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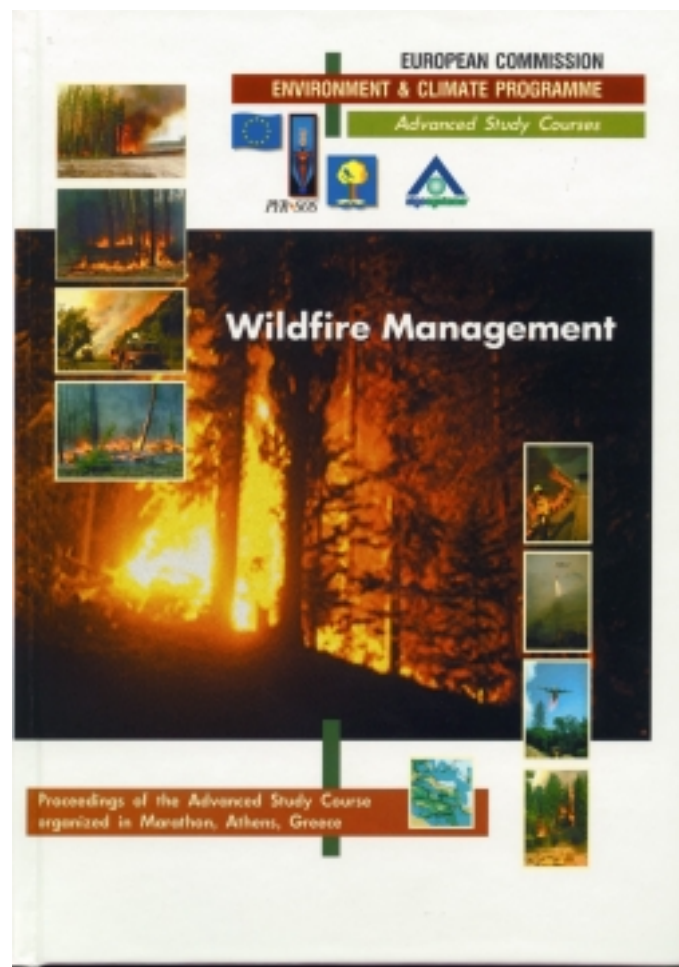
FIRE EFFECTS ON FOREST VEGETATION,

THE CASE OF MEDITERRANEAN PINE FORESTS IN GREECE

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Abstract

Postfire regeneration in Mediterranean pine forests is secured through resprouting and reseeding. Obligate reseeders include Mediterranean pines, rockroses (several Cistus *spp. and other members of the Cistaceae) as well as numerous herbaceous plants (mostly legumes). Seeds are safeguarded by the fire heat in either canopy stores (pines) or long-lived soil banks (rockroses and legumes). Induction of seed germination by fire occurs through: i. pine cone opening (and subsequent dispersal) and ii. seed coat "softening" in the hardseeded plants. Hereafter, seeds are more or less ready to germinate and, consequently, seedling recruitment takes place during the early part of the first postfire wet season. Facultative reseeders (usually species with softcoated seeds) are present as well, in addition to "outsiders" (e.g. several composites) that colonise the burned areas through their anemochorous seeds. Seedling recruitment is also observed during the second postfire year, presumably as the result of an abundant first-year reproduction, particularly in geophytes as well as legumes. Pine seed germination and seedling emergence occur massively in a, usually, single "wave", immediately after the onset of the first postfire rainy period (i.e. during November-January). Moreover, the first postfire summer is by far the most crucial period for the survival of these seedlings (and those of other perennial species).*

Keywords: Regeneration, soil seed banks, canopy seed banks, cone opening, seed dispersal, hardseededness, seed germination, nitrates, seedling establishment, seedling survival and mortality, growth, reproduction, postfire resilience, Mediterranean pines, Cistaceae, Leguminosae.

Introduction

Fire has apparently acted as a powerful ecological factor in the evolution of the Mediterranean flora as well as in shaping the Mediterranean landscapes into their present, mosaic-like patterns with diverse levels of regeneration and degradation (Le Houerou 1987; Naveh 1991). Fire resilience of Mediterranean-type ecosystems (MTE) is generally well documented; thus most of these ecosystems can

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regenerate naturally after a fire, provided that no secondary destructive disturbances (such as additional fires or grazing) will be applied (e.g. Trabaud, Grosman and Walter 1985; Thanos, Marcou, Christodoulakis and Yannitsaros 1989; Moravec 1990; Thanos and Marcou 1991; Ne'eman, Lahav and Izhaki 1993; Saracino and Leone 1993a; Saracino, Leone and Natale 1993; Thanos and Marcou 1993).

