



Life histories of Mediterranean pines

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Abstract

The life history of Spanish pines and their relation to fire as the main disturbance factor in their ecosystems was analysed. The primary ecological attributes studied were the canopy seed bank (onset of cone production, percentage and persistence of serotinous cones), seed and cone morphology, sprouting and bark thickness. Four ecological groups were separated using multivariate cluster analysis and their life-history characteristics are discussed. Serotiny and early flowering in *Pinus halepensis* and *P. pinaster* reflect their evader strategy in relation to fire as this character is advantageous to survive frequent crown fires and to attain successful post-fire recruitment. Late flowering and absence of serotinous cones in *P. nigra*, *P. sylvestris* and *P. uncinata* indicate that their natural forest did not evolve under frequent crown fires. *P. canariensis* and *P. pinea* appeared in two single groups because of their sprouting capability and their seed size respectively. Intraspecific variation in *P. pinaster* was also analysed using the same criteria and high variability was found in its life history traits. A group of *P. pinaster* populations showed high levels of serotiny and thin bark as a possible adaptation to frequent stand-replacing crown fires. In contrast, a group of non- or weakly-serotinous populations seems to have evolved under a low-intensity fire regime where the best fitness corresponds to thick-barked individuals capable of surviving ground fires. Intermediate strategies were also evident in this species and were discussed in relation to the effect of different fire regimes caused by the understorey vegetation.

Introduction

It is widely accepted that pines prevail in areas with adverse climatic and edaphic conditions as well as in first succession stages (Bond 1989, Reich et al. 1995; Keeley and Zedler 1998). The high genetic variability and/or phenotypic plasticity exhibited by Mediterranean pines explains their high colonising ability and the central role they play in vegetation dynamics in the Mediterranean region (Barbero et al. 1998). Following centuries of pine forest depletion for cultivation, grazing, house building or charcoal the pines of western Europe have, since the middle of the twentieth century, become frequent invaders of abandoned farmlands and broadleaved forests. Beyond the Mediterranean Basin, pine invasion also occurs even in

the southern hemisphere (Richardson and Bond 1991, Lepart and Debussche 1992), while in many areas of the southern part of the Basin overexploitation for fuel and timber has led to a drastic decrease in the area populated by pines (Barbero et al. 1998).

The relationship between life histories and colonisation dynamics has been evidenced for different conifers world-wide (Govindaraju 1984, for conifers in general in North America; Richardson et al. 1990 for *Pinus* in South Africa). Moreover, serotiny of some *Pinus* and *Banksia* species has been shown to facilitate their persistence in fire-driven systems in South Africa (Richardson 1988) and in the Mediterranean Basin (Daskalakou and Thanos 1996).

Fire is the principal disturbance in the Mediterranean basin (Naveh 1975; Trabaud 1984; Barbero

et al. 1998) affecting the genus during its radiation and evolution (Keeley and Zedler, 1998). Three main strategies are predominant in fire-prone environments: seedling development, adult tolerance and vegetative regeneration. (Keeley and Zedler 1998). The characteristics related to the survival of adult trees are those, which prevent meristems from the high temperatures of a forest fire. Among these traits, we find the formation of thick bark, which insulates the cambium against lethal temperatures and thus enables the tree to survive low-intensity fires (Ryan and Reinhardt 1988; Agee 1998). Many pines with thick bark also develop thick twigs (McCune 1988) with a high resistance to heat which enable them to provide better protection for buds. These adaptations become effective as the tree reaches maturity and the tree crown rises far enough from the ground. Therefore the species, which employ these strategies, tend to reach a large size thanks to their longevity. A factor related to tree longevity is the existence of durable heartwood (frequently linked to higher wood densities) that prevents wood rotting. Vegetative regeneration occurs in a few species by sprouting from the root collar or stem but may be restricted to juvenile stages (Stone and Stone 1954; McCune 1988). The strategies based on sexual reproduction and seed development are related to seed storage in long-closed cones within the plant canopy (serotiny) (MacMaster and Zedler 1981, Daskalakou and Thanos 1996, Agee 1998). These cones remain closed until exposed to high temperatures ('pyriscence' *sensu* Lamont 1991), which melt their resin (45–60 °C, Keeley and Zedler 1998). Seed release therefore usually occurs after a fire when conditions for seedling establishment are most favourable (i.e. when competition for light, moisture and nutrients is reduced). Some cones however, are 'xeriscent' and open after a variable drying period even in the absence of fires (Nathan et al. 1999). If a fire occurs either before the onset of reproductive maturity or before the accumulation of a canopy seed bank, the population is threatened with extinction; early cone bearing has therefore been selected in many pine species (McCune 1988, Keeley and Zedler 1998; Tapias et al. 2001). Cone, seed and wing morphology, dispersal date as well as viability and dormancy of seed are related both to the dispersal strategy (serotiny or not) and to animal predation (Muir and Lotan 1984, Skordilis and Thanos 1997, Escudero et al. 1999, Thanos 2000).

Life-history traits may vary among species, populations, stands and individuals. For example, most species are polymorphic for cone serotiny, allowing

establishment after disturbances other than fire, such as insect attacks or wind damage (Muir and Lotan, 1984). Schoenike (1976) found that bark thickness was under strong genetic control in different provenances of *P. banksiana*. The ecological classification of pine species has been carried out by other authors (Govindaraju 1984 for conifers in general, McCune 1988, Keeley and Zedler 1998), however, little emphasis has been paid to Mediterranean pines from this point of view. The Iberian Peninsula offers good opportunities for understanding how the various Mediterranean pines have developed different strategies to adapt to fire. Spain, along with the Canary Islands, exhibits all 'Mediterranean coastal pines' except *P. brutia*. Amongst Spanish pines, *P. halepensis* is the only clearly serotinous species (Daskalakou and Thanos 1996, Thanos and Daskalakou 2000), *P. pinaster* and *P. canariensis* can be serotinous or non-serotinous (Gil et al. 1990, Tapias 1998, Gil et al. 2002) and the other pine species are clearly non-serotinous. Serotiny of *P. pinaster* has not been studied in depth in Spain. In some earlier studies by Martin-Bolaños and Vicioso (1956) the presence of serotinous cones had been recorded in some southern Iberian populations. Gil et al. (1990) found several serotinous populations in Spain, the Teleno Mountains in the North-West being where this characteristic was most conspicuous. By contrast, other authors such as Lloret (1996) and Keeley and Zedler (1998), have considered this species non-serotinous. A previous study revealed that the species had both non-serotinous cones (which open at 32 °C) and serotinous ones (which remain closed at 45 °C) (Tapias et al. 2001).

