

Canopy seed banks in Mediterranean pines of south-eastern Spain: a comparison between *Pinus halepensis* Mill., *P. pinaster* Ait., *P. nigra* Arn. and *P. pinea* L.

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Summary

1 Canopy seed banks were analysed in post-fire stands of *Pinus halepensis*, *P. pinaster*, *P. nigra*, and *P. pinea*. We determined age when flowering begins, age of first cone bearing, presence of serotinous cones and cone-opening temperatures.

2 By 15 years after the fire, *P. halepensis* had developed a large canopy seed bank ($3\text{--}100 \times 10^4$ seeds ha^{-1}). Fruiting started at 5 years of age. More than 86% of the cones were serotinous and had opening temperatures from 49.3 to 51.3 °C. Cones from adult trees opened at lower temperatures than those from young trees.

3 A 16-year-old *P. pinaster* stand had a smaller seed bank (12 000 viable seeds ha^{-1}) and a lower percentage of serotinous cones (66.7%), with lower cone-opening temperature (45.8 ± 0.8 °C) and later first fruiting (12 years) than any of our three *P. halepensis* populations.

4 Populations of *P. nigra* and *P. pinea* did not show any fire adaptations: flowering was insignificant even 15 years after fire, and none of the cones produced were serotinous.

5 Serotinous cones represent a fire-survival strategy for *P. halepensis* and *P. pinaster*. Early flowering is also necessary for successful post-fire colonization in species or populations where crown fires are frequent. Late flowering and non-serotinous cones of *P. nigra* and *P. pinea* suggest that they may have evolved where ignition leads only to low intensity ground fires.

Key-words: canopy seed bank, cone-opening temperature, fire, early flowering, serotinous cones

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Introduction

Long-term seed storage in fruits within the canopy (serotiny) is considered the main adaptation of some forest species to recurrent fires (Gill 1981; Lamont *et al.* 1991; Gauthier *et al.* 1996) and is common in families such as *Protaceae*, *Cupressaceae* and *Pinaceae* that dominate the flora of fire-prone areas (Gill 1981; Lamont 1985). Fire plays an important role in the Mediterranean Basin, especially in *Pinus halepensis* forests (Naveh 1975; Barbéro *et al.* 1998), but its vegetation has received less attention than in Australia, South Africa or North America.

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At least 14 species of *Pinus* in North and Central America, plus three in the Mediterranean Basin and one from the Canary Islands (*Pinus canariensis*), bear serotinous cones (Lanner 1998). Cones may remain closed until exposed to high temperatures ('pyriscence' *sensu* Lamont 1991) that melt their resin (45–60 °C, Keeley & Zedler 1998). Seed release therefore usually occurs after a fire, when the conditions for seedling establishment are most favourable (i.e. when competition for light, moisture and nutrients are reduced). Some cones, however, are 'xeriscent' (Nathan *et al.* 1999) and open after a variable period of drying conditions even in the absence of fires. Selection for early reproduction has ensured that a sufficient seed bank develops before the recurrence of fire (McCune 1988; Enright *et al.* 1996).

Serotiny levels vary among and within pine populations, depending mainly on age and fire regime, although factors such as seed predation can also be important

(McMaster & Zedler 1981; Lamont *et al.* 1991; Enright *et al.* 1996). Frequent high-intensity fires which kill all adult trees will favour serotiny (McMaster & Zedler 1981), especially if they affect large areas and there is little seed dispersal from adjacent unburnt areas.

Pinus halepensis, *P. pinaster* and *P. pinea* are common at low and intermediate altitudes in the Iberian Peninsula, whilst *P. nigra* ssp. *salzmannii* and *P. sylvestris* are found mainly at high altitudes. Stands of all except *P. halepensis* are sensitive to fire damage.

Forest fires have increased dramatically in the Mediterranean Basin over the past 50 years, especially in Spain, where about 2300 km² is now burnt each year (Dgcona 1994; Barbéro *et al.* 1998). The area of scrubland and *Pinus halepensis* forest has increased at the expense of other species, such as *Pinus nigra* and *P. pinea* (Barbéro & Quezel 1988; Trabaud *et al.* 1993) and fire frequencies of 20–25 years (Naveh 1990) or less give cause for concern. In Spain *P. halepensis* is the only clearly serotinous species (Trabaud *et al.* 1985), although *P. pinaster* may be (Gil *et al.* 1990), while the other pine species are non-serotinous. Seed production begins earlier in *P. halepensis* and *P. pinaster* (10–15 years) than in *P. nigra* and *P. pinea* (15–20 years) (Ruiz de la Torre 1979; Catalán *et al.* 1991), and *P. halepensis* may bear cones at 6–7 years old (Trabaud *et al.* 1985).

