

# REPRODUCTION IN *PINUS HALEPENSIS* AND *P. BRUTIA*

Costas A. Thanos and Evangelia N. Daskalakou

Department of Botany, Faculty of Biology, University of Athens, Panepistimiopolis, Athens 15784, Greece. E-mail: cthanos@biology.db.uoa.gr

## Introduction

According to Theophrastus (371-286 BC), the founder of Plant Biology, "... some plants come only from seed, as silver fir, fir, pine and in general all those that bear cones..." (Enquiry into Plants II.II.2). This observation holds true not only for the pine species known during classical antiquity but also for almost the entire genus, with the exception of a few resprouters, such as *Pinus canariensis* and *P. edulis* (Mirov 1967). Therefore, sexual reproduction is of paramount importance for the survival and proliferation of pines, and this is even more dramatic under conditions of massive death. Both *Pinus halepensis* Mill. and *P. brutia* Ten. are obligate reseeders and their post-fire resilience relies upon a very powerful regenerative capacity based on both the yearly production of prolific seed crops and the safeguarding of canopy seed banks (Thanos 1999).

## Reproductive Patterns and Fertility Schedules in Mediterranean Pines

The growth and reproduction of *Pinus spp.* (a holarctic genus) is usually restricted to spring and is shifted to cover the summer months for the montane species. However, the cambial activity of Aleppo pine was found to take place throughout the year, provided that growth conditions were favourable (Lipshitz and Lev-Yadun 1986). Interestingly, for reasons pertinent to the evolutionary strategy of the genus, the female part in reproduction of pines is spread over several, usually 3, growth periods whereas pollen is initiated at the end of a growth season and is dispersed early during the following growth season. The Mediterranean pines, *P. pinea* (Francini 1958), *P. halepensis* and *P. brutia* (Panetsos 1981), along with the Mexican species, *P. chihuahuana* and *P. leiophylla* (Perry 1991), require 4 growth seasons, or almost 3 calendar years (Fig. 1). In *P. halepensis* and *P. brutia* the initiation of female conelets seems to take place at the end of the growing season; visualisation of their early development was observed, in the case of Aleppo pine in Italy, in the fall (Francini 1958), and in Israel during November-December (Weinstein 1989). Pollination takes place in March-April whereas fertilisation occurs only the next year, and by the end of that season, the green-coloured cones have almost attained their full size. Seeds ripen during the following season, and cone colour turns

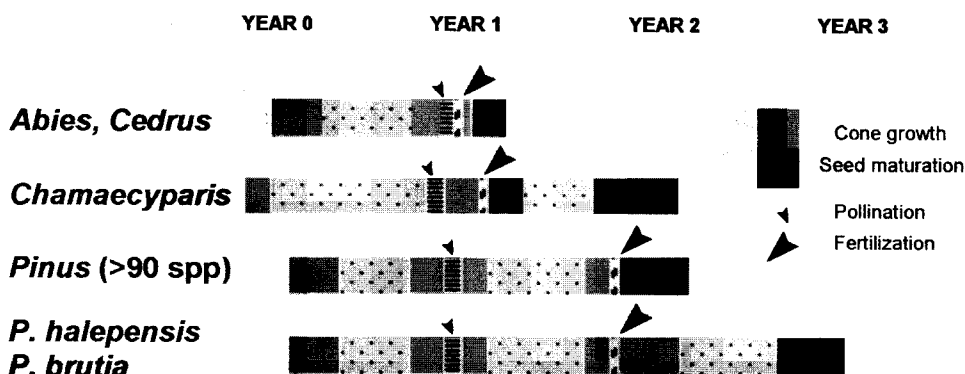


Fig. 1. Typical schedules of female cone formation in gymnosperms. Conelet induction and initiation take place in Year 0; dotted bars represent dormant periods. (Partly adapted from Eremko *et al.* 1989).

brown by the end of spring. Cone opening and subsequent seed dispersal may start, depending on the weather conditions (high temperature and low humidity), early in summer (June–July). However, a percentage of cones remains closed (perhaps ‘forever’, i.e., many decades, Daskalaku and Thanos 1996, Nathan *et al.* 1999), a phenomenon called serotiny or, according to a recently coined term, bradychory (Thanos 1999). The exact timing of when the enclosed seeds have ‘matured’ for germination is still not certain. According to Panetsos (1981), Aleppo pine seeds are ripe (within the cones) as early as in February but a recent work (Panayiotopoulos and Thanos unpublished) places seed maturation almost concurrently with ‘cone-browning’ (May–June). A similar, early-maturation citation for *P. brutia* seeds (Beskok 1970) also requires confirmation. According to that work, cones collected monthly as early as December (before the cone maturation season) contained seeds with high germination ability (>70%).

### Juvenile Period – Individuals and Populations

The duration of the female juvenile phase varies widely within the genus *Pinus*; the record holder for the shortest period (2 years) is *P. densiflora* (Mirov 1967) and that for the longest one (40–80 years) is *P. lambertiana* (Krugman and Jenkinson 1974). Male juvenility lasts longer in most species, a notable exception being *P. tabulaeformis*, which can produce pollen even in the first year (Mirov 1967). The duration of the juvenile phase is, of course, a population parameter. Similarly, the reproductive capacity (number of cones per year) is both environment- and age-dependent, in addition to the variability among individuals. All three factors bear quantitative complications, which have to be taken into consideration when discussing the build-up of the canopy seed bank.