Plant species of MTEs display homeostatic responses towards fire so that in relatively short periods, following a fire, the ecosystem equilibrium is restored and the burned ecosystem cannot be distinguished from the unburned (Trabaud 1987). Recovery of plant species is accomplished by two main mechanisms: a) stimulation of seed germination by fire [through either a scarification effect on the water-impermeable seed coats by high temperatures (e.g. Thanos, Georghiou, Kadis and Pantazi 1992), the inactivation of inhibitors, the change of R/FR ratio of the light reaching the soil (e.g. Thanos and Skordilis 1987) and the promoting action of chemicals] and b) vegetative resprouting of burned plants from intact buds surviving in the crown. The present work concentrates exclusively on postfire regeneration from seed, in the Mediterranean pine forests of Greece.

Postfire seed germination

Hardseeded rockroses and legumes

Hardseededness has been described for many fire-following plant species, including legumes (Doussi and Thanos 1993; Doussi and Thanos 1994; Arianoutsou and Thanos 1996) and rockroses (Thanos and Georghiou 1988; Thanos, Georghiou, Kadis and Pantazi 1992). Most of these species produce seeds with a hard, water-impermeable seed coat, that not only permits the survival of the seed during a wildfire but also requires the high temperatures developed by fire for germination induction. In the absence of fire, either the entirety or a fraction of a seed pool remains dormant, as is the case with the entire family of Cistaceae (Figure 1).
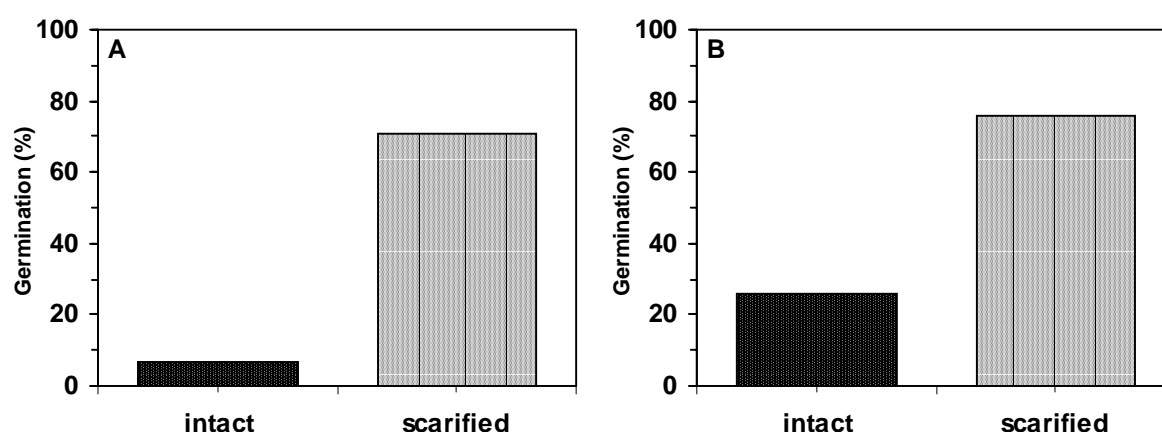

Figure 1   Germinability of intact and scarified seeds of Cistaceae. Pooled germinability for 204 seed lots from 55 taxa is illustrated after 1 week after the onset of imbibition (A) or after 4-6 weeks (B, final germination), at 15 °C and darkness throughout. Scarification of seeds was accomplished with sandpaper. (The graph is based on data presented in Thanos et al 1988).