We compared fire-generated stands of *P. halepensis* and *P. pinaster* in South-eastern Spain with stands of *P. pinea* and *P. nigra*. Four life-history traits related to canopy seed storage were evaluated: onset of cone production; percentage of serotinous cones (if any); cone-opening temperature; and size of the canopy seed banks in young stands. We also compared opening temperatures to determine whether these explain why cones in young trees tend to remain closed longer than in adult ones.

STUDY SPECIES

Pinus halepensis is widely distributed at low and intermediate altitudes (0–1000 ma.s.l.) in eastern Spain but there is little genetic variability between populations (Gil *et al.* 1996). *Pinus pinaster* grows from sea level

to 2000 ma.s.l., forming scattered populations usually separated from each other by hundreds of kilometres. It occurs in almost all the Iberian mountain ranges and its tolerance of a wide range of soils and climates is reflected in considerable genetic variation (Alia *et al.* 1996).

P. pinea grows in unconsolidated soils up to 900 ma.s.l. and forms open forests with sparse understorey (Prada *et al.* 1997), while *Pinus nigra* ssp. *salzmannii* is largely restricted to calcareous soils in the mountains of eastern and southern Spain (Catalán *et al.* 1991).

STUDY AREA

All studied populations were located in the south-east of the Iberian Peninsula, except for one in central Spain (Fig. 1). The climate is typically Mediterranean: mean annual rainfall ranges from 450 (Ayora) to 950 mm (Piedralaves) with a pronounced summer drought (July to September) and mean annual temperature ranges from 12 °C (Villar del Humo) to 15.5 °C (Lujar). Lightning-induced fires are very frequent (> 0.4 fires 100 km⁻² year⁻¹) except at Lujar (0.1 fires 100 km⁻² year⁻¹; DGCONA 1994). Human-induced fires had burnt more than 40% of the forest area at each site in the 10 years previous to the study.

Materials and methods

Three stands of *P. halepensis* and one each of *P. pinaster*, *P. pinea* and *P. nigra* were selected (Fig. 1). All stands had recruited naturally after summer fires 15 or 16 years previously (Forest Administration files). Square plots (100 or 400 m² depending on density) were located at random in order to obtain at least 150 individuals, except in two stands (where density was low) where we surveyed at least 1400 m² (Table 1).

FIELD MEASUREMENTS

In July and August 1995, the altitude, slope, percentage scrub cover and number of trees were recorded

Table 1 Summary data for the studied populations of *Pinus* spp.

Population	Date of fire	Altitude (m)	Plots (n)	Area (m ²)	Trees (n)	Density (trees ha ⁻¹ ± SE)	a.a.g (mm year ⁻¹ ± SE)	Scrub (%)
<i>P. halepensis</i>								
Mira	1980	710	12	1200	1291	11 000 ± 2000	190 ± 20	89
Lujar	1980	580	10	1000	1026	10 000 ± 5500	120 ± 10	84
Ayora	1979	802	8	1400	379	3 000 ± 2000	160 ± 20	93
<i>P. pinaster</i>								
Ayora	1979	802	8	1400	96	700 ± 500	140 ± 40	89
<i>P. pinea</i>								
Piedralaves	1980	690	5	2000	139	700 ± 300	240 ± 20	41
<i>P. nigra</i>								
Villar del Humo	1980	755	5	2000	201	1 000 ± 300	230 ± 60	32

a.a.g. = average annual growth rate of the tallest trees.

