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The effect of fire severity on first-year seedling establishment in a *Pinus canariensis* forest on Tenerife, Canary Islands

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Abstract The Canarian pine (*Pinus canariensis*) exhibits a striking combination of high adult resistance to fire and intermediate serotiny. Hence, the study of its post-fire regeneration can support valuable new insights about functional adaptations to fire. Here, we analyse the first-year seedling establishment after fire in a *P. canariensis* forest on the northern slope of Tenerife, Canary Islands. The effects of fire severity and other explanatory variables on the seedling density recorded 9 months after fire were examined. We detected a clear unimodal relationship between seedling density and fire severity, with maximum regeneration associated with intermediate fire severity and no regeneration associated with very high crown damage. The results suggested that high severity fires may have caused the partial destruction of the aerial seed bank and/or the creation of unfavourable seedbed conditions for germination and seedling emergence. The density of large pine trees, reflecting seed availability, was the second most important factor explaining the distribution of seedlings. Cover of scorched needle litter on the ground correlated strongly and positively with pine seedling density and negatively with fire severity. The complete lack of regeneration at sites most strongly affected by fire does not represent a major threat for the stand recovery of the Canarian pine, due to the very high tree resistance to fire and the tremendous capacity of the Canarian pine to resprout after fire. The observed very high seedling densities at sites with intermediate fire impacts can probably be related to both the complete liberation of the seed bank (including seeds stored in serotinous cones) and favourable micro-environmental conditions for seed germination and seedling establishment.

Keywords Post-fire regeneration · *Pinus canariensis* · Canary Islands · Regression tree · GAM · GLM

Introduction

The importance of fire in influencing the structure and dynamics of Mediterranean ecosystems has long been highlighted (Trabaud et al. 1985; Naveh 1990; Moreno and Oechel 1994; Begon et al. 1996). Disturbances related to wildland fires also determine the regeneration of ecosystems made up of different pine species (Agee 1998; Fernandes et al. 2008), which employ various strategies in response to fire intensity and frequency (Keeley and Zedler 1998). Despite the abundant scientific investigations published for some Mediterranean pine species (Thanos et al. 1996; Eshel et al. 2000; De Las Heras et al. 2002; Ne'eman et al. 1992; Pausas et al. 2003; Daskalakou and Thanos 2004; Nathan and Ne'eman 2004; Vega et al. 2008), there exist very few studies on fire ecology for the Canarian pine (Höllermann 1993, 2000; Arévalo et al. 2001; Climent et al. 2004).

The Canarian pine, *Pinus canariensis* Chr. Sm. ex DC., is an endemic species of the Canary Islands and forms up to 60% of the forest area of the archipelago. Most of the traits associated with fire resistance, such as thick bark, long needles, large buds, a tall growth habit, self-pruning, deep

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rooting and longevity and/or capacity to resprout, are well developed in this species (Climent et al. 2004). It has also been reported that this pine produces a considerable proportion of serotinous cones, similar to Mediterranean serotinous pines such as *Pinus halepensis* and *Pinus pinaster* (Tapias et al. 2004). The degree of serotiny of the Canarian pine seems to be higher for stands in the north of Tenerife, reaching 60% (Tapias et al. 2004), than in the south of the island, which was related to higher levels of productivity and, in consequence, to higher frequency and intensity of fires in the north of the island (Climent et al. 2004). Although this unusual combination of resistance and recovery to fire is striking, quantitative information about the behaviour of the Canarian pine after fire is very scarce and was never studied in natural stands, only in pine plantations (Arévalo et al. 2001).

Fire severity reflects the impact of fire on vegetation and soil (Whelan 2002). However, there exist no generally accepted quantitative indicators or measures for fire severity. Commonly, the degree of fuel consumption in the understory or canopy layer (Pérez and Moreno 1998) or the level of crown damage (Pausas et al. 2003; Vega et al. 2008) is considered, but the degree of mortality of trees and shrubs has also been used to estimate fire severity (Chappell and Agee 1996). Fire intensity and severity usually vary considerably at the landscape scale, producing a patchiness of post-fire biotic and abiotic conditions (Turner et al. 1994), due to topographical and micro-climatic variations and fuel accumulation (Gómez-Tejedor et al. 1999; Miller and Urban 2000).

Several studies have examined regeneration patterns in relation to fire severity in Mediterranean pine forests (Pausas et al. 2003; Broncano and Retana 2004; Fernández et al. 2008; Vega et al. 2008). Initial seedling density can be negatively influenced by high levels of crown damage (Fernández et al. 2008; Vega et al. 2008). This has, on the one hand, been interpreted as a result of a partial destruction of the aerial seed bank due to high fire intensity. Other studies showed no clear relationship between seedling density and fire severity (Pausas et al. 2003; Broncano and Retana 2004). Seedling emergence after fire can be very high despite almost full crown damage for the serotinous *P. halepensis* (Tsitsoni 1997; Ne'eman et al. 1992), while *Pinus ponderosa*, a non-serotinous pine, showed very low regeneration levels in areas with completely damaged canopies (Bonnet et al. 2005).

