

Understanding long-term post-fire regeneration of a fire-resistant pine species

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Abstract

• **Key message** The long-term effect of forest fires in the regeneration of *Pinus canariensis* was studied. Forest fires had little long-term effects on seed production, seedling germination and seedling mortality. The characteristics of different forest stands across the island had influence in some of the regeneration parameters studied.

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Contribution of the co-authors Javier Méndez, Antonio Gallardo and José María Fernández-Palacios designed this study. Javier Méndez, Gustavo Morales, Lea de Nascimento and Rüdiger Otto did the fieldwork. Javier Méndez, Lea de Nascimento and José María Fernández-Palacios performed statistical analysis. Javier Mendez was the principal drafter of the manuscript with the help of the other authors.

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• **Context** Despite the importance of forest regeneration dynamics after wildfires, little is known about its long-term evolution after a fire.
• **Aims** We tested the effect of fire on the long-term regeneration dynamics of *P. canariensis*.
• **Method** In a forest fire chronosequence of five fire ages (time elapsed since the last fire) plus an unburned stand, we monitored seed production, seedling germination and mortality during 2 years.
• **Results** We detected significant differences among forest stands in seed production, seedling density and mortality but not in germination and turnover. These differences were unrelated to fire age. Seed production was conditioned by the number of large adults and elevation, germination by diameter at breast height (DBH) and soil nitrogen content and mortality by DBH.
• **Conclusion** We detected no long-term effect of fire on the regeneration of *P. canariensis* in natural pine forest; however, during the first years after fire, modification of nitrogen availability in soil can reduce germination. Stand conditions in natural pine forests appear to mainly control regeneration dynamics. The regeneration strategies and fire-resistance traits of this species have ensured its persistence in the long term.

Keywords Forest · Fire · *Pinus canariensis* · Chronosequence · Regeneration · PERMANOVA

1 Introduction

Forest fires are one of the most common disturbances in Mediterranean-type ecosystems and the viability of these burned ecosystems is conditioned by species' capacity to ensure their continuity in the ecosystem (Camia et al. 2008). Species survival is also influenced by heterogeneous stand

conditions produced by fire, i.e. changes in light and humidity conditions or in nutrient availability (Eshel et al. 2000; Catovsky and Bazzaz 2002). Early post-fire and subsequent cohorts would, therefore, face different environmental conditions resulting in diverse effects on the main regeneration processes: seed release, germination and mortality rates.

Most Mediterranean pine species can resist fire, but their degree of resistance (the fire intensity they can tolerate) is variable (Fernandes et al. 2008). Pine strategies to cope with fire depend on either species persistence (by sexual reproduction) or individual survival (Keeley 2012). Obligate seeders, like *Pinus halepensis* Mill., survive due to serotinous cones that store seeds in aerial banks and then release them only or mostly after fire, producing an immediate post-fire seedling cohort, whose recruitment gives rise to a new population (Keeley 2012). Species without serotinous cones living in fire-prone environments, such as *Pinus nigra* Arnold or *Pinus pinea* L., have very scarce regeneration after fires and depend exclusively on the ability of reproductive adults to survive and generate subsequent cohorts. The persistence of such populations depends on the recruitment once adults are able to produce new seeds between fires (Retana et al. 2002; Rodrigo et al. 2007). Post-fire studies in pine forests have focused mainly on early regeneration processes or understory vegetation dynamics, whereas long-term changes in regeneration capacity and their implications for population stability have received less attention (Johnstone et al. 2004; Kazanis and Arianoutsou 2004; Lecomte et al. 2005; González-Tagle et al. 2008).

The Canary Island pine (*Pinus canariensis* Sweet ex Spreng.) is a palaeoendemic species phylogenetically close to Mediterranean pines (Wang et al. 1999). It is well adapted to forest fires, although it is not clear whether its regeneration depends on the occurrence of forest fires. This species combines serotinous and non-serotinous cones, moreover, adults have an extraordinary sprouting capacity after fire, resulting in a mixture of stand resilience and individual resistance strategies (Climent et al. 2004). The importance of serotinous cones in this species is lower compared with other Mediterranean obligate seeder pines adapted to fire-prone environments, like *P. halepensis* (less than 40 % vs. between 50 and 100 % of serotinous cones in *P. canariensis* and *P. halepensis*, respectively) (Climent et al. 2004; Nathan et al. 1999). Therefore, serotiny in Canarian pines could be related not just to forest fires but also to adaptation to dry conditions. Abundant seed rain has also been detected in *P. canariensis* in the absence of fires (García-del-Rey et al. 2011), but the dynamics of seed rain, regardless of the cone type involved, has never been studied. Previous studies of Canarian pine forests have focused on post-fire regeneration and the influence of stand conditions at early stages (Höllermann 2000; Arévalo et al. 2001; Peters et al. 2001; Climent et al. 2004; Otto et al. 2010); however, long-term studies of successive regeneration have not been carried out.

We present the first study quantifying long-term post-fire regeneration in *P. canariensis*. The aim of this work is to determine if *P. canariensis* can produce functional regeneration regardless of fire by measuring seed rain, field-germination rate, mortality and turnover. We also measure the temporal dynamics of these processes and evaluate the effect of biotic and abiotic variables. Our hypothesis is that in natural forests of *P. canariensis*, regeneration is independent of the time elapsed after fire and is influenced mainly by environmental factors.