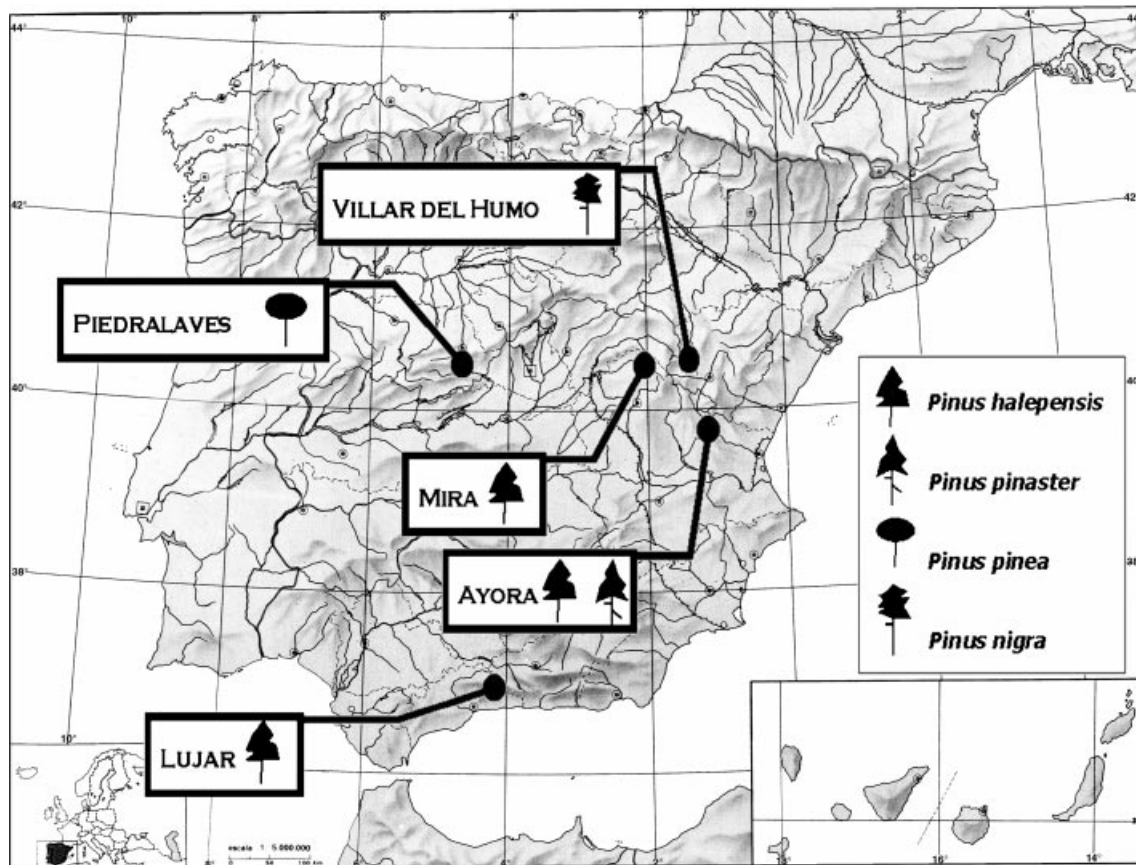


Fig. 1 Location of the study populations of four pine species.

for each plot. For each tree, height, presence of cones or male strobili and height of the oldest cone was also noted (Fig. 2). Each cone was allocated to a crop (i.e. year of ripening) and status (open or closed). All cones able to open would do so in the hot and dry Mediterranean summer. Cones of the 1995 crop were still green and, given that their seeds would not ripen until September–October, were excluded from further analyses.

DETERMINATION OF EARLIEST CONE-BEARING

The ripening year of each cone was determined by counting the number of whorls (Fig. 2, cf. the ‘stem node-ageing’ method of Lamont (1985) for *Banksia* species). Whorl counting is a reliable method for all studied species except *P. halepensis*, which produces several flushes of cones in a year. When whorl counting was not possible, cone age was calculated by counting the number of rings in the stem at the insertion point. Tree height at first flowering time was taken as the average height of the oldest cones. Successful reproduction was assumed to start in the year the oldest cone was produced (2 years after first flowering except in *P. pinea*). Average annual growth (a.a.g., used to represent site quality) was calculated

as the ratio of height to age for the tallest 10 trees in each plot.

EVALUATION OF SEROTINY

In each population the percentage of serotinous cones was estimated for all crops combined, as well as individually for 1993 and 1994, as the proportion of cones that remained closed. Age, height and diameter at breast height (d.b.h.) were measured in 30 randomly selected trees, separated from each other by at least 100 m, in older unburnt areas adjacent to each of the studied stands. The cones of the last two crops were counted and their status recorded. *P. halepensis* and *P. pinaster* were measured in summer 1995 and the other species in 1999.

OPENING TEMPERATURE OF SEROTINOUS CONES

One cone was collected from each of 30 trees in one population of each species in January 1995. The seeds were by then mature but the cones remained closed. After drying to constant weight at a maximum of 28 °C, the temperature was slowly increased to 45 °C (about 2 °C every 10 days at relative humidity < 20%). Cones were weighed and their status monitored twice

