Journal of Vegetation Science 7: 273-280, 1996
© IAVS; Opulus Press Uppsala. Printed in Sweden

Early post-fire regeneration of a *Pinus halepensis* forest on Mount Párnis, Greece

Thanos, Costas A., Daskalakou, Evangelia N. & Nikolaidou, Sotiria

Department of Botany, University of Athens, Athens 15784, Greece;
Tel. +30 1 7284655; Fax +30 1 7234136; E-mail cthanos@atlas.uoa.gr

Abstract. The post-fire regeneration of a 45-yr-old *Pinus halepensis* (Aleppo pine) forest, burned in July 1989, has been studied on Mount Párnis, Attikí, Greece. Four experimental plots at various slopes and exposures were established at altitudes of 400 - 450 m, and monitored for 3 yr at 3-month intervals. Early regeneration took place abundantly, through both resprouting and seed germination of mostly hard-seeded herbs and shrubs; the floristic richness was high with 80 taxa. Pine seedling emergence took place during the winter of the first post-fire year. The mean pine seedling density by the end of the recruitment period (March 1990) was 5 - 6 seedlings/m^2. This density decreased slightly during late spring and considerably during summer. During the second post-fire year only a relatively slight decline was observed; thereafter the density was stabilized to 1 - 2 seedlings/m^2. Mortality follows a negative exponential curve that levels off at ca. 20 %. Height distributions throughout the three post-fire years were all positively skewed as a result of the presence of few very tall saplings. A considerable fraction (20 %) of very short (5 - 15 cm) saplings were still alive 39 months after the fire; these may constitute the sapling bank. Based on the analysis of height distribution curves, it is concluded that the taller seedlings survived significantly better than the shorter ones.

Keywords: Aleppo pine; Attikí; Establishment; Mediterranean forest; Mortality; Seedling; Survival; Wildfire.

Nomenclature: Tutin et al. (1964-1980); Greuter et al. (1984-1989).

Introduction

Fire is a natural event and, apart from human-induced fire, it can be considered as an integrated ecological component of the mediterranean-type ecosystems. Among the latter, the Mediterranean pine forests, built up mostly by *Pinus halepensis* (Aleppo pine) and *P. brutia*, are highly inflammable (Quézel & Barbero 1992). During the period 1955-1990, 22 000 ha/yr were burned, the largest fraction of them attributable to *P. halepensis* forest.

Most Mediterranean plants have developed various adaptive mechanisms to resist fire. In particular, post-fire regeneration is achieved either sexually, through the germination of seeds (stored and protected in the soil or in the canopy) and/or vegetatively by resprouting. *Pinus halepensis* is an obligate seeder and produces large seed crops. Seed release from the cones is controlled by environmental conditions, especially by high temperature and by low air humidity (e.g. Panetsos 1981; Johnson & Gutsell 1993). However, an important portion of the seeds remain enclosed in the cones (serotiny), thus forming an abundant canopy seed bank. Seed viability within the cone is maintained at a high level (Daskalakou & Thanos 1994). Eventually, pine seeds are massively released through the xerochasic opening of the cone induced by fire and dispersed onto the burnt ground. Therefore, a pine seed rain takes place during a short period after the fire (Saracino & Leone 1993b; Daskalakou & Thanos 1994) and, depending on the time of the fire incidence, these seeds remain on the soil surface for a period varying between a few weeks and several months, until the onset of the following wet season.

Seed germination of *P. halepensis* has been studied a great deal in the laboratory (e.g. Thanos & Skordilis 1987; Skordilis & Thanos 1995). The temperature range of germination is rather narrow, but fits well with the temperatures prevailing naturally during most of the wet season. The rate of germination is very low and although germination is possible in darkness it is significantly enhanced by light. These characteristics, and the complete lack of a stratification requirement, led to the prediction of a rather rapid field germination of *P. halepensis* seeds after the onset of the rainy season.

Various aspects of natural post-fire regeneration, particularly in *P. halepensis* forest, have recently been investigated (e.g. Trabaud & Lepart 1980; Arianoutsou & Margaris 1981; Trabaud & Chanterac 1985; Trabaud et al. 1985; Moravec 1990; Ne'eman et al. 1992, 1993; Papavassiliou & Arianoutsou 1993; Saracino et al. 1993; Saracino & Leone 1993a, b, 1994; Daskalakou & Thanos 1994; Garcia-Plé et al. 1995). The present study is a diachronic investigation concentrating specifically on *P. halepensis* seedling emergence, establishment, survival and development.

Methods

Study area

The large wildfire of 25-27 July 1989 on Mount Párnis, at the western border of the Párnis National Park, Attikí (20 km NNW to the centre of Athens) burned 1500 ha forest, mostly *Pinus halepensis*. The forest was then 47 yr old, as it had previously been burned in 1942. The density of the burned forest (determined on the basis of the burned stems) was estimated to be 1000 - 1500 stems/ha. The bedrock of the area consists of hard limestones of Middle Triassic to Lower Jurassic (Anon. 1985).

Four experimental sites of ca. 1 ha, A, B, C and D, were established at an altitude of 400 - 450 m, at the eastern part of the burned area, ca. 2 km NW of the town of Filí, on various slopes and exposures: A: ESE, 15 %, B: E, 45 %, C: WSW, 40 % and D: W, 45 %, respectively. Site D has a very shallow soil and many rocks; it has relatively abundant *Quercus coccifera*. The wildfire was very intensive and, although a few pine trees were left unburned, no live pine trees were found at or near the experimental sites.

