



Fire adaptations in the Canary Islands pine (*Pinus canariensis*)

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Abstract

A wide set of phenotypic characteristics related to life history were studied in mature stands of *Pinus canariensis* throughout its natural range of distribution in the Canary archipelago. Natural forests ranging from those located in xeric areas through to the sub-tropical cloud forests and high mountain stands were classified into eight ecological regions according to their main climatic features. The recent history of forest fires (covering the last 30 years) was taken into account using a categorical factor with three levels. The phenotypic variables studied included those related to seed dispersal (cone size, number of seed scales, seed and wing size and percentage of serotinous trees) and stem growth both on the breast height section (bark thickness, radial growth at various ages and sapwood and heartwood sizes) and on the entire stem (height growth related to age). The average percentage of serotinous trees present in the ecological regions studied varied from 3 to 35%. Average bark thickness in adult trees ranged from 22 to 49 mm and was found to be unrelated to age or diameter. Growth both in height and diameter was found to decline after an average of 25 years, although clear trends in relation to this could not be established across the ecological regions. A high correlation was found to exist between annual rainfall, fire frequency, serotiny and bark thickness at a regional level. Sapwood area per hectare proved to be a valuable indirect site-quality index for the objectives of this paper. Favourable sites (characterised by a high sapwood area per hectare) displayed the highest levels of both bark thickness and serotiny. These particular areas are those, which have suffered more frequent and intense fires over the last decades. The evolutionary implications of this trend and of other general traits of the species, such as vegetative resprouting, are discussed here in relation to the role of understorey vegetation in fire regimes, competition and volcanic history of the islands.

Introduction

The Canary Islands pine (*Pinus canariensis* C. Sm.) is endemic to the Canary archipelago where it is the only existing native pine. Nowadays it spreads mainly throughout the western islands, occupying much of La Palma, Tenerife, El Hierro and Gran Canaria. The climate conditions in natural pine forests are multifarious and result in markedly different vegetation structures. In wet areas, pines form a high canopy over a dense understorey of tree heather (*Erica arborea* L.) and laurel-like broadleaves (*Mirica faya* Aiton, *Laurus azorica* (Seub.) J. Franco, etc.). In contrast, dry pine-woods contain sparse woody shrubs only and, very

often, solely a thick layer of pine litter covers the ground.

Fire may undoubtedly be considered the principal long-term perturbation influencing the entire distribution of the Canary Islands pine. All islands of the Archipelago are of volcanic origin. The volcanic activity of the islands spans 20 million years and is much older in the eastern than in the western islands (Carracedo et al. 1999a and b). Successive volcanic events dating back to the Tertiary have, at varying times and levels of intensity, affected the pine stands on each island. Electric storms, however, are infrequent in the Canary Islands and account for less than 0.5% of incidents of fire. This trend seems to be corroborated

by the magnetic characteristics of rocks taken from a wide range of geological periods (Carracedo pers. comm.). Human intervention has been particularly intense since the European colonisation of the Islands (XV-XVI centuries AD) although the use of fire by aborigines (I-XV centuries AD) is yet to be thoroughly investigated. In recent decades, man-made fires have repeatedly affected pine forests (between 1983 and 1999 alone, more than 20,000 ha were burned), their frequency and intensity varying greatly among as well as within islands (Anonymous 2002).

Fire adaptation in pines has been explained by the use of two different strategies: individual resistance and stand resilience (Keeley and Zedler 1998). The first implies the survival of the adult plants while the second ensures seedling recruitment after the depletion of the original stand. Even when some species seem to have selected predominantly one of the two strategies, both can be simultaneously or alternatively advantageous depending on endogenous factors (age, vigour) or environmental variation (site quality and fire recurrence) (Agee 1998). In *P. canariensis*, numerous traits can be related to fire resistance: thick bark, long needles, thick buds, tall growth habit, deep rooting, longevity and sprouting capability. Moreover, serotinous cones are also present thus ensuring post-fire recruitment. It has been shown that *P. canariensis* seeds resist heat better than small seeds of other pine species and that seedlings developing after heat treatment are larger than those deriving from non-heated seeds (Escudero et al. 2000). Sprouting capability of adult trees is one of the most striking characteristics of the Canary Islands pine (Ceballos and Ortuño 1976). This trait is also exhibited by a few other species located mainly in North and Central America (Keeley and Zedler 1998) and occurs in the Asian *P. merkusii* Jungh and de Vriese (SCBD 2001), a species frequently neglected by bibliographies. Within its natural range of distribution, sprouting is a general trait in *P. canariensis* and occurs exclusively after fire or other damage. Epicormic shoots with juvenile leaves appear in abundance after crown scorching by fire and allow the affected pine canopies to recover in just a few years.

The presence of highly resinous heartwood is a widespread trait in aged *P. canariensis* trees ("pitch pines"). Durable heartwood is characteristic of tree species with a long life span, especially if they grow to a large size (Kozłowski 1971). Indeed, *P. canariensis* can reach considerable dimensions (> 60 m high) and has been known to live more than 600 years. Both re-

sprouting and highly soaked heartwood in this species are features physiologically linked to the accumulation of large amounts of starch in the living sapwood cells (Climent et al. 1998).