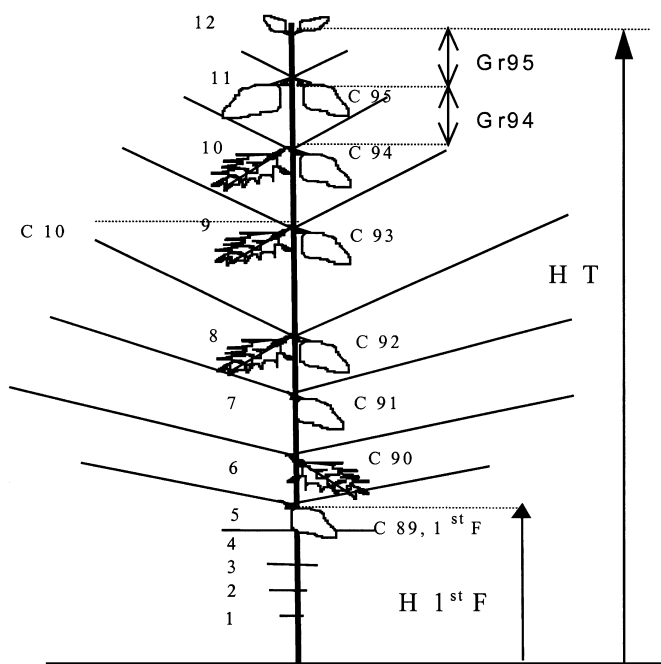


Fig. 2 Schematic representation of data collection of open and closed cones for *Pinus* trees with age estimated by counting whorl. (G r = growth in year t; C = cones ripened in year t, following initiation in previous year; H 1st F = height at first flowering (i.e. of oldest cone); H T = height of tree).

a week: those that opened below 35 °C (a temperature easily reached in a forest canopy) were classified as non-serotinous and those that remained closed at least up to 40 °C were classified as serotinous.

For each serotinous population one closed cone from each crop on five randomly selected trees was harvested during July–August 1995. A protocol based on that of Perry & Lotan 1977 was used to assess the temperature at which resin seal on the scales was broken. An aluminium bowl containing 3 L of water at room temperature was put in a water bath at 70 °C. Cones were placed in the bowl when the water temperature (measured with a thermometer) reached 30 °C. Opening was accompanied by the emission of air bubbles and an audible ‘crack’ as the scales separated abruptly, and the temperature was then noted. Bowl-water temperature typically rose 20 °C within 4 min. Mean cone-opening temperature was calculated for the two younger crops combined (1993 and 1994) and for 1990–92 crops. Mean sample analysis (Tukey HSD $P < 0.05$) was used to compare populations within age groups. Preliminary tests found no violations of the assumptions of normality and homoscedasticity.

ESTIMATION OF THE CANOPY SEED BANK

Cones were heated to a maximum of 45 °C, to promote opening and facilitate seed extraction. Seed viability was assessed in five replicates of 100 seeds per population using tetrazolium chloride solution (Cottrell 1947). The size of the canopy seed bank in 1995, when the trees were 15–16 years old, was then given by this value multiplied by the number of closed and mature

cones and by the mean number of filled seeds per cone.

DIFFERENCES BETWEEN YOUNG AND ADULT TREES OF *PINUS HALEPENSIS*

In November 1998, 20 young *P. halepensis* trees (age 18 years, average height 2.8 m) were randomly selected in the burnt area at Mira and 15 adults (> 40 years, 9.6 m) were found in adjacent areas. Closed cones from the 1994–97 crops were collected at random (where possible two cones per tree per crop). When whorls were not evident, cone age was determined by cutting the cone branch and counting its rings. Cone-opening temperatures were estimated and an average value obtained for each crop and tree age. The data fulfilled the requirements for analysis by ANOVA and a multiple range test (Tukey HSD $P < 0.05$) was used.

Results

CONE PRODUCTION

In *Pinus halepensis* and *P. pinaster*, the number of cones tended to increase with age (Fig. 3), but subsequently decreased in two out of three *P. halepensis* populations (Mira and Lujar). Neither *P. pinea* nor *P. nigra* produced significant numbers of cones below age 15. Highest annual production was recorded for *P. halepensis* at Lujar, three times as many as at Mira, where tree density is similar and 10 times the value for this species at Ayora, where trees are less abundant.

