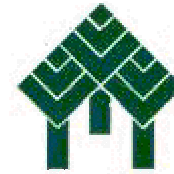


ספרית אורנים



המאמרים במערכת תדפיסים זו מוגנים על-פי

חוק זכויות יוצרים

הדפסת מאמרים תהיה לצרכי לימוד והוראה בלבד

אין לעשות כל שימוש מסחרי במאמרים.

Spatial pattern of seedlings 1 year after fire in a Mediterranean pine forest

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Summary. The spatial distribution of seedlings of the dominant perennial plant species (*Pinus halepensis*, *Cistus salvifolius*, *Rhus coriaria*) and may annual species was studied after a wild fire in an eastern Mediterranean pine forest. The spatial distribution of all seedlings is affected by the location of the old burned pine trees. Seedling density of *Pinus* and *Cistus* is higher at a distance from the burned pine canopy and lower near the burned pine trunk. It is also higher beneath small burned pine trees than under big ones. *Rhus* seedling density is higher under big burned pine trees and also near the burned trunks. Seedlings of *Pinus*, *Cistus* and *Rhus* growing under the burned canopy of big pine trees tend to be taller than seedlings under small ones or outside the burned canopy. Most annual species germinate and establish themselves outside the burned canopies, and only a few annual species are found beneath them. It is suggested that variation in the heat of the fire, in the amount of ash between burned pine trees of different sizes, and in the distance from the burned canopy are responsible for the observed pattern of seedling distribution. The possible ecological significance of the spatial pattern of seedlings distribution and their differential growth rate are discussed.

Key words: *Pinus* – *Cistus* – *Rhus* – Pine forest – Fire – Seedling – Recruitment – Mediterranean

Fire is a dominant factor in the evolution and ecology of Mediterranean-type ecosystems all over the world (Naveh 1973, 1975; Biswell 1974; Fox and Fox 1987; Trabaud 1990). As a result most of those ecosystems are resilient to fire (Keeley 1986; Westnam 1986; Naveh 1989). Plant species are classified, according to their reaction to fire, as “seeders”, “sprouters”, or intermediate types (Keeley 1977, 1984; Trabaud 1987; Keeley and Zedler 1978). Most perennial species of the sclerophyllous Mediterranean vegetation in Israel are

resprouters, not killed by fire (Naveh 1973; Lahav 1988). The consequence is that fire does not change the spatial distribution of these plants. *Pinus halepensis* Mill. and *Cistus salvifolius* L. are classical obligate seeders. The death of the plants as a result of the fire is followed by massive germination in the next winter, but most of the seedlings die during the summer drought (Naveh 1973; Trabaud et al. 1985; Lahav 1988; Trabaud and Oustric 1989; Moravec 1990). Many factors are known to affect seed germination and establishment after fire (Keeley 1987, 1991; Trabaud 1987).

Many studies on post-fire resilience are at the levels of communities or ecosystems and deal with the burned area as a homogeneous and uniform one (Biswell 1974; Fox and Fox 1987; Moravec 1990; Thanos et al. 1989), while other studies are focused on individual plant species (Trabaud 1987; Keeley 1991). In reality, every forest is a mosaic of big trees, small ones, bushes and gaps, causing interactions between species which effect their spatial distribution patterns. As a result of the mosaic pattern of plant distribution, fire intensity varies a lot at different locations in the forest (Christensen 1987). Big trees supply the major part of fuel to the fire, resulting in high temperature during the fire and large amounts of ash after it. Old burned pine trees may have an influence on the germination of different plant species; big black ash circles with only few plant seedlings can be observed under the canopy of the old burned trees for at least 2 years after the fire (Lahav 1988; Kutiel and Kutiel 1989).

Here we present field data on the influence of old burned pine trees on the spatial pattern of seedling recruitment of *Pinus halepensis* Mill., *Cistus salvifolius* L., *Rhus coriaria* L. and some annual species in the pine forest.

Study site

The study site is a natural *Pinus halepensis* forest, located on Mt. Carmel, Israel (32° 44' N 35° 01' E), 320 m above sea level and 7 km from the sea shore.

