Acta Œcologica, 1992, **13** (3), 279-289.

Spatial distribution patterns of *Rhus coriaria* seedlings after fire in a Mediterranean pine forest

I. Izhaki, H. Lahav and G. Ne'eman

Department of Biology, University of Haifa at Oranim,
Kiryat Tivon 36910, Israel

Abstract

Rhus coriaria L. is reported, for the first time, as a post-fire facultative seeder. Two different patterns of seedling distribution were detected during the first 18 months after a wild fire in a natural pine forest on Mt. Carmel Israel: (a) A significant negative correlation was found between the density of *Rhus* seedlings and the distance from the nearest seed source. This pattern fits the expected seed shadow generated by frugivorous birds, which are the dispersal agents. (b) *Rhus* seedling density was higher under big burned pine trees than under small ones and only few seedlings were found outside the canopy of the burned trees. From the seedlings which survived up to the beginning of the first summer after the fire, about 57% were also surviving after it. No difference was detected in the height of the seedlings in the different zones under the burned canopy. The possible causes and ecological implications of the newly reported phenomenon are discussed.

Keywords: *Rhus*, Mediterranean, pine forest, fire, seedling, spatial distribution, seed dispersal

Résumé

Rhus coriaria L. est décrite pour la première fois comme un semencier facultatif après incendie. Deux patrons différents de distribution des jeunes plants ont été mis en évidence au cours des 18 premiers mois suivant un incendie dans une forêt naturelle de pins sur le Mont Carmel en Israel: a) une corrélation négative significative a été trouvée entre la densité de jeunes plants de *Rhus* et la distance à la source de graines la plus proche. Ce patron s'ajuste à l'ombre de graines à laquelle on s'attendait, générée par les oiseaux frugivores qui sont les agents de dissémination; b) la densité de jeunes plants de *Rhus* est plus élevée sous les grands pins brûlés que sous les petits et seuls quelques jeunes plants ont été trouvés à l'extérieur de la voûte formée par les arbres brûlés. Parmi les jeunes plants qui ont survécu jusqu'au début de l'été suivant l'incendie, environ 57 % ont survécu au-delà. Aucune différence quant à la hauteur des jeunes plants n'a été détectée dans les différentes zones situées sous la canopée. Les causes possibles de ce phénomène et ses implications écologiques sont discutées.

Acta Œcologica 1146-609 X/92/03/279/11/$ 3.10/ © Gauthier-Villars

INTRODUCTION

Spatial patterns of plants may be the result of interaction between diverse environmental factors affecting various stages in the plant life history. Microsite heterogeneity concerning resource availability, as well as gradients of various environmental factors, may cause differential responses of seed germination, seedling establishment and plant growth. The result of which may be a spatial distribution pattern of a plant species within a habitat (Auerbach & Shmida, 1987; Olsvig-Whittaker, 1988).

The mode of seed dispersal determines the shape of seed shadow curve and thereby affects seed densities at different distances from seed source. In anemochorous as well as in endozoochorous plants, seed densities decrease exponentially as the distance from seed source increases (Fleming & Heithaus, 1981; Howe & Smallwood, 1982; Holthuijzen & Sharik, 1984; Howe, 1986).

Mediterranean-type ecosystems all over the world are resilient to fire (Naveh, 1973; Keeley, 1986; Westman, 1986). Fire regime characteristics such as frequency, intensity, area and season are suggested to be important in the selection of adaptive traits of plants to fire (Malanson, 1987) and in determining the resilience of the individual plant and the whole ecosystem (Fox & Fox, 1986; Grubb & Hopkins, 1986).

Plant species are classified according to their reaction to fire as "seeders", "resprouters", or intermediate types (Keeley, 1977; Keeley & Zedler, 1978; Trabaud, 1987). Keeley (1991) found a correlation between the reaction to fire and the mode of seed dispersal. Most resprouters have fleshy fruits dispersed by animals, their seeds are big, short living and are killed by fire. Most seeders have dry fruits with small seeds which germinate from seed bank after a heat stimulus caused by fire.

Germination intensity varies with the intensity and duration of the heat treatment, and with depth of burial (Lahav, 1988; Thanos & Georghiou, 1988; Trabaud & Oustric, 1989). Ash of burned trees has an influence on germination (Lahav, 1988; Ne'eman *et al.*, 1992 *c*), growth and reproduction (Kutiel & Naveh, 1987 *a*; 1987 *b*).