It is well known empirically that both Aleppo and brutia pines have a remarkably short juvenile phase, which leads to early cone and seed production. Despite a number of publications stating that Aleppo pine bears cones at an early age (e.g.,

Mouloupoulos (1933): 10 years; Boudy (1950), Nahal (1962), Acherar (1981), Trabaud and de Chanterac (1985): 8 years; Trabaud *et al.* (1985): 7 years; Richardson (1988): 9 years), the well known and quite influential American reviews (Krugman and Jenkinson 1974, Young and Young 1992) erroneously mention 15-20 years (their cone opening and seed dispersal seasons for both Aleppo and brutia pines are also erroneous). In addition, nursery studies (Panetsos 1981, Matziris and Cooling 1982, Matziris 1997, 1998) have provided detailed information on the juvenile phase duration as well as on the reproductive capacity for numerous provenances of both species. Although no kinetic approach had been adopted, it was clearly concluded that under optimal, nursery conditions, the shift to the reproductive phase may take place (in a small fraction of the population) as early as the 3<sup>rd</sup> and 4<sup>th</sup>-5<sup>th</sup> growing seasons for *P. halepensis* and *P. brutia*, respectively, while production of male strobili is considerably delayed. At an age of 7 years, the entire population of nursery-grown Aleppo pine saplings were bearing cones (Panetsos 1981, Matziris 1997). On the other hand, brutia pine showed a considerably higher dispersion: the 12-year-old cone bearing plants reached only 63% overall (Matziris and Cooling 1982).

An early onset of the reproductive phase has been observed in a number of field studies on both species. For Aleppo pine it is usual to observe a few reproductive saplings at the age of 3 or 4 years in fast- and slow-growing, postfire populations, respectively (Thanos *et al.* 1998, Thanos *et al.* 1996). In *P. brutia*, the earliest occurrence of conelets may take place between 4 (Eron 1987, Spanos *et al.* manuscript, Fig. 2B) and 6 years of age (Thanos and Marcou 1993); Nahal (1983) suggests a moderate value, 10 years. A detailed analysis of the kinetics followed by several even-aged, postfire populations of Aleppo and brutia pine saplings has revealed an initial, exponential-like increase of the sexually mature population fraction (Thanos and Marcou 1993, Thanos *et al.* 1995 and 1998, Spanos *et al.* manuscript). This overall exponential trend (Fig. 2A) is expected to turn to sigmoid at a more mature stage; furthermore, the considerable fluctuation through consecutive years (e.g., Fig. 2B) merits additional investigation in regard to the possibility of a weak mast-ing behaviour, already implied for *P. brutia* (Panetsos 1981, Eron 1987).

In conclusion, the juvenile phase in an even-aged Aleppo pine population may end at an age of 3-6 years (Thanos *et al.* 1998) and is estimated to encompass the entire population after 12-20 years (although a small fraction of very low saplings may remain juvenile indefinitely). The  $J_{50}$  value (the age when 50% of the population is reproductive) may vary between 7 and 15 years (close to the approximate values given earlier by Boudy (1950): 10-12, and Acherar (1981): 9.4). The respective  $J_{50}$  values for *P. brutia* are postulated to be in the range of 10-20 years. Therefore, an even-aged Mediterranean pine forest will reach reproductive maturity at an age of 15-30 years, depending on environmental conditions and site quality.

It is well known that reproduction in pines is photoperiodically neutral (Mirov 1967). For reasons of promotion of cone production in commercially important conifers, the effects of a number of techniques and practices have been investigated. The exact timing of the morphological development of trees, including cone formation, is modified by environmental and other factors. However, the approximate time of differentiation must be known before attempts to modify the process are likely to succeed (Lavender and Zaerr 1986). The initial, critical event of the shift