Measurements were carried out during the last weeks of March, June, September and December, from March 1990 until September 1992 (9 and 39 months after the fire). Including a number of additional visits, the total number of visits during the study was 15. At each of the four sites the height of 100 randomly selected pine saplings was measured. Also, the number of pine saplings in 50 randomly selected 1-m^2 circles was recorded. Apart from felling and removing the burned stems (activities that took place during the second but mainly third year after the fire), human impact on the burned area was minimal. Only a single incident of grazing by goats occurred at site A, early in 1991, and hence some plots were not used in measurements thereafter.

Flowering specimens of vascular species were collected at all four sites throughout the investigation period. Species occurrence was assessed in four frequency classes: dominant: found in > 33 % of the 50 1-m^2 circular plots, common: 10 - 33 %, occasional: 5 - 10 %, rare < 5 %. Significance of differences was assessed using the two-sample *t*-test (for two means) and the Newman-Keuls multiple range test (for more than two means); survival curves (Fig. 1b) were fitted by regression analysis (Zar 1974).

Climatic conditions

Data for Tatói (at 237 m, ca. 10 km from the experimental sites) were compiled from average values (1951-1975) provided by Andreakos (1978) and the monthly meteorological bulletins (1976-1992) of the National Meteorological Service of Greece (Anon. 1976-1992). The ombrothermic diagram for Tatói (not shown) indicates a typical Mediterranean climate with mild winters, a rather low total annual precipitation and a markedly seasonal rainfall pattern with a xerothermic period (May - September). The Emberger quotient, Q_2, for Tatói is estimated at 56.6; in connection with the mean minimum temperature of the coldest month (January, 3.3 °C), the climate of the area belongs to the temperate variant of the semi-arid Mediterranean bioclimatic type. Mean annual values (1951-1989) of temperature and precipitation are 16.5 °C and 468 mm. The corresponding values for the first three post-fire years (August to July) were 16.5, 15.7 and 14.6 °C, and 246, 475 and 487 mm. The first post-fire year was particularly dry; the next two years were close to average, although the monthly rainfall pattern was irregular, showing two peaks in both rainy seasons. The second and third years were cooler than average, particularly during the winter months.

Results

Floristics

App. 1 lists the 80 species found in the experimental sites during the three-year investigation. This number should approach the actual number of species present. Table 1 summarizes these data at the family level. The species list includes several elements of typical Mediterranean maquis and phrygana vegetation. There are many more perennials (45 species, among them several geophytes) than annuals (31 species). The former species were recruited (as seedlings or resprouters) almost exclusively during the first post-fire year while the latter occurred throughout the 3-yr period at more or less constant densities. The dominant species (App. 1) are mainly reseeders (either perennials or annuals), represented by large numbers of seedlings:

Asterolinon linum-stellatum	*Euphorbia taurinensis*
Cistus creticus	*Fumana thymifolia*
C. salviifolius	*Malcolmia graeca*
Convolvulus elegantissimus	*Pinus halepensis.*

Only one resprouter is dominant, the grass *Brachypodium retusum*. Reseeders and resprouters (39 species each) were equal in number.

Sapling density, survival and mortality

Maximum density of *Pinus halepensis* saplings was observed in March 1990, 9 months after the fire (Table 2). Despite the variation in density values (which can be

Table 1. Families (and no. of species) represented in the burned pine forest on Mount Párnis (four sites). A/P = Annual/ Perennial; S/V = Seeder/Vegetative resprouter.

Family	Number of species	A/P	S/V
Fabaceae	11	8/ 3	9/ 2
Asteraceae	9	4/ 4	4/ 5
Liliaceae	9	0/ 9	0/ 9
Lamiaceae	8	0/ 8	0/ 8
Brassicaceae	6	6/ 0	6/ 0
Cistaceae	5	1/ 4	5/ 0
Caryophyllaceae	3	3/ 0	3/ 0
Poaceae	3	2/ 1	2/ 1
Primulaceae	3	2/ 1	2/ 1
Other families (18)	23	5 /15	8 /13
Total (27 families)	80	31 /45	39 /39

attributed to the random sampling scheme at each measurement date), a trend towards a gradual decrease in density during the first two post-fire years can be recognized. From 21 months onwards the density stabilized at 1 - 2 saplings/m^2.

Based on the assumption that pine seedling recruitment was completed by March 1990 (justified by literature references and field observations), seasonal mortality was estimated as presented in Fig. 1a. The overall average mortality was highest during the first post-fire summer - nearly two seedlings/m^2 during the period June-September 1990 - and second highest during the first post-fire spring (March-June 1990). Subsequent mortality was considerably lower and amounted to only 25 % of the total death toll during the first two post-fire years (March 1990 - September 1991). Although dead pine saplings were occasionally found from spring 1991 onwards, measurements at subsequent dates could not reveal any significant mortality events.

