

POST-FIRE VEGETATION DYNAMICS IN A NATIVE *PINUS HALEPENSIS* MILL. FOREST ON MT. CARMEL, ISRAEL

GABRIEL SCHILLER,^{a,*} GIDI NE'EMAN,^b AND LEONID KOROL^a

^aDepartment of Agronomy and Natural Resources, Forestry Section, Agricultural Research Organization, The Volcani Center, P.O. Box 6, Bet Dagan 50250, Israel

^bDepartment of Biology, University of Haifa at Oranim, Tivon 36006, Israel

(Received 14 October 1996 and in revised form 22 December 1996)

ABSTRACT

Israel's largest natural *Pinus halepensis* Mill. forest is on the Mt. Carmel range and belongs to the distinct East Mediterranean genetic group. Most of this forest is the result of invasion of abandoned fields and grazing lands, resulting in a heterogeneous pine forest with an understory of broad-leaf shrubs and trees. Species composition, vegetation cover, pine-stand structure, and pine genetic diversity of plots in sites of known fire history, burned 5, 11, and 20 years ago, were studied with adjacent unburned sites forming a chronosequence.

Except for annual species, no species replacement took place during post-fire succession. The main observed changes were in the cover of species and of plant life forms. The ratio of tree/dwarf-shrub cover was found to be linearly related to the number of years elapsed since the last fire. Therefore, this ratio could serve as an index to determine the successional stage of Aleppo pine stands with unknown fire history. It is estimated that 30–40 years are needed for full recovery of Aleppo pine stands after fire, depending upon site quality. The stands of post-fire regeneration are of uniform age and are less variable in their structure than unburned stands. The genetic distance among the various *Pinus halepensis* subpopulations was found to be very small; most of the genetic variability was due to within-subpopulations variability, with almost no variability among subpopulations. Alleles that are typical of West Mediterranean *P. halepensis* populations or of *P. brutia*, were found in two post-fire subpopulations (stands), indicating pre-fire cross pollination between native *Pinus halepensis* trees and trees in adjacent pine plantations of foreign origin.

The conclusion is that fire has little effect on species composition and on vegetation structure, but that it alters the Aleppo pine stand structure.

INTRODUCTION

Abandonment of fields and grazing land and other changes in management practice on large areas of the Mt. Carmel range during the late 19th century and the first half of the 20th century resulted in recovery of the degraded oak scrub which included a few scattered Aleppo pine (*Pinus halepensis* Mill.) (Conder and Kitchener, 1880), and its spread into the abandoned areas. As a result of this succession the oak scrub (Maquis) has become an uneven-aged high Aleppo pine forest with a dense understory of broad-leaved species

(Zohary, 1962). Changes in the area occupied by the forest, or in its density or canopy closure, are also evident from comparison between aerial photographs taken in the 1940s and those taken in 1988 (Sahdot, 1992). This forest is the largest natural forest of the genetically defined East Mediterranean Aleppo pine group (Schiller

*Author to whom correspondence should be addressed. E-mail: vcgabi@volcani.agri.gov.il; gneeman@research.haifa.ac.il
Contribution No. 1915-E, 1996 Series from the Agricultural Research Organization, The Volcani Center, Bet Dagan 50250, Israel.

et al., 1985).

In 1965, part of the forest was designated as a nature reserve and the remainder as a national park. Consequently, forest management practices were neglected in the area, resulting in considerable accumulation of dead biomass. In the last decade, three large wildfires devastated about 7 km² of this unique forest.

Fire is a major factor in the Mediterranean-type ecosystem, which is resilient to fire all over the world (Del et al., 1986). Wildfires resulting from summer thunderstorms are not a feature of the eastern part of the Mediterranean, but fires ignited by man have been a common part of human culture since its earliest ages. Therefore, the Mediterranean landscape in its present form is the result of constant dynamic interactions between human disturbances and the natural regeneration process (Naveh, 1989). Most perennial shrub and tree species of the sclerophyllous Mediterranean vegetation in Israel are post-fire resprouters; however, *Pinus halepensis* Mill. and *Cistus* species are obligatory seeders (Naveh, 1973; Trabaud, 1987; Lahav, 1988). *Pinus halepensis* regenerates from post-fire-dispersed seeds stored in serotinous cones, while *Cistus* regenerates from the soil seed bank. In both species, death as a result of fire is followed by a vigorous regeneration phase. Regeneration and changes due to the secondary succession of Mediterranean pine forests (i.e., *P. halepensis* and *P. brutia*) were studied in many areas (Naveh, 1973; Schiller, 1978; Trabaud and Lepart, 1980; Arianoutsou and Margaritis, 1981; Trabaud et al., 1985; Lahav, 1988; Moravec, 1990; Canas and Limona, 1992; Ne'eman et al., 1992, 1995; Saracino and Leone, 1994; Thanos and Marcou, 1991; Thanos et al., 1989, 1996). These studies reported that the rate of change in post-fire secondary succession was high only during the first years after the fire, afterwards decreas-

ing exponentially. Therefore, and for practical reasons, most of the studies of post-fire changes were carried out during the first post-fire decade by a diachronic method (Prodon and Pons, 1993). In order to study the long-term effects of fire, and the later stages of the secondary succession, we adopted the chronosequence method (Glen-Lewin and van der Maarel, 1992). In this method, plots which are as similar to one another as possible, and differed in the time elapsed since the last fire, were chosen and compared. A basic assumption in this chronosequence method is that differences among plots were mainly the result of differences in their post-fire history. Thus, the time elapsed since the last fire was the major environmental factor explaining the variation in the vegetation data set.

The main objective of the present study was to widen our insight into post-fire changes occurring in a native East Mediterranean *P. halepensis* forest. The specific aims were to analyze changes in species composition, vegetation cover, pine tree stand structure, and to verify whether changes have occurred in the genetic composition of seedlings regenerated after fire, relative to their parent generation.

MATERIALS AND METHODS

STUDY SITES AND PLOTS

Sites with a known fire history and minimal human disturbance were chosen and designated as a chronosequence; the sites are presented in Table 1. Where possible, near each burned site a second site was chosen for comparison, in which no fire had occurred in the last 50 years according to examination of aerial photos and field surveys. We were aware of possible effects on the measured parameters of differences in altitude, the bed-

Table 1
Geographic parameters and fire history of the study sites within the native *Pinus halepensis* Mill. forest on Mt. Carmel

Site	Last fire (years) ^a	Altitude a.s.l. (m)	Bedrock formation	Meridian	Latitude	Aspect no.	Slope (%)
Hai-bar	1989	370	Shamir	1525	2395	280	5
Hai-bar	unknown	400	Shamir	1520	2400	190	20
Oranim	unknown	440	Shamir	1520	2405	150	20
Mitla	1983	340	Shamir	1497	2379	190	10
Mitla	unknown	320	Shamir	1502	2376	190	5
Me'arot	1974	160	Usfiya	1478	2302	—	0
Me'arot	unknown	170	Usfiya	1486	2298	10	5
Etzba	1974	180	Dalia	1486	2349	100	5
Etzba	unknown	180	Dalia	1488	2347	230	10
Arkan	1956	420	Hreibbe	1523	2364	350	30
Sanatorium	unknown	340	Dalia	1513	2352	10	5

^aunknown = fire has not occurred in the last 50 years; a.s.l. = above sea level.

rock-soil complex, slope, and aspect (Schiller, 1982); therefore these factors were included as environmental variables in the canonical ordination analysis, in addition to the number of years since the last fire. However, we are confident that the sites chosen were the best available on the Mt. Carmel range. In the center of each study site a homogeneous study plot of 1000 m² was chosen.