Apart from fire severity, other factors such as topography, exposure, aspect and climatic conditions during the growing season after fire or micro-environmental conditions have been reported to influence post-fire regeneration in pine forests (Tsitsoni 1997; Ne'eman and Izhaki 1998; Eshel et al. 2000; Pausas et al. 2004; Daskalakou and Thanos 2004; Broncano and Retana 2004; Bonnet et al.

2005). Ash deposition under adult trees can have negative effects on pine post-fire regeneration (Eshel et al. 2000), but fire can also increase nutrient availability (Notario del Pino et al. 2008; Durán et al. 2008) and enhance seedling growth (Pausas et al. 2003). Bonnet et al. (2005) described the presence of scorched needle litter on blackened mineral soil as safe sites for ponderosa pine regeneration. Until now, neither the effects of fire severity nor environmental factors on post-fire regeneration for the Canarian pine have been studied.

The aim of this paper is to analyse early post-fire regeneration in natural stands of *P. canariensis* after an intense fire that affected 11,458 ha of pine forest on the northern slope of Tenerife in July 2007, relating the establishment of seedlings in the first year after fire to fire severity and other explanatory variables. Our working hypothesis was that seedling density depended on seed availability, which in turn was determined by the distribution of the aerial seed bank, fire severity and environmental factors such as altitude, substrate age and type. A second objective was to examine pine tree mortality.

Materials and methods

Study area

The study area of about 8,000 ha is located in the north of Tenerife and included the Corona Forestal Natural Park (28°18′40″N, 16°43′19″W), ranging from 300 to 2,700 m and occupying a total area of 46.613 ha (Martín Esquivel et al. 1995; Fig. 1). This area was burned in 1983 and again on the 27th of July 2007 (i.e. 24 years later), affecting 11.458 ha of mostly pine forest. The fire in 2007 spread very fast due to exceptionally high air temperatures (>40°C), very low air humidity (<20%) and strong eastern winds from Africa.

Two main types of pine forests, dominated exclusively by the endemic *P. canariensis* Chr. Sm. ex DC., can be distinguished on the northern slope of Tenerife. The first is the humid pine forest that occurs below 1,400 m and is strongly influenced by the north-east trade winds. The second is the dry pine forest that occurs above 1,400 m and is also found in the south of the island. The understory of the first type can be dense and is characterised by shrubs or small trees such as *Erica arborea*, *Myrica faya*, *Ilex canariensis* and *Daphne gnidium*, all species that are found in the evergreen laurel forest, situated below 1,000 m. Above 1,400 m, the understory is dominated by *Chamaecytisus proliferus* and *Adenocarpus viscosus*, two leguminous shrubs that are well adapted to more arid conditions. Abundant in both pine forests are *Cistus symphytifolius*, *Lotus campylocladus* and *Asphodelus aestivus*, as well as

Fig. 1 Study area of burned pine forest, indicating the distribution of permanent plots and the distribution of managed and natural pine forest areas on the island of Tenerife
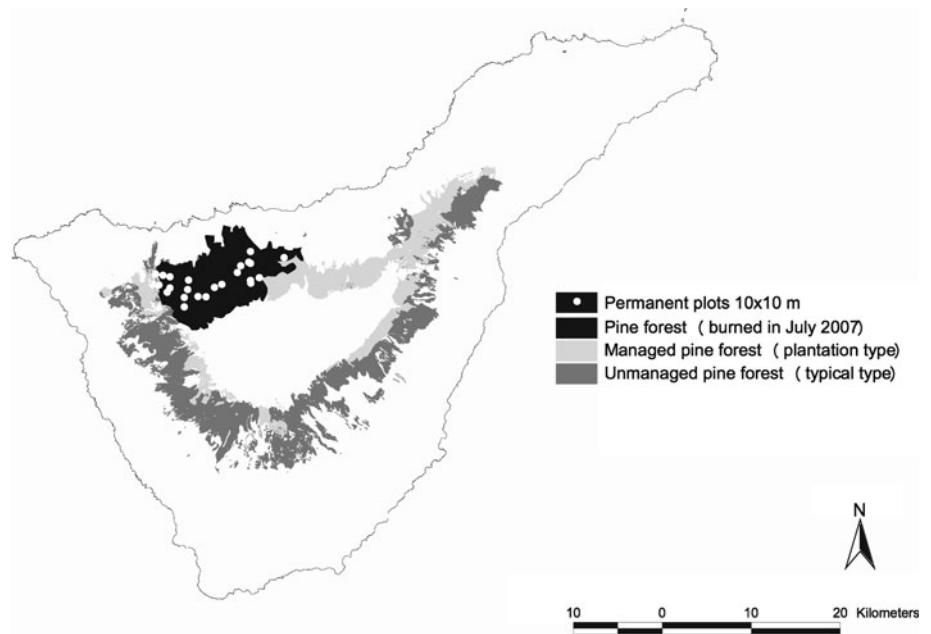
some annuals such as *Wahlenbergia lobelioides*, *Tuberaria guttata*, *Trifolium ligusticum* or *Cardamine hirsuta* (Rivas-Martínez et al. 1993). Annual precipitation reaches 800 mm at the most humid sites on the northern slopes at about 1,000 m, whereas fog drip can substantially increase overall precipitation (Marzol 2008). The drier sites typically receive 400–500 mm of precipitation per year. Mean annual temperature varies between 9 and 15°C within the altitudinal range of the Canarian pine.

