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Aleppo Pine (*Pinus halepensis*) Postfire Regeneration: The Role of Canopy and Soil Seed Banks*

Evangelia N. Daskalakou and Costas A. Thanos[1]

[1] *Author for correspondance: Department of Botany, University of Athens, Athens 15784, Greece*
Tel. 30 1 7284655, 30 1 7284618; Fax 30 1 7234136; e-mail cthanos@atlas.uoa.gr

Abstract. *Pinus halepensis* (Aleppo pine), is the dominant tree of a large fraction (26%) of the Greek coniferous forests; this species is an endemic pine of the Mediterranean Rim and well adapted to fire. Its regeneration is accomplished exclusively through seeds, thus its soil and canopy seed banks are of paramount importance for postfire resilience. Cone opening and seed dispersal were investigated in unburned forests of Attica (Greece) and it was found that *Pinus halepensis* trees maintain a significant percentage of the yearly cone crop (40-80%) closed, thus creating a persistent, canopy seed bank. Full viability of enclosed seeds was maintained for at least three years in canopy storage; moreover, preliminary results concerning the viability of seeds enclosed within the cones for four to more than 50 years showed a gradual reduction of both final percentage and rate of germination. Nevertheless, cones of up to 20 years of age contained a considerable fraction of germinable seeds. On the other hand, Aleppo pine forms only a short-lived (transient) soil seed bank; this bank was particularly abundant after a fire, as a result of the fire-induced cone opening. The germinable seed portion, although quite important prior to the start of the rainy season, was rapidly depleted, and at the end of the rainy season it was virtually absent in both burned and unburned forests. It is therefore concluded that postfire Aleppo pine seedling recruitment takes place almost exclusively during the first year after the fire and depends upon the germination of seeds in a transient soil bank which is produced by the postfire dispersal of pine seeds stored in the canopy seed bank.

Keywords: Regeneration capacity; Cone serotiny; Bradychory; Seed rain; Seed storage; Seed germination; Seed longevity.

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Introduction

In Greece, during the last three decades (1964-89), total burned areas amount to an average of 29300 hectares per year, a large fraction of which (ca. 25%) is Mediterranean pine forest (Efthymiou 1993). Aleppo pine, *Pinus halepensis*, one of the major Mediterranean pine species, has evolved adaptative mechanisms towards "catastrophic" fire events. Being an obligate reseeder (i.e. being usually killed by fire), Aleppo pine depends for its survival upon a very powerful regenerative capacity based on both the yearly production of prolific seed crops and the safeguarding of seed banks. In addition, Aleppo pine seed germination and early seedling establishment are both well adapted to exploit the postfire conditions.

Out of the 95 species in the genus *Pinus*, 23 produce serotinous cones and only six species are considered obligately pyriscent (Lamont et al. 1991). Aleppo pine, although not included in the latter group, does produce serotinous cones, i.e. its seeds are produced, stored and protected in the canopy, within the woody cones. Cone opening and seed release are controlled mostly by environmental conditions (high temperatures and low air humidity). Nevertheless, a significant portion of seeds remains enclosed within the cones (cone serotiny), thus forming a so-called canopy seed bank. Despite the general recognition of the occurrence of cone serotiny in Aleppo pine (e.g. Moulopoulos 1933, Panetsos 1981, Dafis 1987, Klaus 1989, Richardson 1988) it has recently been emphasized that "this phenomenon has not been formally proven" (Trabaud 1987).

The aim of this work was to investigate the dynamics of cone serotiny in *Pinus halepensis* as well as the consequent fate of the seeds present in both canopy stores and soil banks. Moreover, this study intended to illustrate the role of both types of seed banks in the postfire regeneration of Aleppo pine.

Materials and Methods

The six study sites are located in various Aleppo pine forests in the prefecture of Attica, around metropolitan Athens. These are named after the nearest village or town (the mountain where the site belongs is given in parenthesis): Stamata (Pendeli), Villia (Pateras), Avlona and Fyli (Parnes), Kapandriti (Mavrovouni) and Ilioupolis (Hymettus). The mean elevations are 410, 550, 480, 470, 300 and 400 m above sea level, respectively; the distance of each site from the centre of Athens (Acropolis) is, in straight line, 22, 42, 29, 31, 13 and 18 km, respectively. In most sites the soil substrate mainly consists of limestone, except in Stamata and Kapandriti, where the rocks are schists and tertiary deposits, respectively. In all cases the soil varies from deep to shallow, with localized rocky areas, and the slopes are of intermediate values, with no erosion present.