SPECIES COMPOSITION AND VEGETATION STRUCTURE

The presence of plant species was recorded during early and late spring 1994 in all plots. The percentage cover of all perennial species was estimated and recorded along four 25-m line transects in each of the plots. The transects were laid out at equal distances to include most of the variation within each plot. The presence of each plant species was monitored at points 10 cm apart along the transect; a total of 1000 points were counted in each plot, and the percentage cover of each species was calculated. The mean percentage cover of each species in the various sites was square-root transformed and further analyzed. The cover of each species was measured independently, so that wherever the vegetation was composed of several layers of different life forms, one above the other, the total percentage cover could be more than 100%. Average linkage cluster analysis (SAS, 1988) was used to quantify the overall similarity in vegetation cover of the various burned plots, and their adjacent unburned ones. The Montfort index of similarity (I) was used to rank the similarities of these plot pairs (Wolda, 1991).

The effect of the environmental factors (bedrock and soil formation, slope aspect, number of years since the last fire, and altitude) on the vegetation in the various plots, was analyzed by means of the CANOCO computer program (Ter Braak, 1990); this program was specially developed to show the response of multiple species to a set of environmental factors (Ter Braak and Prentice, 1990; Palmer 1993). Canonical correspondence analysis (CCA) with the forward selection option was performed on the square-root transformation of the species percentage cover data. The Monte Carlo test (Ter Braak, 1990) was used to examine the significance of the first canonical axis.

To analyze the structure of the pine stands, the following parameters were measured and/or calculated in all study plots (in unburned plots, only trees taller than 1.30 m were counted and measured): (a) density per 1000 m²; (b) average age as estimated by annual ring counting in cores taken with a Pressler borer at 1.3 m above ground (30–50% of the trees, representing various size classes in each plot, were sampled); (c) average height; (d) average stem circumference at base and at

1.3 m above ground (DBH); (e) average canopy projection as a percentage of plot area was calculated from measurement of four canopy radii. Regressions and correlations among age, height, circumference at base and at DBH, and canopy mean radius were calculated for each plot separately. Regressions of stand density versus stand average age were plotted; and regressions of tree age, circumference at tree base and at DBH versus canopy mean radius were calculated from plotted data at all sites. The regressions versus canopy radius were calculated for future analysis of natural Aleppo pine stands structure using aerial photos.

POST-FIRE GENETIC DIVERSITY OF PINUS HALEPENSIS

The starch gel electrophoresis technique was used to analyze allozyme variation patterns of 15 enzymes encoded by 25 loci extracted from the seeds' haploid megagametophyte tissue according to Conkle et al. (1982). Closed cones were collected from more than 30 trees in each stand at the following sites: Me'arot, Etzba, and Hai-bar. Seeds were extracted from the cones by drying the cones for 48 h at 50 °C. Seeds were stored at 5 °C until used in the isoenzyme analysis; they were then germinated on moist filter paper (Whatman no. 3) in Petri dishes at 20 °C. Analyses were performed using eight megagametophytes per tree from not less than 20 trees per plot. Enzymes were extracted from the germinated seed haploid megagametophyte when the radicle emerged to about 2–3 mm. The maternal tissue was homogenized in a grinding dish together with 35 ml of 0.2 M phosphate buffer (pH 7.5), 0.1% Triton X-100, 1% bovine serum albumin, and 0.1% dithiothreitol for all enzymes. Four different electrophoresis buffer systems were used:

System I: Gel buffer: 0.02 M Tris, 0.02 M boric acid, 0.002 M EDTA, pH 8.4. Electrode buffer: 0.2 M Tris, 0.2 M boric acid, 0.002 M EDTA, pH 8.4. The enzymes assayed: Alcohol dehydrogenase (Adh), Alanine aminopeptidase (Aap), Leucine aminopeptidase (Lap), Menadione reductase (Mnr), phosphoglucosmutase (Pgm), Mannose phosphate isomerase (Mpi).

System II: Gel buffer: 0.01 M Tris, 0.005 M citric acid, pH 8.8. Electrode buffer: 0/05 M NaOH, 0.3 M boric acid, pH 8.0. The enzymes assayed: Glutamate-oxaloacetate transaminase (Got), Glutamate dehydrogenase (Gdh), Superoxide dismutase (Sod).

System III: Gel buffer: 0.002 M citric acid, adjusted with morpholine to pH 6.1. Electrode buffer: 0.04 M citric acid, adjusted with morpholine to pH 6.1. The enzymes assayed: Aconitase (Aco), Isocitric dehydrogenase (Idh), 6-phosphogluconate dehydrogenase (6Pgd), shikimate dehydrogenase (Skdh).

System IV: Gel buffer: 0.002 M citric acid, adjusted

with morpholine to pH 8.3. Electrode buffer: 0.04 M citric acid, adjusted with morpholine to pH 8.3. The enzymes assayed: Malate dehydrogenase (Mdh), Phosphoglucose isomerase (Pgi).

Gels were sliced and stained for each enzyme system according to Conkle et al. (1982). The enzyme systems analyzed were chosen according to previous knowledge of allozyme variation of *Pinus halepensis* growing in the native forest on the Mt. Carmel range (Schiller, et al., 1985; Grunwald et al., 1986); and of *Pinus brutia* (Conkle, et al., 1988) which hybridize with Aleppo pine (Panetsos, 1981; Korol, et al., 1995). An IBM PC version 1.7 of the BIOSYS-1, a computer program for the analysis of allelic variation in genetics (Swofford and Selander, 1981) was used to perform the statistical analysis of the data.

RESULTS

SPECIES COMPOSITION AND VEGETATION STRUCTURE

A total of 249 plant species was recorded in all plots. The list of all species, according to study sites, is with the authors. A comparison between the burned and adjacent unburned plots is present in Table 2. The number of species per 1000 m² five years after a fire was 138 compared with an average of 85 ± 13 species in all the unburned plots. As shown in Fig. 1, there is a significant change in the number of species with time since the fire. In a comparison made between adjacent burned and unburned plots, an average of 36 ± 16 typical species was found in each of the plots. Also, the percentage of typical species was higher in the burned plots (44 ± 3%) than in the unburned ones (28 ± 6%). Unfortunately, because of the small number of plots and categories, no *t*-test could be done. The values of the similarity indices, comparing the burned and the respective unburned plots, were low and similar.