According to Del Arco (2006), natural pine forests originally covered ca. 43,000 ha on Tenerife, of which the majority was destroyed during the first three centuries of European settlement. Since the beginning of the twentieth century, great efforts were made to restore the original pine forest distribution. Pine forests are now considered fundamental for ecosystem stability and conservation and are protected on all Canary Islands (Martín Esquivel et al. 1995). Therefore, they are no longer managed for timber production. However, some silvicultural activities still exist, such as thinning in an attempt to naturalise pine plantations. Pine stands in the study area are considered natural.

Sampling design

In the burned area, a total of 23 UTM quadrats (1 km × 1 km) were selected randomly after stratification by geological age of substrate (Carrecedo et al. 2004). Seven quadrats were situated on very young substrate (<3,000-year-old lava flows), and 16 were situated on older substrate (Fig. 1). The first substrate type is very abundant in the centre of the study area but not at the island level.

Without stratification, this type would have been over-represented in this study.

Within each UTM quadrat, we randomly selected one permanent 10 m × 10 m (100 m²) plot; this plot size is frequently used to study post-fire regeneration in pine forests (Tsitsoni 1997; Arévalo et al. 2001; Pausas et al. 2003). Within these plots, we installed five subplots (1 m × 1 m in each corner and in the centre) to monitor pine seedling emergence and several micro-environmental variables following the sampling design of other studies (Ne'eman and Izhaki 1998; Elliott and Vosse 2005). Since this intense fire had burned all natural pine stands in the north and north-west of Tenerife, from the lower limit at the transition zone with the laurel forest at 600 m to the upper timber line at 2,000 m, and the closest unburned stands in the north of Tenerife consisted of pine plantations, no control plots could be found for comparison. Nevertheless, Srutek et al. (2002) described natural regeneration of pine stands at the tree line above 1,700 m near the study area that may be comparable to our results.

At the plot level (100 m²), we recorded the following biotic and abiotic parameters: altitude, slope (degrees), age of substrate following the geological map of Carrecedo et al. (2004), tree DBH (diameter at breast height), total tree density (individuals with DBH > 5 cm), tree density by DBH ranges (DBH < 25 cm, 25 < DBH < 50 cm, DBH > 50 cm), total shrub cover (although the understory was heavily burned, pre-fire cover was roughly estimated by the structure of the burned individuals), basal area and post-fire mortality of pine trees (DBH > 5 cm).

Within the subplots, we visually estimated litter cover and cover of rocks (pieces > 30 cm in diameter), stones
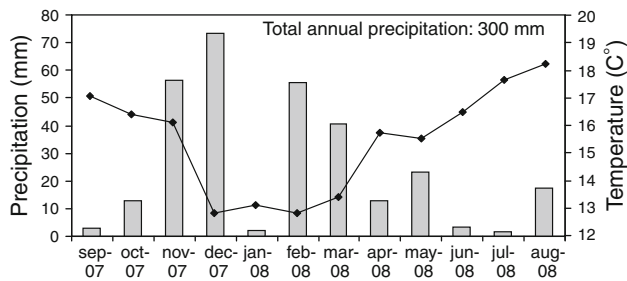
Fig. 2 Mean monthly precipitation and air temperature during the first year after the wildland fire in the north of Tenerife (Meteorological station: Icod de los Vinos, 525 m a.s.l.)

(pieces with diameter between 2 and 30 cm) and uncovered soil (pieces < 2 cm in diameter). Mean canopy cover was measured with a spherical convex densitometer (Lemmon 1956), always from the same corner of the subplot and in the same direction. Fallen cones and pine seeds at the soil surface were counted. All seedlings were tagged in May 2008, 9 months after fire and at the end of the rainy season and just before the summer drought started. *P. canariensis* does not maintain a soil seed bank but an aerial seed bank, and, consequently, all seedlings that emerged from seeds dispersed after fire come from normal or serotinous cones. Germination started with the first heavy winter rains that occurred in November and December 2007 (Fig. 2). There was a second peak of precipitation in February/March 2008. Regeneration was recorded in May 2008, and at 3 and 5 months, respectively, after the two peaks of germination. Therefore, we assume that most of the germinated seedlings were recorded, with the only missing seedlings being those desiccated early in the rainy season between January and March 2008 due to unfavourable micro-environmental conditions. However, we cannot exclude the effect of predation on seeds and seedlings in the first month after fire.