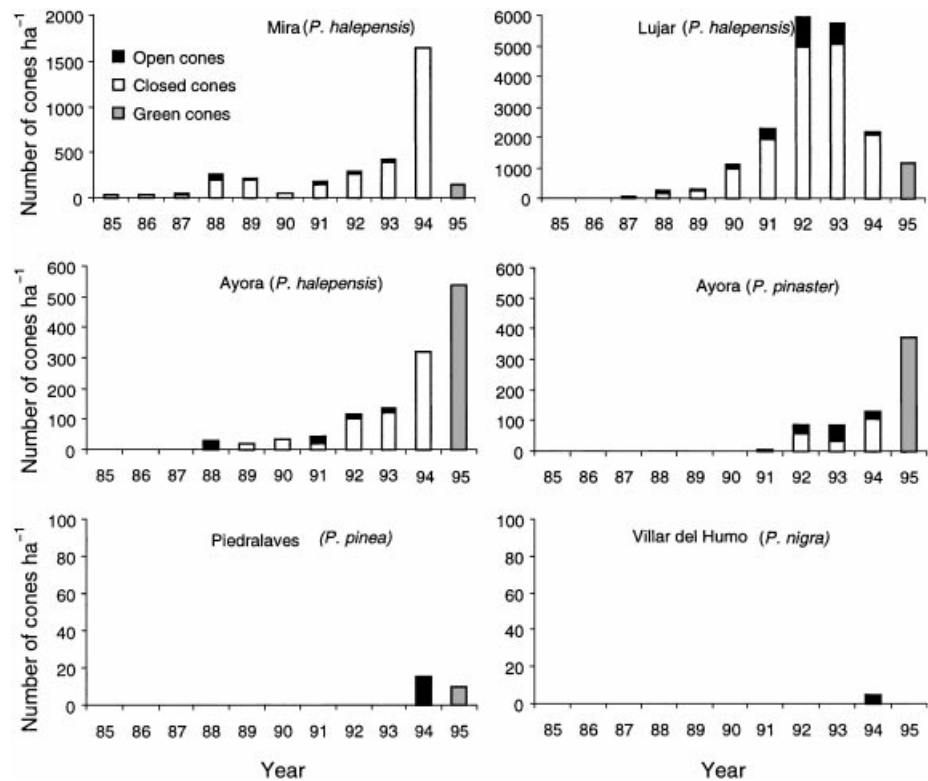


Fig. 3 Variation of number of open and closed cones per hectare with tree age. Stands regenerated after fires in 1970 or 1980. Note: vertical scale differs between species and locations.

Table 2 Flowering characteristics of each population. Plot means are given for age of each tree and its oldest cone and its height at first flowering

Population	Age		H 1st F (cm)	Percentage of reproductive trees (1995)	
	Tree	Cone		F	M
<i>P. halepensis</i>					
Mira	15	5	110 ± 20	8.1	0.0
Lujar	15	7	85 ± 5	8.1	5.5
Ayora	16	9	120 ± 20	17.8	7.4
<i>P. pinaster</i>					
Ayora	16	12	190 ± 50	25.0	7.5
<i>P. pinea</i>					
Piedralaves	15	14	340 ± 50	3.1	1.0
<i>P. nigra</i>					
Villar del Humo	15	14	320	0.5	0.0

H 1st F (mean ± SE); F = trees with cones; M = trees with only male strobili.

EARLY CONE-BEARING

Pinus halepensis was the first species to start yielding seed (Table 2), but age at first reproduction varied from 5 at Mira to 9 at Ayora. Here, and at Ayora, *P. pinaster* first seeded at age 12 and, although both *P. pinea* and *P. nigra* started seed production at 14, amounts were insignificant compared to the other two species.

The height of the trees at first reproduction also varied between *P. halepensis* populations (83–122 cm), and was lowest at Lujar. Values for *P. pinaster* were

192 cm and for *P. nigra* and *P. pinea* were > 3 m. The percentage of reproductive trees (with cones, conelets or male strobili) in 15–16-year-old stands was higher in *P. halepensis* and *P. pinaster* stands than in the other species and was higher in both species at Ayora than in other *P. halepensis* stands.

SEROTINITY

Closed cones were present in all the sampled populations of *P. halepensis* and *P. pinaster*, but both

Table 3 Number and serotiny of cones in young and neighbouring unburnt stands. Only the last two crops (1993–94) were sampled in adult stands

Population	Young stands				Adult stands	
	Number of cones		Percentage of serotinous cones		Number of cones	Percentage of serotinous cones
	All crops	Last two crops	All crops	Last two crops		
<i>P. halepensis</i>						
Mira	379	249	94.2 ± 2.1	98.4 ± 1.8	206	81.0
Lujar	1785	792	86.9 ± 2.6	90.9 ± 2.4	322	59.3
Ayora	98	64	89.8 ± 4.3	96.9 ± 3.6	166	93.9
<i>P. pinaster</i>						
Ayora	43	30	65.1 ± 5.9	66.7 ± 20.9	140	58.7
<i>P. pinea</i>						
Piedralaves	3	3	0	0	147	0
<i>P. nigra</i>						
Villar del Humo	1	1	0	0	214	0

Table 4 Cone-opening temperature in dry air (see Methods) of ripe cones of four pine species. The number of cones of each type is given in parenthesis

Population	Cone-opening temperature ± SE (°C)	
	Non-serotinous	Serotinous
<i>P. halepensis</i>		
Ayora	–(0)	> 45.0 (30)
<i>P. pinaster</i>		
Piedralaves	32.0 (9)	> 45.0 (21)
<i>P. pinea</i>		
Piedralaves	28.0 (30)	–(0)
<i>P. nigra</i>		
Villar del Humo	28.0 (30)	–(0)

number and percentage varied. Neither *P. pinea* nor *P. nigra* produced serotinous cones, even in adult stands where the number of cones was higher (Table 3).