2 Methods

2.1 Study site

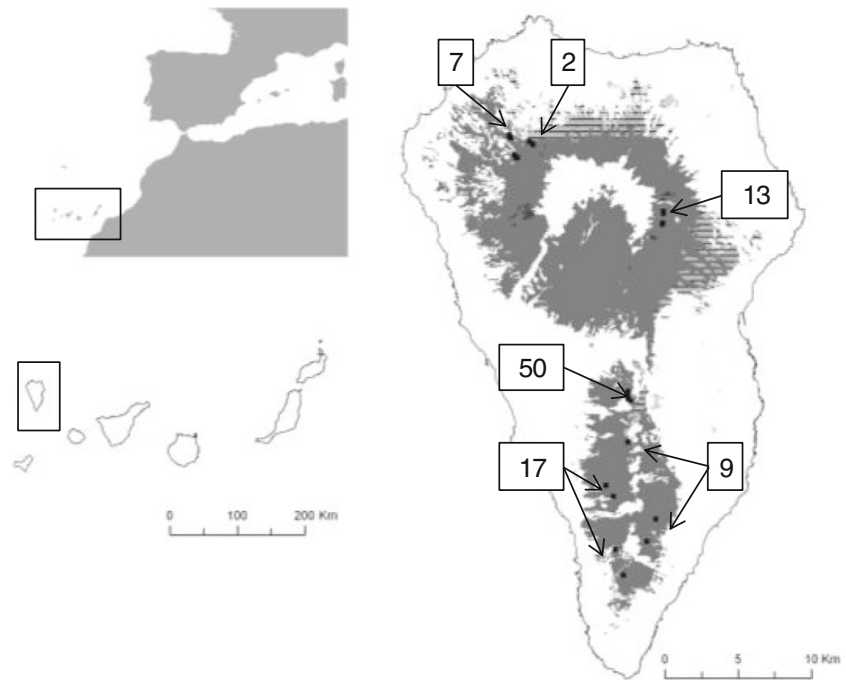
This study was carried out on the island of La Palma (708 km², 2423 m a.s.l.; Canary Islands, Spain), where 69 % of the forested surface of the island is covered by pine forest (ca. 23,600 ha). This represents almost 40 % of the total surface area of natural pine forests in the Canary Islands archipelago (Pérez de Paz et al. 1994). La Palma is the second island most affected by forest fires in the archipelago, with 12,595 ha burned between 1983 and 2008 (18 % of the island's surface) out of a total of 52,345 ha burned in the archipelago during the same period (89 % of the natural pine forest of the Canaries) (Gobierno de Canarias 2011). Consequently, the island of La Palma host the only natural pine forests in the Canaries where it is possible to find a chronological succession of burned areas that have not undergone subsequent fires enabling the study of Canarian pine post-fire regeneration on the long term.

Mean annual temperature in the distribution area of pine forest in La Palma varies between 12.5 and 16 °C, while rainfall ranges between 600 and 1000 mm. Forest soils are of volcanic origin, with leptosols, vertisols and andosols as the prevailing types (IUSS Working Group 2006).

2.2 Experimental design

A fire chronosequence was established consisting of six forest stands burned 2, 7, 9, 13 and 17 years before the beginning of the study (referred to as fire ages) and an unburned control stand (not burned for at least the last 50 years) (Fig. 1). All stands were typically dry pine forest (del Arco et al. 2006). Although the use of chronosequence has some disadvantages (possible pseudo-replication and differences between study plots relative to historical use or microclimate), the chronosequence have proven to be a suitable method in the study of ecological succession (Bermudez et al 2006; Trabaud 2000). Wildfires included in the chronosequence burned more than 20 ha, and none of the zones were affected by later fires

Fig. 1 Study sites on La Palma Island (Canary Island, Spain). Plots comprises a chronosequence of five forest fire ages (2, 7, 9, 13, 17 years after forest fire) and an unburned area (at least 50 years with no fires) located in pine forest. In grey, distribution of the pine forest on the island. *Dark grey* pure (dry) pine; *medium grey with horizontal lines* humid pine; *light grey* pine plantations (Del Arco et al. 2006). All the plots are located in pure (dry) pine forest



nor subjected to silvicultural treatment (Pérez de Paz et al. 1994).

Four 25×25 m plots were randomly established in every stand, except for those with 2- and 9-year-old fires, where, in order to avoid pseudo-replication, only three plots were established due to their smaller burned areas. Altitude, aspect, slope and canopy cover were measured in each plot. The number of living adult pine trees and their diameters at breast height (DBH) were also recorded. Only those trees with over 40 cm of DBH were considered. Canopy height was expressed as the average height of the five trees with the largest DBH in the plot. Litter depth and weight were measured at five 1×1 m random points in each plot. Data were taken four times a year during the study. In each point, litter layer was removed and weighted in the field. A 200-g subsample was dried to constant weight in order to obtain dry weight in tons per hectare. Mean annual precipitation data were obtained from meteorological stations managed by the Spanish Agency of Meteorology (Appendix). Soil nutrients (mg/kg soil) were taken from the study of Durán et al. (2008) carried out in the same plots of this chronosequence.

Five seed traps of 0.2 m² and three subplots (for seedling monitoring) of 25 m² (5×5 m) were randomly placed in each plot (Otto et al. 2012). Monitoring of the trapped seeds and new germinated seedlings was performed every 3 months. The seedlings already present and new ones found in each survey were recorded, mapped and tagged in the subplots. To ensure that mean values contained the natural inter-annual variability, we collected data from September 2005 to February 2007, except in 2-year-old plots, which were monitored until August 2008 to complete two full years of study.