Most of the studies deal with the burned area as a homogeneous and uniform one. In reality, every forest is a mosaic of big trees, small ones, bushes and gaps (e.g., Olsvig-Whittaker, 1988). Consequently fire intensity varies 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 are mentioned to have an influence on the presence of different plant species. Big black ash circles with only some seedlings of a few plant species can be observed under the canopy of the old burned trees for at least two years after the fire (Lahav, 1988; Kutiel & Kutiel, 1989). *Rhus coriaria* L. seedlings are among the few species that grow in those black circles (Ne'eman *et al.*, 1992 *a*; 1992 *b*).

The aim of this study is to reveal the influence of the distance of seed source, and the effect of burned trees' size on the distribution of *Rhus* seedlings after fire in a natural pine forest.

MATERIALS AND METHODS

The plant

Rhus coriaria L. (Sumack) is a small tree ranging from the Canary Islands across southern Europe, and southwestern Asia to Tadzhikistan in central Asia. This tree was cultivated, for tannins and dyes, since the 8th century A.D. *Rhus* populations, in some parts of its area, seem to originate from cultivation. *Rhus* species have a very intensive vegetative reproduction, usually forming dense clones (Borowicz, 1984; Lovett Doust & Lovett Doust, 1988; Luken, 1990). In Israel *R. coriaria* is relatively common in neglected places near villages in the Mediterranean region (Zohary, 1972). Many populations are small vegetative clones. We found no citation mentioning *R. coriaria* in the context of post-fire succession.

Study site

Our study site is a natural *Pinus halepensis* Mill. forest on Mount Carmel, near Haifa in Israel (32° 44′ N 35° 01′ E), at an elevation of 320 m above sea level and 7 km from the sea (Fig. 1). The climate is typical Mediterranean with an annual mean of precipitation of about 700 mm. In September 1989 a large part of the forest was burned in a wild fire. A relatively uniform burned area of 135,000 m^2

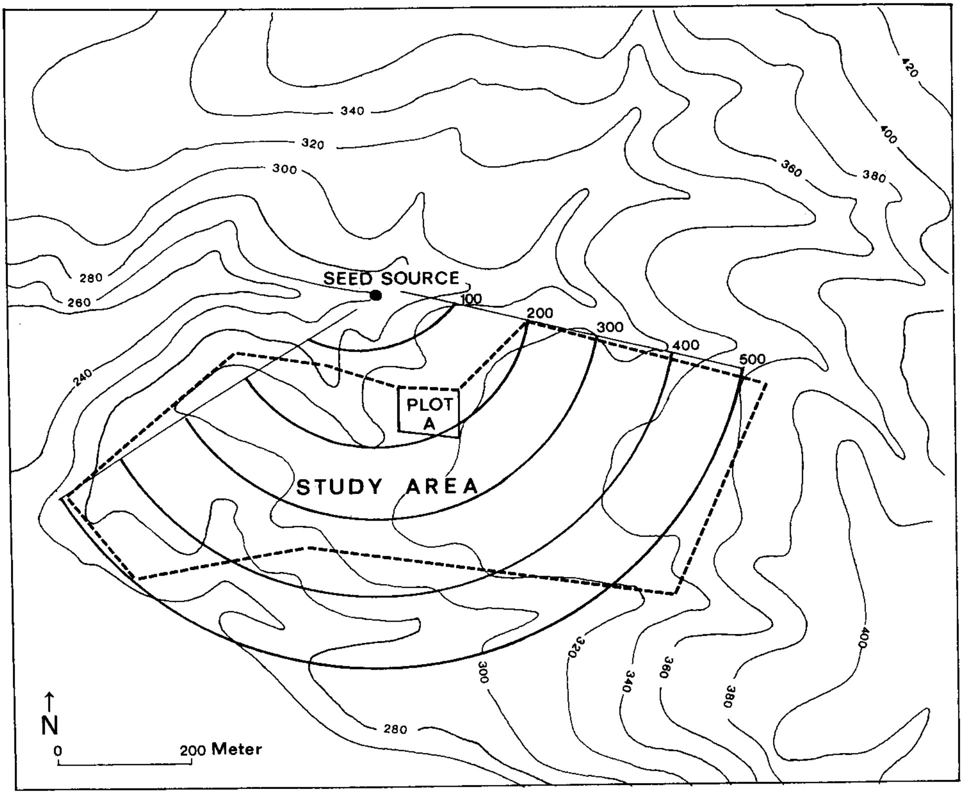

Fig. 1. — Schematic map showing the general layout of the study area, plot A, and the distances from *Rhus* seed source.

and a control area in the unburned surroundings, are used for a long term research on the resilience of the ecosystem to fire. The results reported here were collected during the first 18 months after the fire.