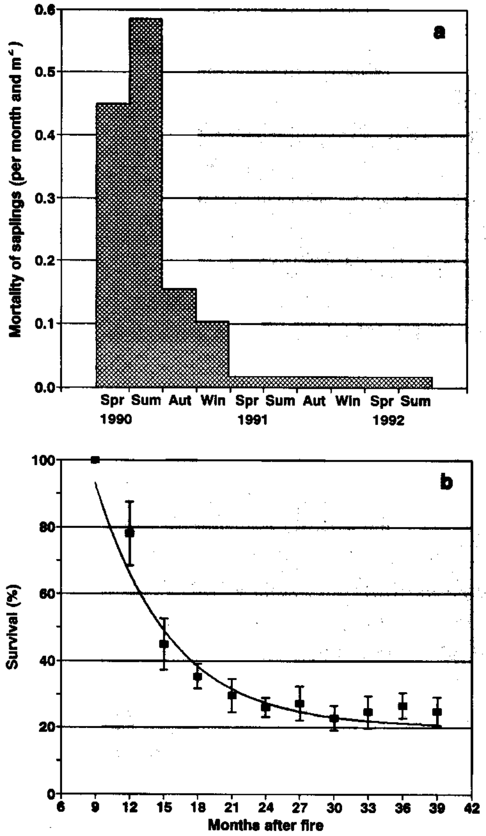

Fig. 1. a. *Pinus halepensis* sapling mortality; **b.** survival, determined every three months from March 1990 to September 1992. In graph **b**, vertical lines represent 2 SE ($n = 4$); regression function of the curve: $Y = 73.145\ e^{-0.154(X-9)} + 20$ (d.f. = 6, $r = 0.978$, $P < 0.001$).

Fig. 1b depicts the survival of the pine sapling populations. The seedling cohort at March 1990 (considered as the end of the seedling recruitment season) is taken as 100 %. After the first post-fire summer, less than 50 % of the seedlings were still alive, while ca. 25 % survived the second summer. Since no significant mortality was assessed during the third year, we estimate that 20 % of the saplings registered in March 1990 were still alive in September 1992. On this basis, the regression analysis resulted in a negative exponential curve (Fig. 1b).

Table 2. *Pinus halepensis* sapling density (seedlings/m^2), determined every three months from March 1990 to September 1992. Lower-case letters indicate significant differences at $P < 0.05$ (Newman-Keuls multiple range test, $n = 200$).

Months after fire	Density ± SE	
9	5.51 ± 0.36	a
12	4.16 ± 0.30	b
15	2.40 ± 0.20	c
18	1.94 ± 0.17	c,d
21	1.63 ± 0.12	d
24	1.38 ± 0.09	d
27	1.39 ± 0.10	d
30	1.24 ± 0.11	d
33	1.35 ± 0.11	d
36	1.54 ± 0.22	c,d
39	1.33 ± 0.10	d

Sapling growth

Pine sapling height increased more or less continuously and was statistically significantly during the first 24 months (Table 3). The average heights of 1-yr, 2-yr and 3-yr old pine saplings were 5 cm, 15 cm and 22 cm. Despite this seemingly rather low average value, maximum heights of pine saplings observed in September 1992 in sites A, B, C and D were 52, 72, 54 and 39 cm. As to the seasonal growth of the saplings, three periods are important, with up to 5 cm height increment: winter and spring 1990, spring 1991 and spring 1992. Virtually no growth was recorded during the three summer periods. A minimum was found in the winter of 1992, presumably due to the low temperatures. Both autumns

Table 3. *Pinus halepensis* sapling height and height increment, during March 1990 to September 1992. Lower-case letters indicate significant differences at $P < 0.05$ (Neuman-Keuls multiple range test, $n = 400$). Asterisks denote a statistically significant difference from 0 of the particular values (t-test, $P < 0.001$; NS: not significant).

Months after fire	Height ± SE (cm)	Season	Height increment (cm/month)
9	3.5 ± 0.0 a	Winter 1990	1.16 *
12	5.1 ± 0.1 b	Spring 1990	0.53 *
15	5.9 ± 0.1 c	Summer 1990	0.27 *
18	8.1 ± 0.1 d	Autumn 1990	0.73 *
21	9.5 ± 0.1 e	Winter 1991	0.48 *
24	14.5 ± 0.3 f	Spring 1991	1.65 *
27	14.9 ± 0.3 f	Summer 1991	0.14 NS
30	16.6 ± 0.3 g	Autumn 1991	0.56 *
33	15.9 ± 0.3 g	Winter 1992	− 0.22 NS
36	21.5 ± 0.7 h	Spring 1992	1.88 *
39	21.9 ± 0.4 h	Summer 1992	0.11 NS

showed intermediate values and may imply a secondary growing season.

The height distributions during the three post-fire years (Table 4) show a positive skewness (i.e. towards higher values) and the dispersion increases with time. The modal height class changes with time as follows:

0 - 5 cm in the first winter and spring	9 - 12 months;
5 - 10 cm in the summer-winter	15 - 21 months;
10 - 15 cm in the second growing period	24 - 33 months;
15 - 20 cm in the third growing period	36 - 39 months.

In this respect it is remarkable that even after three growing seasons a small fraction of extremely small saplings (5-10 cm) was still present.

In order to analyse the increase in height observed during the first post-fire summer (Table 3), the height distribution curves for the beginning and the end of the dry season were drawn (Fig. 2). It is evident, particularly from the graph of survival as a function of height (inset of Fig. 2), that taller seedlings survived much better than shorter ones. Therefore, the apparent height increase could be attributed to the elimination of small seedlings rather than to actual growth.

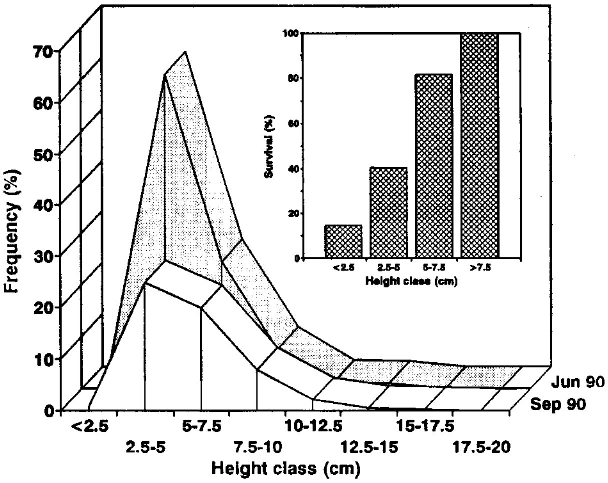

Fig. 2. Height distribution of *Pinus halepensis* saplings, 12 and 15 months after the fire. Height frequency histograms based on pooled data ($n = 400$ per date) from all four sites in 2.5-cm height classes. The histogram of the latter sampling date was proportionately reduced according to the overall mortality during the period 12 - 15 months. In the inset, sapling survival during the first post-fire summer plotted as a function of sapling height at the onset of the summer, 12 months after the fire. Bars based on pooled data ($n = 400$) from all sites.