For each stand, mean annual values of seed rain, germination, field-germination rate (percentage of germinated seedlings per number of fallen seeds) and mortality were calculated by averaging the data of the subplots and traps for seeds for each year. Turnover was calculated using Eq. 1:

$$\text{Turnover} = \frac{\text{Germination} - \text{Mortality}}{\text{Germination} + \text{Mortality}} \quad (1)$$

Turnover shows values from 0 to +1 when the population is growing (high germination), and values from 0 to -1 when the population is decreasing (high mortality). Values equal to zero indicate population stability.

3 Data analysis

Differences among fire ages for each regeneration parameter were tested using a permutational ANOVA analysis (PERMANOVA). PERMANOVA is a procedure for testing the simultaneous response of one or more variables to one or more factors in an analysis of variance (ANOVA) in an experimental design based on resemblances between measures using permutation methods (Anderson et al. 2008). In our design, fire age and year of monitoring were used as fixed factors, and plots as nested ones. The resemblance matrix required for the analysis was based on Euclidean distance for each regeneration parameter. Significant terms and interactions were investigated using *posteriori* pair-wise comparisons with the PERMANOVA *t* statistic. A maximum of 9999 permutations were used to obtain the *p* values (*p*<0.05) in

each dataset, and the Monte Carlo correction was applied where necessary.

To test the relationship between regeneration parameters and environmental variables (Appendix), we used the distance-based linear models (DistLM) procedure. This procedure performs a distance-based analysis on a linear model to obtain a resemblance matrix of each regeneration parameter and predictor variables (Anderson et al. 2008). Environmental variables were normalised to make comparisons. It is then possible to derive meaningful distances between samples, using Euclidean distances. The step-wise procedure was used to add or subtract variables from the model. Akaike's information criterion with second-order correction (AICc) was used to obtain the best model with the smallest number of predictor variables. This modification of the AIC is appropriate when the number of samples is small relative to the number of predictor variables. Marginal tests of environmental variables relationships with each regeneration parameter were performed. Primer 6 and PERMANOVA+ (PRIMER-E Ltd., Plymouth, UK) were used to perform all statistical procedures.

4 Results

We collected 1231 seeds with an average of 7.44 (± 8.08 standard deviation (SD)) seeds $m^{-2} year^{-1}$. The number of collected seeds changed significantly among fire ages (pseudo- $F=7.051$; $p=0.004$). Moreover, seed rain was the only parameter that showed significant interaction between fire age and year of monitoring when the latter was considered as a fixed factor (pseudo- $F=2.441$; $p=0.021$), implying that the differences among ages were not consistent throughout the years of monitoring (Table 1). Pair-wise tests showed that higher values of seed rain occurred 13 years after fire (Fig. 2a). By year, seed rain was highest at ages 9 and 13 in 2005. In 2006, the highest values appeared at age 13; whereas in 2007, ages 2 and 17 had the lowest seed rain. On comparing seasonality, despite seed

rain occurring throughout the year, it was significantly higher during summer and lower in winter for all fire ages (pseudo- $F=8.116$; $p=0.000$) (Fig. 3a).

We recorded the germination of 5193 pine seedlings. Mean germination value was 0.34 (± 0.21 SD) seedlings $m^{-2} year^{-1}$, showing no significant differences among fire ages (pseudo- $F=0.596$; $p=0.736$) (Fig. 2b) and no interaction between fire age and monitoring year. However, significant seasonal differences were found, with maximum germination occurring in autumn and winter, whereas minimum values appeared in summer in all fire ages (pseudo- $F=10.614$; $p=0.000$) (Fig. 3b). Mean germination rate (defined as percentage of new seedlings/number of fallen seeds) was 7.63 % (± 11.27 SD), with no significant differences among fire ages (pseudo- $F=0.553$; $p=0.811$) (Fig. 2c). Seasonally, germination rate was significantly higher on winter and lower on summer (pseudo- $F=15.108$; $p=0.000$) (Fig. 3c).

The dead seedlings detected were 3146 with an average of 0.13 (± 0.15 SD) seedlings $m^{-2} year^{-1}$. Significant differences were found among fire ages (pseudo- $F=4.166$; $p=0.021$) (Fig. 2d) with age 13 recording the highest number of dead seedlings. Seasonal differences were also found with higher values in spring (pseudo- $F=4.054$; $p=0.011$) (Fig. 3d).

Seedling density was significantly different among ages (pseudo- $F=10.086$; $p=0.003$), with an average of 1.01 (± 0.85 SD) seedlings $m^{-2} year^{-1}$. Age 13 shows the highest seedling density, while age 2 the lowest (Fig. 2e). Among seasons, autumn–winter had the highest density (pseudo- $F=3.314$; $p=0.026$) (Fig. 3e). Turnover (Eq. 1) showed no differences for fire ages (pseudo- $F=0.29423$; $p=0.9434$) (Fig. 2f) but a marked seasonality throughout the year (pseudo- $F=161.06$; $p=0.000$) with negative values in the dry season (prevalence of mortality) and positive values in the rainy season (prevalence of germination) (Fig. 3f).