Most of these species have locally dispersed seeds that persist in the soil seed bank until the site is burned; thus in these taxa opportunities for population expansion are generally restricted to postfire conditions. By monitoring the responses of seeds to several heating durations it has been showed that any given seed population is, to a certain degree, heterogeneous in its 'hardcoatedness parameter'. This is considered a significant ecological advantage since germination can, more or less, be manifested after a wide range of fire regimes (Thanos and Georghiou 1988). Thus, the 'window' of germinability can be shifted according to the fire conditions but, in every case, a portion of the seed population will be induced to germinate (Figure 2). Moreover, when thermally pretreated seeds are germinated under various constant temperatures and light regimes, a lack of temperature- and light-mediated control of germination is exhibited (Thanos and Georghiou 1988; Doussi and Thanos 1993).
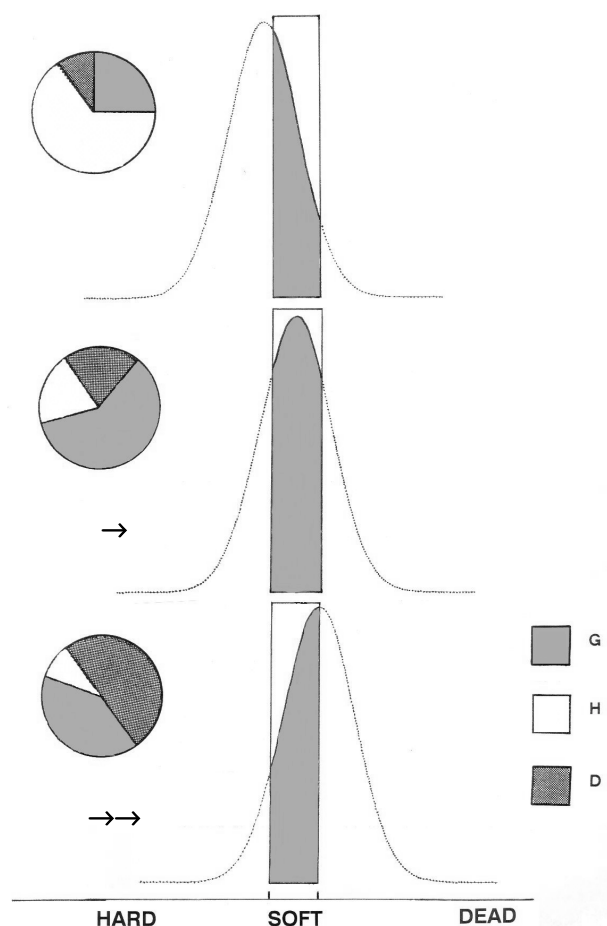

Figure 2   Continuum of hardseededness and 'window' of germinability in *Cistus* seeds. The pies at the left part illustrate the seed population portions of *Cistus creticus*: H - hard; G - germinable (softcoated); D - dead. The three pies (data from Thanos and Georghiou 1988) correspond to untreated (upper chart) and to preheated for 15-30 and 75-90 min at 100 °C (middle and lower chart, respectively).

Composites and weeds

A particular characteristic that allows plant species to exploit newly disturbed sites is the production of large numbers of seeds which may be dispersed to long distances. Apparent adaptations that would allow long-distance dispersal, i.e. small, light seeds with structures such as a pappus, are certainly prominent among pioneers in newly burned sites. In the Mediterranean ecosystems, several annuals may appear in large numbers during the first year after fire; these annuals are apparently opportunistic invaders and are not stimulated by fire *per se*. It has been proposed that the long-term presence of disturbed habitats around the Mediterranean produced pioneer, weedy genotypes that became highly successful invaders.

Helichrysum stoechas ssp. *barrelieri* and *Dittrichia viscosa* are short, composite perennials inhabiting typical Mediterranean ecosystems. Their seeds exhibited a partial and a deep dormancy, respectively (Figure 3, Doussi and Thanos 1997). In the former species, the presence of nitrates resulted in a dramatic enhancement of germinability. The curve of seed germination induction as a function of nitrate concentration (Figure 3A) is similar to that observed in numerous other cases (e.g. in the chaparral fire annual *Emmenanthe penduliflora*; Thanos and Rundel, 1995). It is postulated that a dormancy relief mechanism triggered by an appropriate level of nitrates can serve as a competition-avoiding, gap detector under postfire conditions. In the latter species, the small, deeply dormant seeds of *Dittrichia* were clearly light-requiring. Even a few short exposures to a dim, green safelight strongly promoted germination, suggesting a very low threshold level of photosensitivity and emphasizing the role of light as the principal agent of germination induction (Figure 3B).
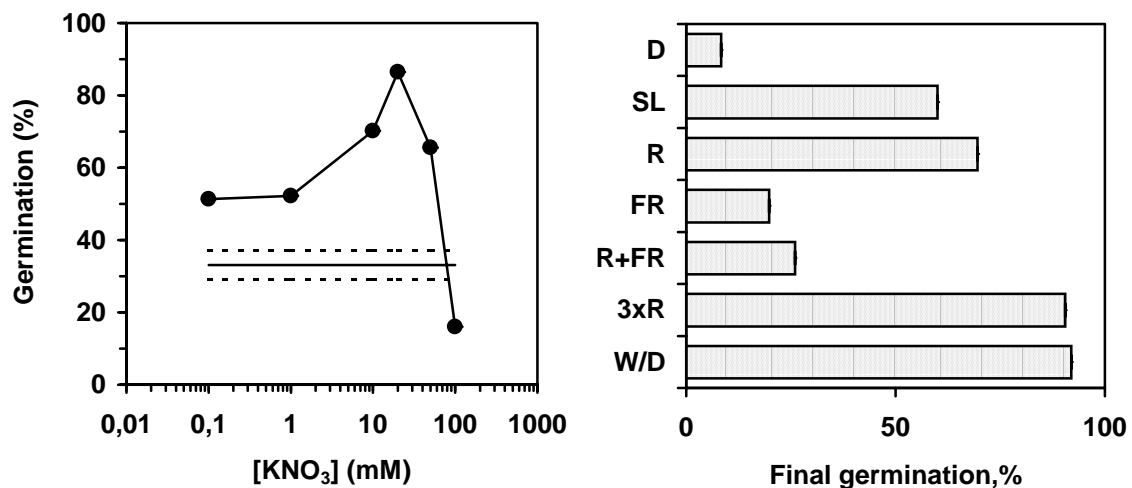

