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Contrasting effects of wildfire and climate on radial growth of *Pinus canariensis* on windward and leeward slopes on Tenerife, Canary Islands

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Abstract Little is known concerning the effects of wildfires on tree radial growth and their climatic response under contrasting regimes of fog water inputs on oceanic islands. On Tenerife, Canary Islands, windward slopes are humid with high-fog frequency due to influence of wet trade winds, while climate on leeward slopes is more arid. We used tree-ring records of *Pinus canariensis* Sweet ex Spreng. to quantify the effects of a fire of known date on radial growth and determine the main limiting climatic factors for growth. Radial growth patterns and their responsiveness to fire severity and climatic variation differed between windward and leeward slopes. Surface fire did not significantly impact growth, while crown fire caused short-term growth reduction, and even cessation, more pronounced on the windward slope. Growth rates, tree-ring common signal, and climate sensitivity were smaller on the windward slope, with cold winters, and summer water stress limiting growth. On the leeward slope, climate explained a greater amount of growth variation mainly due to negative effects of high October–December sea-level pressures causing dry winter conditions. Contrasting growth dynamics on both slopes may result from diverging physiological effects of water inputs and reduced radiation caused by fog drip. Our findings suggest that dating growth suppressions and absent rings are useful to date past high-severity crown fires in *P. canariensis* forests, in addition to ordinary fire scars dating indicative of low-severity surface fires.

Keywords Wildfire · Dendroecology · Absent tree rings · Growth suppression · Growth pattern · Climatic response

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Introduction

Fire regimes in regions with a seasonal aridity are dependent on climate (Kitzberger et al. 2001; Piñol et al. 1998), which implies a synchrony of fire occurrence at a regional or even larger scale. This climatic component, modulated by specific characteristics of the terrain and human-influenced fuel accumulation rates and lightning, will have relevant effects on future fire regimes under a context of global change (Westerling et al. 2006). Wildfire is a fundamental ecological process in conifer forests where the structure, diversity, population dynamics, and nutrient cycling are commonly regulated by the spatial and temporal variations of fire regimes (Drury and Veblen 2008; Yermakov and Rothstein 2006).

Tree-rings are capable of recording historical fire regimes, with fire-history reconstructions relying on proxies of fire timing, extension, and behavior recorded in surviving trees, as well as stumps, logs, and snags (Niklasson and Granström 2000). Fire history is typically

reconstructed based on two types of tree-ring proxies: fire scars created during surface burning and recruitment dates of trees established after crown-opening fires (Brown and Wu 2005; Mast et al. 1999). Fire scars in repeatedly fire-injured trees are the most widely used proxies of local surface burns and can be dated at an annual or even seasonal resolution by means of dendrochronological methods (Drobyshev et al. 2004; Smith and Sutherland 2001).

Despite the effort that has been made to study the relationships of wildfires with climatic variation and human activities (e.g., Veblen et al. 1999), as well as the combined effects of climate and fire on tree regeneration (e.g., Brown and Wu 2005), there is little information and a lack of agreement concerning the effects of wildfires on radial growth patterns. Previous studies report that *Pinus ponderosa* Douglas ex C. Lawson can show both tree-ring growth increases and reductions after surface fires of varying frequency (Peterson et al. 1994). Fires caused growth reductions in *Pinus strobus* L. and *Pinus taeda* L. (Elliott et al. 2002; McInnis et al. 2004). On the contrary, abrupt tree-ring growth increases were found on the surviving *Pinus monophylla* Torr. & Frém. following intense fires (Py et al. 2006).

All previous investigations were performed on pine species without the capability of resprouting after fire, which are usually killed by intense fires. However, the impact of fire severity on the growth of species with the ability to resprout after severe crown reduction has not been studied. This is the case of *Pinus canariensis* Sweet ex Spreng., an endemic species from the western Canary archipelago, which shows traits related to fire adaptation such as thick bark, large buds, tall growth habit, longevity, sprouting capability, and serotiny (Climent et al. 2004). Following severe fires or other injuries, *P. canariensis* develops whorls of new epicormic sprouts from dormant buds located below the bark and form a new canopy.

Pinus canariensis also shows adaptations to xeric conditions, such as very deep root system, tight regulation of transpirational water loss, drought-induced xeromorphic adaptations of the needles, and xeriscent cone opening (Climent et al. 2004; Grill et al. 2004). In spite of these adaptations, however, it is sensitive to prominent water stress, a limiting factor at the upper altitudinal timberline of the species in the Canary archipelago (Gieger and Leuschner 2004; Jonsson et al. 2002). There are prevailing environmental differences between windward and leeward slopes in the Canary Islands that may differentially modulate the effects of fire severity and climatic stress on tree performance and growth. On windward slopes, orographic lifting of moist oceanic trade winds produces adiabatic cooling, condensation, and fog formation, leading to the accumulation of clouds known as "cloud sea" with precipitation mostly occurring by horizontal interception by plant canopies (Aboal et al. 2000). By contrast, leeward slopes are protected from trade winds, and the climate is drier and more arid. While it seems reasonable to expect that *P. canariensis* responsiveness to fire and climate can be different on windward and leeward slopes in the Canary Islands, no investigation has been made to demonstrate the differences.

We use dendroecological methods to assess the effects of fire intensity and climate variation on *P. canariensis* radial growth on windward and leeward slopes on Tenerife, Canary Islands. Our objectives are to quantify the effects of a severity level fire of known date on radial growth and to determine the main growth limiting climatic factors on both slopes. We hypothesize that different fire severities and the contrasted environmental conditions on opposite slopes play a significant role on tree performance and growth dynamics.