Fire severity was determined according to the degree of crown damage measured at the nearest six adult trees from the plot centre; damage was visually estimated by rating the percentage of green needles at the top of the crown with respect to the whole crown (see similar classifications, Pausas et al. 2003; Vega et al. 2008). Instead of dividing arbitrarily the severity gradient into two or three classes (Pausas et al. 2003; Vega et al. 2008), we decided to use a continuous variable.

Since *P. canariensis* has a good capacity to resprout after intense canopy fires, individuals with highly damaged crowns that retain neither green nor scorched needles are rarely dead but rather are able to produce new green needles from the stem or thick branches within a few months after fire. New green needles produced after the fire could be perfectly distinguished from partly undamaged green crowns.

Statistical analyses

In a first step, we constructed a correlation matrix using non-parametric Spearman rank correlation coefficients to explore relationships among explanatory variables. To avoid collinearity (multicollinearity) and eliminate redundant information, we then selected a set of explanatory variables to enter in the GAM and GLM analysis by eliminating those variables that were highly correlated with each other ($r > 0.70$) and exhibited low tolerance statistics (<0.3) in ordinary least squares regression analysis (OLS). This was done in a stepwise procedure, where the variable with the lowest tolerance value was always eliminated, until all the variables in the equation showed a tolerance of >0.4.

In a second step, we used non-parametric models, such as regression trees (Zuur et al. 2007) and generalised additive models (GAM; Hasti and Tibshirani 1990), to evaluate the effect of explanatory variables such as fire severity and environmental factors on seedling density. These regression techniques deal better with non-linearity than ordinary least squares regression (OLS) and can be used to find interactions missed by other methods in ecological studies (Zuur et al. 2007). Most of the diagnostic tests for fitting linear regression models have analogues in fitting GAMs, with the exception of concurvity, the non-parametric analogue of multicollinearity (Hasti and Tibshirani 1990). At present, most statistical programs provide no diagnostic tools for assessing the impact of concurvity on a fitted GAM. However, multicollinearity is strictly a problem in the design matrix and does not depend on the nature of the link to the response. Therefore, it can always be detected with an OLS procedure that provides collinearity diagnostics (Miles and Shevlin 2001; Wood 2006).

Regression trees, a relatively new technique in ecology, were used to explore the relationship between a single response variable (seedling density) and multiple explanatory variables (biotic and abiotic factors) (De'Ath and Fabricus 2000; Zuur et al. 2007). A regression tree is created by a process of repeatedly partitioning the observations into two homogenous groups based on the values (order) of an explanatory variable. This statistical technique also indicates the relative importance of different explanatory variables. Tree models are not affected by transformations of the explanatory variables. Cross-validation was used to select the optimal tree size and to avoid complex suboptimal trees.

Generalised additive models assume that the mean of the dependent variable depends on an additive predictor through a non-linear link function. Generalised additive models permit the response probability distribution to be any member of the exponential family of distributions. AIC (Akaike information criteria) with forward stepwise selection was used to obtain the optimal set of predictor variables, where the lowest AIC value for every possible

combination of explanatory variables was chosen, starting with the explanatory variable with the best fit. The splines used were simplified to a maximum of four degrees of freedom. Partial predictions for significant predictors were plotted, and 95% confidence bands were constructed.

In a third step, parametric generalised linear models (GLM; McCullagh and Nelder 1989; Dobson 1990) were applied, including the same explanatory variables, using linear or quadratic terms in the case of unimodal relationships and best set selection with AIC for the optimal model. For generalised additive and linear models, we selected a Poisson error distribution using a log-link function, as recommended for count data in ecological analysis (Crawley 1993). The use and comparison of several statistical approaches on the same set of ecological data, as applied here, is recommended since it can improve the statistical and ecological conclusions (Zuur et al. 2007). The following statistical programs Brodgar 2.5.6. (www.brodgar.com) and STATISTICA 8 were used for the multivariate analyses.

Results

Variation of explanatory variables

The 23 sampling plots were located between 900 and 1,700 m, within the typical range for pine forests in the north of Tenerife, where the timber line is reached at 2,000 m (Table 1). Plots were not very inclined and were exposed mainly to the north and north-west. The amount of rocks, stones and uncovered soil varied considerably depending on the age of the lava flow; e.g. plots with the youngest lava flows had high rock cover (up to 95%). Basal area ranged between 4 and 75 m²/ha. Since we did not find any fallen trees in our plots, these values represent nearly pre-fire area basal. All pine trees (DBH > 5 cm) within the studied plots were still alive, resprouting from stem and larger branches, meaning that tree mortality = 0%. Post-fire mean canopy cover was 38% (16–59%). Mean density of pine trees (DBH > 5 cm) was 3.83 ind./0.01 ha, reaching 11 ind./0.01 ha in one plot.