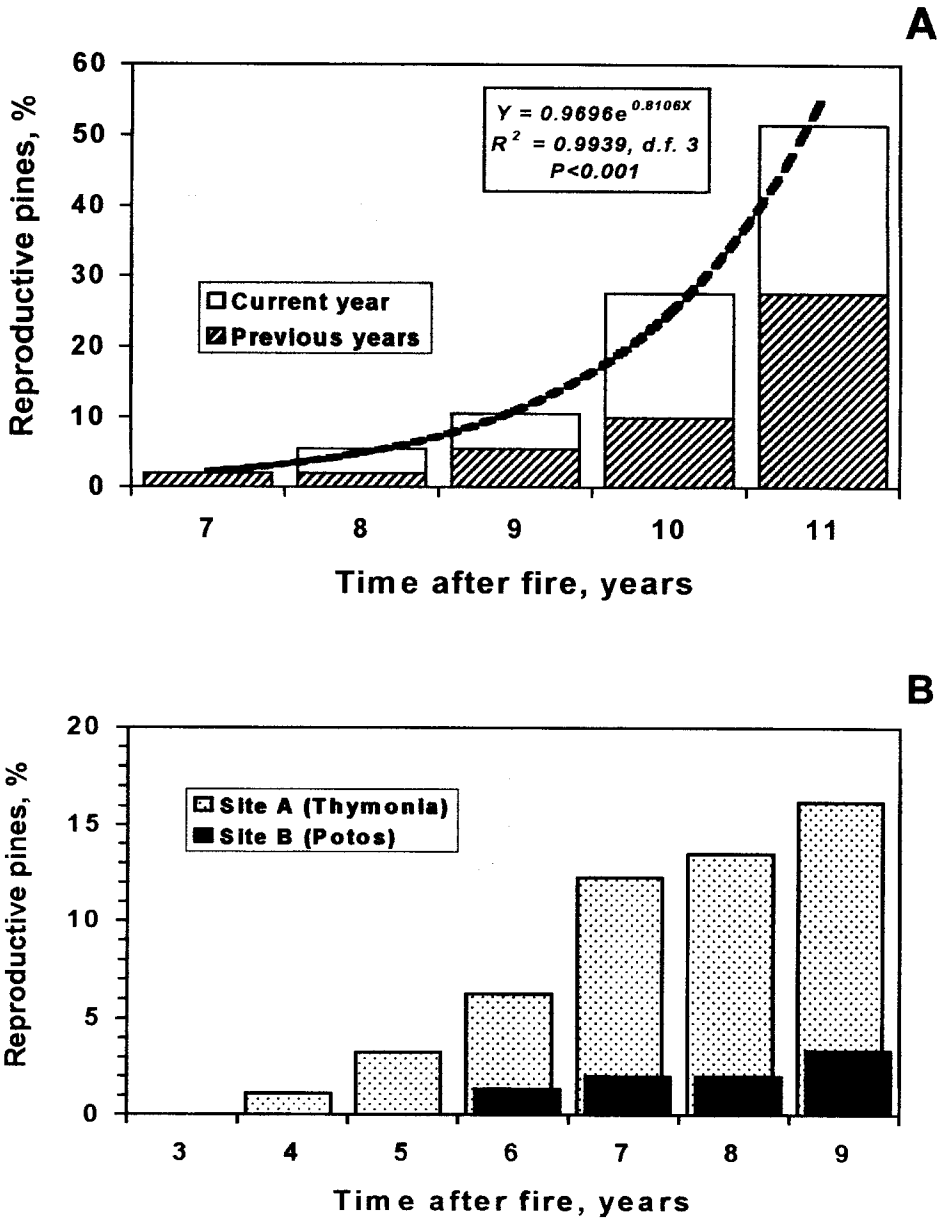


Fig. 2. The shift from juvenile to reproductive phase in populations of *P. halepensis* (A) and *P. brutia* (B) pine saplings in Xylokastro and Thasos, respectively. A: Bars represent current-year and accumulated values; B: bars illustrate the accumulated values for two subpopulations.

to reproductive development is undoubtedly the transformation of the apical vegetative meristems to reproductive ones. This seems to take place in summertime, but the inherent and environmental agents that induce (as well as the mechanisms that mediate and effectuate) the extent and the sex of the transformation are still elusive with the exception of the position effect (Thibaut *et al.* 1992) and the probable impact of high temperatures (Mirov 1967). On the applied level, the promotion of flowering, almost always involves an increase of reproductive capacity but only seldom the enhancement of juvenility termination. Within members of the Pinaceae family, traditional cultural practices, such as water stress, root pruning, N fertilising, girdling and high temperature were most commonly employed (Pharis and Ross 1986). GA<sub>3</sub>, which had been found to promote profuse flowering even in very young seedlings of conifers within Cupressaceae and Taxodiaceae, did not seem to affect species of the Pinaceae family. In natural, even-aged populations (Thanos *et al.* 1995, 1998) an extremely high correlation was found between plant size (stem height) and juvenile/mature status. Thus, both within a specific population (Fig. 3) and at an inter-population level (the case of Fig. 2B) most of the reproductive saplings belong to the tallest class. Certainly a great deal of basic research needs to be oriented towards the investigation and identification of the intrinsic mechanisms mediating the shift from vegetative to reproductive phase in pines. Nevertheless, it does not seem inappropriate to postulate a 'critical mass' trigger effect that would incorporate both the genetic and environmental components.

### Characteristics of Early-Formed Cones and Seeds

An interesting feature of the early reproduction in Mediterranean pines is the dramatically high degree of serotiny (Thanos *et al.* 1998). Figure 4 illustrates this finding; only 5% of cones in Aleppo pine saplings were 'opened' compared with over 50% in mature trees. The respective value for *P. brutia* was less than 15% of the observed, early-formed cones; despite the lack of relevant data for a direct comparison, it is well known that the latter species is, on the average, less serotinous (or bradychorous) than Aleppo pine. Therefore, and although it is too early to address the issue of the underlying mechanism of the phenomenon, this characteristic is of paramount ecological importance; such an extensive increase of cone serotiny during the initial, post-fire population stage contributes significantly to the build-up of the new, canopy seed bank.

Based on numerous cone collections of both species in Greece (Thanos *et al.* 1998, Spanos *et al.* manuscript), it may be suggested that cones formed at an early sapling age are relatively smaller than those produced by the mature plants of the same location. These smaller cones contain, usually, somewhat fewer and smaller seeds (Fig. 5), which nevertheless are almost equally germinable as those produced by mature trees. The slightly decreased cone and seed size may be attributed to the smaller plant biomass and available resources although in comparative terms the reduction is obviously not proportional.