Materials and methods

Study area

Tenerife is the largest island of the Canary archipelago with an area of 2,036 km^2. The island has a steep relief dominated by the volcano Teide (3,718 m) and the Cordillera Dorsal, which splits the island into two main slopes at the south and north sides, causing significant differences in their weather regime (Fernández-Palacios 1992). Climate is Mediterranean, with a mean annual temperature of 12.6°C, maximum amplitude between −4.2 and 31.2°C, and an annual precipitation ranging from 460 to 930 mm (Aboal et al. 2000). Soils associated to humid Canary pine woodlands on Tenerife were classified as Andisols, whereas Inceptisols dominate in xeric areas (Armas et al. 2007).

Altitude and wind-exposure are major determinants of the distribution of well-defined vegetation belts (Fernández-Palacios and de Nicolás 1995). Pine forests surround the highest part of the island with a distribution at 1,300–2,000 m on windward slopes, and 700–2,200 m on leeward slopes (Fernández-Palacios and de Nicolás 1995). On windward areas, pines form a high canopy over a dense understorey of shrubs and frequent laurel-like broadleaves, while leeward pinewoods contain sparse shrubs, and very often only a thick layer of needle litter covers the ground. The study plots are plantations established in 1948 and 1952 on windward and leeward slopes, respectively, located on the Cordillera Dorsal (Fig. 1a) near the north-eastern boundary of the Corona Forestal Natural Park, at elevations ranging between 1,390 and 1,560 m (Table 1).
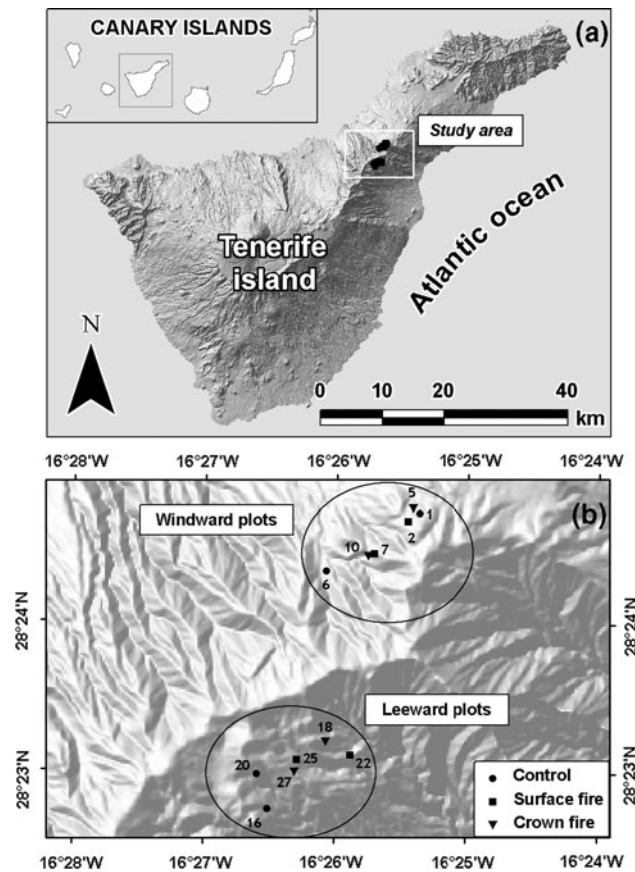
Fig. 1 **a** Location of the study area, **b** location of the windward and leeward study plots with their corresponding fire treatments. Plot numbers refer to plot designations from Arévalo et al. (2001)

Sampling

In June 1995, a big fire affected 2,709 ha in Tenerife for 3 days, burning both at low severity in surface fuels, and at

high severity in the crowns of trees. In a previous study assessing the effects of fire severity on pinewood understorey composition, 27 study plots subjected to three different fire treatments—control not burnt, surface fire, crown fire—from the 1995 fire were selected (Arévalo et al. 2001). In our study, we selected six of these plots on the windward slope and six on leeward, two plots per treatment on both slopes (Fig. 1b; Table 1). We measured DBH (bole diameter at 1.30 m above ground), recorded the presence of epicormic sprouts, and took two wood cores per tree using an increment borer from 22 trees per plot.

Sample processing and tree-ring measurement

The cores were air-dried, glued onto wooden mounts, mechanically surfaced, and then manually polished with successively finer grades of sandpaper, until the xylem cellular structure was visible in the transverse plane. Tree-ring series were absolutely dated by assigning calendar years to the rings. Total ring (TR) widths were measured under magnification to the nearest 0.001 mm with a sliding-stage micrometer (Velmex Inc., Bloomfield, NY, USA) interfaced with a computer.

In addition, earlywood (EW) and latewood (LW) widths were measured on the cores of two control plots, one on windward and one on leeward, which were at a similar elevation, in order to assess the climate/growth relationships free from fire influence. In these cases, TR widths were obtained as the sum of EW and LW on a year-by-year basis. EW to LW transition was defined according to a more or less gradual qualitative contrast in darkening, originated by a change in wood density. The computer program COFECHA (Grissino-Mayer 2001) was used to quantitatively check for crossdating and measuring errors;

Table 1 Characteristics of the studied *Pinus canariensis* plots and trees at windward and leeward slopes on Tenerife based on 22 sampled trees per plot

