ± 27	46.0 ± 21	37.0 ± 27
Production	1991	0.3 ± 0.4	9.0 ± 9	3.8 ± 4.4	30.0 ± 27
	1992	0.0 ± 1.3	33.0 ± 34	7.6 ± 12	28.0 ± 30

^ano th., no thinning; th.pn., thinning of *Pinus*; th.cs., thinning of *Cistus*; th.p.c., thinning of *Pinus* and *Cistus*.

Shoot biomass of pine seedlings was highest in the double thinning subplots, and lowest in the no-thinning plots. The effect of thinning-out on the percentage of

annual shoot biomass production (Table 4) was significant in first and second years ($F_{3,36} = 7.21$, $P = 0.0008$, $F_{3,36} = 3.96$, $P = 0.0162$, respectively). In the

double thinning subplots, pine seedlings had the highest biomass and also grew faster than the seedlings in other treatments, but the effect of thinning decreased with time (Table 4).

4. Discussion

Post-fire recovery of pine forests has been studied for *Pinus halepensis* in almost all its distribution areas around the Mediterranean sea (Trabaud et al., 1985; Lahav, 1988; Moravec, 1990; Ne'eman et al., 1993; Papavassiliou and Arianoutsou, 1993; Saracino and Leone, 1993). However, the effects of post-fire management were almost not studied (but see Canas and Llimona, 1992; Ne'eman et al., 1993).

Post-fire recovery is often referred to as a secondary succession. The main process taking place during succession is species replacement, and several mechanisms were suggested to explain its driving force (e.g. Egler, 1954; Connell and Slatyer, 1977; Tilman, 1990).

In all the studies of post-fire recovery of *Pinus halepensis* forests, no species replacement of the main species was described, but mostly that of annual species or dwarf shrubs such as *Cistus* sp. (Naveh, 1973; Lahav, 1988; Rory and Some, 1992; Papavassiliou and Arianoutsou, 1993). 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 coloniser and a late succession stage species. Although it is a short living tree, it has clear competitive advantages over the broad leaved local oak (*Quercus calliprinos*) on chalky marl in Israel, and will not be substituted (Rabinovitch-Vin, 1986).

Since resprouting species are those that survived the fire and the seeds of most of these species lose their viability as a result of fire, fire does not change their species richness (Trabaud, 1990; Keeley, 1991). Therefore, we performed the analysis of species richness only on annual species and seeders. The increase in species richness during the first 3 years after the fire was significant in all plots. This increase contradicts the general trend of decline in species richness after fire as the forest matures (Naveh, 1973; Westman, 1986; Moravec, 1990; Trabaud, 1990). The higher species richness in the burned and treated plots in relation to

the burned control plots might be the result of new micro habitats emerging owing to the disturbance caused while cutting down the burned trees. The tracks left by tractor wheels, densely populated by annual species, lasted 10 or even 20 years after cutting of the burned trees (personal observations). However, this difference, in species richness, was already small in 1993 and will soon vanish.

Ordination should reveal the connection between the presence of species and the environmental variables (Ter Braak and Prentice, 1988; Palmer, 1993), which in this study are treatments and years. However, since most of the species appeared near the origin of the ordination axis (Fig. 2), it means that the various treatments did not affect them. Even most of the species affected by the environmental variables, located near the arrows' heads (Fig. 2), were common pine forest species. Two of the species near the 1991 arrow are ruderal/segetal species. Only one species, *Asterolimon linum-stelatum*, located near the 'burned control' arrow, is a relatively rare species found more in burned areas (personal observations).

The results demonstrate that cutting down the burned trees, removing the twigs or leaving them in the burned area have only a marginal influence on the total species richness and species. This effect will disappear in the future.

The percentage cover of resprouting species was not affected by cutting the burned trees nor by thinning out seedlings of *Pinus* or *Cistus*, and grew with the years. These results confirm our expectations.