Figure 3   Final germination of *Helichrysum stoechas* ssp. *barrelieri* (A) and *Dittrichia viscosa* (B) seeds, at 20 °C, as a function of potassium nitrate concentration and light regime, respectively. The horizontal line in A represents final germination in water (stippled lines: ± SE); vertical lines are ± s.e. and all experiments were carried out in continuous darkness. Light pulses of Red (R) and Far Red (FR) light were given (B) 1 day after onset of imbibition. (After Doussi and Thanos 1997).

Mediterranean pines

Aleppo and East Mediterranean (or brutian) pine (*Pinus halepensis* and *P. brutia*, respectively) are the two common pines in the eastern Mediterranean rim. Both species do not resprout at all (obligate reseeders) and a typical Mediterranean wildfire usually kills the entire pine population. Therefore, the regeneration of the species, and of the forest as well, is totally dependent upon the recruitment of a postfire cohort of seedlings; and this is indeed what usually happens as a result of prolific seed germination from serotinous cones that burst open in the heat of the fire. Since fire provides an ideal opportunity for their natural regeneration, postfire recruitment strategies in pines are, obviously, of paramount importance for the regeneration of a burned forest. 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 and Leone 1993b; Daskalakou and Thanos 1996).

Cone opening and seed dispersal were investigated in unburned forests of Attica (Greece) and it was found (Daskalakou and Thanos 1996) that *Pinus halepensis* trees maintain a significant percentage of the yearly cone crop (40-80%) closed, thus creating a persistent, canopy seed bank (Figure 4). Full viability of the enclosed seeds was maintained for at least 3 years in canopy storage. For this significant delay in the opening of mature cones a new term has been coined (instead of serotiny): "bradychory", i.e. delayed dispersal, on the basis that seed dispersal is considered the central event. Furthermore, it is noteworthy that cone opening takes place almost exclusively during the first post-maturation summer (and more specifically during the first part of the dry season) while the majority of the cones that remain closed will presumably be induced to open by fire. In *P. brutia*, cone serotiny has not been studied in a detailed way but it is generally believed that this species is considerably less serotinous, on the average, than Aleppo pine.
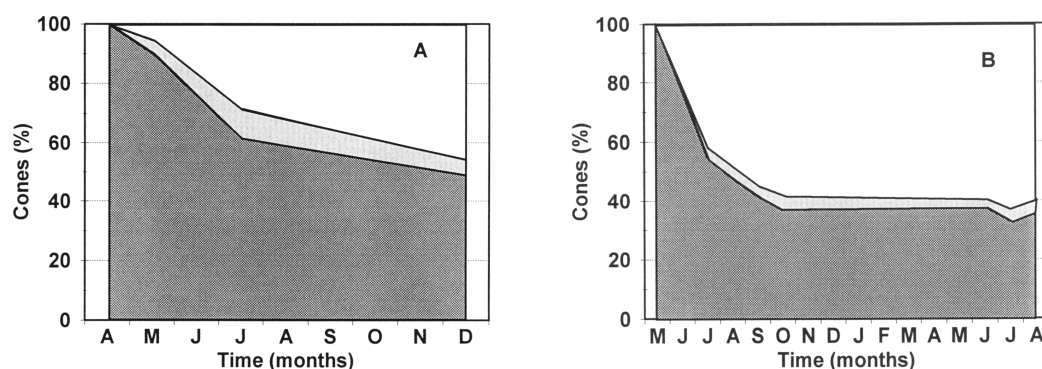

Figure 4   Time course of cone opening on *Pinus halepensis* trees, in two regions of Attica (A: Stamata, B: Ilioupolis). Throughout the observation periods (April 1994 - December 1994 and May 1992 - August 1993, respectively) the same (100 in A and 200 in B), freshly-matured (spring 1994 and spring 1992, respectively) cones were inspected each time (on ten and seven marked trees, respectively). Dark, grey and white areas represent closed, half-opened and fully opened cones, respectively. (After Daskalakou and Thanos 1996).