Table 4. Height frequency distributions (%) of *Pinus halepensis* saplings ($n = 400$ for each date) in 5-cm classes, during a 3-yr postfire period.

Height (cm)	Months after fire 9	12	15	18	21	24	27	30	33	36	39
0 - 5	95	66	47	22	4	1	1	0	0	0	0
5 - 10	5	32	49	57	66	24	25	7	15	8	3
10 - 15	0	2	4	19	26	40	35	41	36	26	16
15 - 20	0	0	0	2	4	21	23	33	33	35	32
20 - 25				0	0	9	11	11	9	17	22
25 - 30						4	3	5	5	9	14
30 - 35						1	1	2	2	4	7
35 - 40						0	1	1	0	1	4
40 - 45							0	0		0	1
45 - 50											1

In order to further investigate the relationship between sapling height and survival, an indirect approach was adopted. As mentioned previously, dead seedlings were occasionally observed throughout the study period. Thus, both live and dead seedlings were measured at two sites; the corresponding height distributions are presented in Fig. 3. It is obvious from both graphs that the height of the survivors differs highly significantly from the height of the succumbers. This is also confirmed by two-sample t-tests between the corresponding means ($P < 0.001$).

Discussion

Floristics

The high number of species (80) appearing in the burned area during the first post-fire years agrees with data from the literature: 42 and 57 in southern France (Trabaud & Lepart 1980), 43 in northwest Algeria (Moravec 1990) and nearly 180 at a highly disturbed site on Mt. Carmel, Israel (Ne'eman et al. 1993). Although the population dynamics were not studied, the flora survey and assessment of frequency classes suggest that, apart from the growth of perennials, no major changes in vegetation and flora occurred during the first

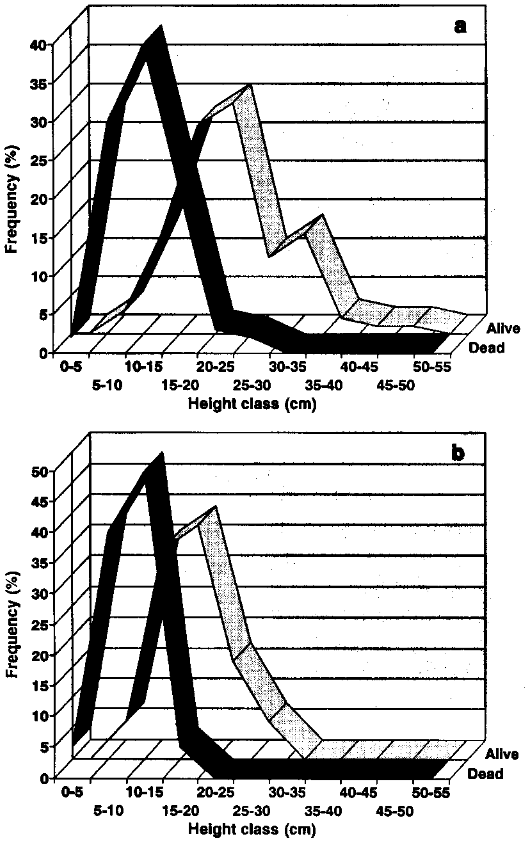

Fig. 3. Height distribution of *Pinus halepensis* saplings, 39 months after fire at sites A (a) and D (b). Along with a live saplings, height frequency ribbons are also presented for dead saplings (dried out during the previous 3-month period but still standing in their place). Means ± 1 SE of alive and dead saplings, respectively ($n = 100$): 22.6 ± 0.7 and 12.7 ± 0.4 cm (Site A); 17.2 ± 0.5 and 10.8 ± 0.3 cm (Site D).

three post-fire years. This is consistent with previous studies: the decline in post-fire floristic richness usually starts after the third year (e.g. Trabaud & Lepart 1980; Ne'eman et al. 1993).

Apart from *Pinus halepensis*, post-fire reseeders from the *Fabaceae* and *Cistaceae* are prominent, as found in many similar studies (e.g. Arianoutsou & Margaris 1981; Trabaud & Chanterac 1985; Thanos et al. 1989; Moravec 1990; Papavassiliou & Arianoutsou 1993). *Cistus*, *Fumana* and other *Cistaceae* (Thanos & Georghiou 1988; Thanos et al. 1992), most legumes (e.g. Doussi & Thanos 1993) and *Convolvulus elegantissimus* [related species being known from other post-fire communities: *C. cantabrica* (Trabaud & Chanterac 1985); *C. pentapetaloides* (Ne'eman et al. 1992)] all have a water-impermeable ('hard') seed coat which enable them to both survive a wildfire and select the post-fire environment for seed germination and seedling recruitment. Other reseeders are not hard-coated and colonize burned areas through either wind-dispersed propagules, e.g. several *Asteraceae*, or from seeds stored in the soil seed bank (e.g. *Anagallis arvensis*, *Euphorbia taurinensis*, *Fumaria officinalis*). Resprouters include the grass *Brachypodium retusum* (Trabaud & Chanterac 1985) in addition to maquis and phrygana shrubs.