The climatic conditions prevailing in the greater region may be represented adequately by the meteorological station of Tatoi, located at a central place from the study sites, at an altitude of 237 m a.s.l. Its ombrothermic diagram shows a typical Mediterranean climate with a mean annual temperature of 16.5 °C, mild winters, a rather low total yearly precipitation (ca. 470 mm) and a markedly seasonal rainfall pattern which results in a xerothermic (virtually rain-free) period (May - September).

Field measurements of cone opening took place in three mature (unburned) Aleppo pine forests of Attica (Stamata, Villia and Ilioupolis). Exceptionally in *Pinus halepensis*, cone development requires three growth (springtime) seasons, in contrast to the vast majority of the pine species where only two are needed. During the third spring, the cones enlarge considerably and their colour is gradually altered from green to brown. Measurements were initiated at the end of the maturation season (late spring) and were carried out on freshly-matured (brown coloured) cones. In two instances (Stamata and Villia) cone measurements took place at the same forest site but, each time, with 100 randomly selected cones (10 cones from each of 10 randomly selected trees). In two subsequent series of measurements (Stamata and Ilioupolis), the same 100 or 200 cones, respectively, were observed each time (on ten and seven marked trees, respectively). The cones were carefully observed with binoculars and were accordingly classified into three classes: opened (all seeds dispersed), closed (no seeds dispersed) and half-opened.

Closed *Pinus halepensis* cones of different maturation years (0, 1, 2 and 3 years old) were collected in the summer months from the above mentioned unburned forests. An additional collection of older cones took place also in the summer from the mature Aleppo pine forest of Fyli. Evaluation of cone age was based on both colour and position on the branch; freshly-matured cones are bright brown while older cones are dull grey. Since Aleppo pine growth is not monocyclic, evaluation of the year of maturation on the basis of cone position on the branch is only a rough estimate. Another characteristic which we have repeatedly observed is that opened cones can re-close entirely at high relative humidity (usually after a rain). Therefore, both the measurements of cone opening on the tree and cone collection as well were carried out after several rain-free and dry days. Finally, for the collection of closed cones, an experienced eye is able to discern the cones that had been previously opened from those that had remained always closed: in the latter the cone scales are firmly sealed.

Cone opening (and seed extraction) in the laboratory was achieved by various durations (30-120 minutes) of thermal treatment of cones at 100 °C, in an oven. Only in the case of the relatively old cones from Fyli, a less intense (but equally successful) treatment, considered to resemble closer the naturally encountered conditions was applied: 10 minutes at 100 °C, in the oven, followed by transfer outdoors (under summer conditions) for two weeks. After cone opening, the morphologically mature (sound) seeds were counted (seeds per cone) and the extracted seeds were used in germination tests.

Germination tests were performed with five replicates of either 20 or 25 seeds per Petri dish (diameter 9 cm); each dish was lined with two discs of filter paper and moistened with 6 ml of deionised water (Thanos and Skordilis 1987). Criterion of germination was visible radicle protrusion; T_{50} is the time required for the manifestation of 50% of final germination. Measurements were taken twice a week and after each count germinated seeds were discarded. Germination experiments were performed either in controlled temperature cabinets (Heraeus BK 5060 EL, Germany) at constant temperatures (5, 10, 15, 20, 25 and 30 °C) and darkness or in temperature- and light-programmable growth benches (Model GB48, Conviron, Canada), equipped with both fluorescent and incandescent lamps. Temperature and light were programmed (Thanos 1993) to change several times daily to simulate as closely as possible the average climatic conditions of Ellinikon (Athens Airport). Far-Red light, FR_I and FR_{II}, obtained by filtering white light through Plexiglas filters, simulated light conditions under a very dense or a somewhat open forest canopy, respectively (Thanos 1993).

The investigation of the postfire soil bank of pine seeds was accomplished through soil sampling, shortly before the onset and after the end of the first postfire rainy season. Fifty samples of soil (14 x 20 cm or 9.5 x 4 cm, 1 cm deep) were collected from four recently burned Aleppo pine forests of Attica (Stamata, Villia, Avlona and Kapandriti; burned in the summer of 1990, 1990, 1991 and 1992, respectively). Sampling took place in Nov. 1990 - Jun. 1991, Nov. 1990 - Jun. 1991, Oct. 1991 - Oct. 1992 and Oct. 1992 - Jun. 1993, for each of the four pairs, respectively. In addition, soil samples were collected in three adjacent, unburned areas of the forests

(Stamata, Villia and Avlona), after the end of the rainy season (June 1991, 1991 and 1992, respectively). Soil samples were transferred to the laboratory and were carefully inspected for pine seeds. Whole seeds were dissected and upon observation classified as sound (i.e. germinable) or empty (aborted). An estimate of consumed seeds was obtained on the basis of the scores of seed coat halves and seed remnants.