Optimal temperatures for seed germination of both pine species have been found to be between 20 and 15 °C; this range of temperatures is usually prevailing during the first part of the rainy season in the Mediterranean climate (Thanos and Skordilis 1987; Skordilis and Thanos 1995). White light irradiation results in a marked promotion of germination, while intense Far-Red light (simulating a dense canopy cover) causes a significant inhibition (Figure 5, Daskalakou and Thanos 1996), in agreement with previous similar results (Thanos and Skordilis 1987).
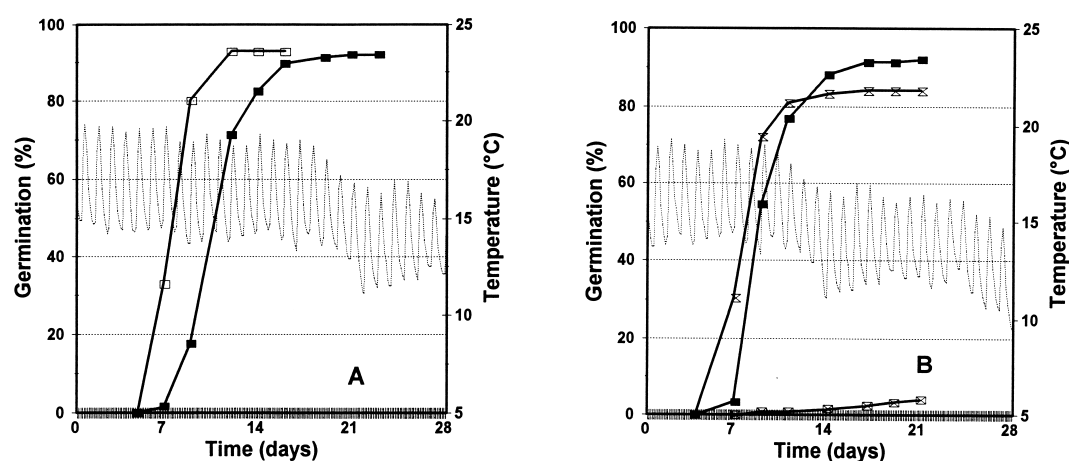

Figure 5   Time course of *Pinus halepensis* seed germination in simulated autumn conditions under different light regimes. A: diurnally alternating white light - darkness (□) and continuous darkness (■); B: diurnally alternating Far-Red (FR) - darkness ("intense", FR_I: ⊠, "mild", FR_{II}: ✕) and continuous darkness (■). The fluctuating lines represent the daily temperature alterations, which simulate the average conditions at Athens Airport; time 0 corresponds to November 1 (A) and November 8 (B), respectively. The seeds used were extracted from freshly-matured cones (0 years old), collected from the forest of Villia. (After Daskalakou and Thanos 1996).

Seedling establishment, survival and growth

Pine seed germination and seedling emergence takes place almost exclusively during the first postfire wet season (Figure 6); more specifically, its occurrence usually takes the form of a massive wave early in the period (October-January), closely following the start of the wet season, as shown by both field (Daskalakou and Thanos 1997) and laboratory works (Thanos and Skordilis 1987; Skordilis and Thanos 1995). During the second postfire rainy period no additional seedlings are usually observed. In *Pinus brutia*, preliminary results show that this pattern may be modified in certain regions with more severe winters: the seedling recruitment profile is shifted to the late winter or early spring months, possibly as a frost-avoiding mechanism of the vulnerable seedlings (Skordilis and Thanos 1995).