After fire, cover percentages had changed with time. Cover percentage of dominant species such as *P. halepensis* ranged between 6 and 76; *C. salviifolius* between 11 and 69; *Calycotome villosa* between 1 and 25. *Pistacia lentiscus* established itself very quickly after fire; there was no difference in cover between the burned and the unburned plots, and cover reached 26 ± 9.4%. *Quercus calliprinos* grew at a slower rate, reaching a cover of only 18 ± 8.1% in the unburned plots. Average percentage of cover of the various plant life forms in each plot are presented in Fig. 2. All plant life

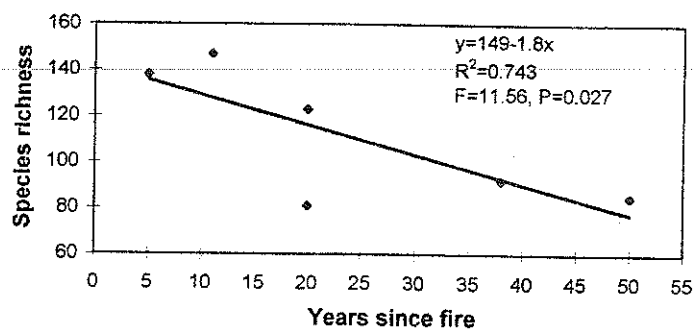


Fig. 1. Regression line and equation relating to number of species in each plot (1000 m²) versus number of years elapsed since the last fire. (The 50-year point represents an average of all unburned plots).

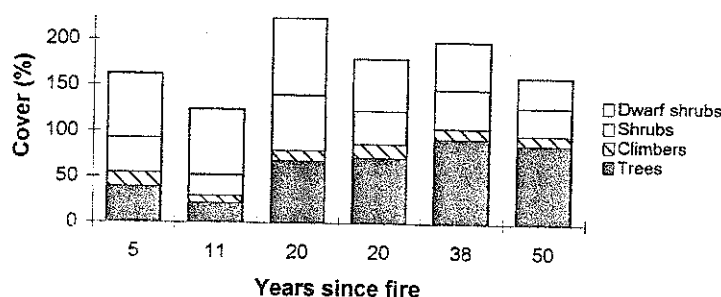


Fig. 2. Cumulative percentage cover of the various plant life forms in the plots classified by the years since last fire.

Table 2
Comparison of species composition between couples of burned and unburned plots

Sites	Hai-bar 89	Oranim	Mitla 89	Me'arot 74	Me'arot	Etzba 74	Etzba	Arkan 56	Sanatorium
Parameters*									
Years	5	>50	11	20	>50	20	>50	38	>50
No. Sp.	138	101	147	81	66	123	93	92	79
Typ. Sp.	65	28	-	35	20	49	19	41	28
Tot. Sp.	160			101		142		120	
Com. Sp.	73			46		74		51	
I	0.0140			0.0234		0.0215		0.0175	

* Years = Years since the last known fire, >50 = unburned; No. Sp. = Number of species in each plot of 1000 m²; Tp. Sp. = Typical species in each plot; Tot. Sp. = Total number of species in each couple of plots; Com. Sp. = Number of common species in each couple of plots; I = Montfort index of similarity.

forms were already present 5 years after fire, and post-fire temporal change affected only their relative proportions; tree cover increased and dwarf shrub cover decreased. The changes in the percentage cover of the two dominant species, i.e., *P. halepensis* and *Cistus* sp., are presented in Fig. 3. The cover of pine trees increased significantly along a logarithmic scale, while *Cistus* cover decreased significantly along a similar scale. The ratio of tree cover to dwarf shrub cover was found to be the best index to describe and predict the successional stage of each plot. This proportion increased from 0.49 (5 years after fire) to 1.8 (38 years after fire), and was 3.2 in the unburned plots. The increase was linear ($y = -0.208 + 0.06x$) and significant ($R^2 = 0.919$, $F = 43.489$, $P < 0.03$). Average linkage cluster analysis performed on the complete percentage cover database failed to reveal obvious clusters. The normalized root mean square distance among the sites varied only between 0.805 and 1.115. However, as shown in Fig. 4, the same analysis performed on percentage cover of *Pinus*, *Cistus*, and *Calycotome* resulted in greater separation (0.257–1.149), clustering Hai-bar 89, Mitla 83, Etzba 74, and Me'arot 74 in one cluster, and Arkan 56 together with all unburned plots in a second cluster.

In the CCA ordination analysis, presented in Fig. 5, the eigenvalue of the first axis was 0.04, and was less than significant according to the Monte Carlo test (F ratio = 1.22, P value = 0.08). It can be seen from the diagram that the vector of years since last fire (YEAR), is located next to the first axis, and both pine cover (Pin) and total cover of trees (Tree) are located close to it, while dwarf shrubs (DwSh), shrubs (Sh), and climbers (Clim) are in the opposite direction. The interpretation of such location is that the years since fire form a major factor in axis 1, and that it had the main positive effect on both pine and total tree cover, and a negative effect on dwarf shrub cover. Shrubs, and especially dwarf shrubs, are located at the opposite side of axis 1, meaning that their cover decreased in the course of the years since the last fire. The topographic environmental factors—slope (SLO) and aspect (ASP) are diagonal to (YEAR), whereas altitude (ALT) is orthogonal to (YEAR), i.e., the vector has a common direction with (YEAR). This means that on steeper slopes, higher elevations, and northern aspect, vegetation renewal was faster. Using the forward selection options in the discriminant analysis, the variable (YEAR) entered first, accounting for 7% of the total variance of the cover data in the ordination; in the bedrock formations, Usfiya (USFI) and Hreibe (HERI), entered next, accounting for an additional 4% and 3%, respectively, but the formations Dalia (DALI) and Shamis (SHAM) did not enter the stepwise analysis. The whole model explained 19%

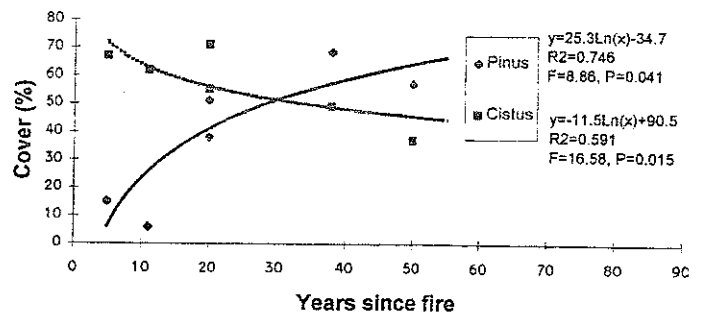


Fig. 3. Regression line and equation relating to percentage cover of *Pinus halepensis* and *Cistus* sp. versus number of years elapsed since last fire. (The 50 years point represents an average of all unburned plots.)