Methods

Distribution pattern of seedlings beneath burned pine trees

The study plot was established after a massive fire in September 1989. The data were collected in August-September 1990 at the end of the summer drought, representing seedling recruitment 1 year after the fire.

A homogeneous (70 m × 70 m) plot was chosen for this study. All the 30 burned pine trees in this plot were numbered. The density and height of *Pinus*, *Cistus* and *Rhus* seedlings were measured along four rectangular belt-transects. Each transect began at the trunk of each tree and continued until outside the burned canopy (Fig. 1). Transect lengths were between 4 m and 10 m according to the size of the burned trees. The measurements were made within a 0.5 m × 0.5 m portable wire quadrat; every second quadrat was counted. About 30 quadrats were counted around each tree. The quadrats were divided into three groups: "zone 1" all quadrats between the trunk and half of the distance to canopy borders; "zone 2", all quadrats between the canopy borders and the first group; and "zone 3", all quadrats outside the canopy borders. The last group represents the area between the trees, not under the direct influence of the burned trees (Fig. 1).

For the calculation of species richness, the presence of all annual plant species in the quadrats was recorded. The distance of each quadrat relative to the border of the burned canopy was measured. The quadrats were numbered according to their distance, in meters, from the border of the burned canopy. The border was set as the zero point, and quadrats under the burned canopy received decreasing negative values, while those outside received increasing positive values.

Data analysis

Mean values of seedling density and height were calculated for each burned tree and also for each zone for each of the 30 studied trees. Further statistical analyses were performed on these means, since the trees were the independent units of observation. Two-way ANOVA was used to analyse both the effects of the zonation and the trunk perimeter on seedling density and seedling height in each

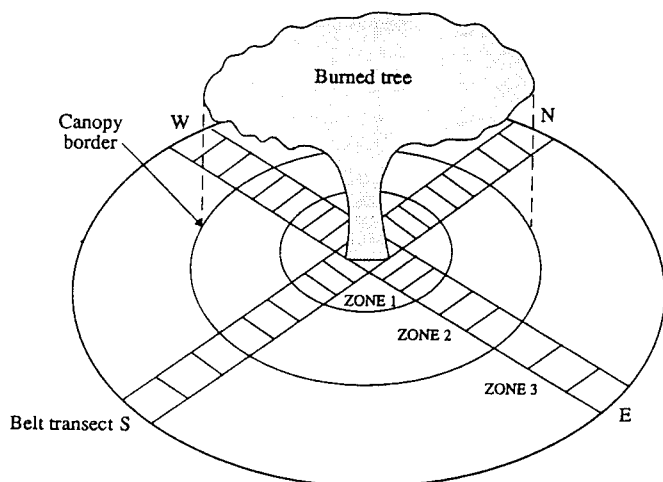


Fig. 1. Schematic representation of the division into three zones according to the location of quadrats relative to the trunk and the border of the canopy of the burned pine tree. *Zone 1*, between the trunk and half of the distance to canopy borders. *Zone 2*, between the canopy borders and the first group. *Zone 3*, outside the canopy borders

perennial species. For this analysis we used the three zones around the burned trunk (see above). For the analysis of the effect of trunk perimeter, only seedlings under the canopy were counted (zones 1 and 2 only). The trunk perimeter was divided into 8 groups (41–60, 61–80, ... 181–200 cm). The results of the two-way ANOVA indicate that the interactions between the two factors (the zonation and the trunk perimeter) on seedling density and on seedling height are not significant for any perennial species except one (Table 1). The results of significant one-way ANOVA tests followed by *a posteriori* comparison for each factor are presented. When significant interaction occurs between the two factors in the analysis (e.g. *Rhus* seedling height, Table 1B), it is misleading to average the effects of one factor over all levels of the second factor (Underwood 1981). In this case the results of the one-way ANOVA followed by *a posteriori* comparison for each factor are not presented.