Aspect	Plot	Treatment	North latitude	West longitude	Elevation (m)	DBH ± SD (cm)	Epicormic sprouts (%)	Absent rings (%)
Windward	1	Control	28°24.738′	16°25.370′	1542	29.2 ± 6.1	0.0	9.1
	2	Surface fire	28°24.681′	16°25.460′	1559	31.2 ± 5.5	13.6	37.5
	5	Crown fire	28°24.770′	16°25.422′	1473	26.3 ± 5.4	100.0	100.0
	6	Control	28°24.345′	16°26.074′	1398	27.6 ± 6.9	13.0	0.0
	7	Surface fire	28°24.464′	16°25.714′	1462	28.6 ± 6.6	8.7	6.6
	10	Crown fire	28°24.448′	16°25.760′	1449	27.5 ± 5.5	100.0	100.0
Leeward	16	Control	28°22.589′	16°26.826′	1390	31.0 ± 5.8	0.0	11.7
	18	Crown fire	28°23.201′	16°26.069′	1535	25.1 ± 3.8	100.0	89.5
	20	Control	28°22.978′	16°26.591′	1525	25.3 ± 6.0	17.4	5.0
	22	Surface fire	28°23.109′	16°25.881′	1435	27.7 ± 7.5	27.3	37.5
	25	Surface fire	28°23.076′	16°26.288′	1490	31.0 ± 6.0	18.2	5.5
	27	Crown fire	28°22.996′	16°26.304′	1540	25.9 ± 4.6	100.0	93.3

Plot numbers refer to plot designations from Arévalo et al. (2001)

only series confidently dated at an annual basis were used for further analyses.

Assessing fire effects on growth patterns

Ring widths were used to calculate mean radial growth rates in order to assess the effects of 1995 fire on tree growth. Due to the great similarity between growth patterns of plot replicates for each treatment and aspect (correlations between plot replicates varied from 0.766 to 0.938, all of them significant at a $P < 0.001$ level), we used tree-ring data from each fire treatment, irrespective of the plot, both on windward and leeward slopes. A modified version of the percentage growth change (PGCs) filter of Nowacki and Abrams (1997) was applied to identify abrupt and sustained growth suppressions (Rozas 2004): PGCs = $[(M_1 - M_2)/M_2] \times 100$, where M_1 and M_2 are, respectively, the preceding and subsequent 7-year ring-width means. PGCs chronologies were calculated by applying this formula to the individual tree-ring series, and mean PGCs chronologies for each fire treatment were separately calculated for windward and leeward slopes. Abrupt growth suppressions were recognized as peaks >200% in the average PGCs chronologies. In addition, the number of absent rings identified by crossdating on the individual tree-ring growth series was summarized at an annual basis. Rings were considered as absent only if identified by crossdating on both cores of each tree.

To assess the short-term effects of fire severity on tree-ring growth, we considered three 5-year periods: pre-fire (1990–1994), post-fire (1996–2000), and recovery (2001–2005). Tree-ring growth data were square-root transformed to achieve requirements of normality and homocedasticity. The effects of plot, treatment, aspect, and period on tree-ring growth were analyzed using repeated-measures ANOVA (Zar 2010), where plot was a random factor, treatment, and aspect were between-subjects factors, and period was a within-subjects factor. The Huynh–Feldt corrected test was applied for within-subjects effects analysis due to the lack of data sphericity. Comparisons among periods, for each treatment and aspect, were carried out using one-way ANOVA and tested with the Tukey's HSD post hoc test. Statistical analyses were performed with the SPSS v15.0 for Windows package (SPSS Inc., Chicago, IL, USA).

Tree-ring standardization and chronology computation

Intra- and inter-annual responses of growth to climate were investigated after standardizing the raw EW, LW, and TR series with the ARSTAN computer program (Cook and Holmes 1996). Asynchronous growth changes such as disturbance signals were unusual within our tree-ring series, and only 50 years of tree-ring data were available. This is why we used for standardization a flexible spline function, which guarantees the removal of most non-climatically related variance, such as the biological trends, by preserving high-frequency climatic information (Cook and Peters 1981). We used a spline function with a 50% frequency response of 32 years and pre-whitened the obtained residuals by autoregressive modeling. The resulting indices for the individual series were averaged by biweight robust mean. The statistical quality of chronologies was assessed for the common interval 1967–2006 using standard basic statistics to measure the common signal (Briffa and Jones 1990): mean sensitivity (ms), first-order autocorrelation (Ac), mean correlation between trees (Rbt), within trees (Rwt), and between all cores (Rbar), signal-to-noise ratio (SNR), and expressed population signal (EPS).

Evaluating tree-ring growth responses to climate

Since the local network of meteorological stations on Tenerife is incomplete and covers mainly low-altitude areas, we used monthly gridded data from the datasets of the Climate Research Unit, University of East Anglia, UK. Mean temperature (T), total precipitation (P), and mean sea-level pressure (SLP) for the period 1967–2006, were taken from the Web site of the Royal Netherlands Meteorological Institute (http://climexp.knmi.nl/). Monthly data from June of the previous year (Jun(-1)) to September of the current growth year (Sep) were used, and also averaged (T and SLP) or summed (P) in periods of 2 and 3 months to identify their main effects on tree-ring growth at monthly, bimonthly, and seasonal scales.

We determined the climatic factors that significantly influenced radial growth, and total growth variance explained by climate on tree-ring chronologies, by redundancy analysis (RDA), a canonical multivariate method that seeks linear combinations of environmental factors correlated to linear combinations of response variables (Legendre and Legendre 1998). EW, LW, and TR chronologies were considered as the response variables in RDA, while the climatic variables were environmental predictors. A forward selection procedure allowed excluding highly redundant and collinear predictors, which could have caused model instability and/or variance overestimation. Stepwise RDAs and Pearson's correlations were calculated to determine the explained tree-ring growth variation for the retained predictors, as well as the sign of climate–growth relationships. The amount of growth variance explained in each RDA was calculated as the proportion of total variance given by the canonical eigenvalue λ (Legendre and Legendre 1998). Total explained variation in tree-ring chronologies for either windward or leeward slopes was obtained under a reduced

RDA model including the significant predictors. For the described analyses, Monte Carlo tests with 9,999 random permutations were used to evaluate the significance of canonical eigenvalues. The sequence of several complementary RDAs was performed using the software CANO-CO v4.0 for Windows (ter Braak and Šmilauer 1998). A scatter plot of the weighting coefficients for the first two RDA axes under an overall canonical ordination displayed the relationships between the significant climatic predictors and chronologies for EW, LW, and TR on both slopes.