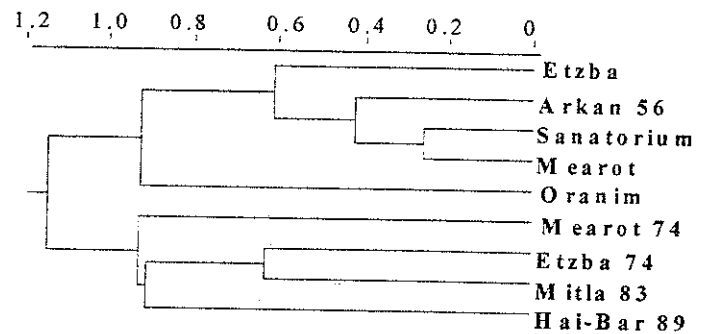


Fig. 4. Average linkage cluster analysis based on normalized mean square root distance performed on percentage cover of *Pinus*, *Cistus*, and *Calycotome*.

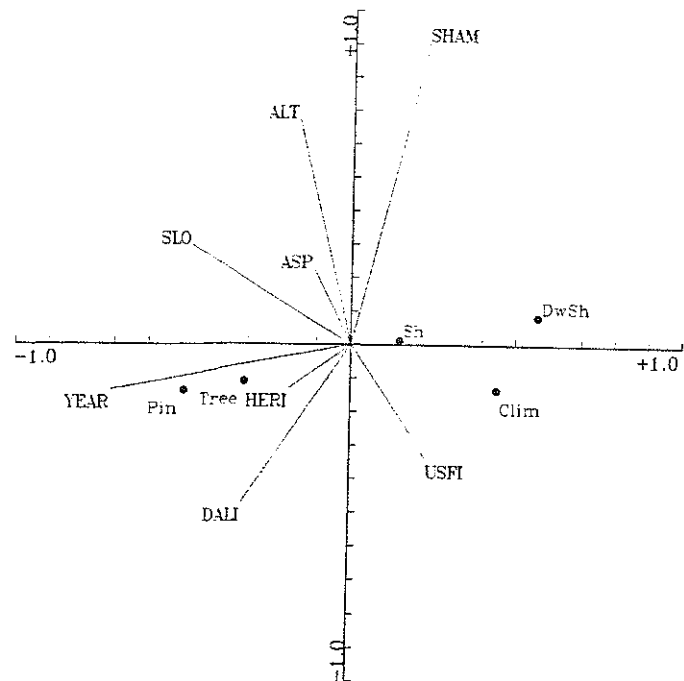


Fig. 5. Canonical correspondence analysis by plot of the square root transformed percentage cover of *Pinus halepensis* and plant life forms and quantitative environmental factors.

Table 3
Age class distribution (%) within plots

Name of the plot	Oranim	Sanatorium	Etzba	Me'arot	Arkan 56
Years after fire	Unburned	Unburned	Unburned	Unburned	38
Number of trees cored	23	19	17	18	14
Age class (years)					
10-19	-	-	-	-	7.1
20-29	-	-	-	33.3	28.6
30-39	21.7	-	5.9	61.1	64.3
40-49	17.3	47.4	41.1	5.6	-
50-59	43.6	52.6	35.3	-	-
60-69	8.7	-	11.8	-	-
70-79	8.7	-	5.9	-	-

of the variance.

The distribution of age classes of Aleppo pine within stands (plots) is presented in Table 3. In the unburned stands at Oranim, Sanatorium, and Etzba, most of the trees were between 40 and 60 years old. Two older trees at Arkan 56 were cored to estimate the approximate age of the pine trees of the former stand at the same place that was destroyed by fire in 1956; these trees were 85 and 96 years old, respectively.

Reduction with time in pine seedlings and tree density is presented in Fig. 6, together with data from yield tables (Rohle, 1991) as reference. Within the first 10 years after fire a rapid reduction in the number of pine seedlings is obvious; the slow reduction afterwards is similar to the dynamics postulated by the yield tables for similar site class quality in plantations (Rohle, 1991). After winter rains had ceased in March 1990, seven months after the fire in September 1989 at the Hai-bar site, an average of 24.7 ± 23.6 seedlings per m^2 was counted; whereas under the canopy of adjacent unburned stands, the average number of seedlings was only 1.72 ± 1.0 per m^2 . Four years later, pine seedling density in the burned stands was only 2.7 per m^2 . The reduction in pine specimen density with age has brought the density to an average of 20 to 30 trees per 1000 m^2 in 50-year-old stands.

Dimensions of pine trees in the unburned plots and 38 years post-fire are presented in Table 4. Tree age ranged from 10 to 76 years. By using the yield tables (Rohle, 1991), which correlate age and tree dimensions under given ecological conditions and enable predictions to be made of further development, significant differences in tree top heights between these stands (i.e., the average height of the 10 highest trees per 1000 m^2) were revealed. These differences in "site class", i.e., the predicted height at age 50, were not the result of differences among stands in mean age, but rather the result of environmental factors, as described in Table 1, i.e., mainly bedrock and soil properties (Schiller, 1982).

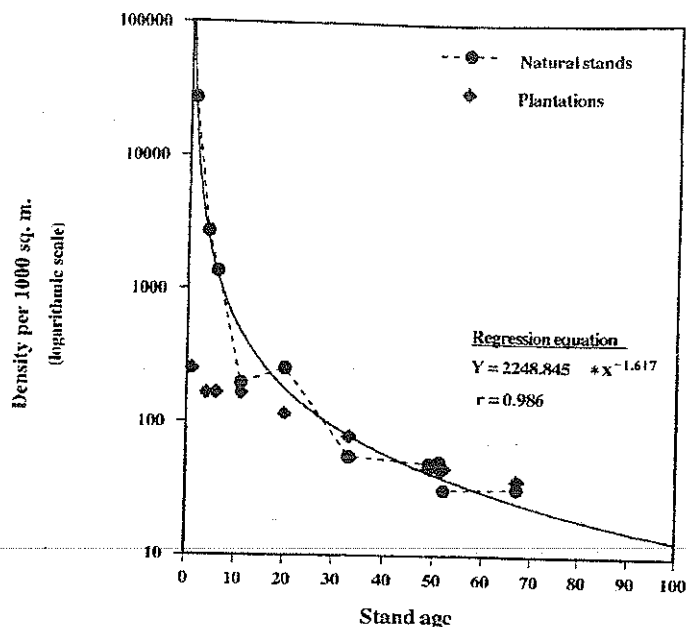


Fig. 6. Regression and regression equation between Aleppo pine density (per 1000 m^2) versus stand age in natural stands and in plantations with equivalent site quality according to Rohle (1991).

The tallest pine trees were measured at Sanatorium and the shortest at Etzba. In all stands canopy projections reached or exceeded 50%. In all the unburned plots, pine seedlings and saplings were found under the older trees; however, they were not included in the measurements because they had not reached the height of 1.30 m.

Linear regressions and correlation coefficients between: canopy projection mean radius (X) and tree age, height, trunk circumference at base and at 1.30 m above ground (Y); and between tree height (X) and trunk circumference at 1.30 m above ground (Y); and regressions between other tree parameters were all significant at a minimum level of $P < 0.05$ in each of the five sites measured. The calculated linear regression lines between the same parameters but for different sites had very similar slopes but different intercepts, as a result of the site factors influencing the growth of trees. Nevertheless, one very significant regression line, which included the data of all sites, could be calculated for eventual use in interpretation of aerial photos, i.e., regression between canopy projected area mean radius, and trunk circumference (Fig. 7). Relations among tree parameters are obvious in forestry science and are, therefore, not discussed.