An evaluation of the postfire regeneration capacity was attempted in the summer 1993 for three unburned forests (Stamata, Villia and Ilioupolis). To determine the number of cones per tree, closed cones (an amount of 5007, 1223 and 1116 freshly-matured or older cones) were counted in 30, 23 and 31, randomly chosen trees, respectively.

Results

Time courses of cone opening on the tree (Figure 1) showed, in both sites, a highly significant percentage

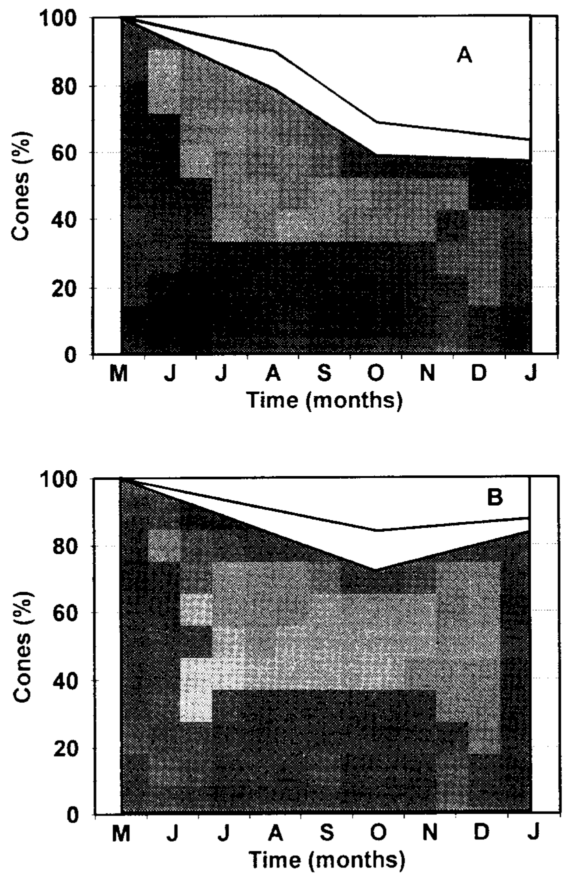


Figure 1. Time course of cone opening on *Pinus halepensis* trees in two regions of Attica (A: Stamata, B: Villia). Four times during the observation period (May 1991 - January 1992) 100 randomly selected, freshly-matured (spring 1991) cones were inspected. Dark, grey and white areas represent closed, half-opened and fully opened cones, respectively.

(about 60% and 80%, respectively) of cones remaining closed at the end of the dry period. In two additional cases (Figure 2), the percentages of closed cones were relatively decreased (to about 50% and 40%, respectively). Moreover, in Ilioupolis (Figure 2B), the cones opened gradually from July to October (from 40% to nearly

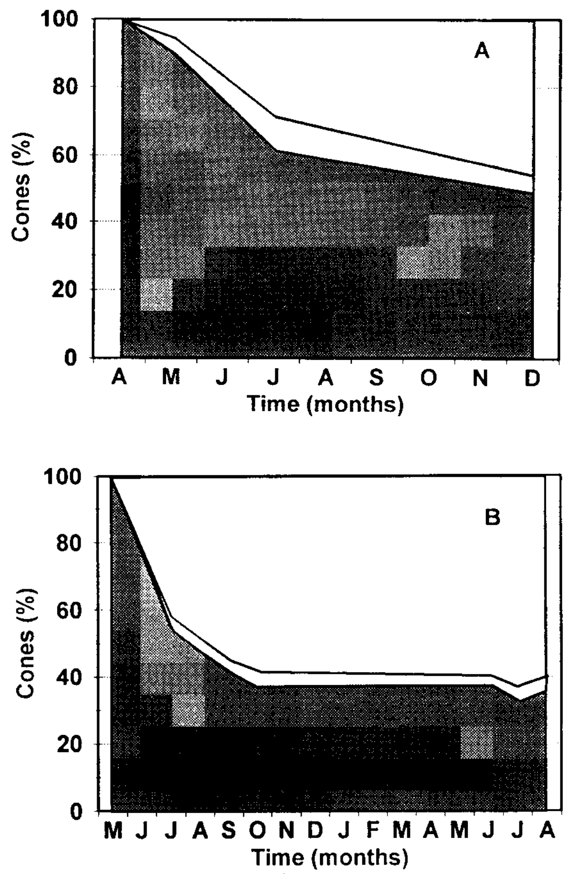


Figure 2. Time course of cone opening on *Pinus halepensis* trees, in two regions of Attica (A: Stamata, B: Ilioupolis). Throughout the observation periods (April 1994 - December 1994 and May 1992 - August 1993, respectively) the same (100 in A and 200 in B), freshly-matured (spring 1994 and spring 1992, 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.