## Results

Fire impact on tree-ring growth patterns

Mean diameters of the sampled trees were quite similar on both slopes, ranging 26.3–31.2 cm on windward and 25.1–31.0 on leeward (Table 1). The proportion of trees with epicormic sprouts greatly differed among fire treatments, with 0.0–17.4% in control plots, 8.7–27.3% in surface fire plots, and 100% in crown fire plots. In control plots, only those trees overtopped or which suffered some

mechanical damage showed sprouts. In surface fire plots, the same cases as in control plots were recorded, but additionally several trees showed basal sprouts due to fire damage in the lower part of the trunk. In crown fire plots, in contrast, crown and bark along the complete stems were scorched, with new sprouts densely and uniformly arranged in whorls with a general aspect of trees resembling "bottlebrushes".

Growth patterns of control and surface fire treatments on the same slope were very similar, with no growth anomalies and the typical ring-width trend of a negative exponential decline with an associated decrease in inter-annual variability (Fig. 2). On both slopes, however, trees suffering from crown fire showed an abrupt decrease in ring width from 1995, and a new increase in mean growth rates, and growth variability from 2000 (Fig. 2).

Growth reductions in the crown fire treatment were evidenced as conspicuous peaks of PGCs with maxima in 1995 and 1994 on windward and leeward, respectively (Fig. 3). Reductions associated with the 1995 burn were more pronounced on windward (613% in mean PGCs) than on leeward (351%). Accordingly, absent rings were identified on both slopes, since 1996 on windward, and in 1975,

Fig. 2 Radial growth patterns of *Pinus canariensis* (mean ring width ± SD) per fire treatment on windward and leeward slopes, with their corresponding sample sizes. *Arrows* indicate the 1995 fire
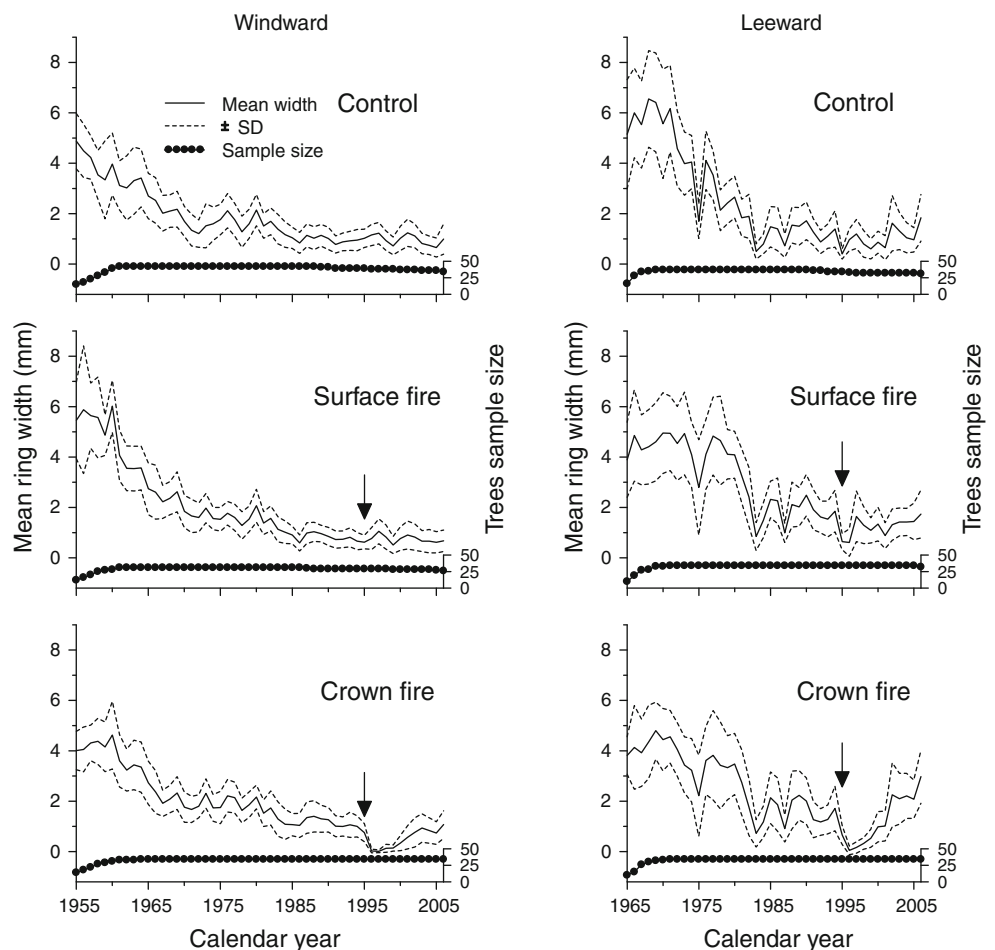
Fig. 3 Mean PGCs chronologies (*lines*) and number of trees with absent rings (*bars*) per fire treatment on windward and leeward slopes. The years of maximum PGCs values and the considered threshold for 200% PGCs are shown
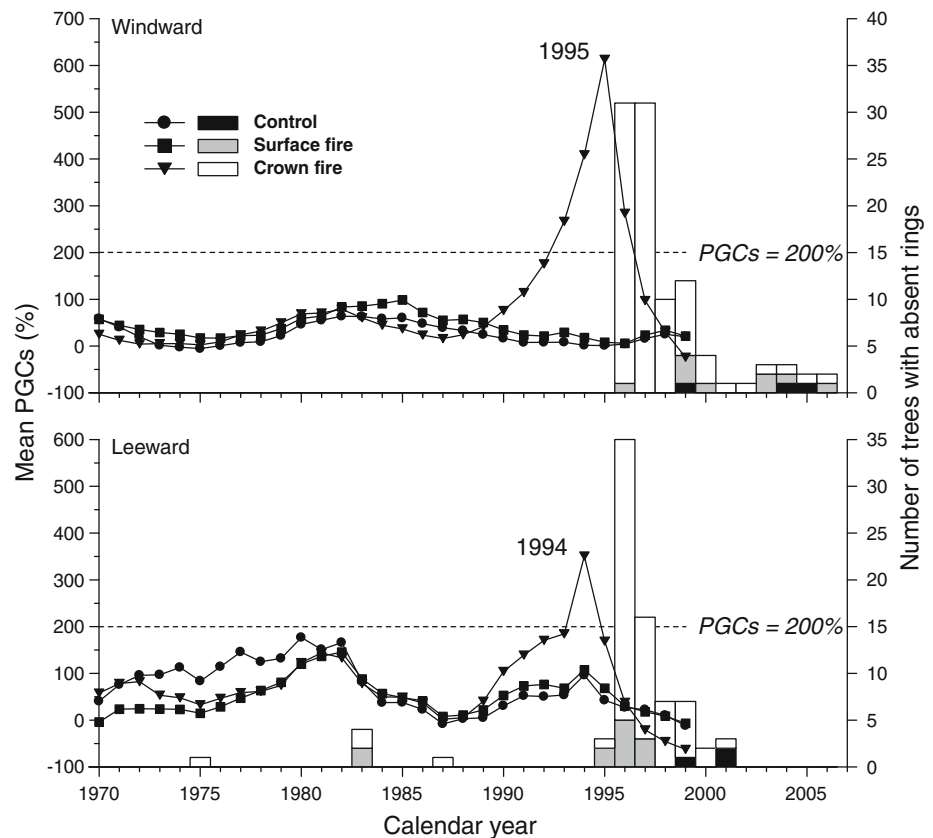
1983, 1987, and 1995–2001 on leeward. Absent rings were mainly recorded for period 1996–2000, mostly from trees that experienced crown fire (Table 1; Fig. 3).