Maximum density of pine saplings is usually observed during the first postfire spring and may amount to an average of several seedlings m^{-2}. Despite the variability among sites and burned areas, the overall trend displayed a gradual decrease of pine sapling density during the first two postfire years. A more or less stabilised average density of around 1-2 saplings m^{-2} is reached at year 2-3 and onwards. By using regression analysis, a nicely fitted, negative exponential curve - with an assumed asymptotic level set at 20% - is obtained (Fig. 7b). Similar exponential kinetics has been obtained with *P. brutia* postfire survival in Samos Island (Thanos and Marcou 1991, 1993).
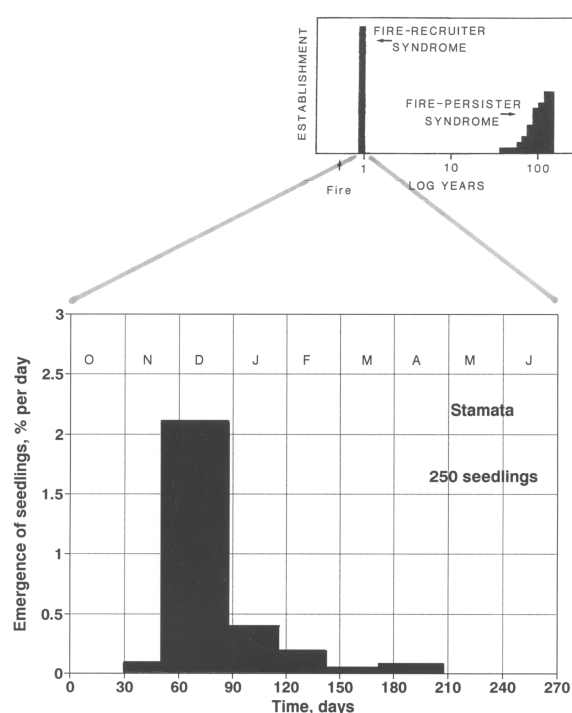

Figure 6   The temporal pattern of pine seedling emergence in a *Pinus halepensis* forest of Attica (Stamata), during the first postfire year (time 0 is set at October 1). (After Daskalakou and Thanos 1997; the upper inset graph after Keeley 1991).

Concerning seasonal analysis of mortality, the case of Mt Parnes is illustrative (Figure 7a). The overall average mortality was highest during the first postfire summer - nearly 2 seedlings m^{-2} perishing during the period June-September 1990, the second highest being during the first postfire spring (March-June 1990). Subsequent mortality was considerably lower than during the early establishment period (March-September 1990) and amounted to only 25% of the total death toll during the first two postfire years (March 1990 - September 1991). Although dead pine saplings were occasionally found from spring 1991 onwards, the measurements at subsequent dates could not reveal any significant mortality events.

It has been found, in several occasions, that the first postfire summer is by far the most crucial period for the survival of seedlings in both Aleppo and East Mediterranean pines (e.g. Thanos, Marcou, Christodoulakis and Yannitsaros 1989; Saracino, Leone and Natale 1993; Daskalakou and Thanos 1997). Another decisive season 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 usually overlooked but it may eventually turn out to be of equal or even greater impact on survival than summer.
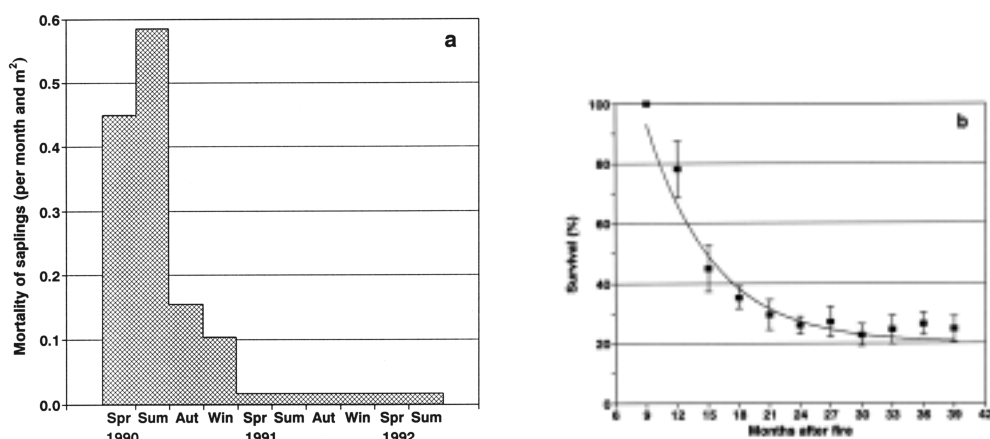