60%). It is noteworthy that during the following dry period (next summer), the percentage of closed cones remained almost unchanged (35-38%), i.e. virtually no cones were additionally opened in the second post-maturation summer. In all these sites, most cones were observed to open during the first 2-3 months of the dry season (Figures 1 and 2).

The period of time at 100 °C in the oven, required for full opening of closed and mature cones (aged from 0 to 3 years) increased gradually with age, from 30 to 120 minutes (Figure 3).

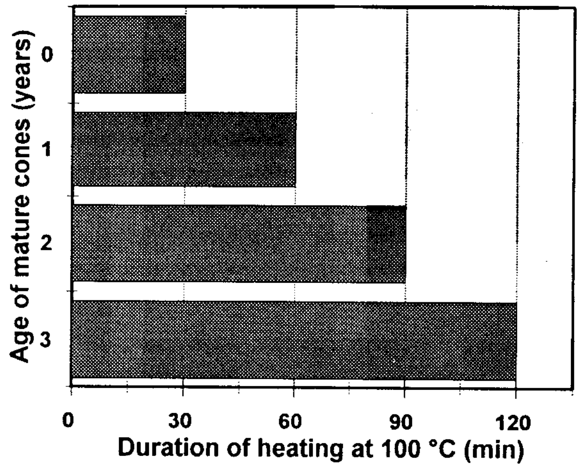


Figure 3. Heat requirements for full opening of closed cones of *Pinus halepensis* as a function of cone age. These cones had matured 0-3 years prior to their collection and had remained closed on the tree canopy.

The mean number of sound seeds per cone extracted from cones collected at various forests of Attica is presented in Table 1. The average seed content ranged between 32 and 70 sound seeds per cone; this diversity may be attributed to a strong correlation between the cone size and its seed content (data not presented).

Pinus halepensis seeds, extracted from closed cones that had matured a few months prior to harvest (0 years old from Stamata), germinated optimally (about 90%) in darkness, at 20 °C (Figure 4A). In addition, seed germination was quite satisfactory at 10 and 15 °C but showed a significant decrease at 25 and 5 °C. Similar final percentages of seed germination were obtained with seeds from Villia (Figure 4B); however, in the latter case, final germination at 5 °C was surprisingly high (90%). Seeds of Aleppo pine from Stamata, extracted from cones that had remained closed on the tree for 0, 1, 2 and 3 years prior to collection, germinated maximally (80-90%) at the optimal temperature range of 15-20 °C, irrespective of their age. Nevertheless, at the suboptimal temperature of 5 °C, final germination was gradually reduced with seed age; however, it has to be borne in mind that older cones (and seeds) had been heated in the oven for longer

Table 1. Average number of seeds in closed, mature cones of *Pinus halepensis* collected from Aleppo pine forests in five regions of Attica. Seeds were extracted from cones by heat treatments at 100 °C; n = number of cones.

Region	Seeds per cone (± SE)	
Stamata	52.8 ± 3.5	(n = 95)
Villia	51.8 ± 2.2	(n = 112)
Ilioupolis	31.9 ± 2.3	(n = 71)
Fyli	56.9 ± 2.3	(n = 100)
Kapandriti	69.9 ± 3.2	(n = 66)

durations than young ones. Older seeds collected from Parnes (Figure 5), estimated to be 4-5 and 6-9 years old, attained a final germination level of ca. 50% at optimum conditions (15 °C and continuous white light). In these seeds, germination rate was significantly reduced (T_{50} = 15 days) in comparison with fresh seeds (T_{50} = 10 days). Aleppo pine seeds 10-20 and over 50 years old germinated to only 30% and 10%, respectively; furthermore the germinants were unable to develop into normal seedlings. Freshly-matured (0 years old) seeds collected from various forests of Attica germinated optimally (81-97%) in darkness (Table 2). Similarly, seeds 1, 2 and 3 years old germinated fully as well (85-99%) at only slightly decreased speed. However, in all seeds tested, the overall rate of germination was slow and T_{50} values ranged between 8 and 16 days.