Fire treatment, aspect, period, and their corresponding interactions had significant effects on tree-ring growth in the periods immediately before and after the 1995 fire (Table 2). By contrast, plot and their interaction with period were not significant, which suggests that replicated plots within each treatment had quite similar ring-width variations. Most conspicuous effects were due to aspect and their interaction with treatment so that different growth responses to fire can be expected on windward and leeward slopes. The highly significant interactions between period and treatment indicate that fire severity differentially impacted on tree growth for the pre-fire, post-fire, and recovery periods.

Windward plots did not show growth differences among periods for the control and surface fire ($P > 0.05$, Fig. 4a); but under crown fire, post-fire growth was significantly lower than for the pre-fire and recovery periods ($F_{2,101} = 89.02$, $P < 0.001$). In contrast, on the leeward slope significant differences among periods were found for all fire treatments (Fig. 4b). Under control and surface fire, a significant reduction of tree growth was noticed in the

Table 2 Results of repeated-measures ANOVA for the effects of plot replicates, treatment (control, surface fire, crown fire), aspect (windward, leeward), and period (pre-fire, post-fire, recovery), on mean tree-ring width

Source of variation	SS	DF	MS	*F*-value	*P*-value
Between-subjects effects					
Intercept	2.627	1	2.627	22.39	<0.001
Plot	0.032	1	0.032	0.27	0.600
Treatment	0.940	2	0.470	4.01	0.020
Aspect	8.141	1	8.141	69.64	<0.001
Treatment × aspect	2.386	2	1.193	10.17	<0.001
Error	22.296	190	0.117		
Within-subjects effects[a]					
Period	0.195	2	0.104	4.26	0.017
Period × plot	0.083	2	0.044	1.81	0.167
Period × treatment	3.362	4	0.896	36.75	<0.001
Period × aspect	0.168	2	0.089	3.67	0.029
Period × treatment × aspect	1.524	4	0.406	16.66	<0.001
Error	8.690	380	0.024		