When analysing the relationship between environmental and regeneration parameters, seed rain, seed germination, seedling mortality and density can be partially explained by the environmental variables measured, while germination rate and turnover cannot. Fire age had no significant relationship with *P. canariensis* regeneration parameters. Nevertheless, the stand elevation, precipitation, canopy cover, density of adults of DBH higher than 40 cm, average DBH of the plot, and soil available nitrogen had significant influence (Table 2).

Seed rain was influenced by elevation, large adults' density, mean annual precipitation and DBH. Distance linear model including the first two variables explain 67.2 % of total variation (Fig. 4a). Soil available nitrogen and average DBH were related to seed germination, explaining 46.83 % of variation (Fig. 4b). As for seedling mortality, 38.3 % of variation was explained by average DBH and elevation (Fig. 4c).

Table 1 Annual seed rain per age (seed m^{-2}) of *Pinus canariensis*

Age	2005	2006	2007	Average
2		3.47 b	2.07 b	2.77
7	1.27 b	0.86 b	8.37 ab	3.50
9	14.55 ab	2.43 b	7.51 ab	8.16
13	33.87 a	23.24 a	12.87 a	23.33
17	0.80 b	3.07 b	1.44 b	1.77
50	4.58 b	2.55 b	8.57 ab	5.23
	11.02	5.94	6.81	7.44

Seed rain at age 2 started to be monitored in February 2006. Letters indicate similar annual seed rain after pair-wise permutational comparison between fire ages ($p < 0.05$)

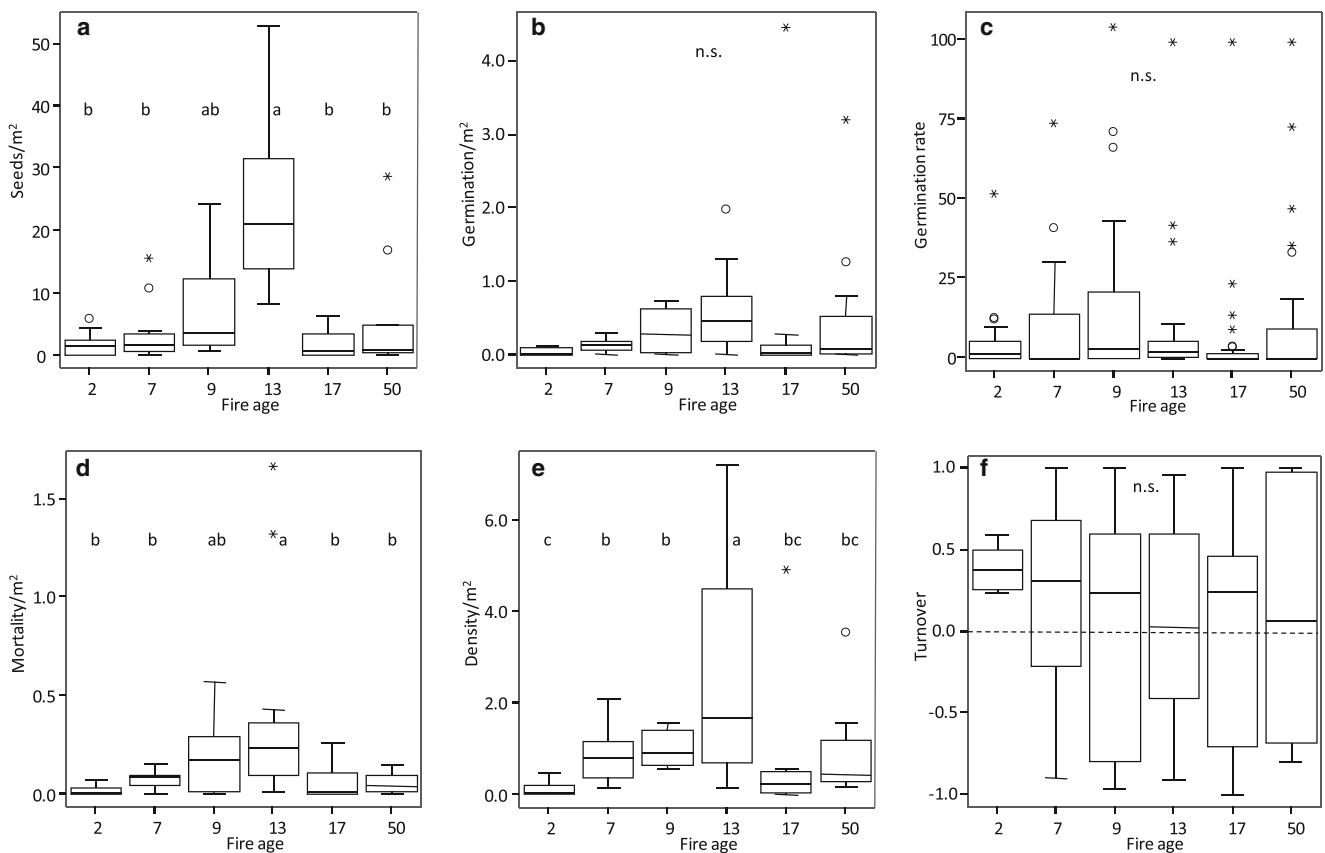


Fig. 2 Average parameters per fire age: **a** seed rain, **b** seed germination, **c** germination rate, **d** seedling mortality, **e** seedling density and **f** seedling turnover. Seed rain, germination, mortality, and density are expressed as seed or seedling per square metre and year. Germination rate is expressed as percentage of number of new seedling/numbers of seeds, and turnover

is defined in Eq. 1. Boxes shows quartiles 1 to 3, the *centre lines* represent the median and intervals indicate the range of 95 % of cases. Circles represent outliers and *asterisks* extreme values. *Similar letters* indicate no significant differences according pair-wise PERMANOVA test ($p < 0.05$) with 9999 permutations