Different studies have shown contrasting behaviour in Mediterranean pines (both between and within species) when faced with typical Mediterranean environmental constraints such as drought. Life-history traits related to fire however, have not so far been considered. The assessment of the genetic variability of these species is also interesting both in terms of conservation and breeding. The objectives of this paper are firstly to analyse the life history of Spanish pines and its relationship to fire as the main disturbance factor. This first part aims to make an ecological classification of species and to describe ecological groups. Secondly, intraspecific variation of cone production, serotiny and bark thickness in *P. pinaster* (the most variable species) is attempted in order to classify ecological groups of populations according to fire adaptation.

Materials and Methods

Plant material

Seven pine species grow spontaneously in Spain (Table 1). *P. halepensis*, *P. pinaster* and *P. pinea* are common at low and intermediate altitudes in the Iberian Peninsula, whilst *P. nigra* ssp. *salzmannii*, *P. sylvestris* and *P. uncinata* are found mainly at high altitudes (Table 1, see Rouget et al. 2001 for more details of *Pinus* distributions in Catalonia, north-eastern Spain). *P. canariensis* is endemic to the western Canary Islands where it occupies much of the territory of La Palma, Tenerife and Hierro (Climent et al. 1996). *P. halepensis* Mill. is widely distributed in eastern Spain (Gil et al. 1996). Maritime or cluster pine (*P. pinaster* Ait.) woods extend around the western Mediterranean basin from France to Morocco and from Portugal to Tunisia (Figure 1) providing some of the most extensive and variable native forests in Spain. It grows from sea level to 2,000 m forming scattered populations usually separated from each other by hundreds of kilometres. It is present in almost all the Iberian mountain ranges and its tolerance to a wide range of soils and climates leads to a high genetic variation (Alia et al. 1996). Baradat and Marpeau-Bezard (1988) have defined three main groups: Atlantic, Mediterranean and Maghrebian (this last including southern Spanish populations). *P. pinea* grows in unconsolidated soils near sea level and up to 900 m forming open forests with sparse understorey (Prada et al. 1997). *P. nigra* ssp. *salzmannii* is largely restricted to the calcareous mountains of eastern and southern Spain (Catalan et al. 1991). *P. sylvestris* occupies vast mountain areas mainly in north-eastern and central Spain and reaches timberline in some central and southern mountains. Finally, *P. uncinata* is the most representative timberline pine in the Pyrenees and Iberian range (north-eastern Spain).

The study of interspecific variation was focused on different numbers of populations for each species located in the main provenance regions (Table 1). Each sampled population consisted of mature natural stands over an ecologically homogeneous area. 25–30 trees, which were spaced at least 100 m apart in order to minimise consanguinity, were studied in each population.

For the intraspecific study of *P. pinaster*, 28 provenances were studied from a common garden experiment in Rio Frio (Ciudad Real, west of central Spain, Figure 1). The trial site enjoys a typical Medi-

terranean climate. This trial consisted of 16-tree plots arranged in 4 randomised complete blocks (Catalan 1969, Alia 1989, Molina 1994, Alia et al. 1995). These 28 provenances included 10 of the Atlantic group (one from France, one from Portugal and 8 from Spain (Figure 1 and Table 2); 13 provenances of the European Mediterranean group including one from Corsica and another from Pisa (Tuscany, Italy) and finally, five provenances of the Maghrebian group (two from Spain, one from Morocco, one from Algeria and one from Tunisia). 32 trees (8 trees in each of four blocks) aged 26 years were studied per provenance.

Data description: interspecific study

Breast height diameter (dbh) and bark thickness was measured and cambium to pith cores were extracted for each tree. Several dominant branches bearing female cones were cut from each tree and needle length and terminal bud thickness were measured. Three sound cones were collected per tree. In the laboratory, length and width of cones, seeds and wings were measured using an image analyser. Average seed weight was obtained. A standard germination test (20 °C and 12 hours photoperiod) was undertaken using 400 seeds per population, and the number of germinated seeds was counted weekly.

Data on aerial seed banks were obtained from young stands of the studied populations (at least 5 plots or 100 trees per population). All cones were counted, their crop or maturation year recorded (by whorl counting) and their open or closed condition (Tapias et al. 2001) identified in order to calculate: the average percent of closed cones with respect to the total number; cone persistence (number of years that cones remain in the canopy) and earliest cone-bearing. The presence of vegetative sprouting in burnt trees was checked to define sprouting ability.

The following complementary data were taken from the published literature:

Height at maturity (average height of the tallest trees in natural stands with the best site quality) and longevity (maximum known age for each species), Ruiz de la Torre (1979).

Wood density (Peraza 1964).

Seed dispersal season and masting (number of years among abundant crops): Ruiz de la Torre (1979) and Krugman and Jenkinson (1974).

Seed viability: how many years viable seeds may be stored in dry and cold conditions (Catalan, 1991).

