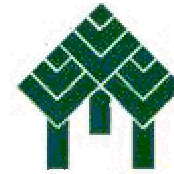


ספרית אורנים



המאמרים במערכת תדפיסים זו מוגנים על-פי

חוק זכויות יוצרים

הדפסת מאמרים תהיה לצרכי לימוד והוראה בלבד

אין לעשות כל שימוש מסחרי במאמרים.

The effect of porcupine and bast scale on Aleppo pine recruitment after fire

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Abstract

The combined effect of a large-scale fire followed by small-scale herbivory by porcupines and bast scales were studied on the recruitment of Aleppo pines (*Pinus halepensis*). A massive fire on Mount Carmel, Israel, in 1989 destroyed 300 ha of a natural pine forest. Although Aleppo pine is fire-adapted, its resilience after fire is jeopardized by other biotic and abiotic hazards. Herbivory by porcupine and scale was responsible for the loss of approximately 6.5% of the saplings at four years post-fire. Porcupine damage was patchy but rather heavy (mean = 15% mortality of pine saplings with a maximum value of 21% mortality) in plots with low vegetation cover and high rock cover while only marginal impact was observed in relatively dense vegetation (mean mortality = 0.5%). Similarly, scale damage was widespread patchy (with maximum of 37% sapling mortality), and not correlated with vegetation cover. While porcupine activity emerged only in the fourth year after the fire, scales infested saplings over a wide range of ages. Porcupine activity was local and distributed over relatively small areas while scale infestation was widespread and general. This study demonstrated that post-fire pine saplings in harsh condition patches (shallow dry soil, high rock cover) are more exposed to the combined damaging effect of porcupine and scales than sapling in patches with more suitable environmental conditions.

Keywords: Herbivory, fire, succession, recruitment, East-Mediterranean ecosystems, Aleppo pine, porcupine, bast scale.

Résumé

On a étudié, sur le recrutement du pin d'Alep, les effets combinés d'un vase incendie et d'une herbivorie localisée due à des porcs-épics et des coccidés. En 1989, un incendie important a détruit 300 ha d'une pinède naturelle au Mont Carmel en Israël. Bien que le pin d'Alep soit adapté aux feux, sa résilience après un incendie peut être compromise par d'autres facteurs, biotiques ou abiotiques. Les porcs-épics et les coccidés sont responsables de la perte d'environ 6,5 % des jeunes plants quatre ans après l'incendie. Les dégâts provoqués par les porcs-épics sont inégaux mais assez importants (en moyenne : 15 % de mortalité chez les jeunes plants, avec une valeur maximale de 21 %) dans les parcelles à faible couvert végétal et recouvrement rocheux élevé, mais seulement marginaux lorsque la végétation est relativement dense (mortalité moyenne : 0,5 %). Les dégâts provoqués par les coccidés sont également très inégaux (avec un maximum de 37 % de mortalité

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chez les jeunes plants) mais ne sont pas corrélés avec le recouvrement végétal. Alors que l'activité des porcs-épics ne se manifeste que la quatrième année suivant l'incendie, les coccidés infestent les jeunes plants au cours d'une période étendue. L'action des porcs-épics est locale et répartie sur des surfaces relativement faibles; l'infestation par les coccidés est très étendue et générale. Cette étude montre qu'après un incendie les jeunes plants de pins sont plus exposés à l'action préjudiciable des porcs-épics et des coccidés dans les parcelles ayant des conditions rudes (sol sec superficiel, fort recouvrement rocheux) que dans celles où les conditions environnementales sont plus favorables.

INTRODUCTION

Plant disturbance is "the mechanisms which limit the plant biomass by causing its partial or total destruction" (GRIME, 1979). Disturbances in the natural environment affect the dynamic of populations, communities and ecosystems (SOUSA, 1984). Disturbances may be abiotic such as fire, storm damage, burial by sand; and biotic such as defoliation by herbivores (CRAWLEY, 1986). These disturbances differ in scale, frequency and intensity. Therefore, a disturbance can affect an individual, a small area, or an entire community. As several disturbances may occur simultaneously or over a relatively short time period, together they may create a complex disturbance regime which governs species abundance and distribution (COLLINS & GLENN, 1988).