Because seedling density has a Poisson distribution rather than a normal one, a square root transformation of this variable was used for the statistical calculations. This transformation makes the variances independent of the means as occurs in a Poisson distribution (Sokal and Rohlf 1981). However, seedling densities in figures are represented by the original values before transformations.

All analyses were performed using GLM and REG procedure provided by SAS (SAS Institute 1988).

Results

The effect of zonation and tree size on seedling density

Seedling density of *Pinus* and *Cistus* per square meter was higher outside the edge of the burned canopy (zone 3) than under the burned canopy itself (zones 1 and 2, Fig. 2A), as indicated by one-way ANOVA tests ($F_{2,85} = 4.20$, $P < 0.05$; $F_{2,85} = 20.38$, $P < 0.001$, respectively).

Seedling density pattern of *Rhus* was the opposite, with a peak under the burned canopy (zones 1 and 2), and with almost no seedlings out of the burned canopy (zone 3, Fig. 2A, $F_{2,85} = 7.45$, $P < 0.01$). Seedling density was ranked as *Cistus* > *Pinus* > *Rhus* in each zone (Fig. 2A).

The mean density of *Pinus* and *Cistus* seedlings under each burned pine tree, was negatively correlated with the perimeter of its trunk ($r = -0.65$, $P < 0.0001$, $n = 30$; $r = -0.51$, $P < 0.005$, $n = 30$, respectively), while the opposite phenomenon was observed for *Rhus* seedlings ($r = 0.52$, $P < 0.005$, $n = 30$, Fig. 2B).

The combined effect of zonation and tree size on seedling density was significant for each plant species as indicated by the two-way ANOVA (Table 1A). The effect of zonation on seedling density was more significant than the effect of tree size in *Cistus* and *Rhus*, but not in the case of *Pinus* (Table 1A). The two-way ANOVA models presented here explain 51–66% of the variation in seedling density.

The effect of zonation and tree size on seedling height

Seedling height of *Pinus*, *Cistus* and *Rhus* were not significantly different between the different zones (one-way ANOVA, $P > 0.05$, Fig. 2C). The mean height of *Cistus* and *Rhus* seedlings under each burned pine tree was significantly correlated with its trunk perimeter ($r = 0.48$, $P < 0.01$, $n = 30$ and $r = 0.59$, $P < 0.01$, $n = 19$ respectively,