Almost all the most recent cones in young stands of *P. halepensis* were serotinous (> 90% for 1993 and 1994 and even larger for 1994 only) compared with

only 66.7% in *P. pinaster* (Table 3). Older *P. halepensis* and *P. pinaster* trees all bore both types of cones, and although serotiny was less marked, especially at Lujar, *P. halepensis* was still the more serotinous species.

CONE-OPENING TEMPERATURE

The preliminary study revealed that all *P. pinea* and *P. nigra* cones opened at the lowest temperature tested (i.e. 28 °C or less) (Table 4). *P. pinaster* had both non-serotinous cones, which opened at 32 °C, and serotinous ones, which remained closed at 45 °C, as did all *P. halepensis* cones.

When opening was measured under water, *P. halepensis* cones opened at higher temperatures (mean: 50.7 ± 0.4 °C) than *P. pinaster* (45.8 ± 0.8 °C) (Table 5). These differences are mainly due to *P. halepensis* cones from the two most recent crops needing 3–4 °C more than older cones of either species. Opening temperatures for *P. halepensis* differed between populations such that the smaller proportion of serotinous cones found at Lujar also required less heat to open.

Table 5 Cone-opening temperature under warm water (see Methods) in serotinous cones of *Pinus halepensis* and *P. pinaster*. Sample size in parenthesis. Means followed with the same letter were not statistically different (Tukey HSD $P < 0.05$)

Population	Cone-opening temperature ± SE (°C)		
	93–94 crops	90–92 crops	All crops
<i>P. halepensis</i>			
Mira	53.2 ± 0.8 (10)a	50.5 ± 1.0 (15)a	51.6 ± 0.6a
Lujar	51.9 ± 0.9 (10)a	47.7 ± 0.6 (15)b	49.3 ± 0.5b
Ayora	53.4 ± 0.8 (10)a	49.7 ± 0.9 (15)a	51.2 ± 0.6ab
<i>P. pinaster</i>			
Ayora	45.3 ± 1.0 (10)b	46.3 ± 1.2 (9)b	45.8 ± 0.8c

Table 6 Size of the canopy seed bank in *Pinus* species in south-eastern Spain (mean \pm SE). All stands were 15–16 years old and originated after fire

Population	Age	Serotinous cones ha ⁻¹ \pm SE	Seeds cone ⁻¹	Seed bank ha ⁻¹ \pm SE
<i>P. halepensis</i>				
Mira	15	3 000 \pm 550	58.4	175 000 \pm 32 000
Lujar	15	15 000 \pm 5 500	66.7	1 000 000 \pm 350 000
Ayora	16	600 \pm 450	53.5	35 000 \pm 25 000
<i>P. pinaster</i>				
Ayora	16	200 \pm 75	62.5	12 000 \pm 4 500

Canopy seed bank in summer 1995 = number of closed cones (up to 1994) \times number of viable seeds per cone.

THE CANOPY SEED BANK

The canopy seed bank for *P. halepensis* differed between populations (Table 6). The large mean number (21.5) of serotinous cones per 15-year-old reproductive tree at Lujar led to a huge canopy seed bank, with more than 1 million seeds ha⁻¹. Similar aged trees at Mira and Ayora had fewer serotinous cones but the canopy seed bank was still important. Most of the differences in the size of the canopy seed bank could be explained by cone production.

Pinus pinaster held a much smaller canopy seed bank than *P. halepensis*, with a mean value of 1.8 serotinous cones per reproductive tree at age 16. Cone production in *P. pinea* and *P. nigra* at age 15 was negligible and although some seeds were produced the absence of serotinous cones precluded formation of a canopy seed bank.

DIFFERENCES BETWEEN YOUNG AND ADULT PINUS HALEPENSIS AT MIRA

Cone-opening temperature differed significantly with both tree age ($P < 0.0001$, $F = 149.2$, $n = 181$) and crop year ($P < 0.0001$, $F = 33.7$) but their interaction was not significant. The cone-opening temperature was 5 °C higher in young individuals (46.6 ± 0.3 °C, $n = 95$) than in adult ones (41.6 ± 0.3 °C, $n = 86$) and, in both, the values decreased with the age of the cone (Fig. 4).