SS sum of squares, *DF* degrees of freedom, *MS* mean square

[a] The Huynh–Feldt corrected test was applied due to the lack of data sphericity
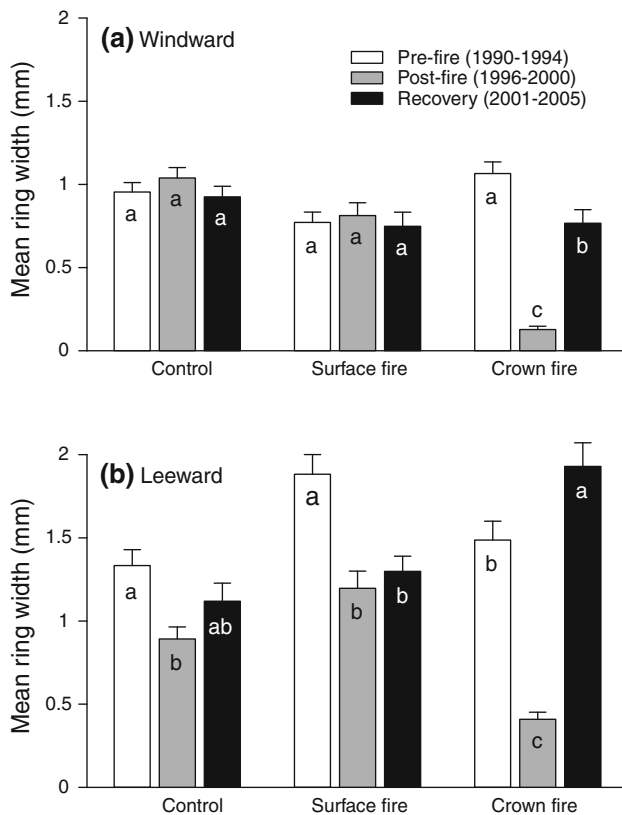
Fig. 4 Comparison of mean ring widths (+1SE) per period and fire treatment on **a** windward and **b** leeward slopes. Different *letters* within each treatment indicate significant differences ($P < 0.05$) among periods according to Tukey's HSD post hoc test

post-fire that was maintained for the recovery period ($F_{2,95} = 6.22$, $P = 0.003$ for control; $F_{2,101} = 12.63$, $P < 0.001$ for surface fire). Under crown fire, a significant reduction of tree growth was also noticed for the post-fire period, but growth was significantly greater for the recovery period than for previous ones ($F_{2,101} = 80.49$, $P < 0.001$).

High-frequency growth variation and climatic response

Mean ring widths and standard deviations were higher on leeward than on windward (Appendix S1). Also, the relative change of EW, LW, and TR widths between consecutive rings was higher on leeward, as indicated by ms values, while Ac was higher on windward. Common signal within and between trees was larger on leeward, as indicated by Rbt, Rwt, Rbar, and SNR statistics for all EW, LW, and TR. EPS values were higher than 0.85 for almost all chronologies, suggesting that the amount of local year-to-year growth variation shared by trees was relatively high, especially for EW and TR chronologies.

A large amount of growth variation was shared by EW, LW, and TR at a local level, with very similar intra-annual

variation patterns within each slope, but quite different between slopes (Appendix S2). The visual assessment was supported by statistical correlations among chronologies, which were highly significant within the same slope, especially between EW and TR; however, no significant correlations among chronologies from different slope were found (Appendix S3).

According to RDA models, climatic variables with a significant effect on tree-ring growth on the windward slope were T in previous December, P in July–August, and P in February, with both December T and July–August P explaining over 17.7% of growth variation (Table 3). Pearson's correlations showed that both variables exerted a positive effect on growth, more pronounced in EW and TR for December T, and in LW for July–August P. By contrast, February P showed a negative effect on LW and TR growth. According to the reduced model, 37.1% of tree growth variation on the windward slope was explained by climate. On the leeward slope, climatic variables with significant effect on growth were P in previous November–December, with a positive effect on tree growth, and SLP in previous October–December, with a negative effect mainly on EW and TR growth. Both variables explained together 43.9% of tree growth variation, while P and SLP explained 25.1 and 40.9%, respectively.

Based on an overall RDA model (F-value $= 6.08$, $P < 0.001$), RDA axis 1 was positively correlated with P in previous November–December and July–August, and negatively with SLP in previous October–December (Appendix S4). RDA axis 2 was positively correlated with T in previous December, and P in July–August, but negatively with P in February. RDA axes 1 and 2 explained, respectively, 74.3 and 20.7% of the growth–climate relationships (Fig. 5). The ordination showed that tree-ring growth on windward was mainly positively related to T in previous December (correlation with TR, $R = 0.45$, $P = 0.003$). On the leeward slope, the main factor affecting tree-ring width negatively was SLP in previous October–December (correlation with TR, $R = -0.66$, $P < 0.001$). The strong relationships between tree-ring growth and SLP in October–December can be also graphically verified (Fig. 6), with wider tree rings following years with low SLP values (i.e., 1990 and 2002), and narrower rings following years with high SLP values (i.e., 1975, 1983, 1987, and 1995).

Discussion

Climate-growth responses of *P. canariensis*

Even in a reduced geographical range, we found big differences in tree growth between windward and leeward

Table 3 Summary statistics of RDA models and Pearson's correlations for the relationships between the variation of tree-ring growth indices on the windward and leeward slopes, and climate predictors for mean temperature (*T*), precipitation (*P*), and sea-level pressure (SLP)

Aspect	Climatic predictors	RDA models			Pearson's correlations[a]		
		λ	*F*-value	*P*-value	EW	LW	TR
Windward	*T* Dec(-1)	0.177	8.18	0.003	0.443**	0.349*	0.449**
	P Jul–Aug	0.176	8.11	0.003	0.335*	0.496**	0.408**
	P Feb	0.099	4.18	0.032	−0.288	−0.333*	−0.323*
	Reduced model	0.371	7.08	<0.001			
Leeward	P Nov–Dec(-1)	0.251	12.72	0.001	0.484**	0.515***	0.506***
	SLP Oct–Dec(-1)	0.409	26.32	<0.001	−0.641***	−0.609***	−0.665***
	Reduced model	0.439	14.49	<0.001			

The proportion of tree-ring growth variation accounted for by each variable and by reduced models was quantified by the eigenvalue λ