The analysis of the correlation matrix revealed that basal area was positively correlated with the number of large trees (DBH > 25 cm) and negatively correlated with rock cover. Pine tree density showed a positive relationship with mean canopy cover, which was negatively correlated with altitude. The amount of scorched needles on the ground correlated positively with basal area, the number of larger trees and the number of cones. There were not any pine seeds found at the soil surface within the subplots ($n = 115$).

Fire severity, considered one of the most important explanatory variables in this study, varied considerably within the area affected by this canopy fire. Mean crown damage reached 77%, but within very short distances

Table 1 Explanatory and response variables recorded in the 23 permanent plots and included (*) in the regression analysis

Explanatory variables		Mean	Min.	Max.	SD
Abiotic factors					
Altitude (m)*	Altitude	1,317.17	900.00	1,700.00	209.27
Slope (°)*	Slope	10.65	0.00	25.00	6.79
Geological age (in thousands of years)*	Geology	5.865	1.240	10.000	2.985
Rock cover (%)*	Rock	37.74	2.00	95.00	24.72
Stone cover (%)	Stone	11.37	0.00	31.00	7.12
Soil cover (%)	Soil	50.80	3.80	95.00	23.68
Fire severity (crown affected %)*	Fireseverity	77.30	40.00	100.00	23.02
Biotic factors					
Basal area (m²/ha)	BA	33.23	3.93	74.82	17.29
Mean canopy cover (%)*	Canopy	38.66	16.20	59.20	12.32
Understory cover (%)	Under	33.13	0.00	83.00	26.04
Density of pine trees (ind./0.01 ha)*	Treedens	3.83	1.00	11.00	2.48
Pine trees DBH > 50 cm (ind./0.01 ha)	T3	0.61	0.00	3.00	0.78
Pine trees DBH 25–50 cm (ind./0.01 ha)	T2	1.30	0.00	4.00	1.26
Pine trees DBH < 25 cm (ind./0.01 ha)	T1	1.87	0.00	10.00	2.60
Pine trees DBH > 25 cm (ind./0.01 ha) *	Largetrees	1.91	0.00	4.00	1.04
Scorched needles at soil surface (%)	Litter	39.42	0.20	89.60	31.34
Response variable					
Seedling density of *Pinus canariensis* (ind./m²) *	Seedl	4.90	0.00	16.20	5.99

(200 m) we could detect areas with almost intact green crowns (50% affected) and areas with completely burned crowns. Fire severity exhibited a positive but not very strong correlation with pre-fire understory cover (Spearman rank coefficient $r = 0.53$, $P = 0.01$) and was also positively related, but not significantly, to higher density of small trees ($r = 0.36$, $P = 0.088$). A high correlation was found between fire severity and needle litter on the ground ($r = 0.61$, $P = 0.002$). To avoid collinearity for the GAM and GLM models, we skipped 10 of the 18 explanatory variables for the regression analysis (see Table 1).

Post-fire seedling density

A total of 564 established *P. canariensis* seedlings were recorded and tagged. The average seedling density was 4.9 ind./m^2, with a maximum value of 16.2 ind./m^2, which is equal to 162.000 ind./ha (Table 1; Fig. 3). No dead seedlings could be detected. The regression tree model with eight explanatory variables and seedling density as the response variable (Fig. 4) selected fire severity as the most important explanatory variable. Seedling density was strongly negatively influenced by a fire severity greater than or equal to 87.5%. That means that the highest seedling densities can be expected for plots with pine canopies affected less that 87.5%. The second most important variable in explaining seedling density was the number of large trees (DBH > 25 cm), which had a positive effect when number of trees was higher than 1.5 ind./0.01 ha. Both factors accounted for 42.6% of the original deviance. The fact that fire severity appeared again further down in the regression tree indicates that the relationship between the two variables is not linear. The highest seedling densities could be found in areas where tree canopies were damaged between 45 and 82.5% and where density of large trees was >1.5 ind./0.01 ha.

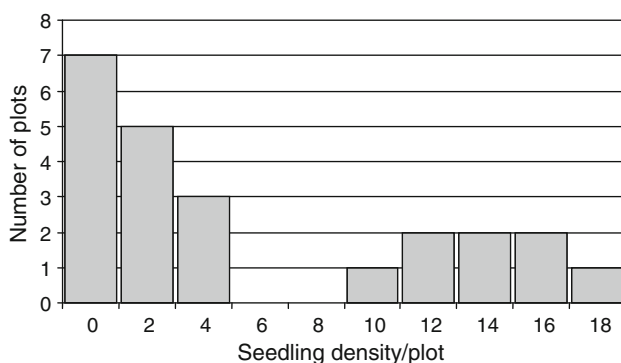Results of GAMs with seedling density as a response variable using the Poisson distribution and a log-link

Fig. 3 Histogram of seedling density of the 23 plots

function are shown in Table 2. AIC methods and forward selection was applied to select the optimal model, which included the same two variables: fire severity and large trees (DBH > 25 cm). Fire severity was again the most important variable in explaining the variation in seedling density. The splines for each significant explanatory variable with the 95% confidence bands are represented in Fig. 5. As indicated by the rather large degrees of freedom for the smoother curve representing fire severity, the corresponding smoothing curve revealed a unimodal relationship between fire severity and seedling density, with a maximum seedling density for areas with 75% crown damage. From this point, seedling density decreased drastically with increasing fire severity. The shape of the smoother for the number of large trees indicates a nearly linear positive relationship. Analysis of the residuals of the optimal additive model showed no clear patterns and a good fit.