Pine sapling density, survival and mortality

Pinus halepensis is an obligate reseeder and a typical Mediterranean tree species. A wildfire usually kills the entire pine population and regeneration of the species and the forest depends on the recruitment of a post-fire seedling cohort. A large fraction of pine seeds can survive the fire, protected by the scales of the closed, serotinous cones; moreover, as a result of heat, these cones open and disperse the enclosed seeds shortly after fire (Saracino & Leone 1993b; Daskalakou & Thanos 1994). Seed germination and seedling emergence takes place almost exclusively during the first post-fire wet season, especially from October to January, when massive establishment follows the start of the wet season. This has been observed in the field (Daskalakou & Thanos unpubl.) and elucidated in laboratory studies (Thanos & Skordilis 1987; Skordilis & Thanos 1995).

Initial field measurements took place in early spring (March), when pine seedling density is maximal. As a result of the drought that prevailed from February 1990, the whole cohort of pine seedlings must have already emerged by the end of March. As in other cases elsewhere in Attikí (Daskalakou & Thanos unpubl.), seedling density decreased moderately during late spring (down to 4 seedlings/m^2) and dropped considerably in the summer, to ca. 2.5 seedlings/m^2. In the second year the density decreased further, but stabilized at ca. 1.5 seedlings/m^2. Taking this value as a basis and assuming that no additional catastrophic events take place, a dense, mature pine forest with an approximate overall density in the order of > 1000 stems/ha may develop.

Previously reported post-fire densities of Aleppo pine seedlings and saplings range widely, apparently related to differences in (1) characteristics of the burned forest, (2) conditions prevailing during post-fire regeneration and (3) post-fire stages inspected. In southern France values equal to, or lower than, 0.1 seedlings/m^2 were measured (Trabaud et al. 1985), with the lowest value of only 0.07 seedlings/m^2 nearly one year after fire (Trabaud 1988). At a site in northwest Algeria, 0.2 seedlings/m^2 were observed 2 yr after a fire, compared with 15.8 in an adjacent protected belt (Moravec 1990). Similar ranges in density were reported from Italy (Táranto) (Saracino et al. 1993; Saracino & Leone 1993a) and on Mt. Carmel, Israel (Ne'eman et al. 1992, 1993), as well as for *Pinus brutia* on the Greek islands of

Thásos (Spanos 1992) and Sámos (Thanos et al. 1989; Thanos & Marcou 1991, 1993).

Several causes of seedling and sapling mortality in Mediterranean pines have been put forward: competition from other plants, attacks by insect and other animals, infection by fungi, as well as water and cold stress (Trabaud 1988), but summer drought is generally considered the prime cause. The present study confirmed that summer drought is decisive.

It has also been stated that the first post-fire summer is by far the most crucial period for the survival of seedlings in both *Pinus halepensis* and *P. brutia* (e.g. Thanos et al. 1989; Spanos 1992; Saracino et al. 1993; Daskalakou & Thanos 1994). Another important time is the first part of the rainy period immediately after the fire when germination and early seedling development and establishment take place; the importance of this critical period is often overlooked but it may eventually turn out to be of equal, or even greater impact on survival than the summer conditions.

The actual mortality values reported show a large variation, evidently resulting from the particular conditions prevailing during the early post-fire years. In a 5-yr study of the survival of pine saplings in different burned sites in southern France, mortality was found to be low: an accumulated total of only 11 % after 3 yr and 20 % after 5 yr (Trabaud 1988). Survival was considered stabilized in the 4th post-fire year, while in the present study stability was reached during the 2nd year.

On the other hand, in an Aleppo pine forest on dunes near Táranto (Italy), mortality was initially very high (an average of 65 % during the first post-fire establishment period, February-August), decreased during the following period (August-January) and increased again somewhat afterwards (Saracino et al. 1993). Similarly, on Mt. Carmel, Israel a high mortality (60 %) was observed between the first and second post-fire year (Ne'eman et al. 1993).

Relatively high rates of mortality have also been reported for burned East-Mediterranean *P. brutia* forests. However, despite the apparently large mortality values, the specific densities of seedlings and the eventual densities of saplings surviving until maturity usually lead to dense pine stands, as is the case in the present study. For instance, on Sámos, survival until the mature stage (10 yr after fire) was ca. 40 % (Thanos et al. 1989; Thanos & Marcou 1991, 1993). Similar results were reported by Neysci (1989) for *Pinus brutia* seedlings planted on clear-felled and subsequently burned pine forest in the province of Antalya (Turkey). On Thásos, the mortality of *P. brutia* seedlings during the first post-fire summer was between 18 % and 36 %, depending on the exposure of the site; here, mortality was attributed mainly to goat grazing while the effect of drought was restricted to between 1.5 % and 4.4 % (Spanos 1992).

From the post-fire trend of pine seedling mortality (Fig. 1a) we conclude that one out of five saplings registered in peak density (March 1990) was still thriving after three growth seasons. A similar mortality curve was found for *P. brutia* seedlings on Sámos: a large fraction of the seedlings perished during the first post-fire summer while overall survival gradually levelled off to 40 % after 2 - 3 yr (Thanos & Marcou 1991).