GENETIC DIVERSITY

Results of isoenzyme horizontal starch gel electrophoresis revealed 25 loci encoding 15 enzyme systems analyzed. Of them, five loci, i.e., Skdh, Gdh, Idh, Mpi, Sod, were monomorphic, and 20 loci were polymorphic; most subpopulations, possessed the same set of alleles.

Table 4
Means and SD of parameters measured on *Pinus halepensis* trees in the various plots

Name of the plot	Years after fire	Mean no. of trees per 1000 sq. m.	Average tree age (years)	Average tree height (m)	Average trunk circumference (cm)	Average canopy radius (m)	Canopy projection (%)	Site class
Oranim	unburned	20	51 ± 12	10.1 ± 3.0	73.4 ± 37.3	2.65 ± 1.27	53.2	14
Sanatorium	unburned	19	49 ± 4	14.0 ± 2.0	90.0 ± 30.0	3.1 ± 1.0	63.6	18
Etzba	unburned	31	52 ± 10	5.9 ± 3.5	78.6 ± 42.8	2.7 ± 1.8	81.3	12
Me'arot	unburned	55	33 ± 6	7.2 ± 3.6	49.4 ± 35.4	2.6 ± 1.6	50	14
Arkan 56	38	67	32 ± 14	10.4 ± 2.6	54.3 ± 28.3	1.7 ± 0.4	66.6	16

However, two subpopulations, the Etzba 74 and the Hai-bar 89 that regenerated after fire, had unique (private) alleles at the 6Pgd₂ and 6Pgd₃ locus. Parameters of genetic diversity in the five subpopulations, based on the identified allele frequencies in the 20 loci, are presented in Table 5. Mean number of alleles per locus (A) was between 1.550 and 1.700; the percentage of polymorphic loci (P) was between 0.500 and 0.600, i.e., 50–60%; and unmodified expected heterozygosity (H_{exp}) ranged between 0.140 and 0.178. Mean genetic identity or distance between subpopulations (Table 6) is very high (0.994 ± 0.002), or the mean genetic distance is very low (0.006 ± 0.002). Still, the Hai-bar 89 subpopulation, which resulted from post-fire regeneration, had

the lowest identity and the greatest distance from all other subpopulations. The highest identity, or the least distance, was found between the burned and the unburned plots at the Me'arot and Etzba sites. The highest mean genetic diversity (H_{ep}) within the five subpopulations was found in the Etzba 74 plot and the lowest in the Hai-bar 89 plot (Table 7); these stands are the result of post-fire regeneration. Genetic diversity at species level (H_{es}) of native *Pinus halepensis* on Mt. Carmel is also presented in Table 7. Genetic diversity among the subpopulations in the various loci is very small; most of the genetic diversity lies within the subpopulations which are very similar in their diversity. Mean genetic diversity within the subpopulations (H_s) is 0.163 ± 0.040; and mean genetic diversity at species level (H_{es}) is 0.169 ± 0.042. F-statistics at all polymorphic loci over all five plots (Table 8) show that excess of heterozygotes is evident in the Aap, Aco, Adh₂, Pgi₂, 6Pgd₂, and 6Pgd₃ gene loci; whereas, in the other loci there is deficiency in heterozygotes. But, the overall mean shows deficiency in heterozygotes within subpopulations and at the species level of *Pinus halepensis* on the

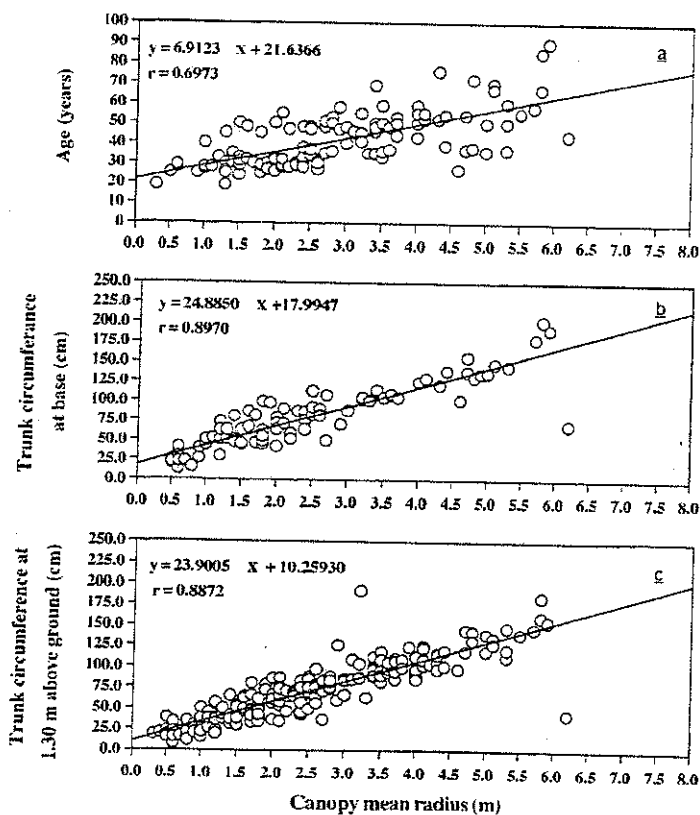


Fig. 7. Regressions and regression equations of tree age (a), trunk circumference at base (b), and at 1.30 m above ground (c), versus canopy's mean radius.

Table 5
Sample size, polymorphic indices, and mean frequencies of private alleles in five subpopulations of native *Pinus halepensis* on Mt. Carmel

Subpopulation	N	A	P	Ap	Hu	U	P(1)	
Me'arot 74	30	1.60	2.091	0.550	0.167	0.000		
Me'arot	23	1.65	2.182	0.550	0.173	0.000		
Etzba 74	46	1.70	2.273	0.550	0.180	1.000	0.022	
Etzba	28	1.55	2.100	0.500	0.165	0.000		
Hai-bar 89	45	1.70	2.167	0.060	0.141	1.000	0.054	
Means	34	1.64	2.162	0.550	0.165	0.400	0.038	
SE		4.6	0.029	0.033	0.016	0.007	0.245	0.016

N = Number of trees analyzed; A = mean number of alleles per locus; Ap = mean number of alleles per polymorphic locus; Hu = unbiased expected heterozygosity; U = number of alleles unique to population; P(1) = average frequency of private alleles.

Table 6
Genetic identities and distance among native *Pinus halepensis* on Mt. Carmel
(genetic identity above diagonal; distance, below diagonal)

	Me'arot 74	Me'arot	Etzba 74	Etzba	Hai-bar 89	Means
Me'arot 74		0.999	0.993	0.993	0.984	0.992
Me'arot	0.001		0.996	0.992	0.991	0.995
Etzba 74	0.007	0.004		0.998	0.997	0.996
Etzba	0.007	0.008	0.002		0.991	0.994
Hai-bar 89	0.016	0.009	0.003	0.009		0.991
Means	0.008	0.005	0.004	0.006	0.009	

Mt. Carmel range; the table also shows that there is very little differentiation among the five subpopulations.