The GLM approach using the Poisson distribution, AIC best set selection and the same explanatory variables, including a quadratic term of fire severity, yielded a model where fire severity (linear and quadratic terms), large trees, altitude and geological age of the substrate were selected (Table 3). Fire severity was the most important factor in explaining seedling distribution, followed by the variable number of large trees.

Seedling density was also strongly and positively related to the cover of scorched needles on the ground (Spearman rank correlation coefficient $r = 0.74$). However, this factor was not included in the previous models due to collinearity with fire severity and the number of larger trees.

Discussion

Fire severity and pine regeneration

All three statistical techniques used confirmed a quadratic response of post-fire pine seedling establishment to fire severity. The GAM smoothing curve showed that maximum seedling density of 14–16 ind./m^2 was found in areas with crowns 70–80% affected by fire. Surprisingly, we could not find any pine seedlings in the seven plots highly affected by crown fire nor seeds on the ground, despite the intermediate level of serotinous cones (35%) reported for the burned pine stands in the north of Tenerife (Gil et al. 2002; Climent et al. 2004). This suggests that the canopy seed bank was either significantly damaged by fire or seedbed conditions were markedly unfavourable for seed germination and seedling emergence (or both factors). The observed negative correlation between fire severity and litter cover on the ground makes it difficult to disentangle the two effects on seedling density 9 months after fire.
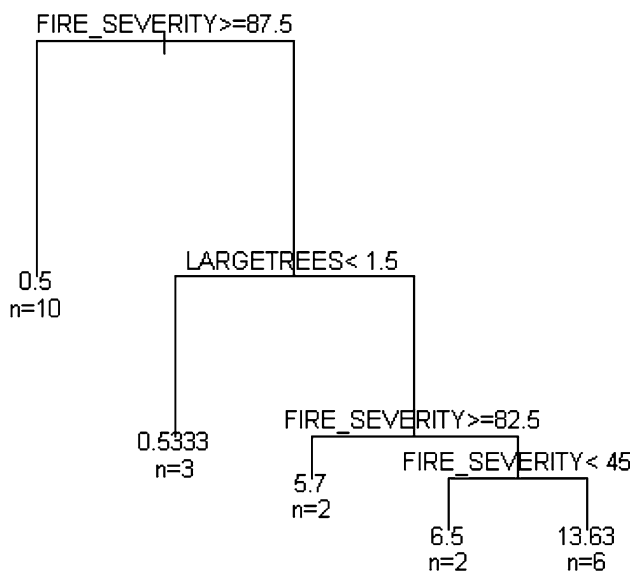
Fig. 4 Regression tree model including eight explanatory variables and seedling density as response variable. The observations are repeatedly split into two groups. If a statement is true, follow the *left* side of a branch, and if false follow the *right* side. The *numbers at the bottom* of a terminal leaf represent the mean abundance value and the number of observations in that particular group (*n*)

Nevertheless, because some favourable micro-sites might always be available for germination and establishment, the complete lack of pine regeneration at these plots suggests that destruction of seeds and cones in the canopy related to high fire intensity could be an important factor in explaining this pattern. However, only experimental studies in early post-fire conditions could clarify the importance of the scorched needle layer for pine regeneration.

There exist very few studies about the effect of fire on natural regeneration for *P. canariensis*. Very low sapling densities (0.014 ind./m^2) in post-fire regeneration were reported for a pine plantation (Arévalo et al. 2001), probably due to low seed and cone production. Seedling/sapling densities (individual height ≤ 10 cm) in unburned natural stands at the tree line in the north-west of Tenerife were

also reported to be rather low (0.34 ind./m^2, Srutek et al. 2002). With respect to Mediterranean pine forests, several studies deal with fire severity and early post-fire regeneration. Pausas et al. (2003) and Broncano and Retana (2004) did not find a clear relation between fire severity (measured by crown tree damage level) and *P. halepensis* seedling density. Fernández et al. (2008) and Vega et al. (2008) found a weak and negative influence of crown damage level on initial *P. pinaster* seedling density after fire. In these latter cases, decreases were explained, on the one hand, by the partial destruction of the aerial seed bank.