Mediterranean-type ecosystems throughout the world are exposed to fires either as a natural feature of the ecosystem (FOX & FOX, 1986) or as a result of human activity and have lasted for millennia (NAVEH, 1984). It is estimated that every woodland or forest in Israel is under fire hazard about every 10-30 years (NAVEH, 1973). Fire can be regarded as the most serious and important disturbance in those ecosystems, leaving its effect for long periods. However, most plant species in these ecosystems possess adaptive traits that make them resilient to fire (MOONEY & HOBBS, 1986). Depending on their post-fire response, plant species are classified as "resprouters" or "seeders" (TRABAUD, 1987; KEELEY, 1991). Resprouters do not die in the fire and resprout from adventive buds formed on the below-ground part of the stem. In seeder species the mature plants die after the fire and regeneration is only by post-fire seed germination.

Fire disturbance may be accompanied by biotic disturbances, such as herbivory. Mammalian herbivores may alter the density, structure, and species composition of a Mediterranean plant community during post-fire succession (QUINN, 1986). MILLS (1983) found that approximately 50% of *Ceanothus greggii* seedlings in the California chaparral were lost to small herbivorous mammals during the first growing season after fire. Since herbivores face increasing levels of plant defenses in later successional vegetation, they prefer to feed regularly on pioneers (CATES & ORIAN, 1975; COLEY, 1983; see also DAVIDSON, 1993); however, mammalian herbivory may also retard succession by feeding on plant species of later seral (DAVIDSON, 1993). The general effects of insect herbivores on natural vegetation have been sparsely studied (CRAWLEY, 1989), so the role of herbivorous insects in the specific case of plant succession and vegetation recovery after fire is not yet clear. A restricted number of studies suggest that the effects of insects are often subtle and are typically less pronounced than the effects of mammals (CRAWLEY, 1989). However, MILLS (1984) reported 10% sapling mortality caused by a psyllid in a post-burn California chaparral.

In the summer of 1993, four years after massive fire on Mount Carmel, Israel, uncommon activity of the porcupine (*Hystrix indica* Kerr) was observed in the burned area. Their feeding activity was concentrated on pine saplings, causing sapling death. The effect of porcupines on natural plant populations after fire has not been previously documented. Aleppo pine saplings also experience bast scale (*Matsuccoccus josephi*) herbivory, during the early years after the fire. The actual damage of bast scales to natural Aleppo pine populations after fire has not been documented previously as well.

The aim of this paper was to study the combined effect of a large-scale fire disturbance followed by small-scale herbivory disturbances by porcupines and bast scales on the recruitment of Aleppo pine in a natural forest system. Specifically, the goals were to determine (1) the actual damage of porcupines and bast scales to pine sapling population after fire, (2) the relationships between this damage and individual pine attributes such as sapling height, (3) the relationships between the damaging activities and vegetation attributes such as percentage cover and density.

STUDY SITE AND ORGANISMS

The study site is a natural forest of scattered *Pinus halepensis* Mill. trees with an understory composed mainly of *Quercus calliprinos* Webb., *Pistacia lentiscus* L., *Rhamnus lycioides* L., *Arbutus andrachne* L., and *Cistus salvifolius* L. The forest is located in the Mount Carmel Nature Reserve, Israel (32° 44'N 35° 01'E), 320 m above sea level and 7 km from the seashore. The climate is mild Mediterranean with a mean annual rainfall of about 700 mm. Mean temperature of the coldest month (January) is 12°C and of the warmest month (August) is 26°C (JAFEE, 1988). The study site was totally burned in September 1989.

The pine

Pinus halepensis Mill. is a species of circum-Mediterranean distribution, including southern Europe, North Africa and the Middle East (MIROV, 1967). Isozyme studies detected differences between Israeli populations and those of the western Mediterranean, probably due to ancient geographical separation (SCHILLER *et al.*, 1986). Local populations were found to have a relatively high resistance of germination to osmotic stress, which was interpreted as adaptation to dry Mediterranean climate (SCHILLER & WAISEL, 1989), or to post-fire germination (NE'EMAN *et al.*, 1993). Aleppo pine is an obligate post-fire seeder (NAVEH, 1973; TRABAUD, 1987; TRABAUD & OUSTRIC, 1989), the mature trees die after the fire and regeneration is only by post-fire seed germination.

The porcupine

Porcupines, which are among the largest rodents in the world, have been recognized as pests in forest and agriculture crops. The New World genus *Erethizon* has been studied extensively because of its damage to forest trees in North America (for review see GREAVES & KHAN, 1978). The Old World porcupines of the genus *Hystrix* have been comparatively little studied, probably because they are nocturnal animals which live in natural caves or excavated burrows in relatively remote or inaccessible locations (GREAVES & KHAN, 1978; ALKON & SALTZ, 1985; HARRISON & BATES, 1991).