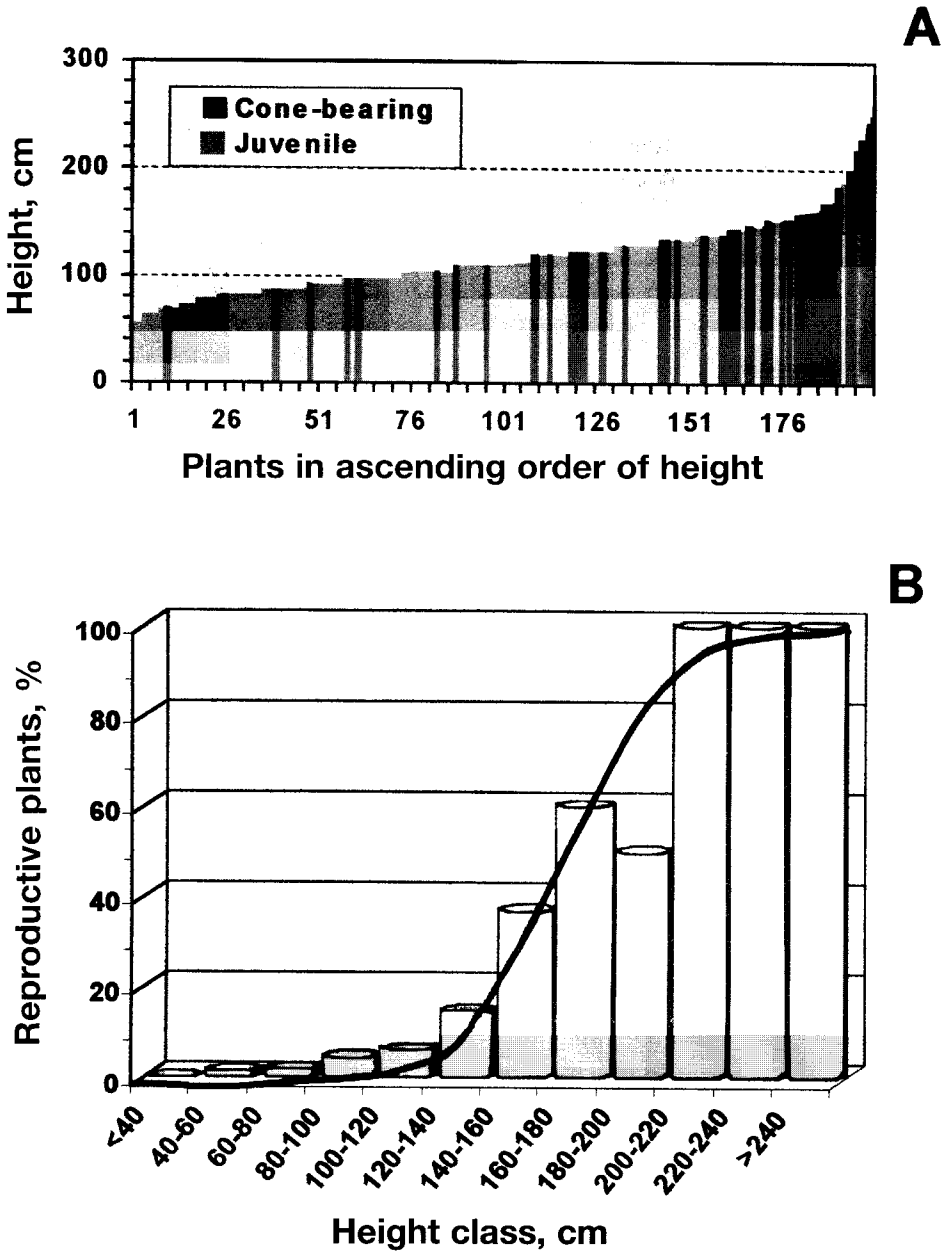


Fig. 3. Plant size and shift from juvenile to reproductive phase in saplings of *P. halepensis* (A) and *P. brutia* (B). Heights in even-aged, post-fire populations of pine plants, 7 and 10 years old, in Samos and Spetses (respectively) are either plotted individually (A) or in classes (B).

