

# POST-FIRE REGENERATION OF *PINUS BRUTIA* FORESTS

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## Introduction

*Pinus brutia* (east Mediterranean or brutia pine) is the most common pine species of the eastern Mediterranean rim. The species does 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 post-fire cohort of seedlings (Nahal 1983, Eron 1987, Thanos 1999). In the present chapter, we will explore the morphological and physiological adaptations that enable the species to regenerate and survive after fires and will consider some of the evolutionary pressures that might have selected for these adaptations. We will also examine the various stages of field regeneration and related topics, and finally will describe representative cases of *P. brutia* post-fire recovery in Greece.

## Adaptations and Mechanisms in Re-establishing Burned *Pinus brutia* Forests

Natural regeneration of *P. brutia* is enhanced by several adaptations to fire, displayed in the whole range of the reproductive biology of the species; these adaptations will be treated under the following three headings: cones, seeds and seedlings.

### Cones

Several species of pines are well known for producing serotinous cones (Mirov 1967). Similarly to its closely related *Pinus halepensis* (Daskalakou and Thanos 1996), this also applies to the brutia pine: the seeds are already ripe by late spring, but the cones open gradually only during late summer and autumn (Selik 1958, Ozdemir 1977, Eler 1990). Moreover, it has been observed that a percentage of cones remain closed for months or even years (Sefik 1965, Neyisci 1993). Despite their rather general acceptance, both previous statements (concerning cone opening kinetics and degree of serotiny) are in need of more solid documentation; for instance, the percentage of closed cones may vary among provenances (an example is furnished by Panetsos 1981). This case of variability is only one among several, due perhaps to the geographic isolation of the respective populations, which have led Mirov

(1967) and Panetsos (1981) to grant to the species the attribute of 'variable'. This is in contrast to the Aleppo pine, which despite its larger geographical distribution was considered by Mirov (1967) as 'stable'. A remarkably large seed reserve is eventually built on the tree canopy for a wildfire emergency. Thus, it is certain that during midsummer, when most of the highly destructive fires take place, a big fraction of the *P. brutia* cones are either completely or partially closed. Due to the high temperatures developed by the fire, the cones burst open and a massive dissemination of the seeds occurs. This was also verified on Samos Island (Greece) after fires in 1983 by a survey of the scorched pine cones, found either on the tree skeletons or on the bare soil but still containing some unburned, sound seeds (Thanos *et al.* 1989). Similarly, the post-fire regeneration of *P. brutia* in burned sites of the Aegean region was achieved by lying scorched, cone bearing branches on the bare ground (Eron and Sarig  l 1992). The endurance of *P. brutia* cones and seeds to the heat of fires is of vital importance. A presumably large fraction of pine seeds can survive fire, protected by the scales of the closed, serotinous cones. This, along with indirect evidence provided by massive seedling emergence, was directly tackled in Samos. Seeds collected from the surface of the burned soil were found to be highly viable; their overall germinability was comparable to that of seeds released from unburned cones: final germination in darkness at continuous 15 or 20  C was 80 and 83%, respectively (Thanos *et al.* 1989). The germination percentage of the seeds decreased significantly when 'bare' seeds were exposed to high temperatures like 70  C and particularly 90  C (Neyisci 1988). Seedling survivorship and growth for *P. brutia* was reduced after the seeds had been exposed to temperatures exceeding 90  C (Hanley and Fenner 1998); with a thermal pre-treatment above 110  C, a rapid decline in germination was also observed. On the other hand, when seeds were left inside the cones and the latter were heated at 125  C, the seeds remained viable (Cengiz 1993). It is, therefore, the protective effect of the cones, rather than the seed coat characteristics of the propagules themselves, that safeguards seed survival and results in post-fire recruitment. In regard to seed longevity, germination tests showed that seeds remaining in closed cones had high germination ability (Eler 1990). Selik (1958) states that even nine-year-old cones contain germinable seeds.