The Indian crested porcupine (*Hystrix indica* Kerr), the largest rodent occurring in Arabia, is widely distributed in western Asia (HARRISON & BATES, 1991). It occurs throughout Israel in natural and man-modified areas in Mediterranean as well as desert habitats (ALKON & SALTZ, 1988). This species is adept in exploiting below-ground plant storage organs for forage but it is also able to consume above-ground plant biomass. Its diet usually consists of roots and bark of succulent plants and it is known to

cause damage to vegetable crops (ALKON & SALTZ, 1985), saplings and mature trees. The most important damage of crested porcupines occurs in forestry and reforestation areas (CHAUDHRY, 1970; CHAUDHRY & AHMAD, 1975). Debarking of trees near ground level in an irrigated forest in Pakistan caused damage to 52.5% in *Melia azedarach*, 24.3% in *Morus alba*, and 1% in *Dalbergia sissoo* (GREAVES & KHAN, 1978). There is some indication of damage to pine trees (*Pinus longifolia*) in Pakistan (KHAN *et al.*, 1992).

The effect of porcupines on natural plant populations has not yet been studied. However, in the Negev desert (Israel) they feed on underground bulbs of geophytes. This leads to plant regeneration, as pockets formed by their digging serve as seed traps, contain relatively high moisture and therefore are suitable microhabitat for germination and growth (GUTTERMAN & HERR, 1981; GUTTERMAN *et al.*, 1990; SHACHAK *et al.*, 1991).

The pine bast scale

Frequently the saplings of *Pinus halepensis* are attacked by the bast scale *Matsucoccus josephi* Bodenheimer & Harpaz (*Homoptera: Matsucoccidae*) which settles on all above-ground parts of pine saplings as well as on adult trees. During feeding it secretes a poisonous saliva that disrupts water transport and results in the death of new growth or the entire plants (MENDEL & LIPHSCHITZ, 1988). *M. josephi* was discovered in Israel in 1933 and a few years later, mass mortality of Aleppo pine saplings in newly reforested areas near Mount Carmel was noted (BODENHEIMER & NEUMARK, 1955). This scale is nowadays considered a serious pest of native Aleppo pine and introduced pines in the Middle East as well as in Greece (MENDEL & SCHILLER, 1993; MENDEL *et al.*, 1994). Although MENDEL *et al.* (1994) estimated that the scale damages 42% of the area of *Pinus halepensis* plantation stands in Israel, there is no information on the actual damage to population of native Aleppo pine.

METHODS

Post-fire pine resilience

Five plots, 4900 m² each, were selected randomly by randomized block design (HURLBERT, 1984) in the burned area in summer 1991, two years post-fire. Two parallel permanent transects (50 m each) were set up in the middle of each plot for recording vegetation cover. Pine and other perennial plant species were recorded at points 10 cm apart, a total of 1000 points for each plot, and percentage cover was calculated. Pine saplings were monitored in the summer of each year (1991-1993).

Pine saplings were counted in ten fixed (1 m × 1 m) quadrates, randomly marked by systematic design along the transects in each plot. The height and the mean of two rectangular diameters of ten pine saplings chosen by the random numbers table in each quadrate were measured.

Reconstruction of the pre-fire forest

The fire that burned the forest was a wildfire and no data on the pre-fire forest are available. Therefore, an attempt was made to reconstruct some of the main characters of the pine forest. The number of burned pine trees was counted in a plot of about 2.5 hectares and the density calculated; the DBH (diameter at breast height) and the radius of the burned crown of all those trees were measured. The regression equation between DBH and the radius of the crown was calculated and the mean percentage of cover of pine trees was found.

Porcupine and bast scale damage

Immediately after porcupine activity was detected in the burned area on Mount Carmel in summer (July-August) 1993, 27 plots, 10 m² each, were selected within the burned area regardless of the location of our five major plots described before. The burned area map was divided into 10 × 10 m plots and the 27 plots were selected by random numbers table. In each plot we visually estimated

the percentage cover of pines, of every other perennial species, and of rocks. We marked each pine sapling and categorized to one of three classes: (1) undamaged, (2) killed by porcupine, (3) damaged by *Matsucoccus josephi*. Sapling mortality from porcupine feeding was identified by the typical teeth marks on the lower bark. Injury by scale was identified by canopy discoloration, bending of apices, and loss of needles. All the saplings were counted, the height and basal stem diameter of each were measured. Pine sapling density was calculated in each plot.