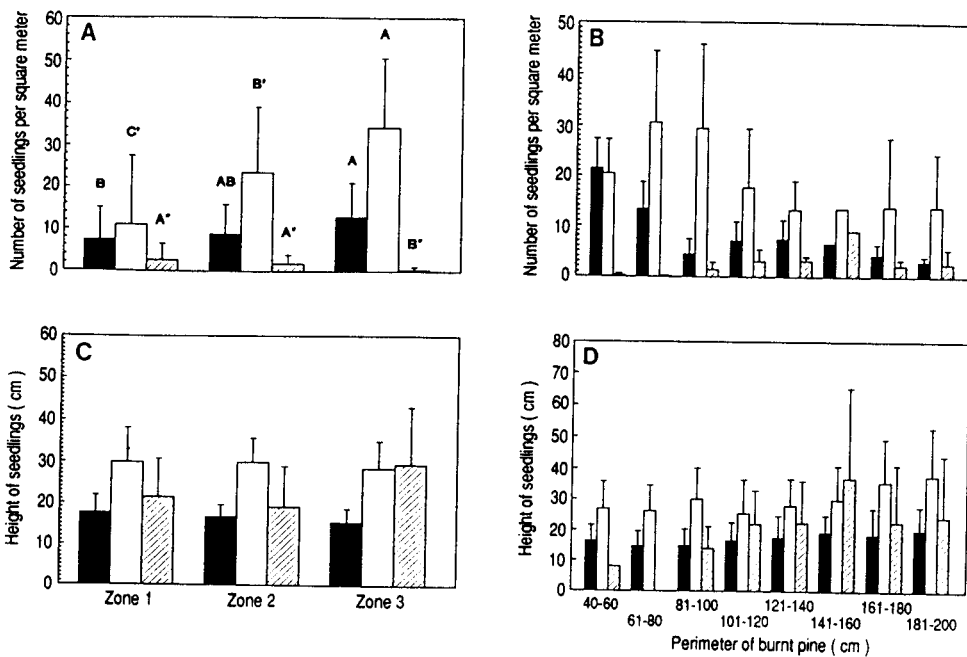


Fig. 2A–D. Seedling density as a function of A different zones beneath the burned pine canopy, and B pine tree perimeter. Seedling height as a function of C different zones beneath the burned pine canopy, and D different pine tree perimeter. Error bars represent standard deviation. See Methods and Fig. 1 for further explanations. Black bars, *Pinus*; white bars, *Cistus*; shaded bars, *Rhus*

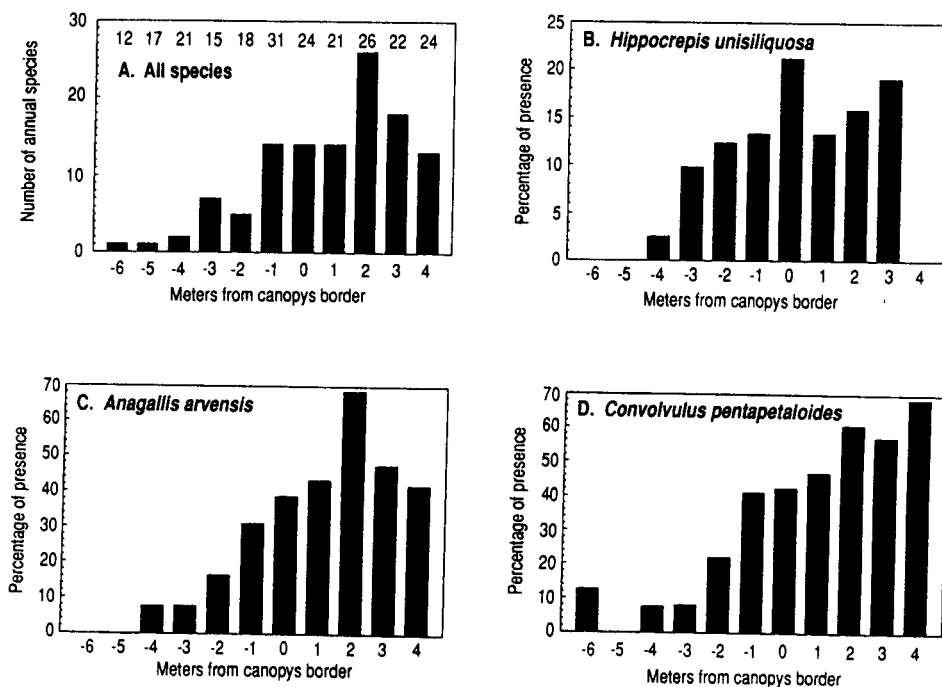


Fig. 3A–D. Distribution of the number of annual species around burned pine trees. A total number of species, B *Hippocrepis unisiliquosa*, C *Anagallis arvensis*, and D *Convolvulus pentapetaloides* (see Methods for further explanations)

Fig. 2D), while the correlation for *Pinus* was not significant ($r=0.32$, $P>0.05$, $n=30$, Fig. 2D).

The combined effect of zonation and tree size on seedling height was significant for *Cistus* and *Rhus*, but not for *Pinus*, (Table 1B). The effect of tree size on seedling height was more significant than the effect of zonation (Table 1B). However, because the interactions of these two factors were significant in the case of *Rhus* (Table 1B) it is impossible to assess the contribution of each factor by itself. It is notable that the two-way ANOVA models explain 35–74% of the variation in seedling height (Table 1B).

Species richness of annual plants

A total of 51 annual plant species were recorded in the burned area. Only few annual species were found under the burned canopy itself (Fig. 3a). The highest number of annual species was observed 2 m away from the burned canopy border (Fig. 3a). Three annual species (*Hippocrepis unisiliquosa* L., *Anagallis arvensis* L., *Convolvulus pentapetaloides* L.) were exceptional by penetrating the burned canopy (Figs. 3b, c, d, respectively).