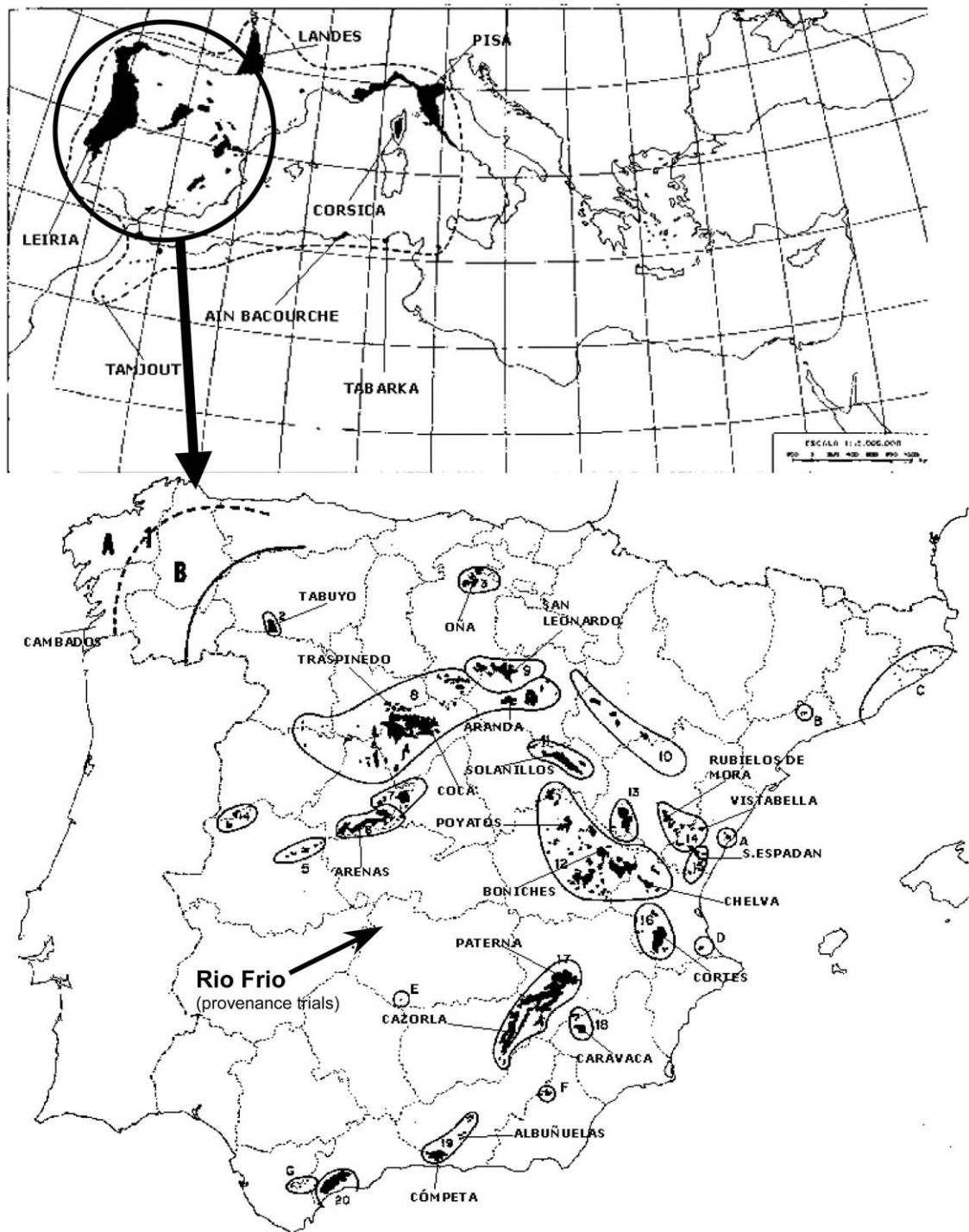


Figure 1. Location of studied provenances. Areas delimited by lines (1 to 20) are the provenances regions defined by Alia et al. (1996). Common garden experiment is located at Rio Frio (Ciudad Real).

Table 1. Summary data for the studied species of Spanish pines (Gandullo and Sánchez-Palomares 1994). Temperature: mean annual temperature. Drought: periods of relative drought (months with rainfall, in mm < mean monthly temperature, in 2x°C), calculated in climate diagram of Walter and Lieth).% of burnt area: area burnt during 1968–1990/total area of species (%) (DGCONA 1994).

Species	Studied populations	Altitude (m)	Temperature (°C)	Annual rainfall (mm)	Summer rainfall (mm)	Drought (months)	% sand in soil	% of burnt area
<i>P. canariensis</i>	23	1190	14.5	519	12	5.1	54.6	38.0
<i>P. halepensis</i>	3	675	13.8	503	76	3.2	35.0	34.1
<i>P. pinaster</i>	10	960	11.4	618	75	2.6	62.5	38.4
<i>P. pinea</i>	1	480	14.3	594	69	4.9	69.8	10.2
<i>P. nigra</i>	1	1070	11.0	882	92	2.1	38.1	6.0
<i>P. sylvestris</i>	1	1266	8.5	919	165	0.8	45.1	24.1
<i>P. uncinata</i>	1	2000	5.5	1000	250	0.6	45.0	0.6

Data description: intraspecific variation in *P. pinaster*

For the study of intraspecific differences in *P. pinaster*, the following attributes were measured: bark thickness (with a Suunto bark gauge) in four cardinal points at breast height, number of open and closed cones in the crown, height and diameter. The percentage of serotinous trees was calculated as the number of trees with serotinous cones divided by the total number of trees.

Data analysis

A matrix of 7 species by 17 phenotypic variables and 7 ecological variables was used to classify the Spanish pine species (Table 3). For the intraspecific study of *P. pinaster*, mean values per provenance were incorporated to a matrix of 28 provenances by 9 phenotypic variables and 9 ecological variables. Firstly, a correlation matrix was obtained to detect strongly related variables. Variables with strong deviation to normality were transformed by logarithmic function (total cones and serotinous cones) and subsequently standardised.

A factorial analysis and cluster analysis were carried out for the variables WOOD (wood density), LONG (longevity), BARK (bark thickness), SPROUT (sprouting capability), CONE (cone length) and SEROT (Serotinous cones) in order to classify all the studied species. Other cluster analysis with the variables BARK (bark thickness), SEROT_T (% of serotinous trees), CONES (cones per tree) and CLOSED (closed cones per tree) were carried out to classify *P. pinaster* provenances. Cluster analysis was undertaken using Euclidean distance and Ward grouping Method. The groups differentiated on the

dendrogram were analysed by discriminant analysis to clarify the differences. ANOVA and multiple range tests (Tukey HSD $p < 0.05$) were used to compare ecological and genetic groups. Preliminary tests found no violations of the assumptions of normality and homoscedacity.

Results

Interspecific variation in Mediterranean pines

A high variability among pine species was found for the traits studied (Table 4). Besides the differences found in bud morphology, needles, cones and seeds, wide differences also existed in variables related to canopy seed banks. Only *P. halepensis*, *P. pinaster* and *P. canariensis* bore serotinous cones, with these last two species displaying a wide variation among their populations. Germination in 1 month as a proxy of germination speed also varied among populations in these two pines.

Three groups of variables were distinguished with significant correlations within them (Table 5). The first group included those traits related to vegetative growth such as BUD, NEEDLE, WOOD and SPROUT; the second group comprised reproductive traits relating to canopy seed banks such as SEROT PRECOC (–), PERSIS (+), VIABIL (+) and MASTING (–) and the third was formed according to ecological variables. Within this third group, mean annual temperature was negatively correlated with annual and summer rainfall ($p < 0.01$). The only significant correlation between vegetative and reproductive pheno-

Table 2. Summary data of ecological characteristics of *Pinus pinaster* provenances studied at the natural location of Rio Frio (Ciudad Real, Central Spain). These 28 provenances include 10 of the Atlantic group; 13 provenances of the European Mediterranean group and, 5 provenances of the Maghrebian group (Baradat and Marpeau-Bezard, 1988). Spanish provenances are 14 out of 20 described by Alia et al. (1996).