5 Discussion

Although seed production differed significantly among fire ages, it did not follow any trend regarding time elapsed after fire. Moreover, differences were evident only in certain years, indicating that seed rain production is not affected by fire age but very likely varies depending on environmental characteristics. The number of large (high diameter) adults with the capacity to produce large numbers of seeds together with elevation and precipitation appear to be the most influential variables. In natural pine forests of Tenerife, tree density was also an essential factor conditioning seed availability (Otto et al. 2010). Other pine species, such as *P. pinea*, produce a larger number of seeds in stands with higher numbers of large adults, which in turn are favoured by high precipitation (Calama and Montero 2007). Directly related to tree size is tree age, which has also been recognised as a key factor determining seed production in the obligate seeder *P. halepensis* (Tapias et al. 2001). Other aspects which could have a role in controlling cone and seed production such as genetic factors or predation have not yet been studied in *P. canariensis*.

In our study, seeds of *P. canariensis* were released all year round, although the number peaked during summer due to cone opening caused by warm temperatures, and is therefore higher in warmer years. This cone opening has also been detected in warm and dry periods at any time of the year (García-del-Rey et al. 2011). In our field research, germination rate from released seeds was 2–18 %, a much lower value compared with germination rates measured under laboratory conditions (20–80 %) (Escudero et al. 2002; Calvo et al 2013). However, this is a typical value for species with recalcitrant seeds in field conditions, which are viable only the first months after release, as is the case for *P. halepensis* (Daskalakou and Thanos 1996).

We do not know the proportion of serotinous and non-serotinous cones in the studied plots, thus we cannot determine the contribution of each cone type to seed rain. In non-serotinous Mediterranean pines (*P. pinea* and *P. nigra*), seed dispersion occurs mainly in late winter and early spring and/or in masting years, while serotinous pines (*P. halepensis* and *Pinus pinaster* Aiton) release their seeds in sporadic episodes of dry weather or masting years