The relationship existing between *P. canariensis* and Mediterranean pines (*P. halepensis* Mill., *P. brutia* Ten., *P. pinea* L. and *P. pinaster* Aiton) and *P. roxburghii* Sarg. (Himalayan Chir pine) has been highlighted by analysis of their morphological traits (Klaus 1989, Frankis 1999) and DNA (Strauss and Doerksen 1990, Krupkin et al. 1996, Liston et al. 1999). Some authors consider *P. canariensis* to be a survivor of a subtropical mountain pine type already present throughout the Mediterranean in the Tertiary (Page 1974, Klaus 1989).

In spite of the many characteristics mentioned which make *P. canariensis* original amongst Mediterranean pines, very little is known about the behaviour of this species in relation to forest fires. Therefore, the first objective of this paper is to determine the variation of life history traits relevant to fire resistance and resilience in *P. canariensis* and, secondly, to confirm whether regional differences can be related to important ecological factors such as climate and fire occurrence in the short and long term.

Materials and Methods

All plant material corresponded to putative natural populations of *P. canariensis* in the Canary archipelago. The natural distribution range of the species (Figure 1) includes basal sub-deserts with less than 250 mm of rain per year, dry pine forests on southern slopes (350 to 500 mm of rain), sub-tropical cloud forests with more than 600 mm of rain per year (plus high throughfall due to mist-capture) and high mountain stands reaching timberline (1700 to 2100 m of altitude) where frosts and snow occur in winter. The influence of wet Trade winds from the northeast determines the different conditions, characteristic of the exposed and sheltered slopes within each island. In addition, annual rainfall increases from southeast to northwest resulting in differences among the islands themselves (Gran Canaria is much drier than La Palma). All soils are of volcanic origin and, with the exception of recent volcanic soils, their evolution is closely related to climatic conditions. Therefore climate is justifiably used as a basis for the definition of a number of ecological regions in this study (Fig-

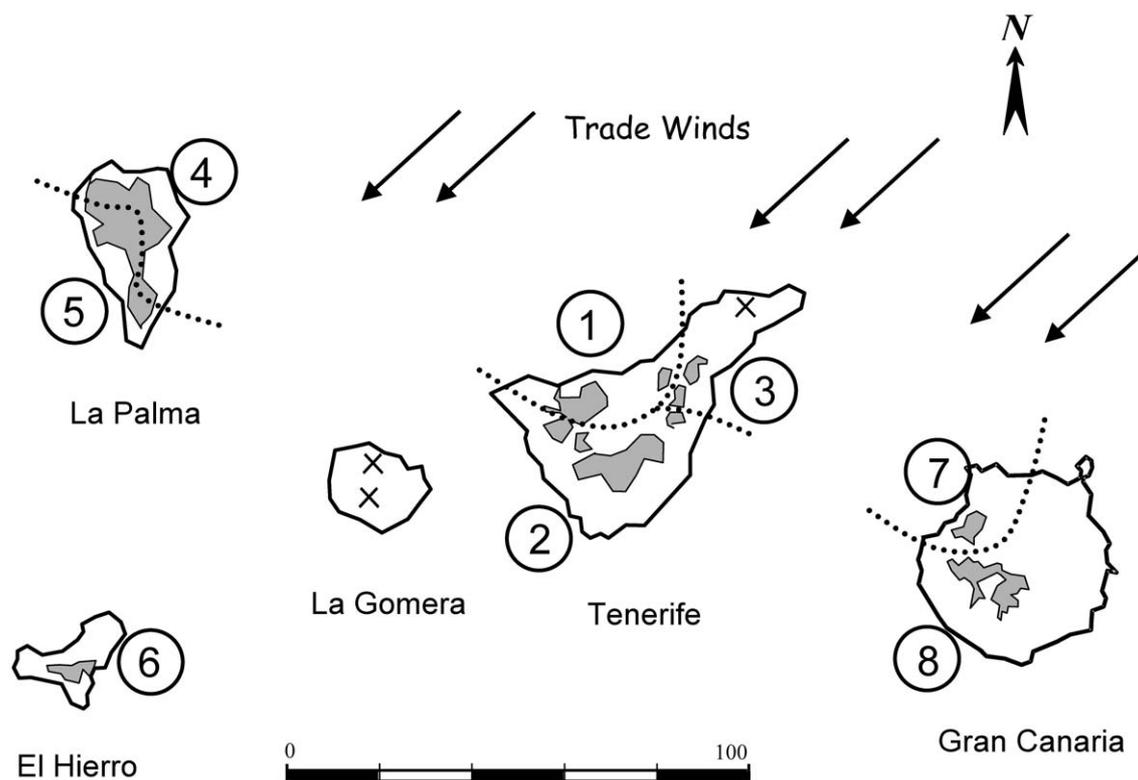


Figure 1. Natural range of distribution of *Pinus canariensis* and ecological regions shown in circled numbers. The pine range extends from 27° 40' to 28° 50' N and from 15° 31' to 18° 05' W. Shaded areas show main natural stands; crosses correspond to relict stands. Main rainfall differences are due to the effect of trade winds (arrows) and geographical position of each island.

ure 1). Mean values of annual rainfall and temperature for each region were obtained from Marzol (1988).