Discussion

All three populations of *Pinus halepensis* showed early flowering (measured as age or height at first seeding),

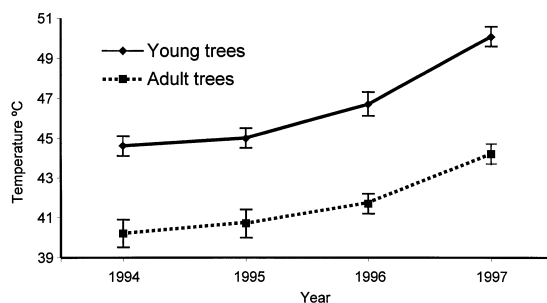


Fig. 4 Cone-opening temperature of young and adult trees of *Pinus halepensis* at Mira according to crop year.

similar to populations in Greece (Panetsos 1981), France (Trabaud *et al.* 1985) and north-eastern Spain (Papió 1994). Progeny trials near Ayora (A. Prada, unpublished data), in which 7% of trees started flowering at 4 years of age, suggest that this species can mature even younger, with earlier seed cone formation possibly prevented by lack of pollen. The 1979 fire at Ayora burnt more than 30 000 ha and left large areas with few remaining adults (none located less than 4 km from the study plot). Thus, the development of fertilized female strobili may have been delayed until the trees could produce sufficient pollen themselves. Other serotinous species (North American pines, Mccune 1988; some *Banksia* species in Australia, Enright *et al.* 1996) give similar results, confirming that early flowering is an important adaptation to fire: the sooner cone production starts, the sooner a large canopy seed bank is formed. *P. pinaster* at Ayora started fruiting later than other Spanish populations (12 vs. 7 years, Tapias 1998). The absence of reproductive precocity in *P. pinea* and *P. nigra* confirms earlier reports (Krugman & Jenkinson 1974; Ruíz de la Torre 1979) and is similar to other non-serotinous pines that grow in low to moderately productive sites (Mccune 1988).

Fifteen or 16 years after the fire, the percentage of reproductive trees in all species was low. The higher percentage found at Ayora for both *P. halepensis* and *P. pinaster*, taking into account their delayed onset of maturity, may compensate for differences in the density of the stands (higher at Mira and Lujar, with more than 10 000 trees ha⁻¹).

Both *P. halepensis* and *P. pinaster* bore serotinous cones. More than 85% of *P. halepensis* cones in young stands and more than 59% of cones in old stands were closed, suggesting that serotiny is higher than in North America species such as *P. contorta* (0–72%, Lotan 1975; Ellis *et al.* 1993) and *P. banksiana* (43–87%, Gauthier *et al.* 1993) and other populations of the species in Israel (Nathan *et al.* 1999) and Greece (Daskalakou & Thanos 1996). The differences among *P. halepensis* populations may be due to genetic differences in the strength of the resin bond as well as to differences in the frequency and intensity of hot and dry spells. The stand at Lujar, with a lower cone-opening temperature, also had the lowest serotiny, and the dry Sirocco-type winds coming from the Atlas Mountains

(Nathan *et al.* 1999) may facilitate faster cone-opening at this site.

Such life history adaptations may be important in moderately productive sites with high intensity fires. Both the abundant cone production and the high serotiny of *P. halepensis* allow the accumulation of a copious canopy seed bank, ranging from 33 000 to 1 million seeds ha⁻¹. Enright *et al.* (1996) have estimated for other species that production of about 100 seeds is needed to establish one adult plant post-fire and, for *P. halepensis*, this would give tree densities in the same order of magnitude as those at our study sites. The seed bank allows intensive recruitment of 50 000–200 000 seedlings ha⁻¹ (Ne'eman *et al.* 1992)

The cones of *P. pinea* and *P. nigra* open at low temperatures (28 °C). When the cone dries, the scale shrinks lengthwise (Dawson *et al.* 1997), finally breaking the resin seal. On a typical dry and hot summer day, this shrinkage is sufficient to open cones of these non-serotinous species, but all cones of *Pinus halepensis* and two-thirds of those of *P. pinaster* remain sealed. The opening temperature of serotinous cones (40–55 °C) was similar to that of the North American *P. contorta* (45–60 °C vs. 25 °C for non-serotinous cones, Crossley 1956; Perry & Lotan 1977). Cone-opening temperature varied among species and, for *P. halepensis* (which had the highest value), both among and within populations. The higher cone-opening temperature observed in young individuals is consistent with the lower percentage of serotinous cones found in older trees at the same site (Mira), but may be related to different environmental conditions during cone formation rather than tree age *per se*. Opening temperatures decreased with the age of the cone and the lack of closed cones more than 5–6 years old on adult trees might be due to changed resin properties such that summer temperatures are now enough to break the seal.