The effect of seed source distance and burned pine tree size on seedling density

Due to our familiarity with the burned area and the surrounding unburned area, we were able to point with high degree of reliability to the nearest and the only seed source of *R. coriaria* in a range of 1.5 km from the center of our burned area (Fig. 1). A total of 340 burned pine trees at different distances from this seed source, were checked. However, the first 100 m from the seed source were not included in the study due to relatively steep topography and uneven burning intensities (Fig. 1). The trunk perimeter of each pine was measured and diameter at breast hight (DBH) was calculated. The total number of *R. coriaria* seedlings growing under the canopy of each tree was counted. The diameter of the burned canopy was measured and the density of the seedlings was calculated per 1 m^2.

One-way analysis of variance (ANOVA) procedure was used to assess patterns of seedling density as a function of the distance from the seed source and of the trunk DBH under which they grow. The distance variable was divided into 5 groups (100-200, 201-300... 501-600 m), and the trunk DBH was divided into 8 groups (12.01-18, 18.01-24, ... 54.01-60 cm). All one-way ANOVA's were followed by *posteriori* comparisons using a Duncan multiple range test ($p<0.05$).

A two-way ANOVA was employed to analyze the combined effects of the distance from the seed source and the trunk DBH on seedling density (dependent variable).

Distribution pattern of seedlings beneath burned pine trees

A relatively homogeneous (70 m×70 m) plot was chosen for this part of the study (Fig. 1). All the 30 lone standing burned pine trees in this plot were numbered and their trunk perimeter was measured. The density and height of *Rhus* seedlings were measured along four rectangular belt-transects facing the four points of the compass. Each transect was located from the trunk and continued to the area outside the canopy of the burned tree (Fig. 2). 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. Because the crown width was different between trees, the quadrats were divided into three groups (Fig. 2): "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 between outside the canopy borders. The last group represents the area between the trees, not under the direct influence of the burned trees (Fig. 2). This method enables to compare the effect of the burned canopy of trees of differents sizes, in relation to the border of the canopy rather than the distance from the trunk.

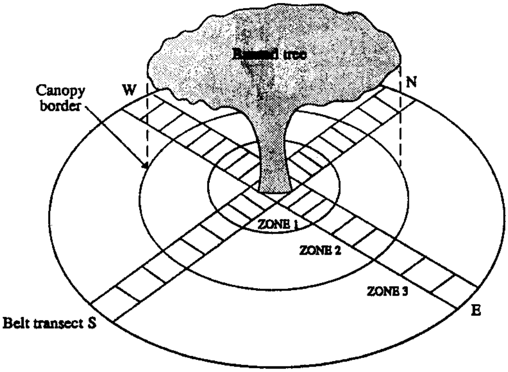

FIG. 2. — Schematic representation of the division into three zones according to the location of quadrates relatively to the trunk and the border of the burned canopy. See text for more details.

Seedling density was counted twice. In the first count (August 1990) dead seedlings were included, so that it could represent the situation at the beginning of the summer. The second count (February 1991) represents the seedlings that survived the first summer drought. Seedlings height was measured only in February 1991. The difference of seedling density between the two dates was compared by T-test.

Mean values of seedling density and height were calculated for each zone for each tree. Because the trees were the independent unit of observation, the statistical analysis on seedling density and height per each zone were performed on these means.

One-way ANOVA was used to determine out the effect of the distance from the burned trunk on *Rhus* seedling density and height.

Data analysis

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 & ROHLF, 1981). However, seedling densities in figures are represented by the original values before transformations. The results of the means are followed by ±S.D. in the text and by error bars in the figures.

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

RESULTS

The effect of seed source distance and burned pine size on seedling density

A significant negative correlation was detected between the square root transformed average number of seedlings per 1 m^2 located in each distance from the seed source ($r=-0.43$, $n=340$, $p<0.001$). Based on the least square regression equation $y^{1/2}=0.686-0.001\,x$ ($n=340$, $p<0.001$), the theoretical maximum distance of seedlings from the seed source was 686 m. But few seedlings were found beneath burned pine trees located more than 500 m away from the seed source (Fig. 3).