Cones and seeds were studied in 21 natural populations thus each ecological region was represented by two to three populations. Two mature cones per tree were collected from twenty-five to thirty trees per population, each tree spaced at least 100 m apart from the other. Further details on methodology can be found in Gil et al. (2002). The percentage of the trees bearing serotinous cones was used to estimate the level of serotinity of each population. Cones (closed), seeds and wings were measured using an image analyser to obtain their projected area. The ratio between seed area and wing area was used as an estimator of wing loading. The total number of seed scales was counted in each cone. Apophysis thickness or height was measured in two seed scales at the middle of the cone in its exposed side.

Bark thickness, age and xylem growth traits were measured at breast height in 1500 trees aged 75 to 265 years. Measurements and radial core extractions were undertaken at 71 plots grouped in 21 populations

covering all the ecological regions defined. Most of the populations (18) coincided with those studied for cone traits. The following dendrometrical variables were measured: age (number of rings), mean radial growth rate of the first 25 years as well as from 25 to 50 years, mean radial growth rate, heartwood radius divided by age, sapwood width, bark thickness and the radial percentage of bark to xylem. Further details on sampling and core analysing can be found in Climent et al. (2002). The number of trees per hectare, basal area per hectare and sapwood area per hectare, were calculated for each plot. Information on fire occurrence was obtained from forest officials and confirmed by visible evidence (burned bark, stumps, etc) at the time of sample collection, thus permitting the definition of a categorical variable of fire frequency. The scale used was 0 if the plot had not been burned in the last 30 years, 1 if burned once and 2 if two or more fires had occurred during that period of time. Dominant height at age 50 was calculated combining data of the four tallest trees per plot (about 15% of sampled trees) and age-height curves (Blanco et al. 1989).

Height growth was studied through stem analysis of 26 trees randomly selected among dominant and co-dominant individuals in the aforementioned populations (3-4 trees per ecological region). Further details including the methods used for obtaining samples are described in Climent et al. (2003). Gompertz functions were adjusted to each height over age data series to calculate the inflexion point, i.e. the age with maximum height growth rate.

All data were first analysed at individual and population level and analysis of variance was applied to detect significant differences among ecological regions. A correlation matrix was then obtained for the mean values per ecological region. The grouping of ecological regions according to four relevant variables (sapwood area per hectare, bark thickness, percentage of serotiny and cone size) was undertaken through a principal component analysis and clustering analysis with the scores for the factors retained. Ward's clustering method and Euclidean distance were used.

Results

Cone and seed traits

All the variables considered showed a high level of individual variation. Trees bearing serotinous cones were present in all the sampled populations with a percentage ranging from 1 to 40 (extreme 0% and 60% values have been observed in relict populations not included in this study). Lower values, sharply different from the rest, corresponded to southern Gran Canaria. At the population level, the level of serotiny was negatively correlated ($p < 0.01$) with mean cone size and apophysis height; (i.e. populations with more serotinous trees displayed smaller cones with flatter apophyses). Significant differences among the ecological regions ($p < 0.001$) were found for cone size, number of seed scales, wing size and apophysis height (Table 1).

Dendrometrical traits

Mean radial growth in mature trees showed a two-fold decrease over the second 25 year period studied and was found to be more pronounced in dry regions (Table 1). Bark thickness at breast height varied greatly among individuals, ranging from 5.3 to 72.3 mm and averaging 35.0 mm. Both at individual and population level (data not shown), bark thickness bore little or no relation to age or stem radius.

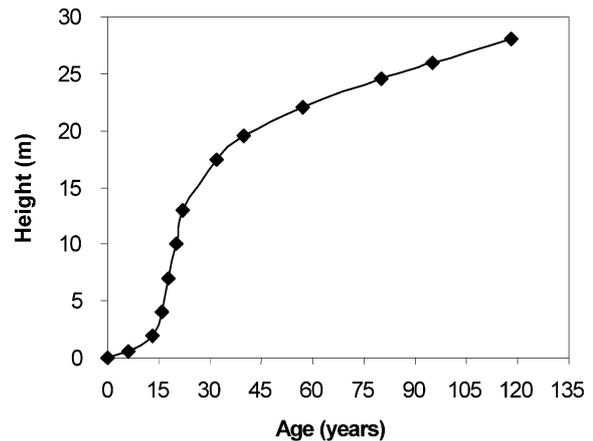


Figure 2. Typical height growth curve for an aged individual of *Pinus canariensis*. Rapid height growth takes place between 15 and 30 years and slows approximately coinciding with the onsets of heartwood formation and cone bearing.