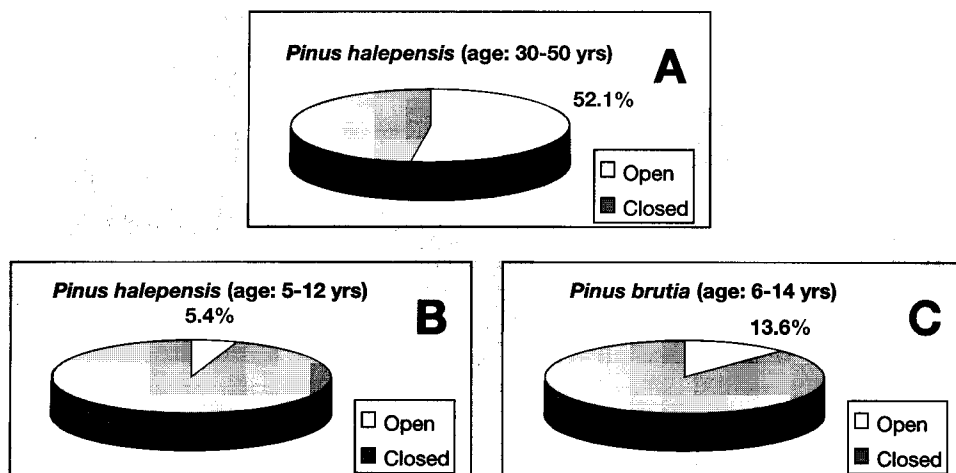


Fig. 4. Degree of cone serotiny in mature (A) and post-fire-regenerating (B, C) Mediterranean pine forests. Observations were carried out after the end of the dispersal season and refer to a total of 587, 184 and 286 cones (4, 13 and 12 cohorts of different maturation years) in 3, 5 and 2 forest areas (respectively). (Adapted from Thanos *et al.* 1995, 1998).

Several sources suggest that even though cones may be produced early, the initial cohorts of fully germinable seeds arise only at around 20 years of tree age (Mouloupoulos 1933, Boudy 1950, Nahal 1962). Nevertheless and despite its quite wide acceptance, this false assumption has been contradicted in several instances by experimental results. As early as in 1933 (Mouloupoulos), seeds extracted from cones of naturally growing, 13-year-old pines were found to display a substantial germinability (46%). In a recent nursery study (Matziris 1998), the cones produced by 10-year-old Aleppo pine saplings showed particularly high values of cone (49g) and seed (28.7mg) weight, which were attributed to the favourable growing conditions. Nevertheless, only 25 seeds per cone were produced (compare with Fig. 5A) and filled seeds amounted to only 67%. On the other hand, from the 11 collections obtained at 6 sites around Athens (cones produced by 5-11 year old trees), 87% of the seeds were filled and 75% (of the initial cohort) were found germinable (Thanos *et al.* 1998). In conclusion, early-formed cones seem to develop normally and the enclosed seeds are also normal; slight deviations from this rule (i.e., increased percentages of unsound seeds) may indeed be observed in cases where pollen supply is presumably not sufficient.

### Large and Lean Cone Crops – Individual and Populations Levels

By compiling data for 52 pine species, Strauss and Ledig (1985) concluded that serotinous species are more likely to bear crops every year than non-serotinous ones. This finding is ecologically plausible and seems to be the case for both the Mediterranean pine species. Nevertheless, Panetsos (1981) assumed that a higher than average seed crop is produced every 3 years in *P. brutia*. Similarly, Eron (1987)