Pausas et al. (2003) showed that fire severity strongly influenced post-fire soil conditions (e.g. needle litter cover, organic matter inputs) that may have implications for germination, emergence, growth and survival of seedlings. A positive effect of needle litter over burned mineral soil was confirmed for post-fire regeneration of *Pinus ponderosa* (Bonnet et al. 2005) and a negative effect of ash layer under adult trees for *P. halepensis* regeneration (Eshel et al. 2000). A positive effect of soil organic cover reduction on initial seedling density after fire was found for *P. pinaster* (Vega et al. 2008) and *P. sylvestris* (Hille and Den Ouden 2004). Regarding *P. canariensis*, we hypothesise that the consumption of litter by fire on the ground and the transformation into an ash layer, combined with the subsequent cover of fallen scorched needles, may favour pine seed germination and seedling establishment by increased nutrient availability (Notario del Pino et al. 2008) and favourable micro-climatic conditions, but the complete lack of a protecting needle layer could negatively influence pine regeneration. However, further studies should focus on the effects of micro-environmental conditions on the regeneration of the Canarian pine in the very early stages of post-fire succession.

Stand characteristics and environmental factors

The second most important variable explaining the distribution of pine seedlings was the number of large trees

Table 2 Results of generalised additive models (GAMs) including each single explanatory variable and seedling density as response variable

Single explanatory variable in GAM	df	GAM coefficient	Final deviance	R^2	Non-linear P value
Fireseverity	**4.09**	**−0.001**	**48.72201**	**71.57**	**<0.0001**
Largetrees	**3.26**	**0.518**	**63.39153**	**63.01**	**<0.0001**
Treedens	4.28	0.116	102.5335	40.18	<0.0001
Canopy	4.53	0.035	118.9286	30.61	<0.0001
Geology	4.33	0.000	121.5742	29.07	<0.0001
Altitude	4.27	−0.001	136.6901	20.25	0.0003
Rock	4.45	−0.014	139.9735	18.33	0.0007
Slope	4.09	−0.038	144.4720	15.71	0.0012

Poisson distribution with log-link function was used. In bold typeface, those variables selected by AIC in the forward stepwise procedure (number of plots: *n* = 23)
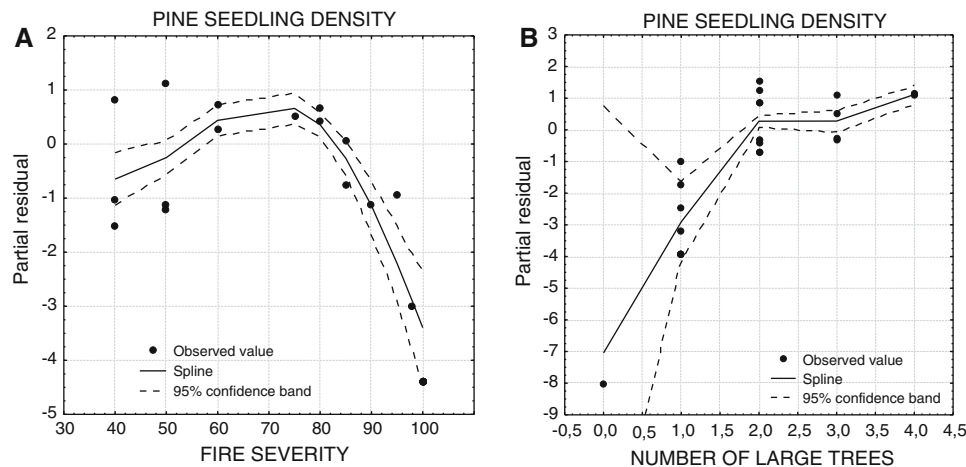
Fig. 5 Splines obtained by generalised additive models (*GAMs*). **a** The effect of fire severity on pine seedling density, **b** the effect of the number of large trees. *Dotted lines* are 95% confidence bands

Table 3 Results of generalised linear models (GLMs), showing the best set of explanatory variables explaining seedling density as response variable, using AIC best set selection and Poisson distribution with log-link function

	Estimate	SE	Wald-stat.	*P* value
Intercept	−4.4513	1.9665	5.1237	0.0236
Fireseverity	0.2439	0.0573	18.1385	<0.0001
Fire*fire	−0.0019	0.0004	19.7779	<0.0001
Largetrees	0.5322	0.1233	18.6236	<0.0001
Altitude	−0.0023	0.0006	12.1072	0.0005
Geology	0.0001	0.0000	5.1148	0.0237

The AIC of the model was 78.80 (corresponding $R^2 = 0.87$) and $P < 0.0001$. Fire severity was introduced both as a linear and as a quadratic term (number of plots: $n = 23$)

(DBH > 25 cm). This variable showed a linear relationship with seedling density and probably reflects the size of the aerial seed bank because the Canarian pine starts to produce flowers and cones quite late (age of first flowering 15–20 years, Tapias et al. 2004). Seed availability has been found to strongly determine post-fire regeneration of pine species (de Groot et al. 2004; Bonnet et al. 2005; Vega et al. 2008). Basal area, here not related to regeneration, possibly reflects better overall site productivity, while abundance of large trees indicates a certain degree of maturity of the stand. Mean canopy cover of natural stands can also be positively related to seed production or to favourable post-fire micro-environmental conditions for germination and survival of seedlings (Bonnet et al. 2005).