Consequently, allometric functions predicting bark thickness through age, radius and/or radial growth performed very poorly (a maximum r^2 of 14% at the individual level). On the other hand, the radial proportion of bark to xylem was negatively and significantly correlated both with age and xylem radius at the individual level ($r = -0.62$ and $r = -0.45$, respectively). The ecological region was a significant ($p < 0.001$) source of variation for all the studied dendrometrical breast height variables.

Maximum height growth was recorded between the ages of 12 to 45 years, the average age being 26 years (Figure 2). No significant differences were found among ecological regions, this feature was therefore excluded from further analyses. It is interesting to note that maximum height growth rates approaching 1 m/year were recorded even in the more xeric conditions (region 8 in southern Gran Canaria, with $R < 350$ mm).

Environmental and stand traits

As expected, significant differences in rainfall, altitude and temperature were recorded among the ecological regions defined. Likewise, these regions displayed significant differences in fire frequency, stand density and both basal area and sapwood area per hectare. Conversely, the dominant height at 50 years did not show significant differences among ecological regions; it was thus excluded from further analyses.

Table 1. Mean values of the variables studied for each ecological region (Figure 1) arranged by decreasing rainfall. Variables with no significant variation among ecological regions and those without any significant correlation (Table 2) are omitted. Ecological and stand data correspond to 21 populations or sampling sites, dendrometrical variables correspond to 1500 individuals and cone traits correspond to 450 individuals.

Region	4	1	3	5	6	7	2	8	Average
Rainfall (mm)	675	630	600	600	525	500	403	335	531.5
Temperature (°C)	12.5	14.0	15.0	16.0	16.0	15.0	11.3	16.0	14.1
Altitude (m)	1525	1150	1200	1075	950	975	1800	925	1260
Fire frequency	1.7	0.7	2.0	2.0	0.7	0.5	0.7	0.0	1.0
Trees per ha (ha ⁻¹)	363	398	353	220	164	158	298	187	280
Basal area per ha (m ² /ha)	45	35	55	19	24	14	22	11	28
Sapwood area per ha (m ² /ha)	31	27	37	14	15	10	16	6	20
Radial growth rate 0-25 years (mm/year)	2.9	2.1	3.5	2.6	3.9	2.6	2.7	2.2	2.8
Radial growth rate 25-50 years (mm/year)	1.6	1.4	1.7	1.5	2.2	1.3	1.5	1.3	1.5
Average radial growth rate (mm/year)	1.0	1.0	0.6	1.1	1.0	0.9	0.7	0.7	0.9
Heartwood radius/year (mm/year)	0.4	0.3	0.6	0.5	0.9	0.5	0.4	0.6	0.5
Sapwood width (mm)	128.9	117.8	113.2	115.0	118.3	99.8	99.6	63.5	106.1
Bark thickness (mm)	39.4	39.8	49.4	36.4	33.9	21.8	36.2	21.6	34.7
Bark percentage (%)	22.9	29.3	19.8	23.0	17.5	14.8	29.1	15.8	22.2
Cone size (cm ²)	66.4	61.8	66.7	66.1	61.8	56.1	82.1	79.9	68.2
Number of seed scales	101	101	104	105	104	104	111	119	106
Wing size (mm ²)	1.04	0.96	0.98	1.04	1.02	0.93	1.05	1.00	1.01
Wing load	0.50	0.49	0.42	0.42	0.36	0.47	0.36	0.42	0.44
Apophysis height (mm)	7.63	6.59	7.49	7.54	7.43	7.02	7.71	8.19	7.45
Level of serotiny (%)	35	20	29	15	19	14	17	3	19

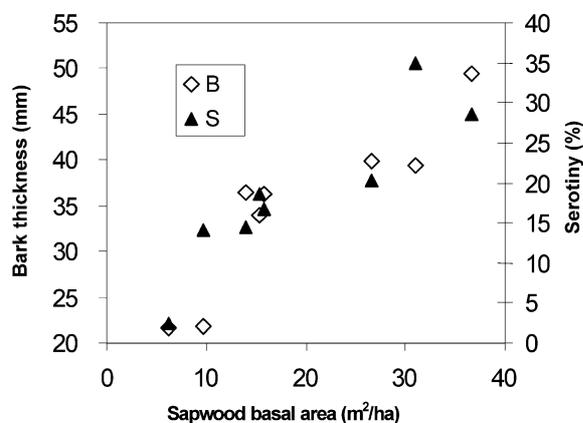


Figure 3. Relationship between sapwood area per hectare, bark thickness, B and level of serotiny, S ($r = 0.9***$ for both pair of variables). Good site conditions, characterised by higher sapwood values, relate to greater bark thickness and a higher percentage of serotinous trees. Each point represents the mean value of each ecological region.