RESULTS

Post-fire resilience

The density of pine saplings in the post-fire area decreased from summer 1991 to summer 1992 by 58%, and by 32% during the next year (table I). The total mortality during these two years was 72%. Expected pine density in the mature forest would be only 250 trees per hectare (table I). Pine cover increased during these two years by 35% but was still 70% behind its pre-fire cover. Sapling height increased by 43% during this time (table I).

TABLE I. – Pine cover, density and height (mean \pm sd) on Mount Carmel, Israel, during succession after the fire of 1989. These data are an average for different study plots in Mt. Carmel, adjacent to those that were studied for the porcupine and scales activity.

Years post-fire	Pine cover (%)	Pine density (n/m ²)	Pine height (m)
0		27.4	
2	8.5 \pm 1.5	6.7 \pm 4.4	0.15 \pm 0.03
3	11.0 \pm 4.0	2.8 \pm 3.5	0.21 \pm 0.06
4	11.5 \pm 4.0	1.9 \pm 2.1	0.27 \pm 0.10
pre-fire*	53.2	0.025	10.01 \pm 3.00**

* for explanations see Methods

** average height of pine trees in nearby unburned forest

General damage estimates

The average porcupine and scale damage to pine saplings were 6.9% \pm 8.0% (range 0-21.1%) and 5.8% \pm 9.9% (range 0-37.2%), respectively, for all 27 sample plots. However, the average damage difference between these two types of herbivory was not significant ($t_{52} = 0.73$, $P > 0.05$, on arcsin square root transformed proportions). There was no significant correlation between these two types of damage ($r = -0.01$, $P > 0.05$, $n = 27$).

The relationships between vegetation cover and porcupine and scale damage

There was a negative correlation between the proportion of damaged pine saplings and vegetation cover (fig. 1). The porcupine damaging activity was concentrated in plots with low total vegetation cover (<36%) and they totally ignored high cover (>60%). The correlation was a step-type function with a steep decrease around the 36% cover (fig. 1).

As two distinctive groups of plots (low vs. high total vegetation cover, $n = 12, 15$ respectively) were identified (fig. 1), we compared them for several parameters. The

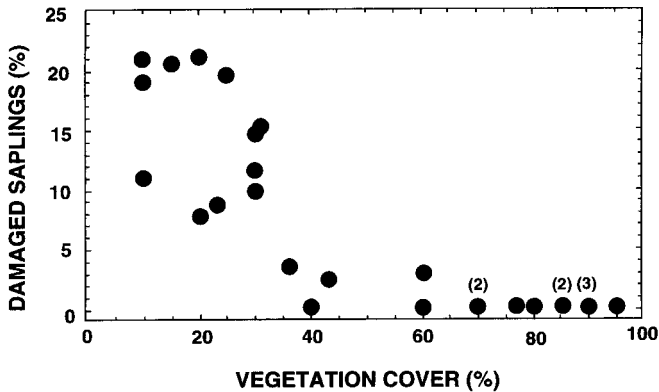


FIG. 1. – The relationships between vegetation cover and the proportion of Aleppo pine saplings killed owing to porcupine feeding in a post-fire area on Mount Carmel, Israel. In parentheses – number of replications of the same point (in case that a point was represented by more than one sample).

TABLE II. – Porcupine and bast scale damage and vegetation attributes (means \pm sd) according to two distinctive groups of total vegetation cover sample plots (for further explanations see text and fig. 1).

	Total vegetation cover		
	Low (n = 12)	High (n = 15)	
Total vegetation cover	21.1 \pm 8.2%	71.4 \pm 19.6%	8.30***
Pine cover	12.0 \pm 7.5%	10.7 \pm 6.8%	0.49 ^{ns}
Rock cover	36.8 \pm 28.9%	6.3 \pm 5.2%	4.02***
Pine density m ⁻²	5.5 \pm 4.4	5.3 \pm 2.9	0.14 ^{ns}
Pine height (cm)	52.1 \pm 18.0	62.2 \pm 23.0	1.25 ^{ns}
Porcupine damage	14.9 \pm 5.1%	0.5 \pm 1.2%	10.52***
Bast scale damage	6.6 \pm 10.8%	5.2 \pm 9.5%	0.37 ^{ns}

*** = $P < 0.001$, ns = not significant

percentage of porcupine damaged saplings in the low total vegetation cover was much higher than in the high cover (table II). The difference between them in total vegetation cover was three fold (table II). The rock cover was significantly higher in the low vegetation cover. However, pine cover and pine density were not significantly different in these two groups (table II). Porcupine damage was more regular in open areas where the coefficient of variation (CV) was only 34% compared to dense plots (CV = 240%) or to scale damage in these two groups of plots (CV = 164% and 183%, respectively).