Genetic groups	Provenance región	Provenance (province)	Altitude (m)	Temperature (°C)	Annual rainfall (mm)	Summer rainfall (mm)	Shrub cover (%)	Sand in soil (%)	Lightning fires (n)	Large fires (n)	Burnt area (%)	
Atlantic	France	Landes	20	13.6	1000	200	80	80	1-4	0	1-10	
	1	Cambados (Po)	60	14.8	1303	153	100	60	1-4	1	1-10	
	Portugal	Leiria	20	14.0	1200	150	80	80	1-4	0	<1	
	2	Tabuyo del Monte (Le)	900	9.7	752	99	80	45	>10	2	10-40	
	3	Oña (Bu)	700	10.8	685	108	70	80	1-4	0	<1	
	6	Arenas S. Pedro (Av)	750	12.2	1187	92	80	60	>10	1	10-40	
	8	Traspinedo (Va)	730	11.5	513	75	80	90	5-10	0	1-10	
	8	Coca (Sg)	810	11.4	474	71	20	90	>10	0	<1	
	8	Aranda de Duero (Bu)	870	10.9	495	84	20	80	1-4	0	<1	
9	San Leonardo (So)	1200	8.7	641	80	40	80	5-10	0	<1		
Mediterranean-European	11	Solamillos (Gu)	1215	11.4	585	99	20	70	5-10	1	1-10	
	12	Boniches (Cu)	1120	10.8	663	105	40	80	>10	0	<1	
	12	Poyatos (Cu)	1400	11.8	654	100	80	70	5-10	1	1-10	
	12	Chelva (V)	790	13.9	494	109	80	40	5-10	1	10-40	
	14	Rubielos de Mora (Te)	800	12.7	495	128	40	80	5-10	0	1-10	
	14	Vistabella (Cs)	1400	12.8	625	150	80	80	5-10	0	10-40	
	15	Sierra Espadan (Cs)	600	15.4	530	131	80	45	5-10	0	10-40	
	16	Cortes De Paya (V)	800	15.5	493	76	80	45	5-10	0	1-10	
	17	Cazorla (Ja)	820	14.0	985	70	80	40	5-10	1	1-10	
	17	Paterna (Ab)	1180	12.3	785	73	80	40	5-10	1	1-10	
	18	Caravaca (Mu)	1100	13.6	510	60	80	40	5-10	0	1-10	
	France	Córcega	700	12.0	900	120	60	50	-	-	-	
	Italy	Pisa	60	13.0	800	106	80	60	-	-	-	
	Maghrebian	19	Cómpeta (Ma)	900	15.7	544	40	60	40	1-4	1	10-40
		19	Albuñuelas (Gr)	1280	14.4	600	46	80	40	1-4	1	10-40
		Morocco	Tamjout	1600	16.0	650	50	70	80	-	-	-
		Algeria	Ain Bacourche	100	18.0	800	90	70	40	-	-	-
		Tunisia	Tabarka	100	18.0	1022	90	80	40	-	-	-

Table 3. Phenotypic and ecological data used in the study of interspecific variation of life histories of Mediterranean pines and the intraspecific variation in *Pinus pinaster*. Only the variables marked with asterisks are used for the cluster analyses.

Phenotypic data		Ecological data	
A interspecific variation		(Table 4)	(Table 1)
BUD: bud width (mm)		ALT: Altitude (m)	
NEEDLE: needle length (cm)		TEMP: Mean annual temperature (°C)	
WOOD: wood density (kg L ⁻¹)*		A_RAIN: Annual Rainfall (mm)	
HEIGHT: maximum mature height (m)		S_RAIN: summer rainfall (mm)	
LONG: longevity (years)*		DROUG: Drought period (month)	
BARK: bark thickness (mm)*		SAND: Sand in soil (%)	
SPROUT: sprouting capability (presence or not)*		BURNT: Burnt area in the last 22 years (%)	
CONE: cone length (cm)*			
SEED: seed weight (mg)			
WING: wing length (mm)			
SEROT: serotinous cones (%)*			
PERSIS: cone persistence in the canopy (years)			
PRECOC: age of first flowering (years)			
MASTING: interval between large crops (years)			
DISPER: dispersion date (season)			
VIABIL: seed viability (years)			
GERMI: seed germination (% germination in 1 month)			
B. Intraspecific variation in <i>P. pinaster</i>		(Table 6)	(Table 2)
DBH: diameter (cm)		ALT: altitude (m)	
BARK: bark thickness (mm)*		TEMP: average temperature (°C)	
XYLEM: radius of xylem (wood): dbh/2-bark (cm)		A_RAIN: annual rainfall (mm)	
BARK/XY: rate bark/xylem radius (mm/cm)		S_RAIN: summer rainfall (mm)	
HEIGHT: tree height (m)		SAND: sand in soil (%)	
SEROT_T: serotinous trees (%)*		SHRUB: shrub cover (%)	
CLOSED: closed cones per tree (cones)*		LIGHT_F: lightning fires (number in 10 years and 10 km ²)	
CONES: cones per tree (cones)*		Large_F: large fires (>500 ha) in the same period	
SEROT: serotinous cones (closed/total cones)		BURNT: burnt area (%) in the same period	

typic variables was that between LONG and PRECOC (–). Ecological variables were significantly related to phenotypical variables in the pairs NEEDLE/S_RAIN (–), CONE/TEMP (+) and CONE/RAIN (–). It is interesting to note that burnt area (BURNT) was significantly correlated ($p < 0.05$) exclusively with reproductive variables such as SEROT, PERSIS and VIABIL.

Four ecological groups were separated using multivariate cluster analysis (Figure 2) according to their life-history traits (wood density, longevity, bark thickness, sprouting capability, cone length and percentage of serotinous cones):

I: Non-serotinous, late flowering pines, including *P. nigra*, *P. sylvestris* and *P. uncinata*.

IV: Serotinous and early flowering pines including *P. halepensis* and *P. pinaster*.

P. canariensis (**III**) and *P. pinea* (**II**) appeared in two single groups for their sprouting capability and the seed size, respectively.