Table 1. Two-way ANOVA comparing (A) seedling density (square root transformed) of *Pinus*, *Cistus* and *Rhus* beneath the burned canopy, and (B) seedling height of the same species across the zone around the burned trunk and trunk perimeter of the burned tree

Source of variation	df	Sum of squares	Mean square	F	P
A Seedling density					
<i>Pinus</i> ($r^2=0.66$)					
Model	23	121.1	5.3	5.51	0.0001
Zonation (Z)	2	16.4	8.2	8.57	0.0005
Trunk perimeter (P)	7	93.6	13.4	13.98	0.0001
Z X P	14	11.1	0.8	0.83	0.63
Error	64	61.2	1.0		
Corrected total	87	182.3			
<i>Cistus</i> ($r^2=0.53$)					
Model	23	216.4	9.4	3.08	0.0002
Zonation (Z)	2	133.5	66.7	21.85	0.0001
Trunk perimeter (P)	7	55.3	7.9	2.58	0.02
Z X P	14	27.6	2.0	0.64	0.82
Error	64	195.5	3.1		
Corrected total	87	411.9			
<i>Rhus</i> ($r^2=0.51$)					
Model	23	22.4	1.0	2.85	0.0005
Zonation (Z)	2	6.6	3.3	9.66	0.0002
Trunk perimeter (P)	7	9.5	1.4	3.98	0.001
Z X P	14	6.3	0.4	1.32	0.22
Error	64	21.8	0.3		
Corrected total	87	44.2			
B Seedling height					
<i>Pinus</i> ($r^2=0.35$)					
Model	23	389.8	16.9	1.39	0.16
Zonation (Z)	2	74.4	37.2	3.04	0.055
Trunk perimeter (P)	7	191.6	27.4	2.24	0.04
Z X P	14	123.8	8.8	0.72	0.74
Error	60	733.7	12.2		
Corrected total	83	1123.5			
<i>Cistus</i> ($r^2=0.41$)					
Model	23	1635.5	71.1	1.85	0.03
Zonation (Z)	2	34.7	17.3	0.45	0.64
Trunk perimeter (P)	7	1267.4	181.1	4.72	0.0003
Z X P	14	333.4	23.8	0.62	0.84
Error	61	2338.9	38.3		
Corrected total	84	3974.4			
<i>Rhus</i> ($r^2=0.74$)					
Model	16	3046.3	190.4	3.97	0.002
Zonation (Z)	2	414.3	207.2	4.32	0.026
Trunk perimeter (P)	6	1469.2	244.9	5.11	0.002
Z X P	8	1162.8	145.3	3.03	0.019
Error	22	1054.4	47.9		
Corrected total	38	4100.7			

Discussion

Spatial patterns in vegetation can be the result of microsite heterogeneity (Auerbach and Shmida 1987). Such heterogeneity is regarded as an important mechanism for species coexistence (Keddy 1984) and can also explain the spatial patterns of plants within a plant community. Correlation between vegetation pattern and environ-

mental conditions is the first step in proving the causes of the vegetation pattern (Olsvig-Whittaker 1988). Trees were found to change soil nutrient status on the forest floor (Klemmedson 1987, 1991; Boettcher and Kalisz 1990). Mediterranean oak trees were found to be the major cause of microsite differentiation of species in their community (Olsvig-Whittaker 1988; Olsvig-Whittaker et al. 1992). Soils in California under the influence of pine forests develop properties that vary in relation to the location and age of the trees (Zinke 1962). Our results prove that the spatial pattern of seedling recruitment after fire depends on the distribution of the pre-existing pine trees which influence post-fire succession even after their death.

As the pine forest includes areas with big trees, small ones, bushes and annuals, fire intensity: temperatures and duration, are not homogeneous (Christensen 1987). Big trees have more biomass, which serves as fuel in a forest fire, than small trees have. The result is a higher temperature for a longer time during the fire, and larger amounts of ash after it. This is also relevant to the comparison of three zones located under and around the burned trees. There is a gradient of fire intensity and ash accumulation from the center of the burned canopy (zone 1), through the periphery (zone 2), to the area outside it (zone 3).