Relationship among variables at regional level

Only 41 out of the 171 possible correlations calculated with the mean values per ecological region were found to be significant (Table 2). Special emphasis was given to the relationships among variables of different groups (environmental parameters - cone and seed traits - growth traits). Among the three ecological variables, rainfall was the only one showing significant relationships with variables of all groups. A marked relationship was found to exist between annual rainfall, sapwood width and sapwood area per hectare. As was expected, significant correlations among the group of radial growth variables were detected. The lack of any relationship between radial growth traits (with the exception of sapwood traits) and the other groups of variables, including environmental variables, is worthy of note. The most relevant group of correlations involved traits related to fire response. Fire frequency and level of serotiny were positively related and were, in turn, related to rainfall, bark thickness, sapwood width and basal area per hectare.

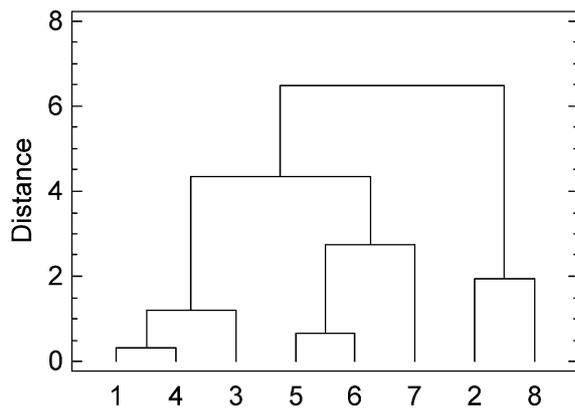


Figure 4. Dendrogram of the ecological regions from a principal components analysis with the variables sapwood area per hectare, bark thickness, level of serotiny and cone size. Two factors were retained, explaining 94% of the observed variation. Ward's grouping method and Euclidean distance were used.

Particularly strong, positive correlations were found between sapwood area per hectare and both level of serotiny and bark thickness (Figure 3).

Grouping of ecological regions

The dendrogram obtained from the clustering and principal components analysis revealed three groups of ecological regions (Figure 4). Particularly striking was the lack of relationship between geographical distance and the Euclidean distances in the dendrogram. Region 1 (North of Tenerife) was very close to region 4 (North of La Palma), while region 2 (South of Tenerife) formed a cluster with region 8 (South of Gran Canaria). Regions 5, 6 and 7, pertaining to La Palma, El Hierro and Gran Canaria, formed another cluster. Moreover, the grouping of the regions in the dendrogram followed almost exactly the arrangement by mean annual rainfall in table 1, even when this variable was intentionally excluded from the analysis.

Discussion

Seeds and cones

Cone serotiny is highly variable in *P. canariensis* both within and between stands, a feature it shares with various other polymorphic serotinous pine species (Keeley and Zedler 1998). In *P. canariensis*, the coexistence of serotinous and non-serotinous individuals in the same population may be related to the extremely variable morphology of cone apophyses

(Gil et al. 2002). Indeed, a similar hypothesis for *P. radiata* in its natural range of distribution has already been put forward by Forde (1964). Compared to other related Mediterranean pines, the level of serotiny is lower in *P. canariensis* than in Iberian *P. halepensis* (40-80%) while interpopulation variability found in *P. canariensis* may be regarded as similar to Iberian *P. pinaster* and much higher than that found in *P. halepensis* (Tapias et al. in press).

A strong correlation has been found in *P. canariensis* between serotiny and recent fire frequency. This is coherent with evidence regarding other pine species such as *P. pinaster* and *P. halepensis* (Tapias et al. 2001) as well as various American species, thus demonstrating that genetic differences in serotiny are related to small-scale differences in fire frequency (Tinker et al. 1994; Keeley and Zedler 1998). Serotiny however is not only a naturally selected strategy in dealing with recurrent fires, but may also be directly influenced by climate, as suggested in *P. banksiana* Lamb (Beaufait 1960). Mild temperatures and high levels of air moisture on northern slopes can prevent cone opening for longer periods in the absence of fire, whilst the opposite would occur in southern, dry pine stands. In fact, serotinous cones in *P. canariensis* are "xeriscent" rather than "pyriscent" (Nathan et al. 1999; Nathan and Ne'eman 2000) since seed dispersal occurs after a variable time lapse without the presence of fire. A certain trade-off has been shown between serotiny and cone size in *P. canariensis*, but this relationship could also be explained by other factors such as adaptation to dry conditions (Gil et al. 2002). Differences in seed and wing sizes however, seem scarcely related to climate or fire occurrence on a regional scale. Furthermore, wing load (estimated through seed area / wing area ratio) does not seem to have been selected by climate or recent fires in this species. Further research helped by common garden experiments might determine the extent of environmental or genetic factors in cone and seed traits in this species.