[a] Significance levels: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Fig. 5 Biplot scores from RDA model for the relationships of tree-ring growth (EW, LW, and TR are, respectively, earlywood, latewood, and total ring indexed chronologies) on windward (W) and leeward (L) slopes with the climatic predictors significantly (*P* < 0.05) related to tree-ring growth variation. The percentage of variance accounted for by each RDA axis is shown
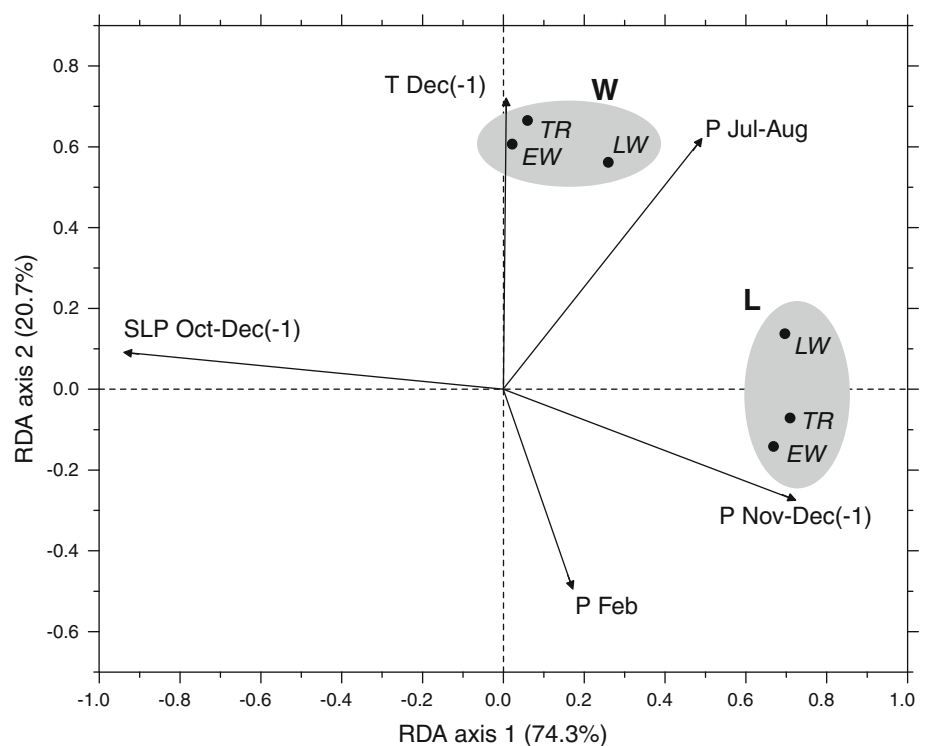

slopes on Tenerife. This is in agreement with previous findings that Canary pine forests on windward and leeward are separate ecosystems, each with its own dynamics, and environmental constraints (Fernández-Palacios and de Nicolás 1995).

The physiological effects of water inputs and reduced radiation caused by fog drip make climate less limiting on the windward slope. The amount of water captured by vegetation from the fog carried by trade winds implies that throughfall can account in average more than twice the incident rainfall (Aboal et al. 2000); therefore throughfall plays a fundamental role in the water relationships of *P. canariensis*. Fog alleviates water stress by reducing

canopy transpiration or evaporation and/or by improving plant water status by direct absorption through the foliage (Burgess and Dawson 2004). Reduced water stress on windward can explain the positive effects of elevated temperatures in previous December and the detrimental impact of February precipitation on *P. canariensis* growth. In Mediterranean pines, carbon assimilation occurs year round, and relatively high rates of winter photosynthesis can occur under warm conditions (Medlyn et al. 2002). In fact, maximum daily net photosynthesis in *P. canariensis* can be higher during winter than in summer, due to higher soil–water availability and a lower evaporative demand as compared with the warm and dry season (Peters et al.

Fig. 6 Comparison of tree-ring growth indices on leeward slope with SLP in October–December of the previous year. Note the inverted scale in the vertical axis for SLP. Years with maximum (1990, 2002) and minimum (1975, 1983, 1987, 1995) growth are shown
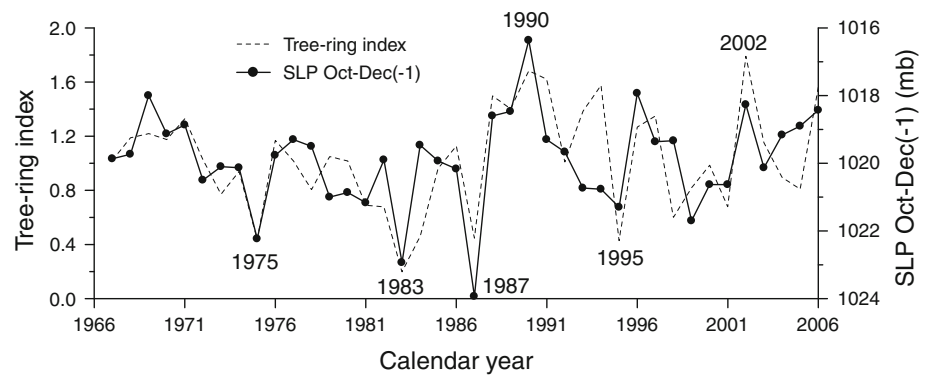
2008). High winter photosynthetic rates and relatively elevated temperatures would result in a greater amount of carbohydrates stored to be used in the following active season (Zweifel et al. 2006).

The negative influence of February precipitation, mainly on LW growth, may be related to reduced solar radiation modulated by cloudiness, which showed to be a primary factor limiting photosynthesis, carbon uptake, and growth during the rainy season (Graham et al. 2003). Trees on windward show a positive response to precipitation in July–August, suggesting that summer water stress limits growth. Probably, summer drought is mitigated by a high relative humidity of the air, and a high frequency of clouds due to trade winds influence. In this species, canopy transpiration is maintained at relatively high rates during the dry season (Luis et al. 2005), suggesting that water stress can negatively affect growth of *P. canariensis* during the warm and dry season, a generalized response of pine species under Mediterranean climate (Bogino and Bravo 2008; Campelo et al. 2006).