Intraspecific variability of P. pinaster

The principal life history traits related to fire varied for the 28 provenances (Table 6). Tree diameter varied between 12 and 19 cm. Bark thickness at breast height in 26 year-old trees varied between 15 mm (Albuñuelas) and 27.8 mm (Traspinedo). The bark thickness/xylem radius rate (mm of bark produced for each cm of xylem) ranged from 2.4 to 4.4 mm cm⁻¹. The percentage of serotinous trees also

Table 4. Life-history traits related to disturbances in the seven Spanish pines. * Ruiz de la Torre 1979, (cm); ^Peraza 1964 (en Kg/L); **Catalán 1991; "Krugman and Jenkinson 1974. (Sp: spring, Su: summer; A: autumn); # (Martínez-Millan et al. 1993, mean DBH of studied trees in parenthesis).

	<i>Pinus</i>						
	<i>uncinata</i>	<i>sylvestris</i>	<i>nigra</i>	<i>pinaster</i>	<i>pinea</i>	<i>halepensis</i>	<i>canariensis</i>
BUD: bud width (mm)	5.0	5.5	8.5	8.2	6.5	5.5	11.5
NEEDLE: needle length (cm)	5.0	4.5	11.5	16.7	15.0	9.0	25.0
WOOD: wood density (kg L ⁻¹)	0,502	0,522	0,598	0,475	0,596	0,548	0,753
HEIGHT: maximum mature height (m)*	25	40	50	40	30	22	60
LONG: longevity (years)*	600	500	>600	300	300	250	600
BARK: bark thickness (mm)#	11 (30)	24 (32)	31 (34)	35 (30)	33 (33)	30 (30)	35 (30)
SPROUT: sprouting capability	no	no	no	no	no	no	yes
CONE-L: cone length (cm)	4.0	4.5	6.5	13.2	11.0	9.0	11.5
SEED: seed weight (mg)	9	11	20	56	666	19	116
WING: wing length (mm)	12	14	17	33	3	18	17
SEED/WING	0,75	0,76	1,14	1,70	222,00	1,06	6,82
PRECOC: age of firsts flowering (years)	>18	10–20	15–20	4–10	10–20	4–8	15–20
SEROT: Serotinous cones (%)	0	0	0	2–82	0	40–80	0–60
PERSIS: Cone persistence in canopy (years)	1–3	1–3	1–3	2–40	1–3	5–20	2–10
MASTING: interval between large crops (years)*"	3–4	2–4	2–4	1–2	3–4	1	3–4
DISPER: Dispersion date (season)*"	Sp	Sp	Sp	Sp-Su	Sp A	Su	Su
VIABIL: Seed viability (years)**	5	5	5	30	5	20	15
GERMI: Seed germination (%. in 1 month)	>95	>95	>95	30-95	>95	>95	80–95

differed sharply among provenances. Only two (Leiria and Cambados) showed no serotinous cones while in others (Tabuyo and North African provenances) nearly all trees were serotinous. Most populations displayed between 3 and 18% of closed cone bearing trees.

The number of cones in the crown also showed wide variation: more serotinous provenances also proved to bear the highest number of cones (9 to 42 cones per tree), while the rest bore less than 6 cones per tree. The exceptions were Oña (Burgos) and Pisa (Italy, Tuscany) the latter bearing more than 20 cones per tree despite being just moderately serotinous (22% of serotinous trees). The number of closed cones per tree showed a variation similar to the last two variables; more serotinous populations bore at least one closed cone per tree (normally more than five cones) while the rest displayed an average lower than one closed cone per tree.

Bark thickness (Table 7) was negatively correlated to the following variables: CLOSED ($p < 0.05$), SEROT ($p < 0.01$), SEROT_T ($p < 0.001$), TEMP ($p < 0.01$) and BURNT ($p < 0.01$) and positively correlated with SAND ($p < 0.05$). CLOSED, SEROT, SEROT_T were correlated among each other ($p < 0.001$) and with BURNT ($p < 0.001$). Both

SEROT and SEROT-T were negatively correlated to HEIGHT and DBH positively correlated to TEMP ($p < 0.05$). Among the ecological variables pertaining to location origin of these provenances, TEMP and BURNT were the most correlated to phenotypical traits. TEMP was negatively correlated with BARK ($p < 0.01$) and positively to SEROT_T and SEROT ($p < 0.05$). BURNT was negatively correlated to BARK ($p < 0.01$) and positively to CONES, CLOSED, SEROT and SEROT_T ($p < 0.001$). BURNT was also strongly correlated ($p < 0.001$) with SHRUB (+) and SAND (–).

Three provenance groups were distinguished by clustering (Figure 3) using only phenotypic variables (bark thickness, total cones per tree, serotinous cones per tree and percentage of serotinous trees) as follows:

I: Highly serotinous provenances (more than 58% serotinous trees), with high cone bearing in spite of their lower vegetative development. Bark thickness is lower here than in any of the other provenances (15–21 mm).

III: Non-serotinous provenances where vegetative growth prevails over cone bearing. Bark thickness is moderate (21.1–23.6 mm), although the bark/xylem rate is relatively low.

Table 6. Life-history traits related to fire in 28 provenances of *Pinus pinaster*.