DISCUSSION

SPECIES COMPOSITION AND VEGETATION STRUCTURE

Fire is a dominant factor in the evolution and ecology of Mediterranean-type ecosystems (Biswell, 1974; Trabaud, 1990); therefore, many studies have been conducted on resilience to fire of plant species, plant com-

munities, and ecosystems in Mediterranean-type climates (Keely, 1994). Among the species studied are *P. halepensis* and *P. brutia*, the two most common pine species growing in the low-to-medium-altitude zone around the Mediterranean basin, which is prone to fires (Naveh, 1973; Schiller, 1978; Trabaud and Lepart, 1980; Arianoutsou and Margaris, 1981; Trabaud et al., 1985; Lahav, 1988; Thanos et al., 1989, 1996; Moravec, 1990; Thanos and Marcou, 1991; Canas and Limona, 1992; Ne'eman et al., 1992, 1995; Saracino and Leone, 1994).

Table 7
Genetic diversity at subpopulation level (Hep) and at species level (Hes) of native *Pinus halepensis* on the Mt. Carmel range

Locus	Hep					Hes	Hs	Dst	Gst
	Me'arot 74	Me'arot	Etzba 74	Etzba	Hai-bar 89				
Aap	0.455	0.423	0.439	0.477	0.364	0.437	0.432	0.005	0.012
Aco	0.207	0.122	0.302	0.356	0.122	0.230	0.222	0.009	0.036
Adh ₁	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	
Adh ₂	0.207	0.340	0.242	0.132	0.302	0.250	0.244	0.005	0.021
Got ₁	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	
Got ₂	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	
Got ₃	0.180	0.269	0.500	0.477	0.518	0.435	0.389	0.000	
Lap	0.207	0.194	0.328	0.132	0.159	0.208	0.204	0.046	0.105
Mdh ₁	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.004	0.021
Mdh ₂	0.064	0.159	0.159	0.069	0.051	0.102	0.100	0.001	0.015
Mdh ₃	0.320	0.439	0.414	0.408	0.362	0.393	0.389	0.004	0.010
Mdh ₄	0.420	0.287	0.352	0.294	0.167	0.313	0.304	0.009	0.030
Mnr ₁	0.542	0.627	0.585	0.539	0.541	0.585	0.567	0.018	0.030
Mnr ₂	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	
Pgi ₁	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	
Pgi	0.278	0.258	0.000	0.000	0.000	0.119	0.107	0.012	0.103
Pgm ₁	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	
Pgm ₂	0.406	0.258	0.177	0.356	0.082	0.271	0.256	0.015	0.056
6Pgd ₂	0.000	0.000	0.000	0.000	0.000	0.021	0.020	0.001	0.044
6Pgd ₃	0.000	0.000	0.064	0.000	0.022	0.017	0.017	0.000	0.016
Means	0.164	0.169	0.178	0.162	0.140	0.169	0.163	0.007	0.039
SE	0.041	0.042	0.045	0.045	0.040	0.042	0.040	0.002	0.009

Hep = genetic diversity within populations; Hes = genetic diversity with species; Hs = mean genetic diversity within populations calculated for polymorphic loci; Dst = gene differentiation among subpopulations; Gst = the proportion of genetic diversity residing among subpopulations.

Table 8
Summary of F-statistics at all polymorphic loci of natural
Pinus halepensis on Mt. Carmel

Locus	Fis	Fit	Fst
Aap	-0.006	0.006	0.012
Aco	-0.139	-0.095	0.038
Adh ₂	-0.125	-0.102	0.021
Got ₃	0.390	0.455	0.105
Lap	0.570	0.579	0.021
Mdh ₂	0.060	0.074	0.015
Mdh ₃	0.409	0.415	0.010
Mdh ₄	0.012	0.041	0.030
Mnr ₁	0.174	0.200	0.031
Pgi ₂	-0.190	-0.068	0.103
Pgm ₂	0.072	0.124	0.056
6Pgd ₂	-0.057	-0.011	0.044
6Pgd ₃	-0.022	-0.007	0.015
Mean	0.144	0.177	0.039

Fit = fixation index of individuals relative to the total population; Fis = fixation index of individuals relative to their subpopulation; Fst = A measure of the degree of differentiation among subpopulations.

Post-fire recovery is often referred to as a secondary succession, a natural process of which species replacement is one of the main features. Several mechanisms have been proposed to explain the species replacement phenomenon (e.g., Egler, 1954; Connel and Slatyer, 1977; Tilman, 1990). However, in all the post-fire studies of Mediterranean natural pine forest, no replacement of the major species has been described (Naveh, 1973; Roy and Some, 1992; Papavassiliou and Arianoutsou, 1993; Ne'eman et al., 1995). The average number of species recorded in our study (102 per 1000 m²) was higher than those recorded in other post-fire studies: about 50 in southern France (Trabaud and Lepart, 1980), 43 in Algeria (Moravec, 1990), and 80 in Greece (Thanos et al., 1996). Species richness was even higher (178–196 spp. per 4900 m²) during the first three post-fire years in the Hai-bar 89 site (Ne'eman et al., 1995). However, because of the use of different research methods, and because species richness is area dependent, no real comparison can be made among the studies. The observed decrease in species richness (Fig. 1) during the early post-fire years fits well into the general trend of decline in the numbers of species as forests mature. This decrease is the result of shading of the light-requiring species, most of them annuals and geophytes, as was found also in other studies (Naveh, 1973; Moravec, 1990; Trabaud, 1990). Burned plots had greater numbers and higher cover percentage than adjacent unburned plots. This fact indicates that the opening of the area by fire causes increased species richness which

declines with time, as can be seen from the linear significant regression in Fig. 1. This conclusion is also supported by the results of the average linkage cluster analysis performed on the data of species cover (Fig. 4). The apparent contradiction between the nonreplacement of perennial species and the high number of typical species can be explained by the high number of annual species typical of this ecosystem (Shmida, 1981). While only minor changes occurred in perennial species composition, major changes took place in their cover (Fig. 2). The increase in cover by trees was mainly the result of the increase in the cover of *P. halepensis* and to a lesser degree the increase in that of *Q. calliprinos*. The decrease in the cover of dwarf shrubs was mainly due to the decrease in *C. salviifolius*. The ratio between the cover of trees and that of dwarf shrubs was found to be highly correlated with the number of years elapsed since the last fire in each plot (Fig. 3). Therefore, this ratio is suggested to be a good indicator of the successional stage of forest plots with unknown fire history. The average linkage cluster analysis (Fig. 4) demonstrated the similarity of vegetation structure among burned and among unburned plots, and the differences between the two groups. In spite of the fact that plots were chosen in pairs (burned and unburned), with the various pairs representing different environmental factors, the results of the canonical correspondence analysis (Fig. 5) further demonstrates the importance of the influence of the "time" factor (i.e., years elapsed since the last fire) on the vegetation structure relative to all other environmental variables. However, one must not underestimate the importance of the topographical and geological-pedological factors. These factors seem to be responsible for the relatively low cover of almost all life forms in the Mitla 83 plot.