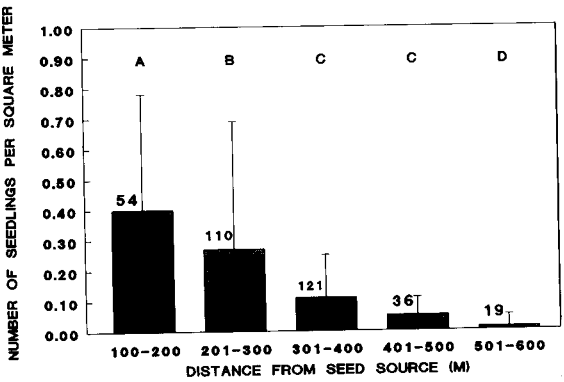

FIG. 3. — *Rhus* seedling density beneath burned pines as a function of distance from the *Rhus* seed source. Significant differences in square root transformed average number of seedlings per 1 m^2 were detected among the difference distance categories ($F_{4,335} = 14.83$, $P<0.001$). Significantly different number of seedlings among distant categories ($P<0.05$, using Duncan multiple range test) are indicated by the letters A–D: A>B>C>D above bars. Sample sizes are given above bars.

A significant positive correlation was detected between the square root transformed average number of seedlings per 1 m^2 beneath the burned trees and the size of the burned pine, expressed by trunk diameter (DBH) (r=0.24, n=340, p<0.001). However, seedling density was relatively higher beneath big trees (trunk DBH>36 cm) than small ones (Fig. 4). It is notable that seedling density beneath the big trees is relatively constant regardless of their trunk DBH (Fig. 4). In addition, seedlings were not found beneath small burned trees with trunk DBH less than 12 cm (Fig. 4).

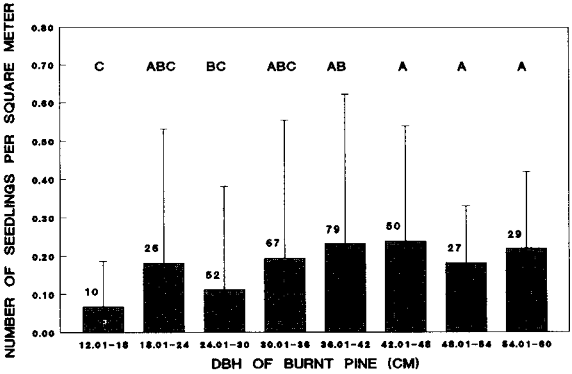

FIG. 4. — The dependency of *Rhus* seedling density beneath pine burned canopy upon pine size as expressed by its trunk DBH. Significant differences in square root transformed average number of seedlings per 1 m^2 were detected among the different trunk DBH categories ($F_{7,332}$=3.43, P<0.01). Significantly different values of seedling density among trunk DBH categories (P<0.05, using Duncan multiple range test) are indicated by the letters A–C: A>B>C above bars. Sample sizes are given above bars.

Both, the distance from seed source, and the trunk DBH, affected the seedling density beneath burned pine trees, as was detected by two-way ANOVA procedure (Table I). Only 33% of the total variation of seedling density is explained by the distance and trunk DBH when each one of these two independent variables alone explains much less variation of seedling density (18% and 6%, respectively).

TABLE I. — Two-way ANOVA comparing square root transformed seedlings density per 1 m^2 beneath the canopy of burned trees across the trunk DBH of the burned tree and the distance from the nearest seed source.

Source of Variation	df	Sum of Squares	Mean Square	F	P
Model	35	10.24	0.29	4.33	<0.0001
Error	304	20.53	0.07		
Corrected total	339	30.77			
Main effects					
Trunk diameter (DBH)	7	2.07	0.30	4.39	<0.0001
Seed source distance (S)	4	6.70	1.68	24.82	<0.0001
Two-way interactions					
DBH×S	24	1.46	0.06	0.90	0.60

Distribution pattern of seedlings beneath burned pine trees

Seedling density per 1 m^2 was recorded around burned pine trees in a 4900 m^2 plot (Fig. 1). All these trees are located at a similar distance (approximately 130 m) from the seeds source. Thus, as the distance variable is almost constant, its expected contribution to the variation of seedling density in this plot is minimal. It is noticeable that most seedlings appeared beneath the canopy of the burned trees with very few exceptions that germinated outside of the burned canopy. Seedling density decreased with the distance from the trunk with significant differences among the three zones around the trunk (Fig. 5). This pattern was consistent both in the beginning and after the first summer after the fire (Fig. 5).