### Seeds

In an experiment attempting to quantify the effective, internal nutrient supply of nitrogen, potassium and phosphorus on seedlings of four Mediterranean plant species, Hanley and Fenner (1997) found that *Pinus brutia* seedlings exhibited no specific requirements for single minerals during the 12 weeks that the experiment lasted. This suggests that the relatively large seeds of brutia pine contain enough essential minerals to supply the seedling through quite an extended early establishment period. In regard to the effect of the osmotic stress on germination, it was found that the estimated value of the germination potential (i.e., the absolute value of the osmotic potential required for inhibition of germination in 50% of the seed population) is extremely high (>1.46 MPa). This finding may indicate an ability for germination under high osmotic stress conditions, such as those presumably encountered in the deep ash cover of intensively burned areas (Thanos and Skordilis 1987), as also has been suggested for Aleppo pine (Ne'eman *et al.* 1993).

### Seedlings

Despite a slow and rather poor aboveground growth (even under laboratory conditions), a very impressive root growth is observed. This may be considered an adaptive mechanism for successful seedling establishment, in response to the water deficiency problems regularly encountered under the Mediterranean climate. *Pinus brutia* has a vertical main root characterised by fast growth, and the species could be registered as a phreatophyte (an attribute often found among desert perennials). It is indicative that the mean root length in 5-6-month-old seedlings is 50-65 cm. During the first growth season, shoot growth is kept slow while the root length is 5-10 times that of the shoot. After the first season, shoot growth seems to accelerate (Boydak 1993). Light demand of seedlings is high; according to Trabaud (1995), the Mediterranean pine species are not exclusively dependent on fire (fire-followers) but are plants occupying open disturbed sites, generally with a scarce vegetative cover, and particularly without the presence of aggressive competitors. Therefore, in the case of wildfires, the heliophilous nature of the species exploits the 'opening' of habitats produced by fire through a massive recolonisation (Thanos 1999).

An important parameter of the overall post-fire 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, which are the outcome of a post-fire recruitment, enter the reproductive stage and produce their first cones. The latter, assuming they contain germinable seeds and are produced in sufficient numbers, will secure, to a great extent, the regeneration of the species (and the forest as well) in case of a future fire incident. In the *P. brutia* population recruited after the great wildfire of 1983 in Samos Island, Greece, the first cones were observed in the 7th annual growth period. After 10 years, on average, about 10% of the plants were found in the reproductive state (Thanos and Marcou 1993). These data conform to previous information furnished by several sources (Panetsos 1981, Nahal 1983, Sefik 1965, Selik 1958).

### Post-fire Germination and Emergence of Pine Seedlings

Experiments under daily alternating conditions of light and temperature resembling those that are naturally met, lead to the conclusion that field germination is feasible throughout the rainy season of the Mediterranean-type climate, though at a lower rate and to an inferior level at cooler temperatures (Thanos and Skordilis 1987). These data fit well with field observations of natural seed germination: an initial small part of the population germinating during the winter months, November to February, and a 'burst' of germination occurring in March and April (Thanos *et al.* 1989, Eler and Senegin 1990). The promotive effect of white light during the 'day' as well as the inhibitory action of far-red light (simulating conditions of dense canopy) verify the heliophilous nature of the species, a nature that allows its germination and establishment mainly in open, well-illuminated places. Stratification has been repeatedly found to have a beneficial effect on subsequent germination performance in *P. brutia* seeds (Sefik 1965, Falusi 1982). In a recent study (Skordilis and Thanos 1995), the inductive effect of stratification was shown to have an escalating

effect from south to north among three Greek provenances. In the seed lot from the southern forest in Lasithi, Crete, stratification simply increased germination rate. In the intermediate lot from Thasos Island, it caused a broadening of the temperature range of germination. In the northern lot from Soufli, Thrace, it caused a dramatic release from a particularly deep dormancy.