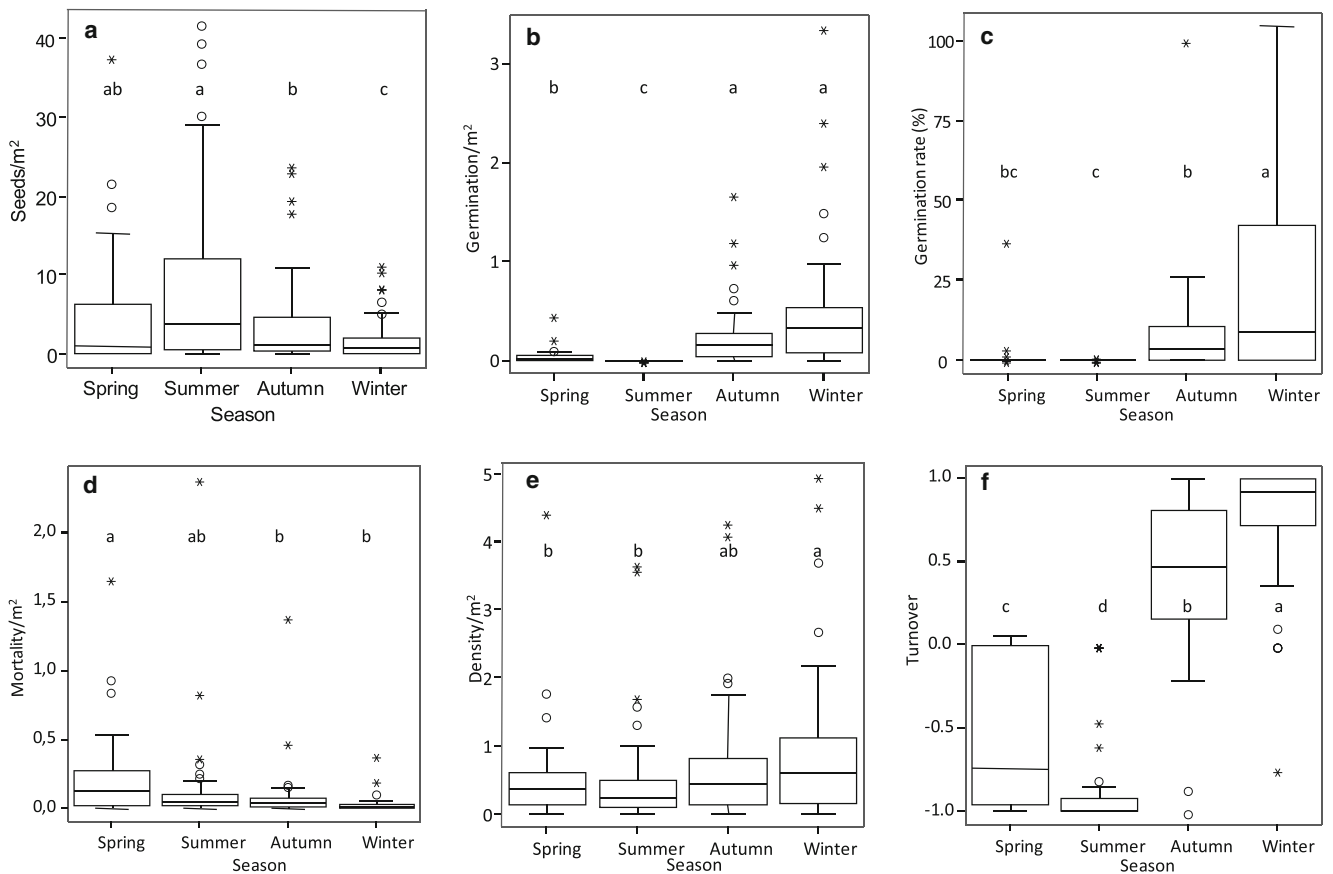


Fig. 3 Seasonal average regeneration parameters of *Pinus canariensis* (seedlings m^{-2}): **a** seed rain, **b** germination, **c** germination rate, **d** mortality, **e** density and **f** turnover (Eq. 1). Boxes show quartiles 1 to 3, centre lines represent the median and intervals indicate the range of 95 % of cases. Circles represent outliers and asterisk extreme values. Similar letters indicates no significant differences according pair-wise PERM ANOVA test ($p < 0.05$) with 9999 permutations

Table 2 Results of marginal test of relationship between regeneration parameters and environmental variables

Variable	Seed		Germination		Mortality		Germination rate		Density		Turnover	
	Pseudo-F	p	Pseudo-F	p	Pseudo-F	p	Pseudo-F	p	Pseudo-F	p	Pseudo-F	p
Fire age	0.151	0.706	1.858	0.194	0.170	0.697	0.001	0.967	0.053	0.807	0.282	0.597
Elevation	19.956	0.001*	0.554	0.448	5.807	0.023*	0.046	0.814	2.672	0.096	3.492	0.066
Precipitation	13.275	0.003*	0.983	0.334	3.195	0.105	0.373	0.564	3.119	0.092	1.464	0.247
Slope	0.083	0.764	0.493	0.484	1.435	0.237	0.780	0.389	1.607	0.225	0.821	0.344
Canopy cover	0.138	0.713	0.899	0.369	1.684	0.202	1.405	0.261	6.890	0.017*	1.845	0.202
Canopy height	2.127	0.142	2.717	0.124	2.864	0.118	0.020	0.886	1.411	0.253	1.818	0.208
Adult density	14.024	0.001*	3.432	0.079	2.127	0.173	0.016	0.896	1.036	0.367	2.317	0.132
DBH	5.191	0.020*	5.420	0.030*	7.840	0.004*	0.859	0.356	5.936	0.026*	3.211	0.078
Basal area	1.008	0.343	0.015	0.903	0.069	0.778	1.220	0.275	0.102	0.739	2.587	0.132
Litter depth	2.921	0.098	0.096	0.762	0.000	0.985	0.035	0.838	0.022	0.887	0.726	0.414
Litter weight	3.072	0.107	0.000	0.986	0.313	0.568	0.004	0.949	0.407	0.509	0.011	0.922
N available	0.881	0.380	7.200	0.018*	0.406	0.489	0.117	0.744	2.087	0.152	0.083	0.782
P available	0.933	0.329	3.472	0.083	0.507	0.474	0.883	0.387	1.508	0.247	1.923	0.167

* $p < 0.05$, significant relationships

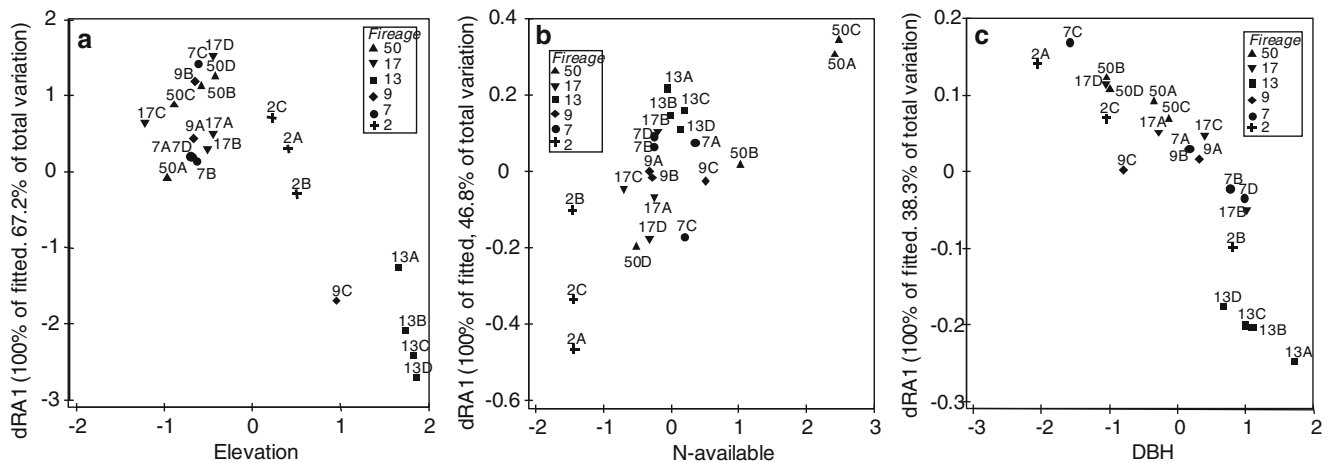


Fig. 4 Distance-based redundancy analysis (dbRDA) plots using the best set of predictor variables. **a** Seed rain, **b** germination and **c** mortality. Euclidean distance resemblance matrix was used