Adult tolerance

P. canariensis bark is, on average, (Figure 5a) of a similar thickness to other fire resistant species such as the American *P. ponderosa* Douglas ex C. Lawson, *P. pseudostrobus* Lindl., *P. serotina* Michx., *P. leiophylla* Schiede ex Schltld. and Cham., *P. palustris* Mill, as well as the Mediterranean *P. pinea* and some provenances of *P. pinaster* (miscellaneous data). On

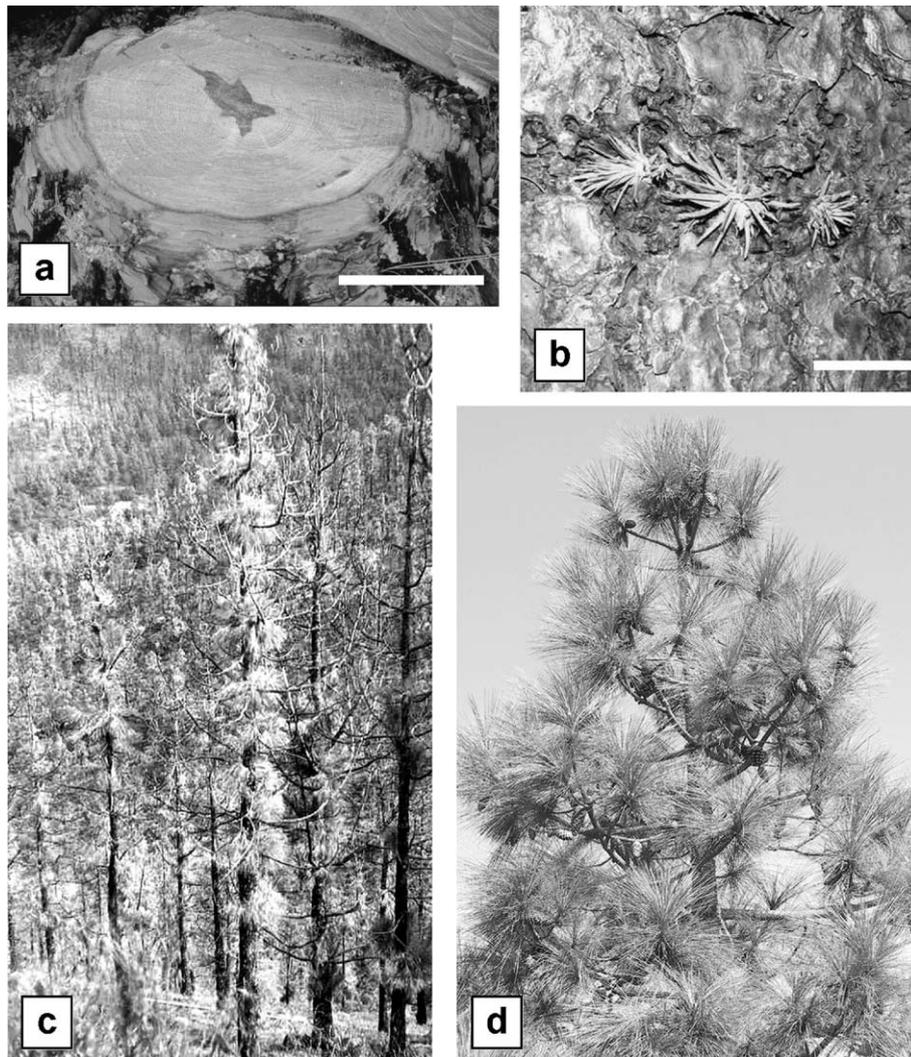


Figure 5. Main traits related to fire adaptation in *Pinus canariensis*. a) Thick bark, insulating the cambium from high temperatures in a 30-year-old individual; bar = 10 cm. b) and c) Epicormic resprouting after crown scorching by fire from preformed, preventitious buds; bar in b) = 5 cm. d) Closed, xeriscent cones in a 45 year-old pine. Only serotinous trees show this profuse cone-bearing, otherwise scarce in this species.

the other hand, significant differences in bark thickness have been recorded among ecological regions in *P. canariensis*. Thick bark provenances of *P. canariensis* coincide with moderately to highly productive areas where forest fires have been frequent and intense over the last decades (Figure 6b). Conversely, thin-barked individuals occur in dry areas where most pine stands are sparse, understorey is scarce or null and fires occur generally as ground fires burning solely the thick litter layer (Figure 6a). The poor relationship between bark thickness and other dendrometrical variables (age or xylem radius) suggests an adaptive

response related to fire regimes rather than an unavoidable consequence of stand growth. Historically, the effects of fire due to human influence have been greater in favourable regions, initially more densely inhabited by aborigines and later by European settlers. Going further back, we can hypothesise less frequent but more destructive fires originated by volcanic activity and very rare lightning storms which affected rather more intensely areas with higher fuel accumulation.