### Timing of Pine Seedling Recruitment – The Effect of Climate

Mediterranean pine seed germination and seedling emergence take place exclusively during the first post-fire wet season (Thanos 1999). More specifically, in Aleppo pine, its occurrence usually takes the form of a massive wave early in the period (October-January), closely following the start of the wet season. During the second post-fire rainy period no additional seedlings are usually observed. In *P. brutia*, on the basis of both a theoretical approach (Skordilis and Thanos 1995) and preliminary results (Thanos *et al.* unpublished), the recruitment timing is changed in regions with more severe winters. Under such climatic conditions, seedling recruitment profile is shifted to the late winter or early spring months, possibly the result of a frost-avoiding mechanism of the vulnerable seedlings.

Significant interactions have been observed between altitude and timing germination and seedling emergence in the field (e.g., Ozdemir 1977); the latter was significantly delayed, till spring arrival, in the mountainous zone of the Antalya region. Latitudinal variation was examined by investigating the stratification requirement and temperature range of germination in seeds of *P. brutia* from three provenances of Greece: a northern continental provenance from Soufli, Thrace, an Aegean provenance from Thasos Island and a southern provenance from Lasithi, Crete (Skordilis and Thanos 1995). Based on laboratory germination behaviour and climatic data (particularly water availability and prevailing temperatures), timing schedules of seedling emergence for the respective pine seed populations were postulated. Thus, in *P. brutia* from Soufli, the inherent (primary) seed dormancy completely prohibits autumn germination; the seeds are expected to germinate in spring after having experienced the inductive, low temperatures of winter. This delay of field germination may be viewed as an evolutionary result of selection by a rather long and severe winter, and may prevent young seedlings from being damaged by freezing temperatures. On the basis of the laboratory data, field germination in Thasos Island may exhibit a bimodal pattern; a fraction of the seed population may start germinating soon after the onset of the rainy season (mid September until the end of October), when temperatures are warm enough. Later, cool temperatures may suppress germination and a second burst in germination is expected in early spring when temperatures warm up again and after the ungerminated seeds have experienced the promotive, low temperatures of winter. The advantage of autumn-over spring-germinating seedlings is the development of an efficient deep root system. However, it may be counterbalanced by the much higher germination rate of the stratified seeds, which is in agreement with the observations of a similar study (Falusi 1982) that indicated a considerable capacity for rapid seedling growth. The ratio of autumn- to spring-germinating seeds is assumed to vary according to the meteorological conditions of each particular year. In the extremely mild climatic

regime of the Lasithi area, it is evident that the non-dormant *P. brutia* seed population of Crete will encounter field temperatures suitable for germination as early as October, provided, of course, that water is available. By the end of December, it is almost certain that even the slowest germinating seeds will already have entered the seedling stage. In this way, between seedling emergence and the onset of the long summer, at least four months would be available for the development of an efficient root system. In regard to an experimental proof of the above postulation, there is only circumstantial or preliminary evidence in favour of an early-peaked germination pattern in Chania, Crete (Thanos and Pendarakis unpublished), as well as a two-peaked or a delayed-peaked pattern in Samos (Thanos *et al.* 1989, Thanos and Marcou unpublished) and at the high altitudes of the Antalya region, Turkey (Ozdemir 1977). It is therefore imperative that field data be collected regarding the timing of seed germination and seedling establishment under natural conditions at several locations. It is also important that germination characteristics be screened in the laboratory for a large and representative specimen of east Mediterranean pine populations. We may conclude that the observed *P. brutia* seed germination responses to stratification and temperature are quite plastic and reflect a climate-adapted strategy on the timing of seedling emergence and establishment (well known to be the most vulnerable life phase).