Sapling growth

The development of *Pinus halepensis* seedlings and the subsequent height growth of the saplings proceeds regularly during the first post-fire year, followed by an arrest of growth in the second winter and a resumption of the growth early in the next spring. Parallel field measurements of seedling heights in several burned Attikí forests showed a similar development, leading to an average height of 10 cm by the end of the first summer and of 16 - 18 cm by the end of the second summer (Daskalakou & Thanos unpubl.). These results are in general agreement with those obtained in southern France; mean increase in height in *Pinus halepensis* here was 10 cm/yr during the first 10 yr, while between 10 and 30 yr of age, growth was much more rapid, up to 40 cm/yr (Trabaud et al. 1985). In another, 5-yr long study near Montpellier, the average heights in the 1st, 2nd and 3rd June after a fire were 4.9, 12.3 and 23.4 cm (Trabaud 1988), which compares well with our values: 5.0, 14.5 and 18.4 cm. Aleppo pine seedlings in the burned forest of Mt. Carmel had reached an average height of 10 cm after 1 yr (Ne'eman et al. 1993). Similarly, in Táranto, mean seedling heights were ca. 6 and 14 cm in the first and second summer (Saracino et al. 1993). In the burned Aleppo pine forests of northwest Algeria, the average height after 2 yr was only 10 cm, against 23 cm in the adjacent protection belt (Moravec 1990). The slow growth reported for the dune forest of Táranto may be related to the nutrient-poor conditions there (Saracino & Leone 1993a).

Pinus brutia saplings, although often considered to grow more slowly (e.g. Panetsos 1981), have been found to grow at comparable rates. During the first 10 yr after a fire on Sámos the yearly increment was nearly 10 cm (Thanos et al. 1989; Thanos & Marcou 1991, 1993). Similar average height values were also reported from the province of Antalya (Neysci 1989) and on Thásos (Spanos 1992).

On Mount Párnis, a considerable fraction of very short saplings were still alive 39 months after a fire: 3.3 % belonged to the 5 - 10 cm class while another 16.5 % were 10 - 15 cm high (Table 4). These short saplings may form a sapling bank that may start growing actively when the particular restraints imposed (e.g. by neighbouring vegetation or soil nutrient shortage) will have been eliminated. Such a sapling bank of *P. brutia* was reported from regenerating forests on Sámos (Thanos & Marcou 1991, 1993).

In this connection it may be mentioned that a large proportion of 3-yr old *P. halepensis* saplings (and particularly most of the shorter ones) had not yet formed secondary needles, this in contrast to the situation with saplings grown in the nursery (Panetsos 1981). Moreover, not even one first-year conelet (out of many thousands of saplings) had been formed.

The growth pattern of *P. halepensis* saplings has been designated as 'monocyclic with a variable number of summer shoots' (Calamassi et al. 1988). According to measurements on young and adult Aleppo pine trees near Marseille (France), apical growth may occur in 1 to 4 cycles (or phases) during a single vegetation season. The first phase is generally the most important and takes place in April and particularly in May; the other phases, if they exist, take place in June and July and the overall growth may extend until September (Serre-Bachet 1992). Nevertheless, under the influence of the much drier climate of Attikí, the growth season for pine seedlings coincides with the spring months (starting from as early as January and extending until late June); however the possibility of a minor growth spurt in autumn should not be entirely excluded.

Finally, it was shown that taller saplings survived significantly better than shorter ones. Therefore, the apparent height increase could be ascribed to the elimination of small saplings rather than to actual growth.

Acknowledgements. This work was partially supported by the General Secretariat of Research and Technology, Greece (grant PENED 91/824) and the European Union: Environment Research Programme (contract EV5V-CT94-0482, project PROMETHEUS). We thank K. Georghiou, M. Arianoutsou, A. Skordilis, K.C. Kadis, M.A. Doussi, P. Delipetrou and G.-A. Tsabassi for help with field measurements.

References

Anon. 1976-1992. *Monthly Climatological Bulletins*. National Meteorological Service of Greece (EMY), Athens. (In Greek.)

Anon. 1985. *Soil Map of Greece. Land Resource map: Athinai-Elevsis.* Ministry of Agriculture, Athens.

Andreakos, K. 1978. *Climatic data of the Greek network*. Nat. Meteorological Service of Greece, Athens. (In Greek.)

Arianoutsou, M. & Margaris, N.S. 1981. Early stages of regeneration after fire in a phryganic ecosystem (east Mediterranean) I. Regeneration by seed germination. *Biol. Ecol. Medit.* 8: 119-128.

Calamassi, R., Falusi, M. & Principe, M. 1988. Relations between apical structure and growth patterns in *Pinus halepensis* Mill. seedlings. *Giorn. Bot. Ital.* 122: 321-338.

Daskalakou, E.N. & Thanos, C.A. 1994. Aleppo pine (*Pinus halepensis*) post-fire regeneration: the role of canopy and soil seed banks. In: Viegas, D.X. (ed.) *Proc. 2nd Int. Conference on Forest Fire Research, Vol. II*, pp. 1079-1088. Coimbra.

Doussi, M.A. & Thanos, C.A. 1993. The ecophysiology of fire-induced germination in hard-seeded plants. In: Côme, D. & Corbineau, F. (eds.) *Fourth International Workshop on Seeds. Basic and Applied Aspects of Seed Biology, Angers, France, 20-24 July, 1992, Vol. 2*, pp. 455-460. ASFIS, Paris.

Garcia-Plé, C., Vanrell, P. & Morey, M. 1995. Litter fall and decomposition in a *Pinus halepensis* forest on Mallorca. *J. Veg. Sci.* 6: 17-22.

Greuter, W., Burdet, H.M. & Long, G. (eds.) 1984-1989. *Med-Checklist. Vols. 1, 3 & 4.* Conservatoire Jardin botaniques, Genève.