Stem analysis shows that *P. canariensis* exhibits a typically fast-growing juvenile stage. Even in dry conditions it can grow 2 cm per year in diameter and 1 m

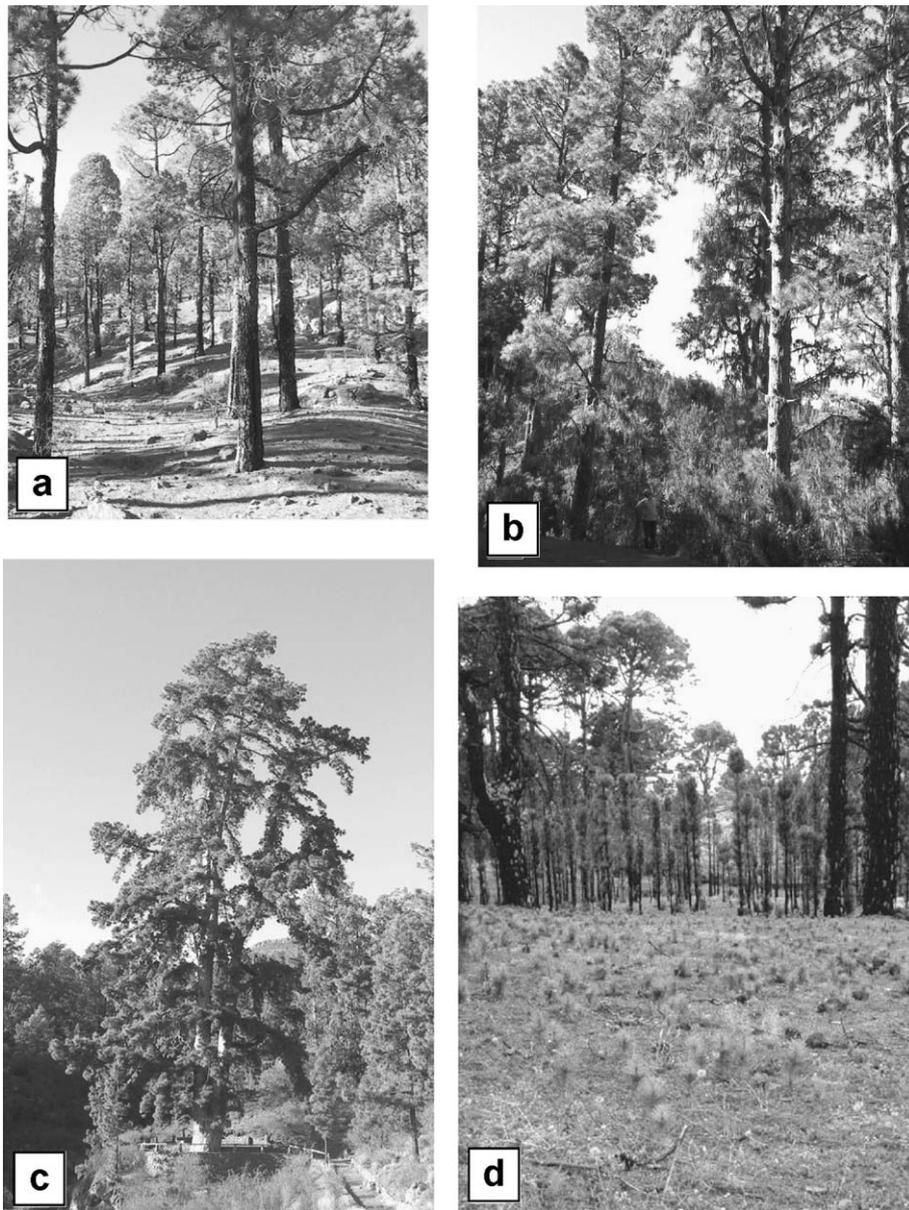


Figure 6. Different aspects of *Pinus canariensis* life history. a) Recently burned dry pine forest at Vilaflor (region 2). Thanks to the absence of understorey only the litter layer was burned in this stand resulting in little damage to the well-isolated stems. b) Typical aspect of a mixed pine stand with a dense understorey of *Erica arborea* and *Myrica faya*. Bark is thicker in these provenances allowing the pine to survive intense crown fires. Serotinous trees are more frequent in these stands. c) One of the largest surviving *P. canariensis* in Vilaflor (region 2), with a height of over 60 m. Bark thickness, 15 to 20 cm, is easily visible because of the woodpecker holes excavated along the stem. d) As a rule even when adult trees survive recurrent burning, recruitment will mainly occur following a fire when the litter layer is eliminated and more light reaches the ground.

per year in height. This growth rate slows at approximately 25–30 years, rather early considering the long lifespan of the species. It is interesting to note that this age coincides with the onset of heartwood formation (Climent et al. 1993) thus corroborating the hypothesis that heartwood formation occurs at the cost of a decrease in growth rate (Helm 2000). Moreover significant cone bearing also tends to occur in this species once this fast-growth stage is over. This would seem to confirm a strong trade-off for carbon amongst vegetative growth, fructification and deposition of extractives during heartwood formation.

On a regional scale, sapwood width and particularly sapwood area per hectare can be considered good, indirect index of site quality for this species. Sapwood is directly related to biomass and leaf area index and, beyond a minimum maturity age, is independent of tree age (Waring et al. 1977, Tausch and Tueller 1989). The sapwood area/leaf area ratio has however been shown to vary among different climate conditions in other pines (Mencuccini and Grace 1994). Thicker sapwood indicates greater tree vigour and a higher storage capacity of reserve carbohydrates (starch) in the xylem (Ziegler 1964). In *P. canariensis* this capacity proves vital to the reconstruction of its fire-scorched crown thus enhancing the resilience of the tree.