### Post-fire Growth of Pine Sapling Populations

The main growth period lasts from late winter until the end of spring or early summer when both temperatures are mild enough and soil moisture is adequate. 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 5–15 years (Neyisci 1989, Thanos *et al.* 1989, Spanos 1994, Spanos *et al.* 2000). Within an individual growth season, the study of post-fire growth kinetics has shown that height kinetics follows a typical sigmoid curve (which is also the case for Aleppo pine, Thanos *et al.* 1995). Concerning annual increment and on the basis of several sets of data (representing different post-fire environmental conditions and regeneration status), height growth of pine seedlings seems to follow linear kinetics, in several cases, at least for the first 10 post-fire years (Thanos and Marcou 1993, Spanos *et al.* 2000). Fig. 1 illustrates the post-fire, vegetative growth of *P. brutia* saplings in the regenerating forest of Samos Island, burned in 1983. From the two linear regression curves shown it is clear that an enhancement of the growth rate is observed at an age between 6 and 10 years (this coincides with the onset of juvenility termination). To illustrate this age-dependent growth rate increase, an additional, hyperbolic regression curve is drawn; although both curves (linear and hyperbolic) are statistically fully acceptable, the latter one has a slightly better regression coefficient value. Because a linear kinetics cannot evidently describe the even-aged population height growth, it is important to collect and analyse longer arrays of measurements, hopefully covering the entire life span of the population. In such a case, they should include all individual trees of the same age; dissimilarly to the current silvicultural practice, the most probable kinetics candidate is perhaps a sigmoid curve.

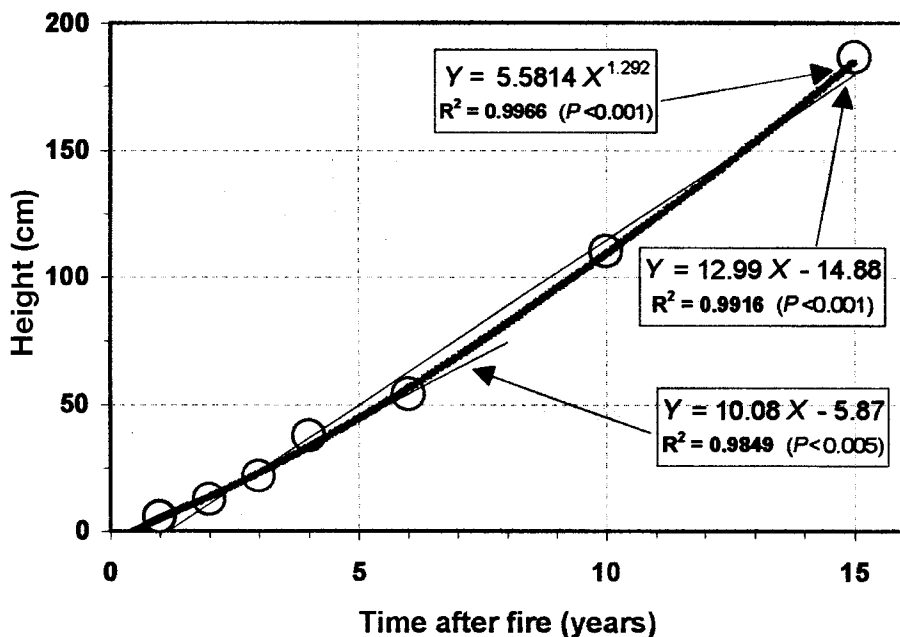


Fig. 1. Post-fire growth of *Pinus brutia* saplings in the regenerating forest of Samos Island, burned in 1983. One hyperbolic and two linear regression curves are shown and equations are given separately for each; the two linear curves extend for 6 and 15 years, respectively. Each point corresponds to the average of at least 400, randomly selected saplings measured in several experimental sites. SE values are smaller than the circle radius. From Thanos *et al.* (1989), Thanos and Marcou (1991, 1993 and unpublished data).

At this point one should not forget to mention the several nursery studies that investigated, among other issues, the growth characteristics of saplings and trees of various provenances (Panetsos 1981, Matziris and Cooling 1982, Eccher *et al.* 1987). These studies have resulted in extremely high rates and annual increments of growth compared with those under 'natural conditions'. The values obtained are useful for comparisons among the different origins of the species although a linking to the 'ecological' measurements is obviously required, and at the same time it would be highly beneficial to both the silvicultural and the ecophysiological approaches.