The high temperatures, up to 1200° C on soil surface and 170° C at 5 cm depth (Raison et al. 1986; Troumbis and Trabaud 1986; Malanson and Trabaud 1987; Uhl 1987) may explain the seed bank mortality of most species. Moderate heat and charred wood are key factors in seedling recruitment after fire (Keeley 1987, 1991). The possible influence of ash on post-fire seed germinations is not mentioned in a recent review (Keeley 1991). Nevertheless ash may reduce germination of seeds (Lahav 1988; unpublished data). Large amounts of ash may cause salinity and high osmotic values which can prevent seed imbibition and germination. Post fire ash provides nutritional conditions which have a positive affect on the development of some plant species (Kutiel and Naveh 1987a, b).

Many annual species growing in pine forests after fire germinate readily after heat treatment and in the presence of ash (Lahav 1988). Nevertheless seed bank mortality and high amounts of ash seem to be the reason for the almost complete absence of annual plant species under big burned pine trees. *Rhus coriaria* is the only species that grows in denser stands under the burned canopies of the big trees, the possible causes for this pattern were already discussed (Izhaki et al. 1992).

Cistus is known to germinate from soil seed bank, accordingly seed germination is dependent upon temperature treatment (Naveh 1973, 1975; Lahav 1988; Trabaud and Oustric 1989). The inner layer of seed coat appears to be responsible for germination control (Arone and Mazzoleni 1989). The low seedling density under the burned canopy of big pine trees may be caused by seed bank mortality due to very high temperatures, or by low germination percentage due to the high osmotic value of the big amounts of ash. Thanos and Georghiou (1988) found that germination of *Cistus incanus* is completely

suppressed by osmotic stress of about 6 bars. Consequently the lower seedling densities under the burned trees may be due to low germination because of the high osmotic potential of the ash. *Cistus* seedlings which do grow under the big burned pine trees are higher, indicating the possible positive effect of ash on seedling growth.

Most *P. halepensis* seeds are dispersed from cones after the fire and therefore may not suffer from the high temperatures. Accordingly *P. halepensis* seed germination was found not to be enhanced by temperature treatment (Naveh 1973, 1975; Lahav 1988). Seed dispersal is by wind, and therefore it can be assumed that most of the seeds were dispersed in the proximity of the mother trees (Augsburger and Franson 1987); thus low seedling density under the burned canopies is the result of post-fire and post-dispersal factors. Pine seedling densities on Mt. Carmel vary from 5 seedlings m^{-2} near the trunk under big burned pine trees up to 22 seedlings m^{-2} outside the canopy of small trees. These are much higher densities than those reported from France of 0.1–1 seedlings m^{-2} (Trabaud et al. 1985), and than those reported for *P. brutia* from Greece of 0.2–0.4 seedlings m^{-2} (Thanos and Marcou 1989). *P. halepensis* seeds from Mt. Carmel were found to have relatively high percentage of germination under moisture stress, up to 9 bar of osmotic potential (Schiller and Waisel 1989). *Pinus halepensis* and *Pinus brutia* in Greece were found to germinate well even up to 14 bar of osmotic stress (Thanos and Skordilis 1987). In both cases the authors point out this ability as an adaptation to the arid Mediterranean environment, whereas *Pinus* actually germinates during the winter and early spring (Thanos and Marcou 1988) when the soil is still wet. Hence, we suggest that this ability to germinate under high osmotic stress may be an adaptation to post-fire germination when high amounts of ash are present. However it seems that the adaptation is not sufficient considering the high ash cover of up to 5 cm (Lahav 1988). This may be the reason for the low seedling densities under the canopies of the big burned trees, as can be seen in our results. A few seeds did germinate under the burned canopies, either as a result of a microsite with less ash, or as a result of adaptation to germination in a medium with high osmotic values.