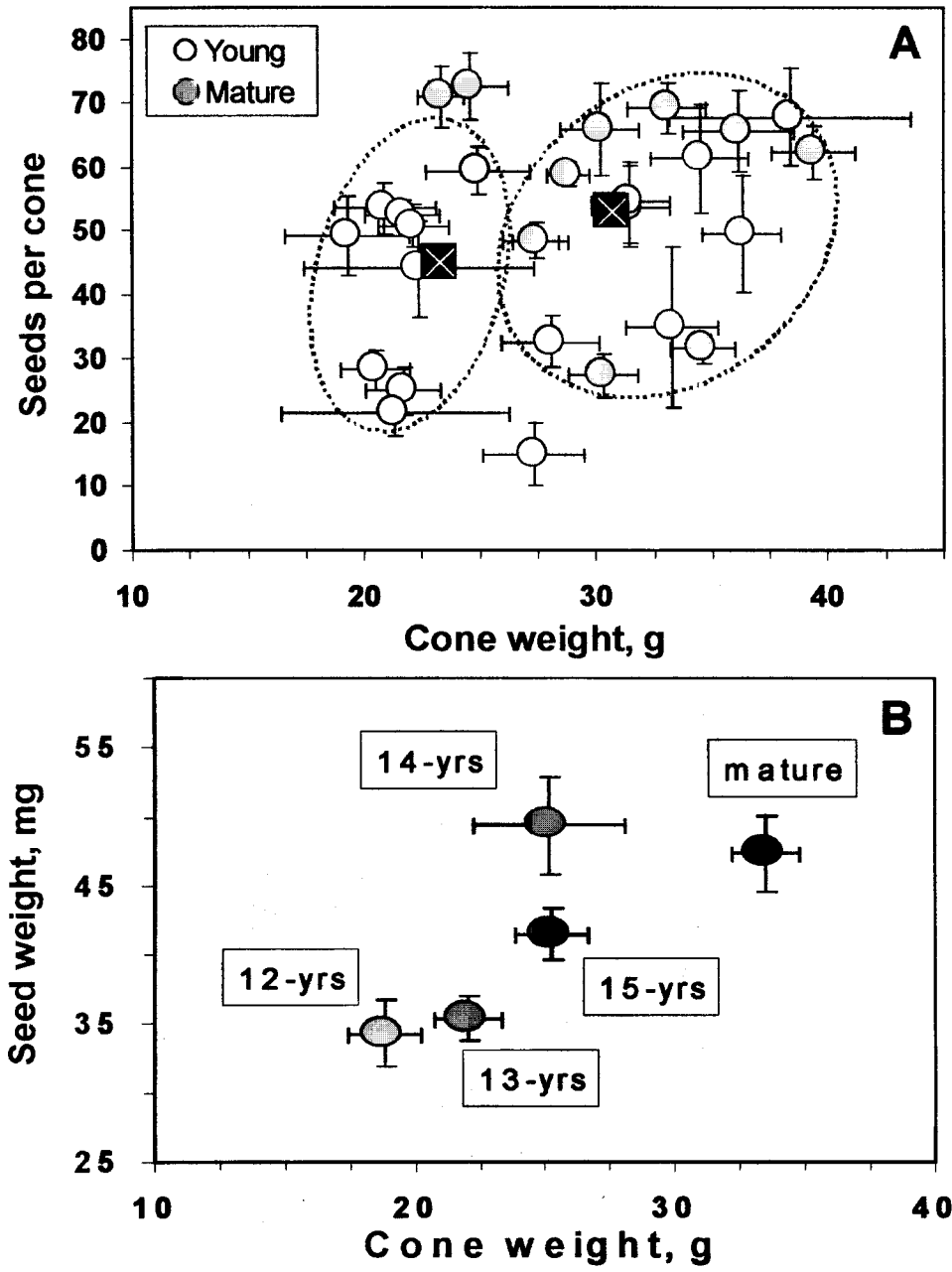


Fig. 5. Characteristics of cones produced by young and mature trees of *P. halepensis* (A) and *P. brutia* (B). Number of seeds per cone (A) and average seed weight (B) are plotted against cone weight. A: Data refer to 11 and 16 collections of cones from young (5-11 years old forest areas) and mature (30-50 years old) respectively; dark squares represent weighed means for each group. B: Cones of young trees (aged as shown) were collected from the same burned forest of Samos; mature refer to cones from an adjacent unburned site (45 years old). Horizontal and vertical bars represent standard errors (SE). (Adapted from Thanos *et al.* 1995, 1998).



claimed that *P. brutia* forests produce an abundant seed crop every 2-3 years; in lower elevations, however, a large amount of seeds are produced every year. Although neither citation is not based on solid evidence, it should be borne in mind that *P. brutia* is probably less serotinous than Aleppo pine. Therefore, cone crop kinetics at the population level require a serious and diachronic investigation prior to any final conclusion on the masting issue.

On the other hand, and besides the recent evidence of inter-annual fluctuations of cone crops (e.g., Fig. 2B), significant inter-annual variability has been detected at the individual level (Thanos *et al.* 1998). These individual fluctuations occur particularly at the very initial phase after the shift from juvenility into reproductive maturity and may be attributed to an 'exhaustion effect', due to the depletion of available resources already consumed by the powerful sinks of cones that developed in previous year(s). To cite a relevant passage from Mirov (1967), 'It is common for many pine species, after their initial outburst of flowering at a tender age, to have a long period of vegetative growth before their permanent reproductive stage is reached at a much older age'.

### Regeneration Potential and Its Build-Up in Post-fire Pine Populations

By examining 18 traits for 34 taxa of North American pines, McCune (1988) has described 5 adaptive modes. His group 4 comprises 11 fire-resilient species (12 taxa) that are precocious reproducers (average first seed-bearing age 6.8 years) with small and light seeds (9.7mg, the smallest value among the 5 groups), often in serotinous cones (by far the highest value among the 5 groups). In a similar study, Richardson *et al.* (1990) considered the factors contributing to the invasive potential of exotic pines in South African mountain fynbos and concluded that the most successful species (*P. halepensis*, *P. pinaster* and *P. radiata*) are fire-resilient, have small seeds, low seed-wing loading, short juvenile periods, moderate to high degrees of serotiny and relatively poor fire-tolerance as adults. Furthermore, they distinguished 5 functional groups, defined primarily by their potential for colonisation and explosive reproduction in fire-prone environments. They showed that these three highly invasive pine species are all classified in one group; taxa belonging in this group have very short juvenile periods, poor fire tolerance, are strongly serotinous and have the smallest seeds. The relatively short juvenile periods of these three pine species facilitate the rapid accumulation of new canopy-stored seed banks that perpetuate local populations. Furthermore, populations are buffered against local extinction following atypically short inter-fire cycles by immigration of seeds from adjacent areas (Richardson *et al.* 1990).

Both Mediterranean pines might be placed in the fire-resilient group of McCune (1988) and the relevant one of Richardson *et al.* (1990). However, it could be argued that the significantly higher (and extremely plastic among provenances) seed weight of *P. brutia* and probably its lower degree of serotiny might be an indication for a rather marginal participation of the latter species in the above-mentioned groups. Post-fire regeneration of both species depends exclusively upon the canopy seed bank, due both to the short life span of their soil seed banks and the destruction of all the seeds that happen to be found in the soil (Daskalakou and Thanos

1996). In a preliminary investigation to estimate the Aleppo pine regeneration capacity (cones/tree) under real forest conditions, a significant, but not unexpected, variation among trees and sites (36-167 cones/tree) was obtained (Daskalakou and Thanos 1996). Evidently, the forest age, the environmental conditions of the particular year and site as well as the location characteristics contribute considerably to this variability. The total amount of post-fire seed rain in a mature Aleppo pine was estimated to be on the order of several hundred seeds per square meter (Daskalakou and Thanos 1996).