No significant correlations were detected between the proportion of pine saplings damaged by the bast scale and cover of vegetation, cover of rock and pine density.

The correlation between size of pine with porcupine and bast scale damage

A significant positive correlation was detected between height and basal stem diameter of the saplings ($r=0.82$, $n=266$, $P<0.0001$). Therefore, the following analyses were conducted only for height but their interpretation is valid for diameter as well.

There was no significant difference in the average height of saplings between the plots with low and high total vegetation cover (table II). Nevertheless, the distribution of sapling height in the population was significantly different from the height distribution of the porcupine damaged saplings ($\chi^2=41.987$, $df=14$, $P<0.001$, fig. 2). The main reason for this difference is that the proportion of small saplings (<20 cm) in the damaged population was much lower than their proportion in the general sapling population (fig. 2).

The scale damaged the tallest saplings with an average of $65.9 \text{ cm} \pm 26.6 \text{ cm}$ ($n=84$), which was significantly higher than the average tallness of those damaged by porcupines ($52.9 \text{ cm} \pm 24.9 \text{ cm}$, $n=284$) and of undamaged saplings ($50.0 \text{ cm} \pm 27.7 \text{ cm}$, $n=1633$; one-way ANOVA on square root transformed sapling height, $F_{2,1998}=17.11$, $P<0.0001$, and Tukey pairwise comparison of means, $P<0.05$). In addition, the distribution of height of saplings damaged by scales was significantly different from that of undamaged saplings (fig. 2, $\chi^2=61.37$, $df=13$, $P<0.0001$).

DISCUSSION

Although pines are fire-adapted, their resilience after fire is jeopardized by many biotic and abiotic dangers. Since Aleppo pine is an obligate seeder it completely depends upon sapling survival for re-establishment. The porcupine and

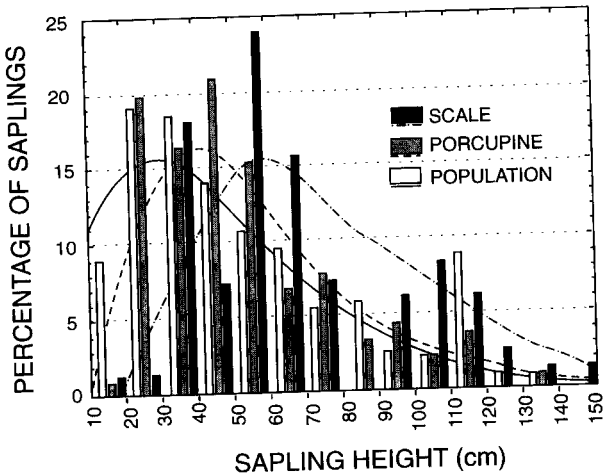


Fig. 2. – Histograms and curves of height distributions of Aleppo pine saplings (1) of the total population (2) only of those damaged by porcupines, and (3) only of those damaged by bast scales. The curves were matched by least square function.

scale episodes described here are only two links in a long chain of hazards that pines may face after fire. Hence, seeds and saplings must pass through critical and very vulnerable establishment phases after fire and only very few saplings will become fully-developed and become members of the mature post-fire pine forest.

Seed predation

Obligate seeders are expected to produce a greater number of seeds and saplings, especially relative to pre-fire abundance (MORENO & OECHEL, 1992). Immediately after the fire Mount Carmel was "flooded" with wind-dispersed pine seeds as their cones opened owing the fire heat. Although no data were collected on seed density immediately after the fire on Mount Carmel, there are indications from other studies that it may reach up to several hundreds per square meter (SARACINO & LEONE, 1993). Granivorous birds are attracted in greater numbers to feed on these seeds owing to their increased accessibility. Flocks of *Columba livia* and *Fringilla coelebs* were seen foraging in the study area several months after the fire (pers. obs.). Predation of pine seeds on the ground by birds may destroy 50% of them in the first two months after fire (SARACINO & LEONE, 1993). In addition, seed mortality due to predation by rodents is possible as well (e.g., VAN DER WALL, 1994). No data are available on post-fire seed predation by birds and rodents on Mount Carmel.