The process of pine tree development after fire is characterized by increase in height and decrease in seedling density (Moravec 1990). However, as was found in earlier cases (Moravec 1990), it is expected that after 5 years pine development will accelerate and will become dominant, and after 20 years it will overtop the shrub layer. Our results indicate that these few pine seedlings under the big burned canopies develop faster than all the rest. Although no significant differences in the height of *Pinus* seedlings between the zones were found, 2.5 years after the fire they reach about twice the height of other seedlings (unpublished data). These seedlings have lower interspecific and intraspecific competition and better mineral nutrition during the first years of growth. It seems that these seedlings have the best chance to become the founders of the new forest. Only long term research will support or reject our hypothesis, and further experimental work will reveal the causes.

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References

- Arone G, Mazzoleni S (1989) The effect of heat exposure on seeds of *Cistus incanus* L. and *Cistus monspeliensis* L. G. Bot Ital 123: 283–289
- Auerbach M, Shmida A (1987) Spatial scale and the determinants of plant species richness. Trend Ecol Evol 2: 228–231
- Augsburger CK, Franson SE (1987) Wind dispersal of artificial fruits varying in mass, area, and morphology. Ecology 68: 27–42
- Biswell HH (1974) Effects of fire on chaparral. In: Koslowski T, Ahlgren C (eds) Fire in Ecosystems. Academic Press, New York, pp 321–364
- Boettcher SE, Kalisz PJ (1990) Single-tree influence on soil properties in the mountains of eastern Kentucky. Ecology 71: 1365–1372
- Christiansen NL (1987) The biogeochemical consequences of fire and their effects on the vegetation of the coastal plain of the southeastern United States. In: Trabaud L (ed) The Role of Fire in Ecological Systems. S.P.B. Academic Publishers, The Hague, pp 1–22
- Fox B J, Fox MD (1987) The role of fire in the scleromorphic forests and shrublands of eastern Australia. In: Trabaud L (ed) The Role of fire in ecological systems. S.P.B. Academic Publishers, The Hague, pp 23–48
- Izhaki I, Lahav H, Ne'eman G (1992) Spatial distribution patterns of *Rhus coriaria* seedlings after fire in a Mediterranean pine forest. Acta Oecol 13 (in press).
- Keddy PA (1984) Plant zonation on lake shores in Nova Scotia: a test of the resource specialization hypothesis. J Ecol 72: 797–808
- Keeley JE (1977) Seed production seed population in soil and seedling production after fire for two congeneric pairs of sprouting and nonsprouting shrubs. Ecology 58: 820–829
- Keeley JE (1984) Factors affecting germination of chaparral seeds. Bull South Calif Acad Sci 83: 113–120
- Keeley JE (1986) Resilience of Mediterranean shrub communities to fires. In: Dell B, Hopkins AJM, Lamont BB (eds) Resilience in Mediterranean-Type Ecosystems. Junk, Dordrecht, pp 95–113
- Keeley JE (1987) The role of fire in seed germination of woody taxa in California chaparral. Ecology 68: 434–443
- Keeley JE (1991) Seed germination and life history syndromes in the California chaparral. Bot Rev 57: 81–116
- Keeley JE, Zedler PH (1978) Reproduction of chaparral shrubs after fire: A comparison of sprouting and seeding strategies. Am Midl Nat 99: 142–161
- Klemmedson JO (1987) Influence of oak in pine forests of central Arizona on selected nutrients of the forest floor and soil. Soil Sci Soc Am J 51: 1623–1628
- Klemmedson JO (1991) Oak influence on nutrient availability in pine forests of central Arizona. Soil Sci Soc Am J 55: 248–253
- Kutiel P, Kutiel H (1989) Effects of a wildfire on soil nutrients and vegetation in aleppo pine on Mount Carmel Israel. Pirineos 134: 59–74
- Kutiel P, Naveh Z (1987a) Soil properties beneath *P. halepensis* and *O. caliprinos* trees on burned and unburned mixed forests on Mt. Carmel, Israel. Forest Ecol Manag 20: 11–24
- Kutiel P, Naveh Z (1987b) The effect of fire on nutrients in a pine forest soil. Plant Soil 104: 274–296
- Lahav H (1988) Renewal of vegetation after fire in a natural pine forest on Mt. Carmel. MSc dissertation, Tel-Aviv University. (In Hebrew)
- Malanson GP, Trabaud L (1987) Vigour of post fire resprouting by *Quercus coccifera* L. J Ecol 76: 351–365