Table 1 extends the previous attempt by incorporating data from two young, regenerating forests (of both species) as well. Moreover, in the case of Xylokastro (northern Peloponnese) forest, an initial approach to a diachronic investigation was made. This long-term study aims at elaborating, establishing and verifying a working model that will, at the same time, describe and predict the build-up of the canopy seed bank. It is proposed that this model should comprise, at least, the following parameters: (1) tree density, (2) reproductive capacity (annual production of cones per tree) and its three components, namely (2a) the population kinetics for the termination of juvenility, (2b) the inter-annual fluctuations caused by environmental and genetic factors, (2c) an age-dependence regulation index, (3) number of germinable seeds per cone, (4) degree of cone serotiny, (5) seed longevity within serotinous cones, (6) seed 'survival' within burned cones. A similar model was recently proposed by Roitenberg and Ne'eman (1999).

*Table 1.* Estimation of the canopy seed bank size in *P. halepensis* and *P. brutia* forests. The first 3 forests of the table are mature whereas the latter 2 were burned and are regenerating. Tree density and cone measurements were made during the summer of 1993 (1997 for Xylokastro). Pre-dispersal canopy seed bank refers to the end of spring whereas fire-free seed rain refers to seed dispersal throughout summer. Post-fire seed rain is given in a range of values; the exact value depends on the actual time of fire occurrence. (Adapted from Daskalakou and Thanos 1996, Thanos *et al.* 1995, 1998).

Pine species	Site	Region	Forest age (years)	Density (stems ha <sup>-1</sup> )	Cones per tree	Seeds per cone	Pre-dispersal seed bank (seeds m <sup>-2</sup> )	Fire-free seed rain (seeds m <sup>-2</sup> )	Postfire seed rain (seeds m <sup>-2</sup> )
<i>Pinus halepensis</i>	Stamata	Attica	40-50	895	166.9	52.8	790	105	685-790
	Villia	Attica	40-50	2365	53.2	51.8	650	50	600-650
	Ilioupolis	Attica	40-50	1000	35.9	31.9	115	25	90-115
	Xylokastro	Corinth	11	4000	0.17	27.0	1.8	0.1	1.7-1.5
			12	4000	0.73	27.0	7.9	0.7	7.2-7.9
			13	4000	1.73	27.0	18.7	1.7	17.0-18.7
<i>P. brutia</i>	Samos Is.	Aegean Sea	12	1500	0.25	48.9	1.8	0.2	1.6-1.8

## References

- Acherar, M. 1981. La colonisation des friches par le pin d'Alep (*Pinus halepensis* Mill.) dans les basses garrigues du Montpellierais. Thèse Doctorat 3<sup>me</sup> cycle, Ecologie, Univ. Sci. Tech. Languedoc, Montpellier, 210 pp.
- Beskok, T.E. 1970. Seed maturation period in *Pinus brutia*, *Picea orientalis* and *Abies bornmuel-leriana* (in Turkish). Turkish Forest Research Institute, Bulletin No 42.
- Boudy, P. 1950. Economie forestière Nord-africaine. II. Monographie et traitement du Pin d'Alep. Larose, Paris.
- Daskalakou, E.N. and Thanos, C.A. 1996. Aleppo pine (*Pinus halepensis*) postfire regeneration: the role of canopy and soil seed banks. International Journal of Wildland Fire 6: 59-66.
- Eremko, R.D., Edwards, D.G.W. and Wallinger, D. 1989. A guide to collecting cones of British Columbia conifers. British Columbia Ministry of Forestry, Research Branch, Victoria, B.C. FRDA Report No. 55.
- Eron, Z. 1987. Ecological factors restricting the regeneration of *Pinus brutia* in Turkey. Ecologia Mediterranea 13: 57-67.
- Francini, E. 1958. Ecologia comparata di *Pinus halepensis* Mill., *Pinus pinaster* Sol e *Pinus pinea* L. sulla base del compartamento del gametofito femminile. Annali dell' Accademia Italiana di Scienze Forestali 7: 107-172.
- Krugman, S.L. and Jenkinson, J. 1974. *Pinus* L. In: Schopmeyer, C.S. (technical coordinator), Seeds of Woody Plants in the United States, USDA, Forest Service, Agriculture Handbook No 450, pp. 598-638.
- Lipshitz, N. and Lev-Yadun, S. 1986. Cambial activity of evergreen and seasonal dimorphics around the Mediterranean. IAWA Bulletin 7: 145-153.
- Lavender, D.P. and Zaerr, J.B. 1985. Temperate conifer forest trees. In: Halevy, A.H. (ed), CRC Handbook of Flowering, CRC Press, Inc., Boca Raton, Florida, Volume I, pp. 1-13.
- Matziris, D. 1997. Variation in growth, flowering and cone production in a clonal seed orchard of Aleppo pine grown in Greece. Silvae Genetica 46: 224-228.
- Matziris, D. 1998. Genetic variation in cone and seed characteristics in a clonal seed orchard of Aleppo pine grown in Greece. Silvae Genetica 47: 37-41.
- Matziris, D. and Cooling, N.E. 1982. Differences among ten-year-old provenances of *Pinus brutia* (in Greek). Forest Research (Greece) 3: 97-121.
- McCune, B. 1988. Ecological diversity in North American pines. American Journal of Botany 75: 353-368.
- Mirov, N.T. 1967. The genus *Pinus*. Ronald Press, New York.
- Mouloupoulos, C. 1933. Observations and investigations on the regeneration of burned forests of *Pinus halepensis* (in Greek). Thessaloniki, pp. 1-24.
- Nahal, I. 1962. Le pin d'Alep (*Pinus halepensis* Mill.). Etude taxonomique, phytogéographique, écologique et sylvicole. Annales d' Ecole Nationale des Eaux et Forêts, Nancy, 19: 1-207.
- Nahal, I. 1983. Le pin brutia (*Pinus brutia* Ten. subsp. *brutia*). Première partie. Forêt Méditerranéenne 5: 165-172.
- Nathan, R., Safriel, U.N., Noy-Meir, I. and Schiller, G. 1999. Seed release without fire in *Pinus halepensis*, a Mediterranean serotinous wind-dispersed tree. Journal of Ecology 87: 659-669.
- Panetsos, C. 1981. Monograph of *Pinus halepensis* Mill. and *P. brutia* Ten. Annales Forestales (Zagreb) 9: 39-77.
- Perry, J.P. Jr. 1991. The pines of Mexico and Central America. Timber Press, Portland, Oregon.
- Pharis, R.P. and Ross, S.D. 1986. Pinaceae. Hormonal Promotion of Flowering. In: Halevy, A.H. (ed), CRC Handbook of Flowering, CRC Press, Inc., Boca Raton, Florida, Volume V, pp. 269-286.
- Roitenberg, D. and Ne'eman, G. 1999. Post-fire seed dispersal in *Pinus halepensis*. In: Ne'eman, G. and Izhaki, I. (eds), MEDPINE, International Workshop on Mediterranean Pines, Book of Abstracts, p. 46.
- Richardson, D.M. 1988. Age structure and regeneration after fire in a self-sown *Pinus halepensis* forest on the Cape Peninsula, South Africa. South African Journal of Botany 54: 140-144.
- Richardson, D.M., Cowling, R.M. and Le Maitre, D.C. 1990. Assessing the risk of invasive success in *Pinus* and *Banksia* in South African mountain fynbos. Journal of Vegetation Science 1: 629-642.
- Spanos, I.A., Daskalakou, E.N. and Thanos, C.A. manuscript. Postfire, natural regeneration of *Pinus brutia* forests in Thasos Island, Greece. (submitted for publication).