Johnson, E.A. & Gutsell, S.L. 1993. Heat budget and fire behaviour associated with the opening of serotinous cones in two *Pinus* species. *J. Veg. Sci.* 4: 745-750.

Moravec, J. 1990. Regeneration of N.W. African *Pinus halepensis* forests following fire. *Vegetatio* 87: 29-36.

Ne'eman, G., Lahav, H. & Izhaki, I. 1992. Spatial pattern of seedlings one year after fire in a Mediterranean pine forest. *Oecologia (Berl.)* 91: 365-370.

Ne'eman, G., Lahav, H. & Izhaki, I. 1993. The resilience of vegetation to fire in an East-Mediterranean pine forest on Mount Carmel, Israel: the effect of post-fire management. In: Trabaud, L. & Prodon, R. (eds.) *Fire in Mediterranean Ecosystems*, pp. 127-140. European Commision, Brussels.

Neysci, T. 1989. *Effects of prescribed burning on soil chemical properties and subsequent growth in Pinus brutia Ten. ecosystems.* Tech. Bull. 205, Turkish Forest Research Institute. Ankara. (In Turkish.)

Panetsos, C.P. 1981. Monograph of *Pinus halepensis* (Mill.) and *P. brutia* (Ten.). *Ann. For. (Zagreb)* 9: 39-77.

Papavassiliou, S. & Arianoutsou, M. 1993. Regeneration of the leguminous herbaceous vegetation following fire in a *Pinus halepensis* forest of Attica, Greece. In: Trabaud, L. & Prodon, R. (eds.) *Fire in Mediterranean Ecosystems*, pp. 119-125. European Commision, Brussels.

Quézel, P. & Barbero, M. 1992. Le pin d' Alep et les espèces voisines: répartition et charactères écologiques généraux, sa dynamique récente en France méditerranéenne. *Forêt Médit.* 13: 158-170.

Saracino, A. & Leone, V. 1993a. Natural regeneration 2 and 4 years after fire of *Pinus halepensis* Miller in dunal environment. In: Trabaud, L. & Prodon, R. (eds.) *Fire in Mediterranean Ecosystems*, pp. 141-150. European Commission, Brussels.

Saracino, A. & Leone, V. 1993b. Ecological features and dynamics of seed dispersal after fire in a *Pinus halepensis* Miller forest. In: Trabaud, L. & Prodon, R. (eds.) *Fire in Mediterranean Ecosystems*, pp. 151-159. European Commission, Brussels.

Saracino, A. & Leone, V. 1994. The ecological role of fire in Aleppo pine forests: overview of recent research. In:

Viegas, D.X. (ed.) *Proc. 2nd Int. Conference on Forest Fire Research, Vol. II*, pp. 887-897. Coimbra.

Saracino, A., Leone, V. & De Natale, F. 1993. Permanent plots for the study of natural regeneration after fire of *Pinus halepensis* Miller in dunal environment. *Ann. Bot. (Roma)* 51: 209-217.

Serre-Bachet, F. 1992. Les enseignements écologiques de la variation de l'epaisseur du cerne chez le pin d' Alep. *Forêt Médit.* 13: 171-176.

Skordilis, A. & Thanos, C.A. 1995. Seed stratification and germination strategy in the Mediterranean pines *Pinus brutia* and *P. halepensis*. *Seed Sci. Res.* 5: 151-160.

Spanos, Y.A. 1992. *Structure analysis and regeneration of brutia pine in Thasos Island.* Ph.D. Thesis, University of Thessaloniki, Thessaloniki. (In Greek.)

Thanos, C.A. & Georghiou, K. 1988. Ecophysiology of fire-stimulated seed germination in *Cistus incanus* ssp. *creticus* (L.) Heywood and *C. salvifolius* L. *Plant, Cell Environ.* 11: 841-849.

Thanos, C.A. & Marcou, S. 1991. Post-fire regeneration in *Pinus brutia* forest ecosystems of Samos island (Greece): 6 years after. *Acta Oecol. Oecol. Plant.* 12: 633-642.

Thanos, C.A. & Marcou, S. 1993. Natural regeneration of *Pinus brutia* forests in Samos island. Key events during the first 10 years of the post-fire period. In: Ministry of Forestry, Turkey (ed.) *Papers of International Symposium on Pinus brutia Ten., Marmaris, October 18-23, 1993*, pp. 176-183. Ministry of Forestry, Ankara.

Thanos, C.A. & 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, C.A., Georghiou, K., Kadis, C. & Pantazi, C. 1992. Cistaceae: a plant family with hard seeds. *Isr. J. Bot.* 41: 251-263.

Thanos, C.A., 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. 1988. Survie de jeunes plantules de pin d'Alep apparues après incendie. *Stud. Oecol.* 5: 161-170.

Trabaud, L. & Lepart, J. 1980. Diversity and stability in garrigue ecosystems after fire. *Vegetatio* 43: 49-57.

Trabaud, L. & de Chanterac, B. 1985. The influence of fire on the phenological behaviour of Mediterranean plant species in Bas-Languedoc (S France). *Vegetatio* 60: 119-130.

Trabaud, L., Grosman, J. & Walter, T. 1985. Recovery of burnt *Pinus halepensis* Mill. forests. I. Understorey and litter phytomass development after wildfire. *For. Ecol. Manage.* 12: 269-277.

Tutin, T.G., Heywood, V.H., Burges, N.A., Valentine, D.H., Walters, S.M. & Webb, D.A. (eds.) 1964-1980. *Flora Europaea, Vols. 1-5*. Cambridge Univ. Press, Cambridge.