On the leeward slope, the presence of narrow/wide rings produced during years of high/low sea-level pressure suggested that annual growth was strongly limited by climatic factors depending on SLP, namely winter precipitation. In fact, precipitation in November–December is negatively correlated ($R = -0.56$, $P < 0.001$) with SLP in October–December. Wider rings were formed after rainy winters (1990 and 2002), while narrower and even absent rings occurred in years following lower winter precipitation (1975, 1983, 1987, and 1995). Narrow rings for these years were also identified by Jonsson et al. (2002) near the upper altitudinal timberline of *P. canariensis* (2,000–2,100 m) on Tenerife, suggesting that they are characteristic of sites beyond the influence of the "cloud sea". When the low-pressure system tends to be stronger, it causes moister and colder conditions than usual during November–December on Tenerife, so that soils are replenished with water before the summer drought. By contrast, high pressures in winter produce the reversed pattern, and lead to anomalous hot and dry winters on leeward.

Leeward populations of *P. canariensis* exhibit xeromorphic traits allowing a tight regulation of transpirational water loss (Grill et al. 2004). Accordingly, annual canopy transpiration lies significantly below the common values for other Mediterranean trees, suggesting a strong adaptation to low soil water availability during periods of great evaporative demand (Luis et al. 2005). The effect of winter precipitation can be due to the pronounced water deficit in the study area, with one-third of the annual precipitation occurring in November–December. The positive influence of moist winters on growth is common in Mediterranean pines and can be attributed to soil water recharge during the wet season (Bogino and Bravo 2008; Martín-Benito et al. 2008).

Fire effects on tree growth

Previous evidences suggest that surviving trees can experience either growth releases or reductions as a function of either the degree of fire injury the trees suffered, or the benefits derived from competitor's decline and release of nutrients to the soil. We observed growth reductions after severe crown fire, with no relevant effects of surface fire on tree growth. Our finding does not agree with previous studies, which showed that *P. monophylla* and *Sequoiadendron giganteum* (Lindl.) J. Buchh. had abrupt tree-ring growth increases on the surviving trees in the early years following intense fires (Mutch and Swetnam 1995; Py et al. 2006); or surface fires caused growth reductions on *P. strobus*, which were directly related to the amount of forest surface litter consumed by fires (Elliott et al. 2002). However, our results agree with a study on *P. taeda*, in which crown fires reduced growth proportionally to the amount of crown scorched (McInnis et al. 2004). In our crown fires, almost 100% of the crown was scorched, while the proportion of crown scorched by surface fire was negligible.

Most conspicuous effects of the 1995 fire on ring-width patterns were due to aspect and its interaction with fire treatment. Crown fire impacted tree growth considerably

on both slopes, but more severely on windward. The reason for growth reduction in 1994 on leeward, as the PGCs filter revealed, is that the big fire in 1995 coincided with a climatically caused narrow ring in the same year on leeward. Thus, the PGCs filter showed its maximum 1 year earlier than the actual date of fire. The harsh reduction of growth rates in the post-fire period, and the absent rings in all trees suffering from crown fire on windward, suggested that fire impact on growth was greater than on leeward. Contrasting growth responses to fire observed on windward and leeward slopes are probably related to the different growth rates, stand structure, understorey composition, fuel accumulation, and flammability on both slopes as a result of cloudiness influence.

As opposed to the post-fire impact, growth recovery was faster on leeward, showing even higher growth rates than for the pre-fire period. In dry Canary pine woodland, understorey shrubs usually die, and soil mineral nutrients become clumped around pine trees after severe fires (Rodríguez et al. 2009), which can improve soil resource content and tree growth in the recovery period. *P. canariensis* is rarely killed by crown fires, with all trees remaining alive after very severe fires (Otto et al. 2010), resprouting from stems and larger branches, and maintaining their ability to intercept nutrients. The outstanding resistance and capability of *P. canariensis* to resprout after severe fires are unusual among pine species. A high proportion of living cells in the xylem, which accumulate large amounts of starch, are responsible for epicormic sprouting from preformed buds, and the production of a new crown after severe fire (Climent et al. 1998, 2004). Our results suggest that the abundant synchronic absent rings are a consequence of severe crown fires, as radial growth ceased and stored reserves were probably allocated for the growth of epicormic sprouts during the post-fire period. Only when the photosynthetic tissue from the new crown produces enough carbohydrates can the surplus be newly allocated to storage and radial growth.

The largest wildfires on Tenerife occurred in September 1983 (6,500 ha) and July 1995 (2,700 ha) following dry winters with high sea-level pressure, which coincided with narrow and absent tree rings on leeward. Dry winters may desiccate coarse forest fuels enough to produce large fires, so that fire occurrence could be phase-locked with sea-level pressure. The relative predictability of fire events in the Canary Islands offers managers and decision makers a useful alerting tool for planning preventive measures to mitigate the effects of large, high-intensity wildfires when dry conditions occur in previous winter. Extensive reconstructions of past fire events in Canary pinewoods, based on dating abundant fire scars and analyzing tree-ring growth sequences from long-lived trees, should be performed to confirm this assumption.

Even if there are previous evidences that abrupt tree-ring growth changes can be found in the surviving trees after intense fires (Mutch and Swetnam 1995; Py et al. 2006), these changes have not been used to reconstruct past fire regimes yet. As our results suggest, dating harsh growth suppressions and synchronic series of consecutive absent rings on surviving trees can also help to date past high-severity crown fires in *P. canariensis* forests and probably also in other tree species with the capability of stem sprouting after fire.

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