- Strauss, S.H. and Ledig, F.T. 1985. Seedling architecture and life history evolution in pines. *American Naturalist* 125: 702-715.
- Thanos, C.A. 1999. Fire effects on forest vegetation, the case of Mediterranean pine forests in Greece. In: Eftichidis, G., Balabanis, P. and Ghazi, A. (eds), *Wildfire Management. Proceedings of the Advanced Study Course on Wildfire Management*, Athens, October 1997, Algosystems and European Commission DGXII, Athens, pp. 323-336.
- Thanos, C.A., Daskalakou, E.N. and Nikolaidou, S. 1996. Early post-fire regeneration of a *Pinus halepensis* forest on Mount Parnis, Greece. *Journal of Vegetation Science* 7: 273-280.
- Thanos, C.A. and Marcou, S. 1993. Natural regeneration of *Pinus brutia* forests in Samos Island. Key events during the first 10 years of the postfire period. In: *Papers of International Symposium on Pinus brutia* Ten., Ministry of Forestry (Turkey), Marmaris, 18-23 October, 1993, pp. 176-183.
- Thanos, C.A., Skordilis, A. and Daskalakou, E.N. 1995. Comparative ecophysiological study of the postfire regeneration of Mediterranean pines (in Greek). Technical Report of Research Project PENED 91/824, Athens.
- Thanos, C.A., Skordilis, A. and Daskalakou, E.N. 1998. The regeneration potential of Aleppo pine (at young age stages) and the postfire resilience of Mediterranean forests (at gradually decreasing interfire periods) (in Greek). Technical Report of Research Project PENED 95/295, Athens.
- Theophrastus, *Enquiry into Plants*, vol. I. Hort, A.F. (translator, 1916), William Heinemann – Harvard University Press, London – Cambridge, Massachusetts.
- Thibaut, B., Loup, C., Chanson, B., and Dilem, A. 1992. La valorisation du pin d'Alep en zone méditerranéenne française. *Forêt Méditerranéenne* 13: 226-233.
- Trabaud, L. and de Chanterac, B. 1985. The influence of fire on the phenological behaviour of Mediterranean plant species in Bas-Languedoc (southern France). *Vegetatio* 60: 119-130.
- Trabaud, L., Michels, C. and Grosman, J. 1985. Recovery of burnt *Pinus halepensis* Mill. forests. II. Pine reconstitution after wildfire. *Forest Ecology and Management* 13: 167-179.
- Weinstein, A. 1989. Geographic variation and phenology of *Pinus halepensis*, *Pinus brutia* and *Pinus eldarica* in Israel. *Forest Ecology and Management* 27: 99-108.
- Young, J.A. and Young, C.G. 1992. *Seeds of woody plants in North America*. Dioscorides Press, Portland, Oregon.