In contrast to *P. halepensis*, *P. banksiana* only shows serotiny in adult trees with d.b.h. > 7 cm and its degree increases with age (Gauthier *et al.* 1993). The differences may be due to *P. halepensis* forests having evolved with shorter intervals between crown fires (about 25 years, Agee 1998) than *P. banksiana* forests (50–150 years, Heinselman 1981). The latter grows in boreal forests where there is limited shrub production, whereas the continuous understorey in *P. halepensis* forests may reach 1–1.5 m. Serotiny is an advantage in young *P. halepensis* because it allows rapid development of a sufficient seed bank to ensure recruitment. Moreover, *P. halepensis* produces an abundant cone crop every year (compared with only every 3–4 years in *P. banksiana*, Krugman & Jenkinson 1974), so that, in older trees, the previous years crop is enough to enable post-fire regeneration. If no fire occurs, the less serotinous (xeriscent) cones open in the dry and hot summer and dispersed seed may colonize gaps due to winds, storms, landslides, diseases or pests. The woody understorey that grows in *P. halepensis* (and *P. pinaster*) stands leads to high intensity fires that scorch 100% of the crowns (Agee

1998), but serotinous cones allow re-establishment even of young stands.

Our data confirm that *P. pinaster* populations can be serotinous (Gil *et al.* 1990; Tapias 1998) where, as in Spain, it can be of adaptive value, but they may otherwise be non-serotinous (Keeley & Zedler 1998). The presence of serotinous and non-serotinous individuals in the same population explains why only two-thirds of the cones from Ayora trees are serotinous. Other pines, such as *P. contorta* (Muir & Lotan 1984; Tinker *et al.* 1994) have similar serotinous and non-serotinous populations, depending on the natural fire regime.

Both *P. pinaster* and *P. halepensis* were present at Ayora, but the lower percentage of serotiny and lower cone-opening temperature in *P. pinaster* suggest that its cones are more likely to open on hot summer days, and that *P. halepensis* will thus be able to maintain a greater canopy seed bank in xeric locations. The warmer and dryer climate throughout the last 50 years may have allowed expansion of *P. halepensis* at the expense of *P. pinaster*, whereas it had previously been confined to lower altitudes (Bosch 1866).

Early flowering and serotiny have no ecological advantage in *P. pinea* and *P. nigra*. Natural *P. pinea* forests grow on nutrient-poor, highly drained sandy soils, where the growth of shrubby species is limited by water and nutrient deficits (Prada *et al.* 1997). The understorey is therefore sparse and can not sustain ground fires, and their thick bark and self-pruning of low branches make adult pines resistant. Natural *P. nigra* forests show a similarly sparse overstorey and, if present, the woody understorey reaches only up to 0.5 m in height (Regato-Pajares & Elena-Rosselló 1995). *P. nigra* is one of the longest-lived Iberian plants, with extant individuals more than 1000 years old (Creus 1998), and like *P. pinea* can withstand low-intensity fires. Prolific seeding every 3–4 years compensates for low seed production in the intervening period, and shade-tolerance (Regato-Pajares & Elena-Rosselló 1995) may allow colonization of tree-fall gaps following dispersal of the small winged seeds. *P. pinea* has large heavy seeds, dispersed by animals, whose development takes 2 full years. However, the reserves enable rapid root development so that the seedling reaches the water layer sooner.

Other ground-fire resistant pinyon pines, such as *P. monophylla* and *P. cembroides*, have similar life-history characteristics to *P. pinea* (McCune 1988), whereas *P. nigra* is more like *P. ponderosa* and *P. palustris*. None of these species have serotinous cones because flames do not reach the canopy and adult trees are able to survive ground fires (McCune 1988).

Dense stands of all four species were widely planted in Spain during the 1950s, and under these conditions ignition can spark off an intense crown fire. Species with serotinous cones are more likely to survive than those that lack canopy seed banks (Trabaud & Campant 1991). The distribution area of *P. nigra* ssp. *salzmannii* has indeed decreased due to the expansion of *P. pinaster*

after fires (Barbéro & Quézel 1988). Traditional Spanish forest management practices which increase canopy density have increased the frequency and intensity of fires and are thus threatening species such as *P. nigra*.

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