Diurnal white light, similar in quality and quantity to natural daylight, resulted in a certain increase of germi-

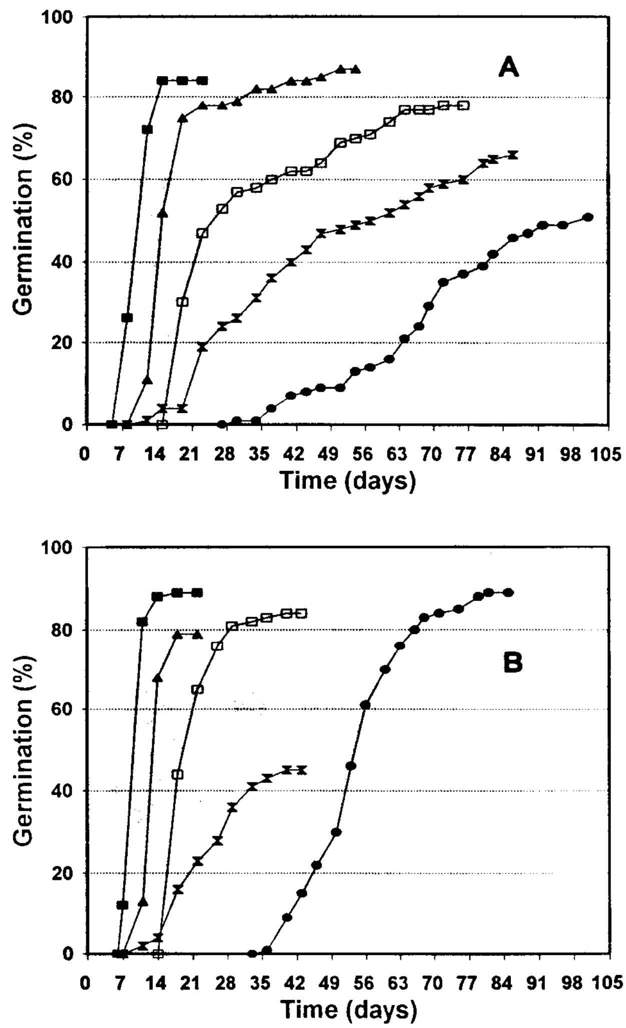


Figure 4. Time courses of *Pinus halepensis* seed germination at various constant temperatures, in the dark (● 5, □ 10, ▲ 15, ■ 20 and X 25°C). The seeds used were extracted from closed cones, collected during the summer of their maturation year (cones aged 0 years) from the forests of Stamata (A) and Villia (B).

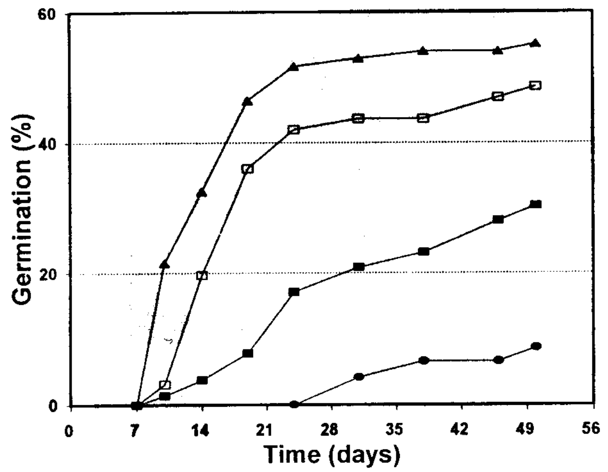


Figure 5. Time course of *Pinus halepensis* seed germination as a function of seed age. The seeds used were extracted from closed cones (collected in the pine forest of Fyli) of an estimated age of 4-5 (□), 6-9 (▲), 10-20 (■) and ca. 50 (●) years. Germination took place at 15 °C, under continuous white light.