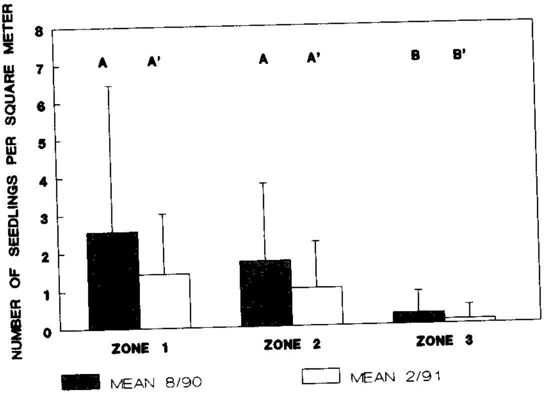

FIG. 5. — *Rhus* seedling density, in the different zones (see Fig. 2) as a function of zone under the burned pine canopy in two sampling dates. Significant differences in square root transformed average number of seedlings per 1 m^2 were detected among the three different zones (in August 1990, $F_{2,85}=8.85$, $P<0.001$; in February 1991, $F_{2,85}=9.43$, $P<0.001$). Significantly different density values among different distances from the trunk ($P<0.05$, using Duncan multiple range test) are indicated by the letters A–B: A>B in August 1990 and by A′–B′: A′>B′ in February 1991. Sample sizes in both dates were 28 for zone 1, and 30 for zones 2 and 3.

Seedling survival

Seedling density decreased during the first summer. The average seedling density in zone 1 and 2 beneath pine canopy was higher in the beginning than after the summer (2.06±2.37, $n=30$; 1.16±1.22, $n=30$; respectively). But the difference is not significant ($T=-1.8$, $P=0.08$). However, seedling survival during this summer was 57% for all zones. The differences between these two dates are not significant when testing in each zone separately (Fig. 5). Almost no seedlings outside the canopy of the burned trees succeeded in surviving until the first summer and after it. The mean height of the seedlings that survived up to February 1991, in all zones was between 19.0 and 29.59 cm without a significant difference (One-way ANOVA, $F_{2,36}=2.02$, $P=0.15$). In summer 1992 some seedlings are above 2 m high (pers. obs.).

DISCUSSION

The results of this study demonstrate for the first time the ability of *Rhus coriaria* to function as a post-fire pioneer species. *R. coriaria* seedlings can be found immediately after the fire under the burned pine canopies up to a relatively long distance from the seed source. Nevertheless, *R. coriaria* has also a very vigourous vegetative reproduction forming dense clones, and a post-fire resprouting ability. Similar ecological behavior was reported for the American *R. laurina* which is mainly a post-fire resprouter but also a seeder. However, most of its seedlings die as a result of summer drought (DESOUZA *et al.*, 1986; FRAZER & DAVIS, 1988; THOMAS & DAVIS, 1989). Other *Rhus* species such as the Japanese *R. trichocarpa* and *R. javanica* are also reported both as resprouters and seeders (NAKAGOSHI *et al.*, 1983; 1987).

Most of seeder species have small seeds dispersed by wind or by autochorous means. The seeds are long living, accumulate in the seed bank and do not germinate unless a stimulus of high temperatures for short time was given. Many of the resprouters have big seeds and endozoochorous seed dispersal mode, unless germinating close to dispersal time the seeds loose viability, and no seed bank can be established (Keeley, 1986; 1991).

Rhus coriaria red fruit is similar to the fruit of *R. integrifolia* and to the fruit of the relative genus *Pistacia* which is dispersed by frugivorous birds (Izhaki,, 1986; Lloret & Zedler, 1991). Fruits of *R. coriaria* were also observed to be dispersed by fruit-eating birds (pers. obs.). Because the fire occurred in September before fruit ripening, and burned the seed-source trees, we assume that seed dispersal took place before the fire. Thus, the seedlings we measured probably came from seeds which germinated from a soil stored seed bank. It was observed that large numbers of *R. javanica* and *R. trichocarpa* seeds germinated from the seed bank in the soil after fire in a pine forest in Japan (Nakagoshi *et al.*, 1983). The germination of seeds of "seeders", which disperse their seeds before the fire, like *Cistus* sp. (Lahav, 1988; Thanos & Georghiou, 1988; Trabaud & Oustric, 1989) and *R. javanica* (Washitani & Takenaka, 1986) is stimulated by thermal treatment. Fleshy fruits with big seeds are exceptional in the reproductive syndrome of post-fire seeders (Keeley, 1991). The ability of *R. coriaria* to renew itself from seed bank after the disturbance of fire points to its potential as a pioneer species.