Provenances	Sampled trees	HEIGHT (m)	DBH (cm)	BARK (mm)	XYLEM (cm)	BARK/XY (mm/cm)	CLOSED	CONES	SEROT (%)	SEROT_T (%)
Landes (France)	32	6.0	18.43	22.41	6.97	3.21	0.44	4.84	9.03	18.8
Cambados (1)	28	5.1	15.39	21.11	5.59	3.78	0.00	2.18	0.00	0.0
Leiria (Portugal)	32	5.8	17.30	23.63	6.29	3.76	0.00	0.72	0.00	0.0
Tabuyo Del Monte (2)	32	5.7	17.00	21.13	6.39	3.31	18.28	42.22	43.30	96.9
Oña (3)	32	5.0	17.75	24.91	6.38	3.90	0.31	8.22	3.80	12.5
Arenas S. Pedro (6)	32	6.2	19.72	26.44	7.21	3.66	0.69	2.31	29.73	18.8
Traspinedo (8)	32	5.0	18.09	27.78	6.27	4.43	0.06	5.84	1.07	6.3
Coca (8)	32	4.9	18.35	26.09	6.57	3.97	0.03	4.75	0.66	3.1
Aranda De Duero (8)	32	4.3	15.95	24.19	5.55	4.35	0.59	3.22	18.45	18.8
San Leonardo (9)	32	5.5	19.04	23.84	7.13	3.34	0.06	1.72	3.64	6.3
Solanillos (11)	32	5.1	15.34	19.22	5.75	3.34	0.22	3.37	6.48	6.3
Boniches (12)	32	5.2	17.11	21.41	6.41	3.34	0.28	1.62	17.31	12.5
Poyatos (12)	30	4.8	15.65	22.07	5.62	3.93	0.27	1.50	17.78	10.0
Chelva (12)	32	5.0	19.29	25.47	7.10	3.59	0.09	2.28	4.11	6.3
Rubielos D Mora (14)	31	4.9	19.52	26.19	7.14	3.67	0.03	2.71	1.19	3.2
Vistabella del M. (14)	32	5.6	17.62	20.44	6.76	3.02	0.03	2.66	1.18	3.1
Sierra Espadan (15)	32	4.8	16.60	23.44	5.96	3.93	0.47	3.34	14.02	28.1
Cortes De Palla (16)	32	5.0	18.15	21.13	6.96	3.03	0.06	2.22	2.82	6.3
Cazorla (17)	32	5.3	16.55	22.56	6.02	3.75	0.16	1.41	11.11	12.5
Paterna (17)	32	5.1	18.77	21.69	7.22	3.00	0.44	6.12	7.14	12.5
Caravaca (18)	32	5.3	17.18	21.28	6.46	3.29	0.19	1.44	13.04	6.3
Córcega (France)	31	5.2	18.48	20.81	7.16	2.91	0.10	3.71	2.61	6.5
Pissa (Italy)	32	5.4	18.47	21.22	7.11	2.98	0.47	20.56	2.28	21.9
Cómpeta (19)	32	5.7	18.96	21.88	7.29	3.00	0.28	8.50	3.31	12.5
Albuñuelas (19)	19	4.7	15.56	15.05	6.28	2.40	1.74	6.84	25.38	57.9
Tamjout (Morocco)	31	5.4	18.43	19.00	7.32	2.60	6.48	24.45	26.52	74.2
AinBacouche (Algeria)	12	3.4	12.92	16.08	4.85	3.32	12.25	16.83	72.77	91.7
Tabarka (Tunisia)	16	3.4	12.08	18.56	4.18	4.44	5.69	9.06	62.76	81.3

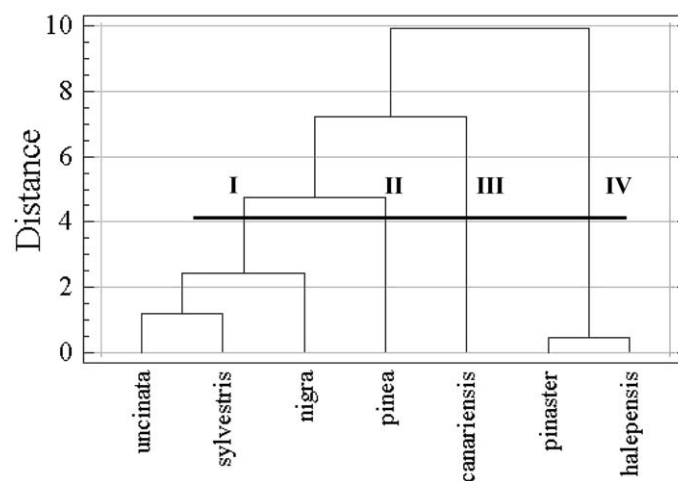


Figure 2. Dendrogram of the cluster analysis (Ward's distance, Euclidean) of Spanish pine species according to their life histories: WOOD (wood density), LONG (longevity), BARK (bark thickness), SPROUT (sprouting capability), CONE (cone length) and SEROT (serotinous cones).

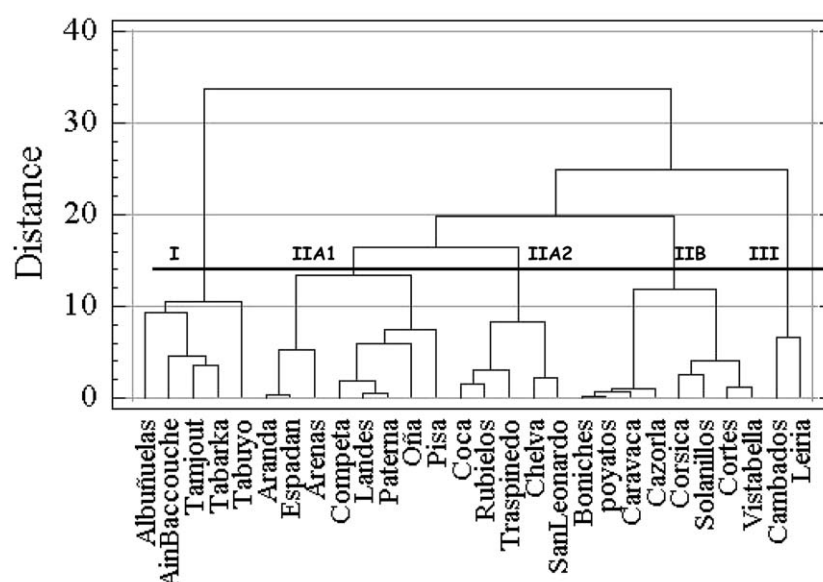


Figure 3. Dendrogram of the cluster analysis (Ward's distance, Euclidean) of 28 provenances of *Pinus pinaster* according to their life-history traits related to fire (BARK, SEROT_T, CONES, CLOSED).

II: Weakly to moderately serotinous provenances with variable bark thickness. Within this large group, three sub-groups can be distinguished:

IIIB: Weakly serotinous provenances (3–12% of serotinous trees) with moderately low bark thickness (19.2–22.6 mm).

IIA1: Moderately serotinous provenances (12–28% of trees) with thick bark (21.2–26.4 mm).

IIA2: Very low-serotinous provenances (<6% of trees) with the thickest bark (23.8–27.8 mm).

Life history traits showed less significant differences among genetic groups (Table 8) than among ecological groups (Table 9).

Discussion

Native Spanish pines have shown a wide range of life histories related to fire adaptation, which may in turn be related to different fire types and frequencies. Strategies related to cone bearing and seed dispersal were the most variable between species of all the studied attributes.