Figure 7   Aleppo pine sapling mortality (a) and survival (b) determined every three months during the period March 1990 (9 months after fire) to September 1992 (39 months after fire). In graph **b**, vertical lines represent 2 SE (*n*=4); the plotted curve was obtained through regression analysis and is described by the formula $Y = 73.145\ e^{-0.154(X-9)} + 20$ (d.f.=6, r=0.978, *P*<0.001), where *Y* is survival, in %, and *X* is time after fire, in months. (After Thanos et al. 1996)
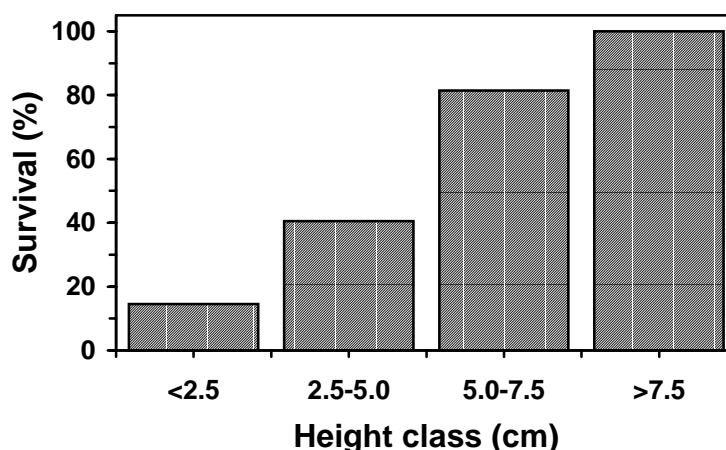

Figure 8   Survival of Aleppo pine saplings during the first postfire summer. The graph refers to the period 12 to 15 months after fire in Mt. Parnes (i.e. before and after the first postfire summer) and is plotted as a function of sapling height (at the onset of summer) in 2.5 cm height classes (*n*=400). (After Thanos et al. 1996).

Several causes of mortality for seedlings and saplings of Mediterranean pines have already been cited in general: competition by other plants, predation by insects and other animals, infection by fungi, as well as water and cold stress (Trabaud 1988). Nevertheless and despite the lack of solid and causal evidence, it is almost unanimously assumed that the most prominent reason of mortality is summer drought; almost all non-surviving seedlings are usually found dried but intact (e.g. Thanos, Daskalakou and Nikolaidou 1996). By using the height distribution curves for the beginning and the end of the first postfire summer it is revealed that taller seedlings survived significantly better than shorter ones (Figure 8). Another interesting feature is the discovery of numerous, very short *P. halepensis* and *P. brutia* saplings, 3 and 6 years after fire, respectively (Thanos, Daskalakou and Nikolaidou 1996; Thanos and Marcou 1991); this finding leads to the postulate that a pine sapling bank may be formed during the early post fire recovery stage. Since pine seed supply during this stage is absent or scarce, a pine sapling bank may be proven an important or indispensable adaptive strategy for the regeneration of burnt Mediterranean forests.
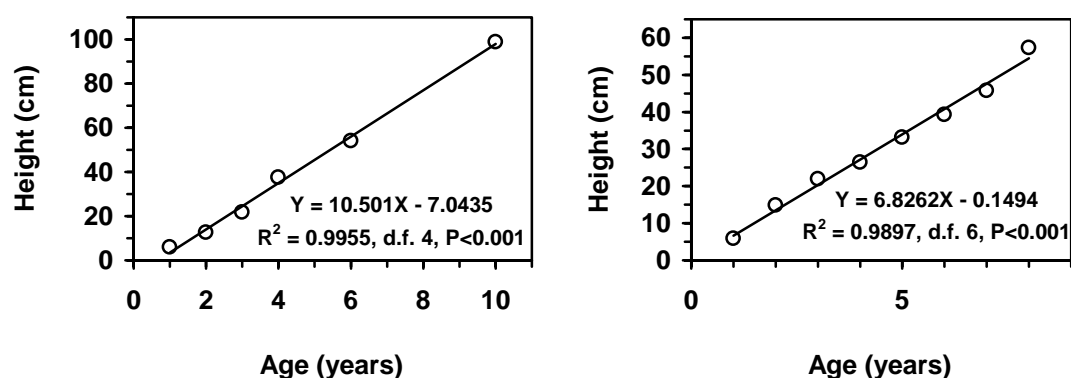

Figure 9 Early postfire, annual growth of pine sapling in Samos island (left and Mt. Parnes (right). Annual heights of *Pinus brutia* (A) and *P. halepensis* (B) were obtained after the end of the respective growth period. (After Thanos and Marcou 1993 and Thanos et al. unpublished, respectively).