### Survival and Mortality – Climate, Soil and Competition

The post-fire time-course of pine seedling mortality, plotted in several cases, seems to follow a negatively exponential curve leveling off asymptotically, within 2-4 years after fire, to a level around 10-40% (Fig. 2) of the initial peak of establishment (Thanos and Marcou 1993). It was further found that the first post-fire summer is by far the most crucial period for the survival of seedlings in *P. brutia* (e.g., Thanos *et al.* 1989). Another decisive season is the first part of the rainy season, immediately after fire, when germination and early seedling development and

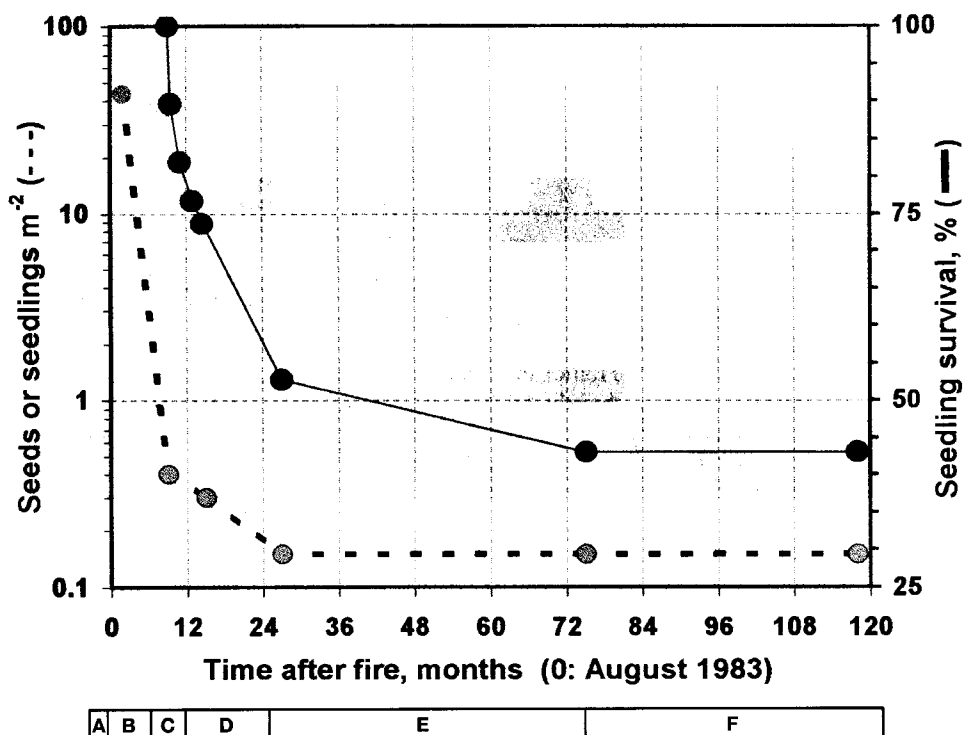


Fig. 2. Pine seeds on the ground (October 1983) and seedling density for the 10-year long post-fire period (stippled line). The survival of the seedlings already established after the first rainy season is illustrated in solid line (i.e., 100% of survival corresponds to the seedling population in May 1984). The timing of phases A-F (see text) is displayed in the horizontal bar. From Thanos *et al.* (1989), Thanos and Marcou (1991, 1993 and unpublished data).

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. Several causes of mortality for seedlings and saplings of Mediterranean pines have already been cited in general: water and cold stress conditions, competition from other plants, infection by fungi and pests as well as predation by insects and other animals. Pine seeds are thought to be consumed by animals even at an early stage of post-germination growth; the seed coat (containing the megagametophyte and enclosing part of the cotyledons) frequently has been observed missing (presumably having been eaten) (Thanos *et al.* 1989).