The most important changes in the pine forest vegetation after fire concern seedling densities, height, and cover. During this process the dominant species changed from *Cistus* to *Pinus*, and shrubland changed to forest (Trabaud et al., 1985; Moravec, 1990; Thanos and Marcou, 1991). *Pinus* cover was affected both by years and treatments, owing to the thinning of their seedlings. However, it is noteworthy that the cover of *Pinus* in the plots where both *Pinus* and *Cistus* were thinned out was highest in 1993. This shows one aspect of the effectiveness of this treatment. The results of the ordination also demonstrate the higher correlation between the relative abundance (cover) of the species located along the first axis and the years, rather than treatments. Only *Pinus* and *Cistus* cover were affected by the treatments and are therefore located opposite the arrows of treatments where they were thinned out.

Intraspecific competition for water (Naveh, 1973) and interspecific competition with *Cistus* (Lahav, 1988; Thanos et al., 1989; Moravec, 1990; Thanos and Marcou, 1991) may explain growth depression of pine seedlings and their mortality. The results supported this hypothesis (Lahav, 1988), but could not prove that the intensity of interspecific competition differed from that of intraspecific competition (Katz, 1993).

Removal treatments are a test for competitive release (e.g. Keddy, 1987). Thus, the positive reaction of *Pinus* to the thinning out of *Pinus* seedlings indicates intraspecific competition, while the positive reaction of *Pinus* seedlings to the thinning-out of *Cistus* seedlings indicates interspecific competition. *Pinus* seedlings responded to the thinning of both seedling species better than to the thinning of either one separately. The clearest effect was in the double thinning treatment subplots. In these subplots there was no mortality, seedlings were higher, had a higher shoot biomass and still were growing faster than seedlings in all other plots. *Cistus* reacted similarly to the thinning out of *Pinus* (Ne'eman, 1994).

Since individual plants with high biomass have a competitive advantage over individuals with a low biomass (Gaudet and Keddy, 1988), it seems logical that pine seedlings with the highest biomass would also tend to compete better and grow higher in the future. The nature of the interactions among the numerous seedlings of both species is not yet clear. However, thinning out of seedlings may enhance the natural process of pine seedlings overtopping the *Cistus* bush layer (Trabaud et al., 1985; Moravec, 1990).

Pine seedling densities on Mt. Carmel in the first 2 post-fire years reached 20 seedlings m⁻² at the beginning of the second year, and decreased to about 10 seedlings m⁻² 2 years later. These densities are higher than those recorded for another site on Mt. Carmel (Lahav, 1988) and are also higher than values reported for other locations (Trabaud et al., 1985; Moravec, 1990; Thanos and Marcou, 1991). Consequently, there is no need to plant new seedlings in a burned pine forest; treating the natural population of pine seedlings is an ecologically preferred alternative.

Other studies on the same site have shown the locations of the large burned pine trees to be a bad germination site, as only few pine seedlings germinated there (Izhaki et al., 1992; Ne'eman et al., 1992). However, the growth of these pine seedlings was quicker. Five

years after the fire, most of the young pine trees grew in groups around the old big burned stems, and they were higher than the young trees elsewhere (Ne'eman and Ishaki, unpublished data). A similar phenomenon is still evident in other sites, 11 and 20 years after fire (Ne'eman and Ishaki, unpublished data).

As a result of this research, and the above cited works, the following preliminary management recommendations are proposed to enhance the natural development of a post-fire pine forest.

(1) Since natural seed germination and seedling density are high, no additional planting is necessary to retain the natural genetic composition and variability.

(2) Thinning pine seedlings in the second post-fire winter will enhance the development of pine seedlings. The tallest pine seedlings should be left, since they may also continue to grow faster. Further thinning of pine seedlings should be done with special care since they are still exposed to the danger of mortality in the future, mainly due to pests, drought, and competition.

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

(4) Pine seedlings growing near the old burned pine trees should be carefully maintained since they may grow to be the natural replacers of the old burned pine trees.