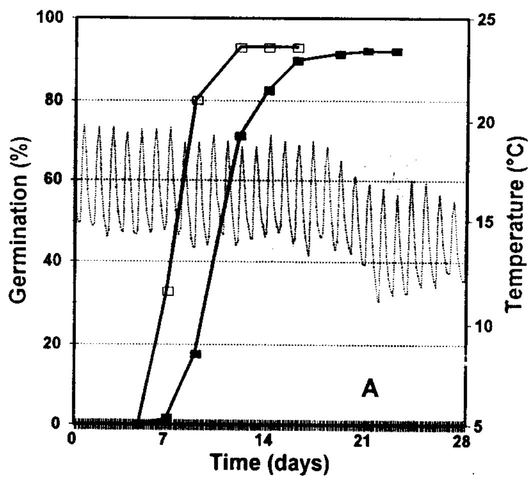
nation rate (T_{50} about 7 days), while the final percentage of germinated seeds reached 90%, similar to the dark control (Figure 6A). The germination of *Pinus halepensis* seeds was fully suppressed (4%) by diurnal FR_I illuminations (light conditions simulating the dense forest canopy); on the other hand, mild Far-Red irradiation (FR_{II}) was entirely ineffective to germination (Figure 6B).

The pie charts of Figure 7 show that shortly before the onset of the rainy season, Aleppo pine seed density in the burned soil varied considerably (151, 129, 63 and 405 seeds/m^2 in Stamata, Villia, Avlona and Kapandriti, respectively). In all four sites, despite the fact that the portion of sound seeds was by far the smallest one (8-18%), the absolute values were quite significant (10-74 seeds/m^2). On the other hand, at the end of the rainy season, it is remarkable that pine seed density in the soil was dramatically reduced (0-4 seeds/m^2). A similar depletion of the soil seed bank occurred (inset of Figure 7) at the end of the rainy season in neighbouring, unburned sites of the three forests (Stamata, Villia and Avlona). Furthermore, the absolute values of seed density were fairly comparable to those found in the burned sites (1.4-2.1 sound seeds/m^2).

In a preliminary study of the canopy seed bank dynamics, freshly-matured and older cones were counted in three unburned forests (Stamata, Villia and Ilioupolis). The average number of closed cones per tree varied widely in the three forests (167, 53 and 36, respectively). Nevertheless, the relative contribution of fresh and older cones was remarkably similar in the three forests; the percentage of the older cones was 62, 66 and 67%, respectively, while the contribution to the canopy bank of the freshly-matured ones ranged between 33 and 38%. The postfire regeneration capacity of the previously

Table 2. Final germination levels of *Pinus halepensis* seeds extracted from 0- to 3-year-old, closed cones, collected in pine forests of five regions of Attica. Seeds were extracted from cones by heat treatments at 100 °C and were germinated in darkness, at 15 (marked with an *) or 20 °C.

Region	Final Germination (% ± SE)			
	Cone Age (years)			
	0	1	2	3
Stamata	84.0 ± 8.5	85.0 ± 3.5	94.0 ± 4.8	88.0 ± 5.1
Kapandriti	96.8 ± 2.3*	88.0 ± 1.8*	88.0 ± 2.0*	—
Fyli	88.8 ± 3.8*	94.4 ± 2.4*	99.0 ± 1.0*	—
Villia	89.0 ± 4.0	—	—	—
Ilioupolis	81.0 ± 4.0	—	—	—



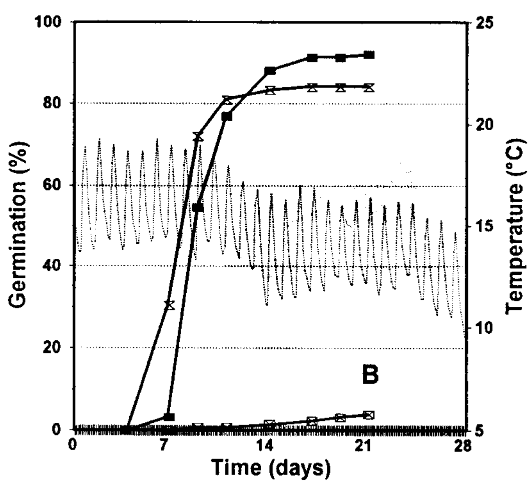


Figure 6. Time course of *Pinus halepensis* seed germination in simulated autumn conditions under different light regimes. A: diurnally alternating white light and darkness (□) and continuous darkness (■); B: diurnally alternating Far-Red (FR) and darkness ("intense", FRI_I:⊠, "mild", FRII:⊠) and continuous 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.