The fact that there was only one seed source in all the surrounding enabled us to analyze the pattern of seedling density beneath burned pine trees as a function of the increasing distance from the fruit source. The leptokurtic shape of the distribution of the established seedlings as a function of the distance from seed source, 9 months after germination (Fig. 3), is similar to the expected seed shadow pattern generated by frugivores and other dispersal modes (Fleming & Heithaus, 1981; Howe & Smallwood, 1982; Holthuijzen & Sharik, 1984; Howe, 1986). It was suggested that the frugivorous birds are especially important because they extend the tail of the seed shadow far away from the parental crown (Howe, 1986). However, the distances of dispersal we report here, up to 650 m, are much longer than those reported for vertebrate frugivores (Howe & Primack, 1975; Hudler *et al.*, 1979; Fleming & Heithaus, 1981; Holthuijzen & Sharik, 1984; Willson & Crome, 1989; Fleming & Williams, 1990). Appropriate methodological difficulties in several of these studies might be the reason for their data on shorter dispersal distances. However, such a long distance seed dispersal in our case suggests that *R. coriaria* is a pioneer species that has the potential to colonize deeply into disturbed areas.

One year after the fire *R. coriaria* seedlings were found to grow almost only under the canopies of burned pine trees. Seedlings density was found to be higher under the canopy of big burned trees, than under small ones. This is in contrast to other species present in the study area that were found in much lower densities under the burned canopies than outside them (Ne'eman *et al.*, 1992 *a*; 1992 *b*). We speculate some possible explanations to this exceptional pattern of distribution.

(a) Frugivorous birds may be attracted to big pine trees rather than to the small ones. Therefore, high dropping accumulation and higher seed density beneath big trees is expected.

(b) High temperatures under the big trees stimulate the germination of the seeds, while those under the smaller trees fail to germinate because of lack of proper thermal stimulus.

(c) High amounts of ash, up to 5 cm cover under big trees (LAHAV, 1988) may cause high salinity and exclusion of some plant species from germination and growth under these trees (NE'EMAN *et al.*, 1992 *c*). *R. coriaria* grow almost only under the canopies of big trees, where they reach a height of up to 2.50 m during two growing seasons (unpublished data). Their development is the best under the canopy where most of the ash accumulates. Similar results were detected also for *P. halepensis* and *C. salviifolius* (NE'EMAN *et al.*, 1992 *a*; 1992 *b*). It is obvious that *R. coriaria* germination occurs in high ash concentrations which creates high osmotic stress.

(d) It may also be that high mineral concentration is an obligatory factor for germination of *R. coriaria* seeds, as is the case for some halophytes (WAISEL, 1972).

Water stress was found to be the cause of the death of many *R. laurina* (FRAZER & DAVIS, 1988; THOMAS & DAVIS, 1989), *Pinus* and *Cistus* seedlings (KARSHON, 1973; LAHAV, 1988) during their first summer. Since seedling density under the burned pine trees is rather low, water stress may explain seedling death also in *R. coriaria*.

CONCLUSIONS

Two different spatial patterns were discovered in the distribution of *R. coriaria* seedlings after fire. The first is the negative correlation between the distance from the seed source and the number of seedlings. The second is the dependence of establishment upon the presence of big burned trees. It is the first time that such a behavior is described. If those patterns are valid for wide range of Mediterranean habitats, which suffer from frequent fires (NAVEH, 1973), *R. coriaria* should have been a much more common tree in the maquis.

To conclude, it seems that *R. coriaria* has a unique advantage as a post-fire pioneer species by its ability to germinate near the trunk of the burned pines. This microhabitat stays almost free of plants during the first year after fire. A plant species that has adapted itself to germinate in these conditions, from a seed bank, has the advantage of establishing ahead of other species when very low interspecific competition occurs. However, since this species is relatively rare in mature Mediterranean forests in Israel, it seems that its ability to compete with other species is limited, and it is probably excluded by other tree species during the post-fire succession.

Future experimental work on the influence of temperature and ash on the germination and establishment of *R. coriaria* will reveal the attributes that enable this species to colonize near the burned pine trees.

ACKNOWLEDGEMENTS

We thank O. ZOHAR for his assistannce in field work, Mrs M. CATZ for revising the manuscript, and two anonymous reviewers for their fruitful comments. This study was supported by the Carmel Foundation, Ministry of Environmental Affairs, Israel and by The Society for Protection of Nature in Israel.

REFERENCES

AUERBACH M. & SHMIDA A., 1987. – Spatial scale and the determinants of plant species richness. *Trend. Ecol. Evolut.*, **2**, 228-231.