Zar, J.H. 1974. *Biostatistical Analysis.* Prentice-Hall, Englewood Cliffs, NJ.

Received 3 May 1995;
Revision received 28 July 1995;
Accepted 12 October 1995.

App. 1. Species found in the burned pine forest of Párnis (four sites), during the 3-yr post-fire period. A/B/P = Life form: Annual/Biennial/Perennial; F = Frequency: Dominant (D), Common (C), Occasional (O), Rare (R); S/V = Seeder/Vegetative resprouter; - = not determined.

Species	Family	A/B/P	F	S/V
Pinus halepensis	*Pinaceae*	P	D	S
Quercus coccifera	*Fagaceae*	P	C	V
Aristolochia microstoma	*Aristolochiaceae*	P	R	V
Arenaria serpyllifolia	*Caryophyllaceae*	A	C	S
Cerastium illyricum	*Caryophyllaceae*	A	O	S
Silene vittata	*Caryophyllaceae*	A	R	S
Aethionema saxatile	*Brassicaceae*	A/P	C	S
Alyssum spec.	*Brassicaceae*	A	O	S
Clypeola jonthlaspi	*Brassicaceae*	A	C	S
Erophila verna	*Brassicaceae*	A	O	S
Hornungia petraea	*Brassicaceae*	A	O	S
Malcolmia graeca ssp. *bicolor*	*Brassicaceae*	A	D	S
Erica manipuliflora	*Ericaceae*	P	R	V
Anthyllis hermanniae	*Fabaceae*	P	C	V/S
A. vulneraria	*Fabaceae*	A	C	S
Bituminaria bituminosa	*Fabaceae*	P	R	S/V
Cercis siliquastrum	*Fabaceae*	P	R	V
Coronilla scorpioides	*Fabaceae*	A	R	S
Coronilla spec.	*Fabaceae*	A	R	S
Hippocrepis ciliata	*Fabaceae*	A	C	S
Lotus ornithopodioides	*Fabaceae*	A	R	S
Medicago spec.	*Fabaceae*	A	R	S
Ononis reclinata	*Fabaceae*	A	O	S
Trifolium campestre	*Fabaceae*	A	O	S
Euphorbia taurinensis	*Euphorbiaceae*	A	D	S
Ruta graveolens	*Rutaceae*	P	C	V
Pistacia lentiscus	*Anacardiaceae*	P	C	V
P.terebinthus	*Anacardiaceae*	P	C	V
Thymelaea tartonraira	*Thymelaeaceae*	P	O	V
Hypericum empetrifolium	*Hypericaceae*	P	C	V
Cistus creticus	*Cistaceae*	P	D	S
C.salviifolius	*Cistaceae*	P	D	S
Fumana thymifolia	*Cistaceae*	P	D	S
Helianthemum syriacum	*Cistaceae*	P	R	S/V
Tuberaria guttata	*Cistaceae*	A	R	S
Daucus involucratus	*Apiaceae*	B	C	S
Anagallis arvensis	*Primulaceae*	A	C	S
Cyclamen graecum	*Primulaceae*	P	C	V
Asterolinon linumstellatum	*Primulaceae*	A	D	S
Olea europaea ssp. *oleaster*	*Oleaceae*	P	O	V
Convolvulus elegantissimus	*Convolvulaceae*	P	D	S
Ballota acetabulosa	*Lamiaceae*	P	R	V
Coridothymus capitatus	*Lamiaceae*	P	O	V
Micromeria spec.	*Lamiaceae*	P	O	V
Phlomis fruticosa	*Lamiaceae*	P	O	V/S
Satureja thymbra	*Lamiaceae*	P	O	V
Stachys spruneri	*Lamiaceae*	P	O	V
Teucrium divaricatum	*Lamiaceae*	P	O	V
T. polium	*Lamiaceae*	P	O	V
Scrophularia spec.	*Scrophulariaceae*	-	C	-
Orobanche spec.	*Orobanchaceae*	-	R	-
Fumaria officinalis	*Papaveraceae*	A	C	S
Crucianella spec.	*Rubiaceae*	A	C	S
Valantia muralis	*Rubiaceae*	A	C	S
Lomelosia brachiata	*Dipsacaceae*	A	O	S
Anthemis chia	*Asteraceae*	A	R	S
Centaurea orphanidea	*Asteraceae*	B	R	V
C. raphanina	*Asteraceae*	P	O	V
Crepis neglecta	*Asteraceae*	A	O	S
Crupina crupinastrum	*Asteraceae*	A	O	S
Helichrysum stoechas	*Asteraceae*	P	O	V
Leontodon tuberosus	*Asteraceae*	P	O	V
Phagnalon graecum	*Asteraceae*	P	O	V
Senecio spec.	*Asteraceae*	A	O	S
Allium (2 spp.)	*Liliaceae*	P	C	V
Asparagus aphyllus	*Liliaceae*	P	C	V
Asphodelus aestivus	*Liliaceae*	P	C	V
Gagea reticulata	*Liliaceae*	P	R	V
Muscari commutatum	*Liliaceae*	P	C	V
M.comosum	*Liliaceae*	P	C	V
M.neglectum	*Liliaceae*	P	C	V
Urginea maritima	*Liliaceae*	P	C	V
Crocus laevigatus	*Iridaceae*	P	C	V
Romulea linaresii	*Iridaceae*	P	R	V
Carex spec.	*Cyperaceae*	P	O	V
Brachypodium retusum	*Poaceae*	P	D	V
Briza minor	*Poaceae*	A	O	S
Lagurus ovatus	*Poaceae*	A	O	S
Ophrys spec.	*Orchidaceae*	P	R	V