Late flowering and absence of serotinous cones in *P. nigra*, *P. sylvestris* and *P. uncinata* indicate that their natural forests did not evolve under conditions involving frequent crown fires. By contrast, serotiny and early flowering in *P. halepensis* and *P. pinaster* reflect their evader strategy in relation to fire. The

woody understorey which grows in *P. halepensis* and in some *P. pinaster* stand leads to high intensity fires that scorch 100% of the crowns (Agee 1998), serotinous cones however allow the re-establishment of even young stands. While serotiny is a general trait in *P. halepensis*, both *P. pinaster* and *P. canariensis* showed high intraspecific variability. Although 26 out of 28 of the studied populations of *P. pinaster* bore serotinous cones, stark differences between them are evident. We found that 0 to 96% of trees were serotinous. These values in some populations of *P. pinaster* and in *P. halepensis* are higher than in North American species such as *P. contorta* (0–72%, Lotan 1975; Ellis et al. 1994) and *P. banksiana* (43–87%, Gauthier et al. 1993) and other populations of Aleppo pine in Israel (Nathan et al. 1999) and Greece (Daskalidou and Thanos 1996). The differences among species and populations may be due to genetic differences in the strength of their resin bond as well as to differences in the frequency and intensity of hot and dry spells (Nathan et al. 1999). Serotiny may be important in moderately productive sites with high intensity fires. Both the abundant cone production and the high serotiny of *P. halepensis* allows for the accumulation of a copious canopy seed bank which in turn promotes intensive recruitment of over 50,000 to 200,000 seedlings ha⁻¹ (Ne'eman et al. 1992).

Both *P. halepensis* and certain populations of *P. pinaster* showed early flowering, as do *P. halepensis*

Table 7. Correlation coefficients between phenotypical and ecological traits at the provenance level of *Pinus pinaster*. All coefficient values are significant at 95% (in bold: significant at 99%; with an asterisk: 99.9%).

	HEIGHT	DBH	BARK	XYLEM	BARK/XYLEM	CLOSED	SEROT	SEROT-T	ALTITUDE	TEMPER	A-RAIN	S-RAIN	SHRUB	SAND	BURNT
HEIGHT	1														
DBH	0,75*	1													
BARK	0,62*	0,95*	1												
XYLEM	0,75*	0,95*	0,57	1											
BARK/XYLEM	0,57	-0,55	0,57	-0,55	1										
CLOSED	-0,38	-0,41				1									
CONES						0,86*	1								
SEROT	-0,56	-0,67*	-0,52	-0,6*		0,76*	0,48	1							
SEROT-T	-0,41	-0,52	-0,58*	-0,40		0,89*	0,77*	0,89*	1						
ALTITUDE									1						
TEMPER	-0,44	-0,44	-0,44	-0,49			0,43	0,39	-0,54	1					
A-RAIN									-0,53		1				
S-RAIN										0,42	0,47	1			
SHRUB										0,50	-0,38		1		
SAND										-0,38	0,49			1	
BURNT										0,49	0,75*	0,71*	0,85*	-0,73*	1
											0,54*	-0,65*	-0,65*	-0,65*	1

populations in Greece (Panetsos 1981), France (Traud et al. 1985) and eastern Spain (Prada 1999). Other serotinous species (North American pines, McCune 1988; some *Banksia* species in Australia, Enright et al. 1996) gave 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. The absence of reproductive precocity in *P. pinea*, *P. nigra*, *P. sylvestris* and *P. uncinata* confirms earlier reports (Krugman and Jenkinson 1974; Ruíz de la Torre 1979) and is similar to other non-serotinous pines growing on low to moderately productive sites (McCune 1988). Late cone bearing in the moderately serotinous *P. canariensis* requires further investigation.

Early flowering and serotiny offer no ecological advantage to *P. pinea*, *P. sylvestris* and *P. nigra*. Natural *P. pinea* forests grow in low-nutrient, 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 cannot sustain crown fires (or intense ground fires) and the thick bark and self-pruning of dead branches aid fire resistance in these adult pines. Natural *P. nigra* forests show a similarly sparse high canopy and, when present, the woody understorey reaches only 0.5 m (Regato-Pajares and Elena-Roselló 1995). *P. nigra* is one of the longest-lived Iberian plants with extant individuals more than 1 000 years old (Creus 1998) and like *P. pinea*, it 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 and Elena-Roselló 1995) may facilitate the colonisation of tree fall gaps following dispersal of small winged seeds. *P. pinea* has large heavy seeds, dispersed by animals, and its development takes two full years. Abundant seed reserves provide rapid root elongation enabling it to reach deep soil layers.

Other ground-fire resistant pinion pines, such as *P. monophylla* and *P. cembroides*, have similar life-history characteristics to *P. pinea* (McCune 1988) whereas the strategy of *P. nigra* and *P. sylvestris* is closer to that of *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).

Intraspecific variation in *P. pinaster*

A high intraspecific variability has been found in *P. pinaster*. Our data confirm that *P. pinaster* populations can be serotinous or non-serotinous (Gil et al. 1990, Tapias 1998). Other pines, such as *P. contorta* and *P. coulteri* provide evidence about the existence of serotinous and non-serotinous populations and the significant effects of fire on their development and location (McMaster and Zedler 1981; Muir and Lotan 1984; Tinker et al. 1994). In *P. pinaster*, variation in serotiny seems to be unrelated to the latitude, longitude or altitude of the population. High levels of serotiny were found in populations located in northern and southern extremes and from lowlands to highlands (up to 1200 m a.s.l.). Furthermore, different degrees of serotiny appear in all the main genetic groups described by Baradat and Marpeau-Bezard (1988) (Table 8) indicating that these are ancient characteristics of this species and that their expression depends on local 'forces' of selection. Particularly surprising are the stark differences in serotiny found between the populations of Tabuyo and Coca. Despite the relatively short geographical distance (150 km) and very short genetic distance (evaluated through isozymes) separating these populations (Salvador et al. 2000), serotiny is almost fixed in the first population while it is absent in the second. This Atlantic genetic group shows the highest variability regarding fire adaptations with provenances in all the ecological groups. By contrast, in group I (highly serotinous) the Maghrebien genetic group is most prevalent. Frequency of lightning fires cannot entirely explain the results of serotiny and precocity found in this study. High levels for these traits were found in locations with a high frequency of lightning fires ($> 1 \text{ fires} \cdot 100 \text{ km}^{-2} \cdot \text{year}^{-1}$) such as Tabuyo, but also in other locations with low lightning fire frequency such as the Albuñuelas Mountains ($< 0.1 \text{ fires} \cdot 100 \text{ km}^{-2} \cdot \text{year}^{-1}$). On the other hand, low levels of serotiny and precocity were found in populations with a high frequency of lightning fires such as Coca and Solanillos ($> 1 \text{ fires} \cdot 100 \text{ km}^{-2} \cdot \text{year}^{-1}$).