The resistance of aged individuals when confronted by fire is enhanced by extremely thick bark (> 15 cm, authors' unpublished data), tall habit (> 60 m), self-pruning and deep rooting (ensuring root survival even after intense fires). Moreover, resinous heartwood prevents heart rotting and allows these monumental trees to live for several centuries, even up to 600 years (Figure 6c).

Vegetative regeneration

Resprouting after fire has been observed at all ages of *P. canariensis* except in juvenile seedlings (Figure 5b and c). As in other resprouting pines, epicormic shoots derive from preformed preventitious buds isolated from heat under its thick bark (Ledig and Little 1979). Resprouting also occurs in stumps and even in cut logs, which can maintain living needles for some years. The huge accumulation of reserve carbohydrates (starch) in the sapwood parenchyma cells explains this remarkable behaviour (Climent et al. 1998). Nevertheless, recurrent fires can lead to decay in aged individuals especially in harsh environmental conditions.

Several pine species have the capacity to resprout from the root collar at the seedling or sapling stage as reviewed by Keeley and Zedler (1998), *P. clausa* (Chapm. ex Engelm.) Sarg., *P. pungens* Lamb., *P. oocarpa* Schiede ex Schltdl, *P. serotina* and even *P. halepensis* and *P. brutia* (Klaus 1989). However, very few pines are able to resprout as adult trees; these are *P. echinata* Mill. (Cain and Shelton 2000), *P. rigida* Mill. (Ledig and Little 1979), *P. merkusii* Jungh and de Vriese (SCBD 2001) and *P. leiophylla* (Perry 1991, Farjon and Styles 1997). It is interesting to note that the last two species live in ecosystems similar to the wet regions of the *P. canariensis* range, i.e. pure or mixed forests (the latter with a dense understorey of broadleaves) in volcanic areas. This last feature points strongly to the significant role of volcanism in the adult sprouting ability in pines. In fact, a close relationship would appear to exist between the volcanic history of the Canary archipelago and the differences in bark thickness encountered in *P. canariensis*. While in Tenerife and La Palma sixteen eruptions have taken place since the European conquest of the XV century, volcanic activity in Gran Canaria and El Hierro ceased much earlier (Carracedo et al. 1999a and b). Further research on the role of volcanism could provide a deeper insight into the life history of the Canary Islands pine and other similar species.

Evolutionary implications

The clustering undertaken which was based solely on cone size and serotiny, bark thickness and sapwood area per hectare was fully congruent with the ranking of climatic conditions of the ecological regions. Our hypothesis is that this reflects direct environmental influences but, moreover, indicates the differential evolutionary pathways, which are related to fire occurrence.

The maintenance of thick bark together with resprouting ability is generally considered an alternative strategy which is complementary to cone serotiny related to fire resilience in the genus *Pinus* (Keeley and Zedler 1988, Schwilk and Ackerly 2001). Furthermore, a negative correlation among bark thickness and level of serotiny has been evidenced in Iberian *P. pinaster* (Tapias et al in press). The trade-off between persistence and recruitment strategies regarding fire has been also postulated in other fire-adapted genera, such as *Banksia*, by comparing obligate-seeders and resprouter species (Zammit and Westoby 1988). However, these quite logical patterns are apparently in

contrast to that of *P. canariensis*, where both serotiny and bark thickness seem to have been simultaneously selected in fire-prone areas. The question arising is, how can serotiny increase fitness in *P. canariensis* if adult trees survive fire? It is worth recalling that cone bearing is usually low in this species; thus a delayed seed release will significantly increase the aerial seed bank (Figure 5d). Seed germination and seedling survival in the absence of fire is very low due to the thick needle layer preventing germination and the high light demands of young *P. canariensis* seedlings (Peters et al. 2001). Hence, the probability of serotinous trees contributing to stand recruitment will always be higher (Figure 6d). This is especially true in mixed stands with resprouter broadleaves (Figure 6b) where the chances of pine seed germination drop rapidly following a fire. If fires become less frequent or less intense, their serotinous condition is liable to be maintained as, unlike thick bark or fruitfulness, it is not costly in terms of carbon. Nevertheless, both serotinous and non-serotinous individuals could sporadically find opportunities to reproduce in gaps created by the fall or death of old trees, thus contributing to the polymorphism of this trait within each population.

It is striking that all the above-mentioned resprouting pines and also resprouting *Banksia* species (Zammit and Westoby 1988) are serotinous to various degrees. This corroborates the compatibility of both strategies and strengthens the idea that a combination of adult resistance and variable, slight serotiny provides high fitness in certain ecological circumstances. The unpredictable fire regime deriving from volcanism in subtropical areas seems to have particularly selected this combination of traits in a few *Pinus* species. It is the contrasting intensity and frequency of fires caused by different vegetation structures, human activity and volcanism, which is postulated to account for the differences encountered both within and between ecological regions in *P. canariensis*.

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