Sapling mortality

At the early stage after the fire Aleppo pine had enough saplings to ensure its maintenance in the stand. In the second, third, and fourth summer post-fire, the pine had approximately 268, 112 and 76 times more saplings, respectively, than would be needed to restore its total pre-fire density. Competition, drought and herbivory, were probably the major processes responsible for this massive sapling mortality.

An intensive intraspecific competition among Aleppo pine saplings as well as interspecific competition between saplings of pine and *Cistus salviifolius* were observed during the first 4 years post-fire on Mount Carmel (LAHAV, 1988; KATZ, 1993). These processes probably caused density-dependent mortality.

The results of this study support the hypothesis that herbivory by porcupine and bast scale influences the establishment of Aleppo pine saplings after fire. However, although only about 6% and 7% in average of young saplings were killed by porcupines and bast scales, respectively, their damage in certain plots was above 35%. Therefore, it seems that their impact is rather heterogenous and depends on vegetation structure. Porcupine damage is particularly severe in open sites, especially those with high rock cover. Sapling density in these sites, 4 years post-fire, was similar to its density in sites with higher total vegetation cover. However, pine saplings which succeeded in germinating in shallow soil on these rocks would probably face difficulties reaching adequate resources such as water and nutrients. Thus, it is expected that their number will decrease when the saplings grow up. Therefore, porcupine damage in these relatively open areas (15% in average of the left saplings) is additional to the severe abiotic conditions already occurring, which further greatly reduces the chances of the saplings' survival.

While porcupine activity emerged only in the fourth year after the fire and lasted for only one summer (pers. obs.), scales infested saplings over a wider range

of ages, especially between the second and fifth year and between 20 and 40 years of age (MENDEL *et al.*, 1994). It should be emphasized that porcupine activity was local and distributed over a relatively small burned area while scale infestation is widespread and common in post-fire areas (pers. obs.). These two types of herbivory also differ in their impact on pine saplings. Porcupines usually cause immediate death while infestation by scales may last for several years, usually ending in death.

The scale damage is undifferentiated with regard to total vegetation cover, rock cover and pine density. There is no clear trend in scale infection. By contrast, although porcupine damage seems to be uncommon, it appeared in much more defined areas (open habitat, see above), probably owing to foraging limitations. Since it is a large rodent of heavy external build (12.8 kg body mass, 88 cm body length, HARRISON & BATES, 1991), largely covered by long spines, it is probably unable to maneuver in dense vegetation. Therefore, pine saplings that were densely surrounded by individuals of other plant species evaded porcupine predation. In addition, digging out pine saplings in shallow soil demands far less energy than in a relatively deep soil.

Porcupine activity was restricted to saplings and was not observed for adult Aleppo pines. However, debarking of adult pine trees by porcupines has been reported elsewhere (KHAN *et al.*, 1992). Saplings may have a superior nutritional quality over adult plants and over dry plant material. Since fire can release large quantities of important plant nutrients, saplings in post-fire habitat may contain nutrient-rich tissues (STEIN *et al.*, 1992 but see McCULLOUGH & KULMAN, 1992). Furthermore, they probably contain a smaller amount of secondary compounds (e.g., CATES & ORIANS, 1975; COLEY, 1983).

What were the factors limiting the timing of porcupine feeding activity on pine saplings to summer in general, and to summer 1993 in particular? Shortage of available fresh plant material in the dry summer of east Mediterranean ecosystems may be the dominant factor explaining this foraging behavior. Furthermore, pine saplings in contrast to other perennials (like *Cistus*) grow during the summer (KATZ, 1993) and therefore may have higher water content in their tissues. The size of four-year-old saplings may suit porcupine requirements for feeding while the younger saplings may be too small.

In California chaparral, obligate seeding species seem to suffer greater mortality than facultative or obligate sprouting species (MORENO & OECHEL, 1992). It is likely that herbivory in east Mediterranean ecosystems is an important factor in counteracting the greater drought tolerance of the obligate seeding species, such as Aleppo pine, as was suggested for several obligate species in the chaparral (MORENO & OECHEL, 1992).

To conclude, both mammal and insect herbivory decreased survival of Aleppo pine saplings and constitute a major controlling factor of post-fire sapling establishment especially in relatively open areas. Both herbivores preferred taller saplings which had, also, higher biomass and thus, also, a better chance to survive through intra- and interspecific competition. Higher mortality rates among these saplings may cause a delay in the development of the forest to its pre-fire condition.

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