(Daskalidou and Thanos 1996; Skordilis and Thanos 1997; Tapias et al. 2001). The release of Aleppo pine seeds during dry weather events (also called weak serotiny or xeriscence) is considered an advantage for the establishment in an ecological scenario where potential competitors have been suppressed (Espelta et al. 2011; Nathan et al. 1999). This gives an idea of the behaviour of *P. canariensis*, in which both serotinous and non-serotinous cones combine to produce seed rain over the whole year. This continuous supply of seeds allows a transient seed bank throughout the year, offsetting the problem of rapid loss of seed viability on the ground, which is typical of many pine species on field conditions (Keeley and Zedler 1998). Additionally, seeds can be wind dispersed over distances of 1.6 km, allowing low-productive stands to receive seed inputs from near high-productive stands (López de Heredia et al. 2010). As a result of this pattern, Canarian pine forests always appear to have available seeds, both in the canopy and on the ground, able to germinate at any time of the year.

In contrast to seed production, no significant differences were detected in seed germination among fire ages. From the set of environmental variables measured, average adult diameter and soil nitrogen content were the most important. In the same fire chronosequence used in our study, Durán et al. (2008) found that soil nitrogen content is affected by forest fires, showing lower values in burned than unburned stands and suggested that these differences could cause long-term reductions in productivity. If so, very frequent fires could prevent recovery of nutrients available in the soil, and, consequently, affect and hinder seed germination, as well as altering its spatial distribution. Correlation with this modification of nitrogen content could be established only at extreme fire ages (2 and 50 years after fire), with the germination trend being lowest in the younger age group (2 years after fire) and highest in the older

one (50 years). However, intermediate ages showed no relation to fire age. In fact, age 13 displayed even higher germination values than control areas. The recovery of nitrogen content in the long term may be masked or exceeded in importance by other stand conditions such as the modification of nutrients spatial heterogeneity (Rodríguez et al. 2009). Consequently, the existence of suitable microsites for germination and recruitment seems crucial for *P. canariensis* regeneration, as shown in other pine species (de Groot et al. 2004; Bonnet et al. 2005; Vega et al. 2008). Thus, fertilisation experiments on seeds of *P. canariensis* would be required to test the influence of nutrient soil content on germination rates.

Seedling mortality differed significantly among fire ages, but was unrelated to time elapsed after fire. Again, stand characteristics seem to be responsible for seedling mortality; however, the low variability explained by our model, including elevation and diameter of adults as the most important variables, point to the influence of other variables not considered here. Higher rates of mortality are concentrated in the dry season most likely due to water stress (Luis et al. 2001). It has also been shown that different tree species seedlings show higher mortality when subjected simultaneously to shade and drought conditions (Sack 2004). Additionally, Canarian pine seedlings show limitations in their development under these conditions, affecting their survival (Climent et al. 2006). Despite favouring seed production, high adult density can produce adverse conditions for regeneration by reducing light in the understory, or by competing for water and nutrients, thus increasing seedling mortality, as has already been shown for *P. canariensis* (Arévalo and Fernández-Palacios 2008; Peters et al. 2001).

Few studies that simultaneously consider the four regeneration processes (seed rain, seedling germination,

mortality and density) can be found in the literature (Miller and Cummins 1982; Boydak 2004; Neeman et al. 2004). This is the first study carried out on *P. canariensis* including all of them, giving a more complete picture of the dynamics of its forest regeneration. Previous studies on this ecosystem found how regeneration in the absence of fire is notable, but these only focused on a single parameter: seedling germination (Arévalo et al. 2001, 2005; Arévalo and Fernández-Palacios 2005, 2008; Otto et al. 2010). Despite of the high environmental variability found on the island of La Palma and the risk of inherent pseudo-replication in the establishment of a chronosequence, we expected fire to be the main factor controlling regeneration parameters overriding the possible effects of environmental variability; however, our results show that stand characteristics are more important.

From our results, a seasonal pattern of Canary Island pine regeneration can be drawn, although some variability exists among stands. A substantial summer seed release is followed by germination during the rainy season (autumn–winter), until the next dry season when most of the germinated seedlings die mainly due to water stress. Intra-specific competition may also possibly appear among surviving seedlings. Occasionally, introduced herbivores, mainly European rabbits, can feed on seedlings; however, this effect was rarely observed in our study. Although seedling density fluctuates during the year, the continuous supply of seeds and seasonal turnover allows the existence of a permanent seedling bank, which ensures stable, mature populations of *P. canariensis*. The regeneration dynamic pattern shown by *P. canariensis* combines a mixture of fire tolerant and fire embracer Mediterranean pine regeneration strategies (Keeley 2012).

The continuously renewed seedling bank and the presence of long distance seeds dispersal allow this species to maintain stable populations. These features also allow it to act as a pioneer species exploiting new opportunities to establish after disturbances, such as forest fires or canopy gaps created by storms or dead adult trees. This ability is especially useful in volcanic territories allowing the rapid colonisation of new areas originating from lava flows, which is indeed the case for the Canary Islands. Accordingly, Canarian pine stands described in some works as having high tree density but low regeneration might actually be young populations replacing old ones damaged by past disturbances (Höllermann 2000; Climent et al. 2004).