Serotiny and its influence on regeneration of *P. canariensis* has not been analysed in detail thus far (Tapias et al. 2004). Although serotiny was not measured in this study, the maximum seedling density of *P. canariensis* in areas with intermediate fire severity could indicate the liberation of the total aerial seed bank, including an important part stored in serotinous cones. For the clearly serotinous Mediterranean pine *P. halepensis* (Daskalakou and Thanos 2004; Tapias et al. 2004), massive regeneration has also been reported after fire (14.0 ind./m², Tsitsoni 1997; 5–20 ind./m², Ne'eman et al. 1992; 5.5 ind./m², Thanos et al. 1996; 4 ind./m², Daskalakou and Thanos 2004), values similar to the observed densities in the present study.

Very young substrate had a negative effect on pine seedling density. This environmental factor was also negatively correlated with basal area and the number of large trees, indicating a smaller aerial seed bank compared to more productive sites. Moreover, favourable micro-environmental conditions probably are scarce and hydric stress could increase with increasing rockiness. A negative effect of rockiness on post-fire regeneration was reported for *P. pinaster* (Vega et al. 2008).

Altitude influenced weakly and negatively seedling density independently from fire severity and the number of large trees. Since fire severity was not related to tree cover or altitude, we suggest that environmental factors such as precipitation and temperature could explain this weak trend. The area above 1,400 m is less influenced by the cloud layer caused by the trade winds and, therefore, the climate is drier and colder and favours the formation of dry pine forests. While analysing unburned natural Canarian pine stands along an elevational gradient between 1,700 and 2,000 m in the same region at La Guancha in the northwest of Tenerife, Srutek et al. (2002) observed a decrease in basal area, tree density, canopy cover and seedling/sapling density with altitude, which was interpreted as a response to environmental stress, i.e. decreases in productivity. The decrease in canopy cover could also represent lower levels of shading and, as a consequence, a reduced

number of favourable micro-sites for germination and establishment of seedlings.

Results show that the influence of rockiness and altitude on seedling density was only significant when applying GLMs. Furthermore, we could confirm that GLMs also cope very well with non-linear relationships, if quadratic terms are included, but data should first be explored by means of regression trees or GAMs to detect non-linear relationships as suggested by Zuur et al. (2007), otherwise there is a risk of missing important explanatory variables.

Fire severity and tree mortality

According to the applied classification of fire severity by the degree of crown damage, the wildland fire of 2007 in the northern region of Tenerife could be characterised by a high severity ground fire (understory: 100% affected) and a medium-to-high severity canopy fire (crowns: 77% affected). Even in the seven plots where needles and small branches of the crowns were completely consumed (real crown fire), we could not detect any tree mortality, which reflects the extraordinary fire resistance of *P. canariensis* in burned natural stands. Although mentioned before (Ceballos and Ortuño 1976; Höllermann 2000) and related to several life history traits (Climent et al. 2004), here we confirm this functional adaptation with quantitative data. The ongoing monitoring of pine regeneration will reveal if all the trees that were highly affected by fire will survive the next years. Fire severity, therefore, negatively affects the vitality of the Canarian pine but rarely causes mortality of individuals.

Conclusions

With respect to post-fire seedling distribution in natural *P. canariensis* stands, we propose a hierarchical scheme: The aerial seed bank, i.e. seeds stored in normal and serotinous cones, determine the potential level of seed rain that can fall to the ground after release to be transformed into a seedling bank. Fire severity modifies this potential seed rain by liberating seeds enclosed in serotinous cones or by partially destroying seeds and cones in the canopy. In a second step, post-fire micro-environmental conditions such as the amount of pine needle litter on the ground or the degree of rockiness of the substrate determine the success of germination and establishment in the first year.

The complete lack of regeneration at sites most affected by fire does not represent a major threat for the stand recovery of the Canarian pine, due to its very high tree resistance to fire and its tremendous capacity to resprout after fire. The observed very high seedling densities at sites with intermediate fire impacts can probably be related to

both the complete liberation of the seed bank (including seeds stored in serotinous cones) and favourable micro-environmental conditions for seed germination and seedling establishment. However, we hypothesise that regeneration at these sites will not be functional due to relatively fast canopy closure in the next years.

The occurrence of the striking combination of the two main strategies to cope with wildland fire, high adult resistance and variable light or intermediate serotiny, has been related to the unpredictable fire regimes deriving from volcanism in subtropical areas (Climent et al. 2004). This highlights the importance of serotinous trees for contributing to stand recruitment after fire. Our observation, that no recruitment seems to occur in highly burned areas where seeds released from serotinous cones would have high light availability for several years and, therefore, good chances to establish, calls into question this functional adaptation to fire in case of the Canarian pine. Long-term monitoring of post-fire regeneration will probably reveal which are the best conditions for pine seedling establishment after fire.

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