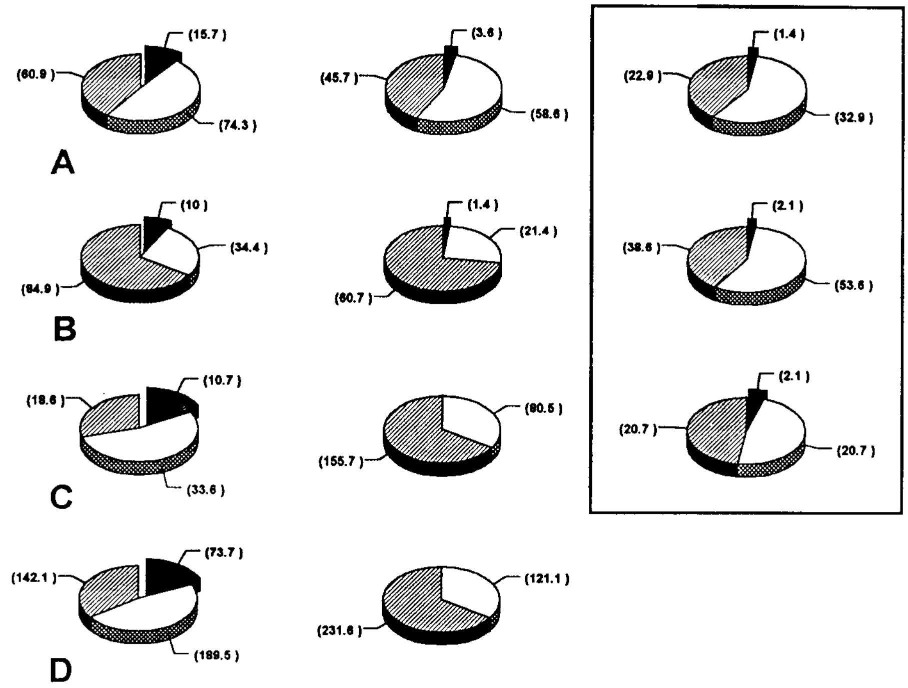


Figure 7. Soil banks of *Pinus halepensis* seeds in Stamata (A), Villia (B), Avlona (C) and Kapandriti (D). The four pairs of pies in the left part illustrate the composition of the seed bank just prior to the onset (left column) and after the end of the first postfire rainy season (middle column), respectively. Sampling took place in Nov. 1990 - Jun. 1991 (A and B), Oct. 1991 - Oct. 1992 (C) and Oct. 1992 - Jun. 1993 (D), for each of the four pairs, respectively. The three pies of the inset illustrate the soil seed banks in adjacent, unburned areas of the corresponding forests, after the end of the rainy season (June 1991, 1991 and 1992, respectively). The contribution of sound (germinable), empty and consumed pine seeds is depicted by black, white and stippled sectors, respectively; values in parentheses are the actual densities (seeds/m^2).

mentioned pine forests (Table 3) was evaluated on the basis of the following parameters: (a) the density of trees, (b) the mean number of cones produced per tree, (c) the mean number of seeds per cone and (d) the rate of cone opening during the dry season (as well as the assumption that only freshly-matured cones can open without a fire). Despite the large variations observed, particularly in the former two variables, the overall potential of the canopy store was of a similar order of magnitude in all three cases (several hundred seeds per square meter) while the estimated annual seed rain (dispersed in fire-free conditions) ranged from 25 to 105 seeds per square meter.

Discussion

Aleppo pine populations overcome the "destruction" caused by a fire event by the yearly production of large seed crops. In addition, a large fraction of pine seeds survive the lethal wildfire temperatures as a result of the insulation provided by the scales of the serotinous cones (C.A. Thanos et al. unpublished).

The significant delay encountered in the opening of maturing cones (a phenomenon called serotiny) could as well be termed as "bradychory" (i.e. delayed dispersal) if seed dispersal was considered as the central event. In Aleppo pine, a significant percentage of the yearly cone crop (45-80%) was found to remain closed on the tree. Furthermore, it is noteworthy that cone opening took place mostly during the first post-maturation summer only (and more specifically during the first part of the dry season) while the majority of the cones that remained closed will presumably be induced to open by a fire heat. A similar situation has been found with serotinous cones of *Pinus pungens* which remain closed for 2 years after maturity and then about 40% open without fire, while the rest remain closed on the tree, for a decade or more, maintaining their seeds in a viable state (Barden 1979).

Pinus halepensis forms a long-term, permanent seed bank in the canopy, a very important feature for the postfire regeneration of the forest. Cone opening performed in the laboratory (at 100 °C) showed that heating requirements for full opening ranged between 30-120 min and were strongly and positively correlated to cone age.