- 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. Annual Tall Timbers Fire Ecological Conference 13:131–170
- Naveh Z (1975) The evolutionary significance of fire in Mediterranean region. *Vegetatio* 9:199–206
- Naveh Z (1989) Fire in the Mediterranean a landscape ecological perspective. In: Goldammer JG, Jenkins MJ (eds) *Fire in ecosystem dynamics*. SPB Academic Publishing, The Hague, pp 1–20
- Olsvig-Whittaker LS (1988) Relating small-scale vegetation patterns to the environment. In: During HJ, Werger MJA, Willems JH (eds) *Diversity and Patterns in Plant Communities*. SPB Academic Publishing, The Hague, pp 87–94
- Olsvig-Whittaker LS, Naveh Z, Giskin M, Nevo E (1992) Microsite differentiation in a Mediterranean oak savanna. *J Veg Sci* 3:209–216
- Raison RJ, Woods PV, Jakobsen BF, Bary GA (1986) Soil temperatures during and following low intensity prescribed burning in a *Eucalyptus pauciflora* forest. *Aust J Soil Res* 24:33–47
- SAS Institute (1988) *Sas/Stat user's guide*. Cary, NC, USA
- Schiller G, Waisel Y (1989) Among-province variation in *Pinus halepensis* in Israel. *For Ecol Manag* 28:141–151
- Sokal RR, Rohlf FJ (1981) *Biometry*. W.H. Freeman, San Francisco
- Thanos CA, Georghiou K (1988) Ecophysiology of fire-stimulated seed germination in *Cistus incanus* spp. *creticus* (L.) Heywood and *C. salvifolius* L. *Plant Cell Environ* 11:841–849
- Thanos CA, Skordilis A (1987) The effects of light, temperature and osmotic stress on the germination of *Pinus halepensis* and *P. brutia* seeds. *Seed Sci Technol* 15:163–174
- Thanos CA, Marcou S, Christodoulakis D, Yannitsaros A (1989) Early post-fire regeneration in *Pinus brutia* forest ecosystems of Samos island (Greece). *Acta Oecol Oecol Plant* 10:79–94
- Trabaud L (1987) Fire and survival traits in plants. In: Trabaud L (ed) *The Role of Fire in Ecological Ecosystems*. SPB Academic Publishers, The Hague, pp 65–90
- Trabaud L (1990) Fire as an agent of plant invasion? A case study in French Mediterranean vegetation. In: di Castri F, Hanes AG, Debssche M (eds) *Biological invasions in Europe and the Mediterranean Basin*. Kluwer Academic Publishers, pp 417–437
- Trabaud L, Oustric J (1989) Influence du feu sur la germination de semences de quatre espèces ligneuses méditerranéennes a reproduction sexuelle obligatoire. *Seed Sci Technol* 17:589–599
- Trabaud L, Michels C, Grossman J (1985) Recovery of burned *Pinus halepensis* Mill forests. II. Pine reconstitution after wild-fire. *For Ecol Manag* 13:167–179
- Troumbis A, Trabaud L (1986) Comparison of reproductive biological attributes of two *Cistus* species. *Acta Oecol* 7:235–250
- Uhl C (1987) Factors controlling succession following slash and burn agriculture in Amazonia. *J Ecol* 75:377–407
- Underwood AJ (1981) Techniques of analysis of variance in experimental marine biology. *Oceanogr Mar Biol Ann Rev* 19:513–605
- Westnam WE (1986) Resilience concept and measures. In: Dell B, Hopkins AJM, Lamont BB (Eds) *Resilience in Mediterranean-Type Ecosystems*. Junk, Dordrecht, pp 5–21
- Zinke PJ (1962) The pattern of influence of individual forest trees on soil properties. *Ecology* 43:130–133