Woody understorey in very serotinous populations of *P. pinaster* stands may easily grow up to 1-2 m tall and would therefore be sufficient to produce fires capable of scorching 100% of their crowns in summer. Lightning during summer thunderstorms may easily provoke these devastating and extremely intense crown fires. The presence of serotinous cones storing the aerial seed bank makes the re-establishment of

Table 8. Mean values for life history traits related to fire in the main three genetic groups of *Pinus pinaster* after Baradat and Marpeau (1988). Values followed by different small case letters are statistically significant.

Genetic groups	Number of provenances	Bark thickness (mm)	Xylem radius (cm)	Bark/xylem (mm/cm)	Height (m)	% of serotinous trees	Cones per tree	Closed cones per tree	% of serotinous cones
Atlantic	10	24.1 ± 0.7 b	6.44 ± 0.25 a	3.8 ± 0.2 a	5.36 ± 0.18 b	18.1 ± 6.7 b	7.6 ± 2.8 a	2.0 ± 1.2 a	11.0 ± 4.8 a
Mediterranean European	13	22.1 ± 0.6 b	6.56 ± 0.2 a	3.4 ± 0.2 a	5.14 ± 0.16 ab	10.4 ± 6.1 b	4.1 ± 2.4 a	0.2 ± 1.1 a	7.8 ± 4.2 a
Maghrebien	5	18.1 ± 1.0 a	5.98 ± 0.35 a	3.1 ± 0.2 a	4.53 ± 0.26 a	63.5 ± 9.8 a	13.1 ± 3.9 a	5.3 ± 1.7 a	38.2 ± 6.8 b
All groups	28	22.1	6.43	3.5	5.11	22.6	6.9	1.8	14.3
Significance level (p)		0.0002	n.s.	0.040	0.0455	0.004	n.s.	n.s.	0.0026

Table 9. Mean values for life history traits related to fire in the main ecological groups of *Pinus pinaster*. Values followed by different small case letters are statistically significant.

Ecological groups	Number of provenances	Bark thickness (mm)	Xylem radius (cm)	Bark/xylem (mm/cm)	Height (m)	% of serotinous trees	Cones per tree	Closed cones per tree	% of serotinous cones
I	5	18.0 ± 0.7 a	5.80 ± 0.33 a	3.2 ± 0.2 a	4.53 ± 0.27 a	80.4 ± 3.3 a	19.9 ± 3.1 a	8.9 ± 1.2 a	46.2 ± 4.9 a
IIA1	8	23.3 ± 0.6 bc	6.71 ± 0.26 a	3.5 ± 0.2 a	5.32 ± 0.21 a	18.0 ± 2.6 b	7.1 ± 2.4 b	0.5 ± 0.9 b	10.9 ± 3.9 b
IIA2	5	25.9 ± 0.7 c	6.84 ± 0.33 a	3.8 ± 0.2 a	5.09 ± 0.27 a	5.0 ± 3.3 c	3.5 ± 3.1 b	0.1 ± 1.2 b	2.1 ± 4.9 b
IIB	8	21.1 ± 0.6 b	6.39 ± 0.26 a	3.3 ± 0.2 a	5.19 ± 0.21 a	7.9 ± 2.6 bc	2.2 ± 2.4 b	0.2 ± 0.9 b	9.0 ± 3.9 b
III	2	22.3 ± 1.2 bc	5.94 ± 0.52 a	3.8 ± 0.4a	5.43 ± 0.42 a	0.0 ± 5.2 c	1.4 ± 4.8 b	0.0 ± 1.9 b	0.0 ± 7.7 b
All groups	28	22.1	6.43	3.5	5.11	22.6	6.9	1.8	14.3
Significance level (p)		0.0000	n.s.	n.s.	n.s.	0.0000	0.0018	0.0000	0.0000

the species possible where the survival of adult trees is negligible. Woody understorey vegetation growing in moderate serotinous populations such as Arenas may easily reach the same height. In high site qualities however (rainfall > 1000 mm), the crown of certain trees will typically reach a height sufficient to enable them to avoid a crown fire and thus allow some individuals to survive. Consequently, recruitment comes from serotinous and non-serotinous trees. Furthermore, woody understorey vegetation, growing in weakly serotinous populations is sparse and low and therefore does not facilitate crown fires. In these locations lightning fires are very frequent but are of low intensity and usually affect only the accompanying vegetation. As a result, most of the mature trees survive these fires and individuals with closed cones are not naturally selected.

A negative correlation between serotiny and bark thickness indicates alternative strategies for the species as a whole. However, important exceptions are evident in groups IIA1 (thick-barked and moderately serotinous populations) and IIB (moderately thin-barked and weakly serotinous populations). These intermediate patterns appear in completely unconnected populations and could reflect either an intra-provenance heterogeneous directional selection or a true combined adaptation responding to variable or unpredictable fire regimes. This last hypothesis has been proposed to explain the high variability of similar traits in *P. canariensis* (Climent et al. in preparation).

Life history traits and vegetation dynamics

In Spain, the abandonment of agricultural land and the implementation of afforestation programs over the last half-century have given rise to two different processes. On one hand forests (especially pine forests) have increased significantly while, on the other hand, fuel accumulation and forest continuity have lead to frequent and catastrophic fires. About 2300 km² are burnt each year in Spain (DGCONA 1994). The area of shrubland, *P. halepensis* and *P. pinaster* forests has increased at the expense of other species such as *P. nigra*, *P. sylvestris* and *P. pinea* (Barbero and Quezel 1988, Barbero et al. 1998) and fire return periods of 20-25 years (Naveh 1990) or less give cause for concern. Hence, serotinous species are more likely to survive than those lacking canopy seed banks.

In eastern Spain, *P. halepensis*, which had previously been confined to lower altitudes, has now expanded at the expense of *P. pinaster* (Bosch 1866).

The lower percentage of serotinous cones and lower cone-opening temperatures in *P. pinaster* compared to *P. halepensis* (Tapias et al. 2001) demonstrates that *P. halepensis* is able to maintain a greater canopy seed bank in xeric locations. The warmer and drier climate of the last 50 years may have accelerated this process.

Against this backdrop it is easy to appreciate the importance of in-depth knowledge of the different fire adaptations developed by these trees and their practical applications if we are to promote a sound management of Mediterranean pines ecosystems.

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