BOROWICZ K., 1984. – *Chorology of Trees and Shrubs in South-West Asia and Ajucent Regions.* Polish Scientific Publishers, Warzawa, vol. 3, p. 88.

CHRISTENSEN N. L., 1987. – The biogeochemical consequences of fire and their effect on the vegetation of the coastal plain of the southeastern United States. *In*: TRABAUD L., (Ed.), *The Role of Fire in Ecological Systems*, SPB. Academic Publishing, The Hague, 1-22.

DESOUZA J., SILKA P. A. & DAVIS S. D., 1986. – Comparative physiology of burned and unburned *Rhus laurina* after chaparral wildfire. *Oecologia*, **71**, 63-68.

FLEMING T. H. & HEITHAUS E. R., 1981. – Frugivorous bats, seed shadows, and the structure of tropical forests. *Biotropica,* Reproductive Botany Supplement, **13**, 45-53.

FLEMING T. H. & WILLIAMS C. F., 1990. – Phenology, seed dispersal,and recruitment in *Cecropia peltata* (Moraceae) in Costa Rican tropical dry forest. *J. Trop. Ecol.*, **6**, 163-178.

FOX B. J. & FOX M. D., 1986. – Resilience of animal and plant communities to human disturbance. *In*: DELL B., HOPKINS A. J. M. & LAMONT B. B. (Eds.), *Resilience in Mediterranean-Type Ecosystems*, Dr. Junk Publishers, Dordrecht, 65-83.

FRAZER J. & DAVIS S. D., 1988. – Differential survival of chaparral seedlings during the first summer drought following wildfire. *Œcologia*, **76**, 215-221.

GRUBB P. J. & HOPKINS A. J. M., 1986. – Resilience at the level of plant community. *In*: DELL B., HOPKINS A. J. M. & LAMONT B. B. (Eds.), *Resilience in Mediterranean-Type Ecosystems*, Dr. Junk Publishers, Dordrecht, 21-39.

HOLTHUIJZEN A. M. & SHARIK T. L., 1984. – The red cedar *(Juniperus virginiana* L.) seed shadow along a fenceline. *Am. Midl. Nat.*, **113**, 200-202.

HOWE H. F., 1986. – Seed dispersal by fruit-eating birds and mammals. *In*: MURRAY D. R. (Ed.), *Seed dispersal*, Academic Press, New York, 123-189.

HOWE H. F. & PRIMACK R. B., 1975. – Differential seed dispersal by birds of the tree *Caearia nitida* (Flacourtiaceae). *Biotropica*, **7**, 278-283.

HOWE H. F. & SMALLWOOD J., 1982. – Ecology of seed dispersal. *Ann. Rev. Ecol. Syst.*, **13**, 201-228.

HUDLER G. W., OSHIMA N. & HAWKSWORTH F. G., 1979. – Bird dissemination of dwarf mistletoe on ponderosa pine in Colorado. *Am. Midl. Nat.*, **102**, 273-280.

IZHAKI I., 1986. – Seed dispersal in an Eastern Mediterranean scrub in Israel. Ph. D. dissertation, The Hebrew University of Jerusalem (In Hebrew).

KARSHON R., 1973. – Renewal of pine forest after fire. *Lyaaran*, **23**, 8-16 (In Hebrew).

KEELEY J. E., 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 J. E., 1986. – Resilience of Mediterranean shrub communities to fires. *In*: DELL B., HOPKINS A. J. M. & LAMONT B. B. (Eds.), *Resilience in Mediterranean-Type Ecosystems.* Dr. Junk Publishers, Dordrecht, 95-113.

KEELEY J. E., 1991. – Seed germination and life history syndromes in the California chaparral. *Bot. Rev.*, **57**, 81-116.

KEELEY J. E. & ZEDLER P. H., 1978. – Reproduction of chaparral shrubs after fire: A comparison of sprouting and seeding strategies. *Am. Midl. Nat.*, **99**, 142-161.

KUTIEL P. & NAVEH Z., 1987 *a*. – Soil properties beneath *P. halepensis* and *Q. caliprinos* trees on burned and unburned mixed forests on Mt. Carmel, Israel. *Forest. Ecol. Manage.*, **20**, 11-24.

KUTIEL P. & NAVEH Z., 1987 *b*. – The effect of fire on nutrients in a pine forest soil. *Plant soil.*, **104**, 274-296.

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.