The main growth period lasts from late winter till the end of spring; when soil moisture is available, an extension of the growth period may take place until well into summer. The height distributions for each particular population are all positively skewed (e.g. Thanos, Daskalakou and Nikolaidou, 1996). With the unusual exception of extremely rich soils, an average growth in the range of 5-20 cm per year has been observed in most cases, for the first 5-10 years. In all these cases, the study of postfire growth kinetics showed that, within an individual growth season, height kinetics follows a typical sigmoid curve. Concerning annual increment and on the basis of several sets of data (representing different postfire environmental conditions and regeneration status), height growth of pine seedlings seems to follow linear kinetics, in all cases and at least for the first 10 postfire years (Figure 9). Despite a slow and rather poor aboveground growth (even under laboratory conditions), a

very impressive root growth is observed. This may be considered as an adaptive mechanism for successful seedling establishment, in regard to the water deficiency problems regularly encountered under the Mediterranean climate.

Pine sapling reproduction

An important parameter of the overall postfire regeneration capacity of a pine forest - especially in those cases where fire frequency is relatively high - is the duration of the juvenile stage for pines. In other words, it is of crucial importance to know when young pines - the outcome of a postfire recruitment - enter the reproductive stage and produce their first cones. The latter, assuming that they are mature (i.e. contain germinable seeds) and produced in sufficient numbers, will secure to a great extent the regeneration of the species (and the forest as well) in the not unusual case of a second fire incident in the near future.
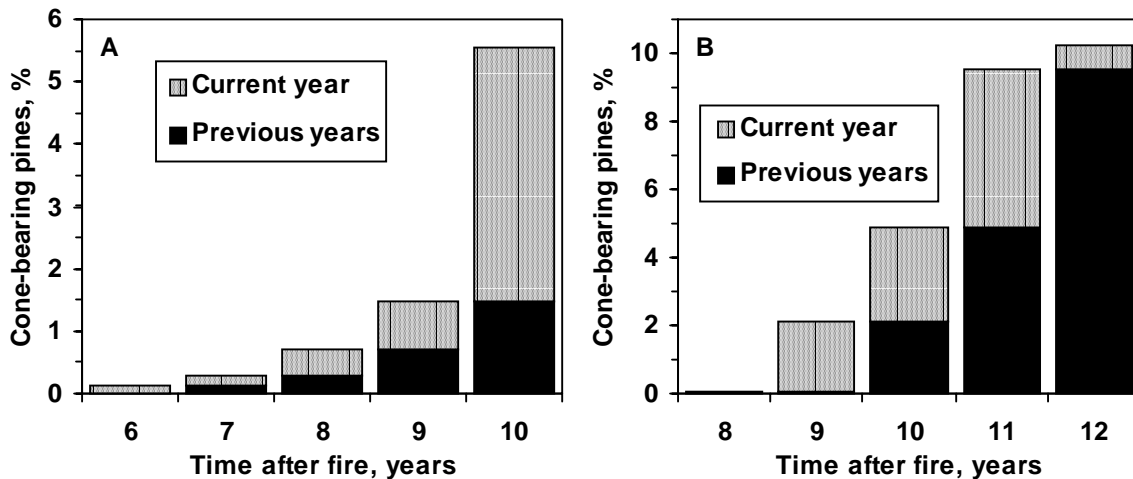

Figure 10 The reproductive shift in even-aged pine sapling populations at early postfire conditions in Samos island (A) and Mt. Parnes (B). Cone-bearing, illustrated both at an annual rate and cumulatively, is based on sample sizes of 464 and 4979 plants, respectively. (After Thanos and Marcou 1993 and Thanos et al. unpublished, respectively).

The reproductive shift in Aleppo pine has been investigated in the nursery, and only recently under field conditions. Nevertheless, it is well known that both Aleppo and brutian pine have a remarkably short juvenile phase, a fact leading to an early cone (and seed) production. In the burned forest of Parnes, as early as 4 years after germination, a very few pine saplings are seen to produce female conelets; in a very exceptional case, an Aleppo pine sapling in Ag. Stefanos (Attica) was observed forming a female conelet during the third growth period. The kinetics followed by the sapling population show an exponential-like increase of the population fraction of sexually mature saplings (Figure 10). Nevertheless, and despite the overall exponential trend, considerable fluctuations

among consecutive years may occur, a fact that merits further investigation in regard to the possibility of a weak masting behavior, only implied for *P. brutia* in the past (Panetsos 1981).

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