Pinus halepensis has a thin bark which varies in thickness and shape among provenances (Panetsos, 1981). The thin bark allows the quick heating of the cambium by fire, which results in the death of trees even after relatively low intensity fires (Zohar, 1992). Therefore, after fire events, regeneration depends solely on the availability of a seed crop. Aleppo pine produces a huge seed crop every year: the seed crop of a dominant 50-year-old tree may reach between 300 and 500 cones or more; each cone bears between 50 and 80 seeds. Some of the cones are serotinous (Tucovic and Stilinovic, 1973) and shed their seeds only after fire events. However, also in the non-serotinous cones, about one-third of the seed crop is kept in the upper closed part which bursts open only as a result of fire events. This behavior provides a huge amount of seeds, which then germinate if favorable conditions occur soon after the fire event, producing a seedling crop of up to

300 ± 160 per m² (Schiller, 1978; Richardson, 1988).

Mortality of seedlings (Fig. 6) is most marked in the spring and early summer months after germination (Schiller, 1978; Thanos et al., 1996), owing mainly to the micro-site conditions which prevent the establishment of seedlings. Later on, seedlings, saplings, and trees succumb to site factors such as soil-bedrock complex characteristics (Schiller, 1982), drought, intra- and interspecific competition (Schiller, 1978; Katz, 1993), the pine bast scale *Matsucoccus josephi* Boden. et Harpaz (Mendel et al., 1997), and porcupine damage (Izhaki and Neeman, 1996). Still, enough seedlings per unit-area survive and grow into closed canopy stands with a density much higher than that of plantations (Rohle, 1991). From the results presented in Tables 4 and 5 it can be deduced that stands differ in their structure according to fire history and to differences in site qualities. Stands which resulted from invasion of abandoned areas are much more heterogeneous in tree numbers, ages, and dimensions than stands which were the result of post-fire regeneration.

Genetic identity among the subpopulations of Aleppo pine was very high, i.e., the genetic distance was very small (Table 6). However, the Hai-bar 89 stand, which is the result of post-fire regeneration, diverged from the other stands because of the occurrence of private alleles at locus 6Pgd₂ allele two and locus 6Pgd₃ allele three. Allele three in locus 6Pgd₃ occurs also in the Etzba 74 stand, which is also the result of regeneration after fire. The occurrence of these two alleles points to eventual intraspecific hybridization with planted *P. halepensis* originating from the West Mediterranean group, which possess these alleles (Schiller et al., 1985; Grunwald et al., 1986) or interspecific hybridization with hybrids between *P. halepensis* and *P. brutia* (Conkle et al., 1988; Korol et al., 1995) or with *P. brutia* (Moulalis et al., 1976). These two sites were only a few hundred meters away from plantations which included the above-mentioned pines. The occurrence of alleles alien to the native Israeli *P. halepensis* within the natural regeneration raises the possibility of change in the unique genetic composition of the native Aleppo pine forest on the Mt. Carmel range. These alleles, which are present in populations peripheral to the main area of distribution, occur due to hybridization with other provenances of Aleppo pine or with other pine species. This hybridization endangers the natural genetic structure of *P. halepensis* stands which have evolved under the East Mediterranean ecological setting.

In conclusion, depending on site quality, it will take between 30 and 40 years for a burned natural Aleppo pine stand on the Mt. Carmel range to reach the composition and structure of a mature unburned stand, from

both the species and vegetation points of view. Fire events endanger the unique uneven-aged, much diversified forest structure and turns it to an even-aged, more homogeneous forest. However, if the original, burned forest had been heterogeneous, that would be reflected in the spatial pattern of the new regenerating forest (Ne'eman, 1997). Because of large afforestations, with overseas *P. halepensis* provenances in the proximity of the native, naturally regenerated *P. halepensis* forest, the unique genetic composition of the latter is endangered. Careful attention must be given, if this native forest is to function as a nature reserve, to solve management problems and to apply active conservation to prevent structural and genetic changes.

ACKNOWLEDGMENTS

This research project "Resilience via succession of a semi-arid Mediterranean Aleppo pine forest ecosystem to fire on Mt. Carmel, Israel"—GR-01089; DISUM 00025—was partially supported by grants from the Israel Ministry of Science and KFA-BEO-Forschungszentrum Juelich GmbH/ Germany, Projekttraeger fuer Biologie, Energie und Oekologie.

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: Koslowski T.T. and Ahlgre, C.E., eds. *Fire and ecosystems*. Academic Press, New York, pp. 321–364.
- Canas, J. and Limona, F. 1992. Dynamic des communautés végétales du massif Monserat après les incendies de 1986. In: Trabaud, L. and Prodons, R., eds. *International Workshop on the Role of Fire in Mediterranean Ecosystems*. Banyuls-Sur-Mer, France, September 1992 (Abstract).
- Conder, C.R. and Kitchener, H.H. 1880. Map of Western Palestine in 26 sheets, from the surveys conducted for the Committee of the Palestine Exploration Fund. Palestine Exploration Fund, London.
- Conkle, M.T., Hodgskiss, P.D., Nunnally, L.B., and Hunter, S. 1982. Starch gel electrophoresis of conifer seeds: a laboratory manual. USDA For. Serv., Pacific Southwest For. and Range Exp. Stn., Gen. Tech. Rep., PSW-64.
- Conkle M.T., Schiller, G., and Grunwald, C. 1988. Electrophoretic analysis of diversity and phylogeny of *Pinus brutia* and closely related taxa. *Sys. Bot.* 13: 411–424.
- Connell, J.H. and Slatyer, R.O. 1977. Mechanisms of succession in natural community, stability and organization. *Am. Nat.* 111: 1119–1144.
- Dell, B., Hopkins, A.J.M., and Lamont, B.B., eds. 1986. *Resil-*