Seeds retained within cones of North American pines may remain viable for up to 20-30 years (Lamont et al. 1991), whereas it has been suggested that cones of many pine species (e.g. *P. radiata*) do not open, even for 50

Table 3. Estimation of the canopy seed bank size of *Pinus halepensis* in the pine forests of three regions of Attica. Tree density and cone measurements were accomplished during summer 1993. Canopy seed bank size at the start, middle and end (May, July and October, respectively) of the dispersal season is expressed as seeds per m^2 of forest surface; the last column represents an estimate of seed rain (for the particular dispersal period 1993) at fire-free conditions.

Region	Trees per ha	Cones per tree	Seeds per cone	Canopy Seed Bank (seeds / m^2) May	July	Oct.	Annual Seed Rain (seeds / m^2)
Stamata	895	166.9	52.8	790	745	685	105
Villia	2365	53.2	51.8	650	630	600	50
Ilioupolis	1000	35.9	31.9	115	100	90	25

years (Frankis 1991). Similarly, Aleppo pine seed longevity was not apparently affected by either the exposure to heat (up to 2 hours at 100 °C) or, more importantly, by cone age (at least up to three years). Nearly half of the seeds 4-5 and 6-9 years old were found still viable, while a dramatic reduction of germinability was observed in older seeds. On the other hand, *Pinus halepensis* seeds were all killed when subjected to a 10 min thermal treatment at 100 °C (M. Fenner personal communication). Similarly, viability of *Pinus rigida* seeds was unaffected when serotinous cones were subjected to temperatures as high as 200 °C; on the other hand unprotected seeds were killed after 3 min at temperatures equal or higher than 125 °C (Fraver 1992).

Optimal temperatures for Aleppo pine seed germination were found to be 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). At suboptimal temperatures (5 or 10 °C) both final percentage and rate of germination were reduced, particularly with increased seed age. However, such a loss of germination vigour might be attributed to an artificial ageing caused by the increased thermal treatment applied for cone opening. White light irradiation results in a marked promotion of germination, while Far-Red light causes a significant inhibition, in agreement with previous similar results (Thanos and Skordilis 1987; Skordilis 1992).

Postfire regeneration of *Pinus halepensis* depends exclusively upon the canopy seed bank due both to the short life span of the soil seed bank and the destruction of all the seeds that might happen to be found in the soil (mainly as a result of seed dispersal during the previous part of the dry season). The latter is further enhanced by the relatively large seed size which does not facilitate the penetration and subsequent accumulation of pine seeds in the soil (as is the case with the fire-adapted, hardcoated seeds of Cistaceae; Thanos et al. 1992). Postfire pine seed rain (judged from the soil seed bank) ranged from 63 to 405 seeds/m^2 in the four locations studied. All seeds had been dispersed shortly after the fire which explains why they were found at or near the soil surface, and many seeds were observed with their wings still intact. Similarly, seeds of *Pinus brutia* (Samos, Greece) and *P. pinaster* (SE Spain) in burned forests of Samos, Greece and SE Spain, respectively were found in the upper (0-2 cm) layers of soil (Thanos et al. 1989; Ferrandis et al. 1994). A significant density of viable seeds (10-74 seeds/m^2) was found in the soil, prior to the first postfire rainy season. The observed density of emerged Aleppo pine seedlings, at experimental plots established in these same forest locations, attained a maximum of 3-5 seedlings/m^2 (Daskalakou and Thanos 1995). Although this value may seem controversial in regard to the relatively high seed availability, the great toll paid to consumers and abiotic factors could simply resolve the matter. In addition, the eventual seedling density observed would correspond to a very densely regenerated forest (of the order of several tens of thousands of stems per hectare). In a postfire community of Taranto, the observed density of Aleppo pine seeds per square meter did not vary significantly from the corresponding values of the present study (Saracino and Leone 1994).

A preliminary approach to estimate the Aleppo pine regeneration capacity in real forest conditions, showed a significant variation among trees and sites (36-167 cones/tree). Evidently, the age of the forest, the environmental conditions of the particular year and site as well as the location characteristics would greatly contribute to this variability. Although there exists a gap of knowledge concerning the probable "incineration" of a portion of seeds (within the closed cones) during a wildfire, the evaluated total amount of the Aleppo pine postfire seed rain (on a 0% seed mortality basis) was not particularly variable, on the order of several hundred seeds per square meter. It is notable that these theoretical values are very close to the real ones (63-405 seeds/m^2) measured in the soil seed banks prior to the onset of the rainy season. According to Saracino and Leone (1994), seed density on the postfire ground was significantly correlated with the available cones per tree. Finally, the present estimations of the annual seed rain, in fire-free conditions, were significantly lower than the postfire ones, ranging from 25 to 105 seeds/m^2 in a particular year.

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