LAHAV H., 1988. – Renewal of vegetation after fire in a natural pine forest on Mt. Carmel. M. sc. dissertation, Tel-Aviv University (In Hebrew).

LLORET F. & ZEDLER P. H., 1991. – Recruitment pattern of *Rhus integrifolia* populations in periods between fires in chaparral. *J. Veg. Sci.*, **2**, 217-230.

LOVETT DOUST J. & LOVETT DOUST L., 1988. – Modules of production and reproduction in dioecious clon shrub *Rhus typhina*. *Ecology*, **69**, 741-750.

LUKEN J. O., 1900. – Gradual and episodic changes in structure of *Rhus* clons. *Bull. Torrey Bot. Club.*, **117**, 221-225.

MALANSON G. P., 1987. – Diversity, stability and resilience: effect of fire regimes. *In*: TRABAUD L. (Ed.), *The Role of Fire in Ecological Systems*, SPB Academic Publishing, The Hague, 49-63.

NAKAGOSHI N., NEHIRA K. & NAKANE K., 1983. – Regeneration of vegetation in the burned pineforest in southern Hiroshima Perfecture, Japan IV: Buried viable seeds in the early stage of succession. *Mem. Fac. Integrated Arts and Sci. Hiroshima Univ.*, **49**, 23-33 (in Japanese with English summary).

NAKAGOSHI N., NEHIRA K. & TAKAHASHI F., 1987. – The role of fire in pine forests of Japan. *In*: TRABAUD L. (Ed.), *The Role of Fire in Ecological Systems*, SPB Academic Publishing, The Hague, 89-119.

NAVEH Z., 1973. – The ecology of fire in Israel. *Ann. Tall Timbers Fire Ecol. Conf.*, **13**, 131-170.

NE'EMAN G., LAHAV H. & IZHAKI I., 1992 *a*. – The effect of burned pine trees on post fire germination and establishment. *Proceedings of the VI MEDECOS conference*, Crete., 361-366.

NE'EMAN G., LAHAV H. & IZHAKI I., 1992 *b*. – Spatial pattern of seedlings one year after fire in a Mediterranean pine forest (in press).

NE'EMAN G., MEIR I. & NE'EMAN R., 1992 *c*. – The influence of pineash on the germination and early growth of *Pinus halepensis* Mill. and *Cistus salviifolius* L. *Environmental Quality and Ecosystem Stability, Proceedings of the Fifth International Conference of the Israel Society for Ecology & Environmental Quality Sciences*, 771-778.

OLSVIG–WHITTAKER L., 1988. – Relating small-scale vegetation patterns to the environment. *In*: DURING H. J., WERGER M. J. A. & WILLEMS J. H. (Eds.), *Diversity and Patterns in Plant Communities*, SPB Academic Publishing, The Hague, 87-94.

SAS Institute, 1988. – *SAS/Stat user's guide*, Cary, NC, USA.

SOKAL R. R. & ROHLF F. J.., 1981. – *Biometry*. W. H. Freeman, San Francisco, CA, USA.

THANOS C. A. & 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.

THOMAS C. M. & DAVIS S. D., 1989. – Recovery patterns of three chaparral shrub species after wildfire. *Oecologia*, **80**, 309-320.

TRABAUD L., 1987. – Fire and survival rats in plants. *In*: TRABAUD L. (Ed.), *The Role of Fire in Ecological Systems*, SPB Academic Publishing. The Hague, 65-90.

TRABAUD L. & OUSTRIC J., 1989. – Influence du feu sur la germination de semences de quatre espèces ligneuses méditerranéennes à reproduction sexuée obligatoire. *Seed Sci. Technol.*, **17**, 589-599.

WAISEL Y., 1972. – *Biology of Halophytes*. Academic Press, N.Y., 395 p.

WASHITANI I., & TAKENAKA A., 1986. – 'Safe sites' for the seed germination of *Rhus javanica*: a characterization by responses to temperature and light. *Ecol. Res.*, **1**, 71-82.

WESTMAN W. E., 1986. – Resilience concept and measures. *In*: DELL B., HOPKINS A. J. M. & LAMONT B. B. (Eds.), *Resilience in Mediterranean-Type Ecosystems*. Dr Junk Publishers, Dordrecht, 5-21.

WILLSON M. F. & CROME F. H. J., 1989. – Patterns of seed rain at the edge of a tropical Queensland rain forest. *J. Trop. Ecol.*, **5**, 301-308.

ZOHARY M., 1972. – *Flora palaestina, Vol. II*. The Israel Academy of Sciences and Humanities, Jerusalem.