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References

- Arianoutsou, M. and Margaris, N.S., 1981. Early stages of regeneration after fire in a phrygic ecosystem (East-Mediterranean) I. Regeneration by seed germination. *Biol.-Ecol. Medit.*, 8: 119-128.
- Biswell, H.H., 1974. Effects of fire on chaparral. In: T.T. Koslowski and C.E. Ahlgren (Editors), *Fire and Ecosystems*. Academic Press, New York, pp. 321-364.

- Canas, J. and Llimona, F., 1992. Dynamique des communautés végétales du massif de Monserat après les incendies de 1986. In: L. Trabaud and R. Prodon (Editors), Int. Workshop on the Role of Fire in Mediterranean Ecosystems. Banyuls-Sur-Mer, France, September 1992. (Abstr.)
- Connell, T.H. and Slatyer, R.O., 1977. Mechanisms of succession in natural community stability and organization. *Am. Nat.*, 111: 119-1144.
- Egler, X.X., 1954. Initial floristic model. *Vegetatio*, 4: 412-417.
- Gaudet, C.L. and Keddy, P.A., 1988. A comparative approach to predicting competitive ability from plant traits. *Nature*, 334: 242-243.
- Haim, A., 1993. The resilience of small mammals to fire in an East-Mediterranean pine forest on Mount Carmel, Israel: the effects of post-fire management regimes. In: L. Trabaud and R. Prodon (Editors), Proc. of the Int. Workshop on the Role of Fire in Mediterranean Ecosystems. Commission of the European Communities, Brussels, pp. 127-141.
- Izhaki, I., 1993. The resilience of passerine birds to fire in an East-Mediterranean pine forest on Mount Carmel, Israel: the effects of post-fire management regimes. In: L. Trabaud and R. Prodon (Editors), Proc. of the Int. Workshop on The Role of Fire in Mediterranean Ecosystems. Banyuls-Sur-Mer, France, September 1992, Commission of the European Communities, Brussels, pp. 303-315.
- Izhaki, I., Lahav, H. and Ne'eman, G., 1992. Spatial distribution patterns of *Rhus coriaria* seedlings after fire in a Mediterranean pine forest. *Acta Oecol.*, 13: 279-289.
- Katz, G., 1993. The interaction between *Pinus halepensis* and *Cistus salvifolius* in the first stages of post-fire succession on Mount Carmel. M.Sc. Dissertation, Tel-Aviv University, 92 pp. (In Hebrew with English abstract.)
- Keddy, P.A., 1987. Effect of competition of shrubs on herbaceous wetland plants: a 4-year field experiment. *Can. J. Bot.*, 67: 708-716.
- Keeley, J.E., 1986. Resilience of Mediterranean shrub communities to fires. In: B. Dell, A.J.M. Hopkins, and B.B. Lamont (Editors), Resilience in Mediterranean-Type Ecosystems. Dr. Junk, Dordrecht, pp. 95-113.
- Keeley, J.E., 1991. Seed germination and life history syndromes in the California chaparral. *The Bot. Rev.*, 57: 81-116.
- Kutiel, P. and Naveh, Z., 1987. Soil properties beneath *P. halepensis* and *Q. calliprinos* trees on burned and unburned mixed forests on Mt. Carmel, Israel. *For. Ecol. Manage.*, 20: 11-24.
- Lahav, H., 1988. Renewal of vegetation after fire in a natural pine forest on Mt. Carmel. M.Sc. Dissertation, Tel-Aviv University, 77 pp. (In Hebrew.)
- Moravec, J., 1990. Regeneration of N.W. Africa *Pinus halepensis* forests following fire. *Vegetatio*, 87: 29-36.
- Naveh, Z., 1973. The ecology of fire in Israel. *Annu. Tall Timbers Fire Ecol. Conf.*, 13: 131-170.
- Naveh, Z., 1989. Fire in the Mediterranean landscape, an ecological perspective. In: J.G. Goldammer and M.J. Jenkins (Editors), Fire in Ecosystem Dynamics. S.P.B. Academic, The Hague, pp. 1-20.