A noteworthy feature for one- and two-years-old *P. brutia* seedlings is their apparent grazing-tolerance, though both the extent of this tolerance and the long-term effects of non-lethal grazing are still unknown. The absence of the apical primary needles and the concurrent necrosis of the apical part of the stem easily detect grazing in first year seedlings. In the case of Samos Island (Greece) fires, a rather high proportion of seedlings were found grazed but still growing. The survival and recovery of grazed seedlings was achieved (to an unknown degree) by the growth

of one or two lateral stems which had a negative effect on seedling and tree shape (Thanos *et al.* 1989). Nevertheless and despite the lack of solid and causal evidence, it is almost unanimously assumed that the most prominent reason for mortality is summer drought; almost all non-surviving seedlings are usually found dried but intact (Spanos 1994, Spanos *et al.* 2000).

### Pine Sapling Banks

An interesting feature was the discovery of numerous, very short (10-20 cm) *P. brutia* saplings, evidently suppressed by neighbouring vegetation (in particular *Cistus* spp. plants) 6 years after fire (Thanos and Marcou 1991). Such saplings still endured at the age of 15, with a stem height 50-70 cm (Thanos and Marcou unpublished). These particular *Cistus* stands consist of virtually even aged plants, and because their maximal longevity is believed to be around 10-15 years, their senescence may start 10-15 years after fire eventually relieving the suppression of pine saplings permitting a normal growth of the pines. This finding leads to the postulate that a pine sapling bank may be formed during the early post-fire recovery stage. Because the pine seed supply during this stage is absent or scarce, a pine sapling bank may be proved an important adaptive strategy for the regeneration of burned Mediterranean forests.

Only recently has the concept of sapling bank emerged as a regeneration pathway in addition to soil or canopy seed bank and vegetative resprouting. The suppressed saplings are suggested to be, like seeds in the ground, awaiting the removal of inhibition of their development, with light, water and nutrients being the possible limiting factors. The postulated advantages of a sapling bank over the seed bank are lower predation losses and the detection and subsequent exploitation of a small opening in the shading canopy by a suppressed young plant (impossible for a seed in the soil). Both these advantages seem to fit nicely in the case of *P. brutia*. The pine sapling bank postulate requires, undoubtedly, further and rigorous studies towards the determination of the degree of its occurrence and related factors, as well as the ecophysiological mechanisms pertaining to the suppression and resumption of sapling growth.

### Selected Case Studies from Greece

*Pinus brutia* grows in the northeastern part of the Greek mainland, the islands of the east Aegean Sea and Crete. The recovery of *P. brutia* forests of Samos Island (Greece) was followed after the great wildfire of August 1983 that burned an area of more than 2,500 ha. After 10 years, the survival of pine seedlings was 43%, the overall density was around 0.15 saplings m<sup>-2</sup> and the average height was 100 cm (Thanos and Marcou 1993). The major conclusion reached was that pine seedling emergence, establishment and survival were significant and predictably adequate for complete natural reforestation, for most of the sites of the area burned. Fig. 2 summarises the major events in regard to natural regeneration of *Pinus brutia*. In October 1983, just prior to the onset of the rainy season, a mean number of 43 seeds m<sup>-2</sup> were found on the burned ground. Pine seedlings emerged on the burned ground as early as December 1983, about one month after the start of the rainy season. During January and February 1984, seedling



emergence was even scantier but a burst of germination was observed from mid March until the end of the rainy season (beginning of May). This bimodal pattern was presumably imposed by the inhibitory temperatures of winter. By the end of May, only 0.4 pine seedlings  $\text{m}^{-2}$  had been established. The observed difference between the available germinable seeds and the emerged seedlings  $\text{m}^{-2}$  is attributed to the considerable losses due to biotic and abiotic factors. The seedling survival curve (Fig. 2) shows a steep decrease during the subsequent first summer, followed by a rather moderate one for the next 12-month period (November 1984–November 1985). Therefore, the survival curve of tagged pine seedlings revealed a considerable drought tolerance: more than half had survived 18 months after tagging whereas 43% were found alive after 6 years; after 10 years virtually no further mortality was observed.