Although *P. canariensis* seems to tolerate the current fire regime, it is uncertain how fire regime changes will affect its regeneration in the future. Charcoal palaeo-records reveal how fire regimes have been modified since humans first arrived on the Canary Islands (de Nascimento

et al. 2009; Nogué et al. 2013). At present, forest fire frequency has significantly increased over the last few decades in the Mediterranean region (Camia et al. 2008). This scenario is also shared by the Canary Islands, and in La Palma, the number of fires has increased by 50 % compared with previous decades (Gobierno de Canarias 2011). Predictions about climate warming in the Mediterranean region suggest an increase in air temperature and a reduction in summer rainfall, consequently, forest fire frequency is expected to increase significantly (Stocks et al. 1998; Flannigan et al. 2000; Gillet et al. 2004). Changes in fire regimes have been confirmed as affecting growth and reproductive traits of fire-adapted pine species as *P. halepensis* (Eugenio et al. 2006) and other Mediterranean species not so adapted to fire, such as *P. pinea* and *Pinus sylvestris* L. (Pausas 2004). Similar changes in fire regime or intensities may have unexpected effects on regeneration and related ecological processes in *P. canariensis*. In this context, the need to maintain long-term monitoring is clear, as a basic part of the correct management of Canarian pine forests.

6 Conclusions

We conclude that fire has little effect on long-term regeneration of *P. canariensis* in natural forests of La Palma, although a negative impact has been detected on early post-fire regeneration. Between 2 to 7 years after fire, regeneration dynamics are controlled primarily by stand conditions such as elevation, number of seed producer trees and density of adults. However, there are still some unknown aspects of the regeneration of this species, where the recurrence of fire can play an important role, as for example, in the pattern of seedling survival or the occurrence of intra or inter-specific competition in the seedling bank. The studied chronosequence offers an excellent opportunity for such studies. Data obtained in the future and the results presented here are of great interest because they provide novel information regarding reference conditions for Canarian pine forests, especially considering that pine forests in La Palma are natural and have mainly been subjected to low intensity of use and management.

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Appendix

Table 3 Biotic and abiotic characteristics of the permanent plots (mean values)

F. age	Alt. (m)	G. age. (kyrs)	Or.	Exp.	Slp. (°)	Prec. (mm)	Dens. (Ind. ha ⁻¹)	Dens. >40 (Ind./ha)	Can. height (m)	Can. cov. (%)	DBH±std error (cm)	Basal area (m ² ha ⁻¹)
2-1	1509	400-800	NWNW	ww	30	800	576	48	5.6	31	46.6±12.0	12.2
2-2	1535	400-800	NW	ww	21	800	112	80	16.2	29	45.4±13.9	19.6
2-3	1457	400-800	NW	ww	23	800	512	32	12.5	15	29.0±11.3	24.4
7-1	1208	400-800	NW	ww	9	660	272	112	18.7	53	38.4±10.1	32.1
7-2	1224	400-800	NE	ww	21	660	160	112	20.3	56	44.9±10.6	26.6
7-3	1226	400-800	NW	ww	4	660	640	32	9.4	39	48.7±38.3	27.3
7-4	1204	400-800	SW	ww	18	660	144	112	19.5	55	47.6±9.5	26.5
9-1	1214	20-125	SE	ww	15	730	224	96	15.5	70	41.2±16.7	32.2
9-2	1219	20-125	E	ww	22	510	128	48	16.9	64	50.1±25.9	20.1
9-3	1659	20-125	SW	lw	13	630	1008	144	15.8	68	31.1±9.1	60.2
13-1	1852	400-800	NE	ww	9	1380	80	80	21.2	45	56.9±8.6	20.7
13-2	1874	400-800	N	ww	15	1380	144	128	17.1	44	49.1±9.1	28.1
13-3	1898	400-800	SE	ww	8	1380	192	144	19.4	64	47.8±11.6	36.3
13-4	1909	400-800	SE	ww	20	1380	272	160	22.2	69	43.7±11.0	43.3
17-1	1274	0.5-20	SE	lw	5	720	560	80	19.8	69	32.9±7.6	47.1
17-2	1257	0.5-20	N	lw	24	670	112	96	21.6	61	48.1±13.1	21.6
17-3	1062	0.5-20	SW	lw	5	420	208	112	20.2	69	45.7±8.6	30.1
17-4	1275	0.5-20	W	lw	17	720	784	16	14.0	52	26.9±5.4	33.7
50-1	1132	0.5-20	N	lw	6	1050	384	144	14.7	63	38.0±11.6	36.5
50-2	1238	0.5-20	NW	lw	30	1050	496	48	9.1	52	34.3±10.2	25.0
50-3	1153	0.5-20	SW	lw	7	1050	320	80	16.5	65	40.6±13.1	36.6
50-4	1282	0.5-20	SW	lw	21	1050	448	32	12.4	43	30.5±6.3	22.0

Rainfall data were obtained from the nearest meteorological station of the Spanish Agency of Meteorology (AEMET)

F. age fire age plot, Alt. altitude (m), G. age geological age (kyr), Or. orientation, Exp. wind exposure (leeward (lw), windward (ww)), Slp. slope (deg), Prec. annual average precipitation (mm), Dens. adult trees density, Dens. >40 adult tree density with DBH>40, DBH diameter breast height (cm), Can. height canopy height (m), Can. cov. canopy cover (%)

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