- Ne'eman, G., Lahav, H. and Izhaki, I., 1992. Spatial pattern of seedlings one year after fire in a Mediterranean pine forest. *Oecologia*, 91: 365-370.
- Ne'eman, G., Lahav, H. and Izhaki, I., 1993. The resilience of vegetation to fire in an East-Mediterranean pine forest on Mount Carmel, Israel: the effect of post-fire management. In: L. Trabaud and R. Prodon (Editors), Fire in Mediterranean Ecosystems. Commission of the European Communities, Brussels-Luxembourg, pp. 127-141.
- Ne'eman, G., 1994. The effect of thinning out on the survival and development of *Pinus* and *Cistus* seedlings after fire on Mt. Carmel, Israel. Proc. of the 2nd Int. Conf. on Fire Research, Coimbra, Portugal, November 1994. Viegas, Coimbra, pp. 1021-1031.
- Palmer, M.W., 1993. Putting things in even a better order: the advantages of canonical Correspondence analysis. *Ecology*, 74: 2215-2230.
- Papavassiliou, M. and Arianoutsou, M., 1993. Regeneration of leguminous herbaceous vegetation following fire in a *Pinus halepensis* forest of Attica, Greece. In: L. Trabaud and R. Prodon (Editors), Fire in Mediterranean Ecosystems. Commission of the European Communities, Brussels-Luxembourg, pp. 127-141.
- Rabinovitch-Vin, A., 1986. Parent rock, soil and vegetation in Galilee. Nature Reserve Authority and Kibbutz Haneuchad Publishing House, Tel-Aviv, 254 pp. (In Hebrew.)
- Rory, J. and Some, L., 1992. Germination and population dynamics of *Cistus* species in relation to fire. *J. Appl. Ecol.*, 29: 647-655.
- Saracino, A. and Leone, V., 1993. Natural regeneration 2 and 4 years after fire of *Pinus halepensis* Miller in dunal environment. In: L. Trabaud and R. Prodon, (Editors) Fire in Mediterranean Ecosystems. Commission of the European Communities, Brussels-Luxembourg, pp. 141-150.
- Statistical Analysis System Institute Inc., 1988. SAS/STAT User's Guide. SAS Institute Inc., Cary, NC, 1028 pp.
- Ter Braak, C.J.F. and Prentice, I.C., 1990. A Theory of Gradient Analysis. *Advances in Ecological Research*, Vol. 18. Academic Press, London, pp. 271-313.
- Thanos, C.A., Marcou, S., Christodoulakis, D. and Yannitsaros, A., 1989. Early post-fire regeneration in *Pinus brutia* forest ecosystems of Samos Island (Greece). *Acta Oecol.*, 10: 79-94.
- Thanos, C.A. and Marcou, S., 1991. Post-fire regeneration in *Pinus brutia* forest ecosystem of Samos island (Greece): 6 years after fire. *Acta Oecol.*, 12: 633-642.
- Tilman, D., 1990. Constraints and tradeoffs: toward a predictive theory of competition and succession. *Oikos*, 58: 3-15.
- Trabaud, L., 1987. Fire and survival traits in plants. In: L. Trabaud (Editor), The Role of Fire in Ecological Systems. S.P.B. Academic, The Hague, pp. 65-90.
- Trabaud, L., 1990. Fire resistance of *Quercus coccifera* garrigue. In: J.G. Goldammer and M.J. Jenkins (Editors), Fire in Ecosystem Dynamics. S.P.B. Academic, The Hague, pp. 21-32.
- Trabaud, L. and Oustric, J., 1989. Influence du feu sur la germination de semences de quatre espèces ligneuses méditerranéennes a reproduction sexuée obligatoire. *Seed Sci. Technol.*, 17: 589-599.
- Trabaud, L., Michels, C. and Grossman, J., 1985. Recovery of burned *Pinus halepensis* Mill forests. II. Pine reconstitution after wild-fire. *For. Ecol. Manage.*, 13: 167-179.
- Westman, W.E., 1986. Resilience concept and measures. In: B. Dell, A.J.M. Hopkins and B.B. Lamont (Editors), Resilience in Med-