The average density of pine seedlings measured in the second post-fire autumn was 0.30 seedlings  $\text{m}^{-2}$ , 6 years after the fire, the overall density was around 0.15 saplings  $\text{m}^{-2}$ , whereas 10 years after, a similar density was observed. The six phases (A–F) marked on the horizontal bar in Fig. 2 represent the major events of post-fire regeneration. During the first period, phase A (*seed dispersal*), seeds are liberated from within their cones, through the action of fire, and are subsequently disseminated on the burned ground. In phase B (*germination*), virtually all seeds germinate during the first post-fire wet season. During this period there exists, presumably, a very high rate of mortality due both to animal consumers of various types and to erratic germination as well as unsuccessful seedling establishment. Thus, phase B is the most critical for the final recruitment of a post-fire cohort of pine seedlings. Afterwards, 2 phases of seedling establishment follow: C (*seedling establishment 1 – first summer*) and D (*seedling establishment 2 – second year*), with gradually decreasing mortality risks. The pine sapling population is virtually stabilised in phase E (*stable sapling density*) and starts being reproduced in phase F (*reproduction*). At 10 years after fire, on average about 10% of the plants (depending on the particular site) were found in the reproductive state with a mean number of 2.5 cones (of various maturation stages) per non-juvenile plant (or 0.25 cones per plant when all the saplings were taken into consideration).

The climatic and edaphic conditions in the island of Thasos (Greece) are especially favourable for the growth of the natural *Pinus brutia* stands. In August 1989, a great wildfire swept away 5,700 ha of *P. brutia* forest in NW Thasos. The post-fire recovery was monitored during the four subsequent years (Spanos 1994, Spanos *et al.* 2000). Pine seedling establishment took place as late as May 1990; the unusually long dry period between October and April 1990 resulted in very late seed germination. By the end of the recruitment period (May 1990), mean pine seedling density was considerably high (2–6 seedlings  $\text{m}^{-2}$ ) whereas a significant drop in the first summer was observed. Thereafter, a relatively smooth decline was obtained, and the density was almost stabilised to about 0.6–2 seedlings  $\text{m}^{-2}$  after 5 years: the kinetics of survival was found to follow a rectangular hyperbola. Significant differences in seedling density values were detected among site groups of varying orientation or quality: north-facing and index I sites showed the highest density values while south-facing and index V sites were lowest. Similarly, height kinetics showed a significant divergence among site groups; again, the north facing and the index I sites were the fastest growing. Annual growth showed a linear regression kinetics throughout the 5-year-long post-fire period of study, with a yearly increment of 17 cm. Starting at

an age of 4-6 years an increasing fraction of the sapling population became reproductive (Spanos *et al.* 2000).

In conclusion, the natural regeneration of *P. brutia* is accomplished exclusively by seeds and is enhanced by a number of adaptations to fire. (1) The cones are serotinous, thus most seeds survive inside the cones and are disseminated by the wind immediately after fire. (2) The seeds are mainly non-dormant and can germinate throughout the rainy season. (3) The heliophilous nature of both seed germination and seedling establishment is promoted by the opening of habitats produced by fire. (4) Pine seedlings show a considerable drought tolerance and, once settled, their survival chance is quite high – the average density of pine seedlings measured in several cases is high enough for complete natural reforestation of most burned areas. (5) In certain cases, and to a varying extent, a post-fire sapling bank may be formed acting as an important auxiliary strategy. (6) The remarkably short juvenile phase that leads to an early cone and seed production ensures, to a great extent, the regeneration in cases where fire frequency is relatively high. Naturally, there are a number of exceptional cases where post-fire regeneration is not adequate, as on steep slopes or poor soils, heavily affected by erosion. Other factors contributing to the non-recovery of the pine forest are of course: grazing, additional subsequent fires and human 'management'.

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