- ience of Mediterranean-type ecosystems. Dr. Junk, Dordrecht.
- Egler, F.E. 1954. Vegetation science concept. I. Initial floristic composition—a factor in old field vegetation development. *Vegetatio* 4: 412–417.
- Glen-Lewin, D.C. and van der Maarel, E. 1992. Patterns and processes in vegetation dynamics. In: Glen-Lewin, D.C., Peet, R.K., and Veblen, T.T., eds. *Plant succession theory and prediction*. Chapman & Hall, London.
- Grunwald, C., Schiller, G., and Conkle, M.T. 1986. Isozyme variation in native stands and plantations of Aleppo pine in Israel. *Isr. J. Bot.* 35: 161–174.
- Izhaki, I. and Ne'eman, G. 1996. The effect of porcupine and bast scale on Aleppo pine recruitment after fire. *Acta Oecol.*, in press.
- Katz, G. 1993. The interaction between *Pinus halepensis* and *Cistus salvifolius* in first stages of post-fire succession on Mt. Carmel. M.Sc. dissertation, Tel Aviv University, Tel Aviv (in Hebrew, English summary).
- Keely, J.E. 1994. Seed germination patterns in fire-prone climate regions. In: Kalin-Arroyo, M.T., Zedler, P.H., and Fox, M.D., eds. *Ecology and biogeography of Mediterranean ecosystems in Chile, California and Australia*. Springer-Verlag, New York, pp. 239–273.
- Korol, L., Madmony, A., Rivon, Y., and Schiller, G. 1995 *Pinus halepensis* X *Pinus brutia* subsp. *brutia* hybrids? Identification using morphological and biochemical traits. *Silvae Genet.* 44: 186–190.
- Lahav, H. 1988. Renewal of vegetation after fire in a natural pine forest on Mt. Carmel. M.Sc. dissertation, Tel Aviv University, Tel Aviv (in Hebrew, English summary).
- Mendel, Z., Assael, F., Saphir, N., Zehavi, A., Nestle, D., and Schiller, G. 1997. Seedlings mortality in natural regeneration after fire of Aleppo pine in Israel. *J. Wildl. Fire* 7: 327–333.
- Moravec, J. 1990. Regeneration of N.W. Africa *Pinus halepensis* forests following fire. *Vegetatio* 87: 29–36.
- Moulalis, D., Bassiotis, C., and Mitsopoulos, D. 1976. Controlled pollinations among pine species in Greece. *Silvae Genet.* 25: 95–107.
- Naveh, Z. 1973. The ecology of fire in Israel. *Annu. Proc. 13th Tall Timbers Fire Ecology Conf.*, Tallahassee, FL, pp. 131–170.
- Naveh, Z. 1989. Fire in Mediterranean landscape, an ecological perspective. In: Goldammer, J.G. and Jenkins, M.J., eds. *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. 1995. Recovery of vegetation in a natural east Mediterranean pine forest on Mount Carmel, Israel as affected by management strategies. *For. Ecol. Manage.* 75: 17–26.
- Ne'eman, G. 1997. Regeneration of natural pine forest—a review of work done after the 1989 fire on the Mt. Carmel, Israel. *Int. J. Wildl. Fire*, 7: 295–306.
- Palmer, M.W. 1993. Putting things in even a better order: the advantages of canonical correspondence analysis. *Ecology* 74: 2215–2230.
- Panetsos, C.P. 1981. Monograph of *Pinus halepensis* Mill. and *P. brutia* Ten. *Ann. For. Zagreb* 9(2): 39–78.
- Papavassiliou, S. and Arianoutsou, M. 1993. Regeneration of the leguminous herbaceous vegetation following fire in a *Pinus halepensis* forest of Atica, Greece. In: Trabaud, L. and Prodons, R., eds. *The role of fire in Mediterranean ecosystems*. European Commission, Brussels, pp. 119–125.
- Prodons, R. and Pons, P. 1993. Post-fire bird studies: methods, questions and perspectives. In: Trabaud, L. and Prodons, R., eds. *The role of fire in Mediterranean ecosystems*. European Commission, Brussels, pp. 332–344.
- Richardson, D.M. 1988. Age structure and regeneration after fire in self-sown *Pinus halepensis* forest on the Cape Peninsula, South Africa. *S. Afr. Tydskr. Plantk.* 54: 140–144.
- Röhle, H. 1991. Yield tables for *Pinus halepensis* in Israel. Faculty of Forestry, University of Munich, Germany, 65 pp.
- Roy, J. and Some, L. 1992. Germination and population dynamics of *Cistus* species in relation to fire. *J. Appl. Ecol.* 29: 647–655.
- SAS. 1998. Statistical Analysis System Institute Inc. SAS/STAT Users guide. SAS Inst. Inc., Cary, NC, 1028 pp.
- Saracino, A. and Leone, V. 1994. The ecological role of fire in Aleppo pine forests: overview of recent research. In: Viegas, D.X., ed. *Proceedings of the 2nd International Conference on Forest Fire Research*, Coimbra, Portugal, Vol. II, pp. 887–897.
- Sahdot, E. 1992. Changes in vegetation cover in the "Galim" (Mt. Carmel) catchment area during the last thirty years. *Bull. Nat. Reserve. Authority* 123: 33–39 (in Hebrew).
- Schiller, G. 1978. Factors involved in natural regeneration of Aleppo pine. Ph. D. thesis. Tel Aviv University, Tel Aviv, 90 pp. (in Hebrew, English summary).
- Schiller, G. 1982. Significance of bedrock as a site factor for Aleppo pine. *For. Ecol. Manage.* 4: 213–223.
- Schiller, G., Conkle, M.T., and Grunwald, C. 1985. Local differentiation among Mediterranean populations of Aleppo pine in their isoenzymes. *Silvae Genet.* 35: 11–19.
- Shmida, A. 1981. Comparison between the Mediterranean vegetation of Israel and California. *Isr. J. Bot.* 30: 105–123.
- Swofford, L.D. and Selander, B.R. 1981. BIOSYS-1, A computer program for the analysis of allelic variation in genetics. Dept. of Genetics and Development, University of Illinois, Urbana.
- Ter Braak, C.J.F. 1990. CANOCO—a FORTRAN program for canonical community ordination by correspondence analysis, principal component analysis and redundancy analysis. Agricultural Mathematics Group, Wageningen.
- Ter Braak, C.J.F. and Prentice, I.C. 1990. A theory of gradient analysis. *Advances in Ecological Researches*, Vol. 18. Academic Press, London, pp. 141–150.
- Thanos, C.A. and Marcou, S. 1991. Post-fire regeneration in *Pinus brutia* forest ecosystem in Samos island (Greece): 6 years after fire. *Acta Oecol.* 12: 633–642.
- 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: 79–90.
- Thanos, C.A., Daskalakou, E.N., and Nikolaidou, S. 1996. Early post-fire regeneration of a *Pinus halepensis* forest on Mount Parnis, Greece. *J. Veg. Sci.* 7: 273–280.
- 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: Trabaud, L., ed. *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: Goldammer, J.G. and Jankins, M.J., eds. *Fire in ecosystem dynamics*. S.P.B. Academic, the Hague, pp. 21–32.
- Trabaud, L. and Lepart, J. 1980. Diversity and stability in garrigue ecosystem after fire. *Vegetatio* 60: 119–130.
- 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.
- Trabaud, L. and Oustric, J. 1989a. Influence du feu sur la germination des semences de quatre espèces ligneuses méditerranéennes à reproduction sexuée obligatoire. *Seed Sci. Technol.* 17: 589–599.
- Tucovic, A. and Stilinovic, S. 1973. A contribution to the study of interpopulational variability of Aleppo pine. *Sumarstvo* 26: 3–10.
- Wolda, H. 1991. Similarity indices, sample size and diversity. *Oecologia* 50: 296–302.
- Zohar, Y. 1992. Prescribed burning as a tool in forest management. Annual report, project 274-0010-92, submitted to the Forest Department of the Jewish National Fund, Jerusalem.
- Zohary, M. 1962. *Plant life of Palestine, Israel and Jordan*. Ronald Press, New York, 262 pp.