

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21

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

Vicente Rozas <sup>1,\*</sup>, Gonzalo Pérez-de-Lis <sup>2</sup>, Ignacio García-González <sup>2</sup>, José Ramón  
Arévalo <sup>3</sup>

<sup>1</sup> Misión Biológica de Galicia, Consejo Superior de Investigaciones Científicas, Apdo. 28,  
E-36080 Pontevedra, Spain

<sup>2</sup> Departamento de Botánica, Escola Politécnica Superior, Campus de Lugo, Universidade  
de Santiago de Compostela, E-27002 Lugo, Spain

<sup>3</sup> Departamento de Ecología, Facultad de Biología, Universidad de La Laguna, E-38206  
La Laguna, Tenerife, Spain

\* Corresponding author: E-mail [vrozas@mbg.cesga.es](mailto:vrozas@mbg.cesga.es) , Telephone +34 986 854800, Fax  
+34 986 841362

22

23 **Abstract**

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

42

43 **Key words** Wildfire, dendroecology, absent tree rings, growth suppression, growth  
44 pattern, climatic response

45

46 **Introduction**

47 Fire regimes in regions with a seasonal aridity are dependent on climate (Kitzberger et al.  
48 2001; Piñol et al. 1998), which implies a synchrony of fire occurrence at a regional or  
49 even larger scale. This climatic component, modulated by specific characteristics of the  
50 terrain and human-influenced fuel accumulation rates and lightning, will have relevant  
51 effects on future fire regimes under a context of global change (Westerling et al. 2006).  
52 Wildfire is a fundamental ecological process in conifer forests where the structure,  
53 diversity, population dynamics, and nutrient cycling are commonly regulated by the  
54 spatial and temporal variation of fire regimes (Drury and Veblen 2008; Yermakov and  
55 Rothstein 2006).

56 Tree-rings are capable of recording historical fire regimes, with fire-history  
57 reconstructions relying on proxies of fire timing, extension and behaviour recorded in  
58 surviving trees, as well as stumps, logs and snags (Niklasson and Granström 2000). Fire  
59 history is typically reconstructed based on two types of tree-ring proxies: fire scars created  
60 during surface burning, and recruitment dates of trees established after crown-opening  
61 fires (Brown and Wu 2005; Mast et al. 1999). Fire scars in repeatedly fire-injured trees are  
62 the most widely used proxies of local surface burns, and can be dated at an annual or even  
63 seasonal resolution by means of dendrochronological methods (Drobyshev et al. 2004;  
64 Smith and Sutherland 2001).

65 Despite the effort that has been made to study the relationships of wildfires with  
66 climatic variation and human activities (e.g., Veblen et al. 1999), as well as the combined  
67 effects of climate and fire on tree regeneration (e.g., Brown and Wu 2005), there is little  
68 information and a lack of agreement concerning the effects of wildfires on radial growth  
69 patterns. Previous studies report that *Pinus ponderosa* Douglas ex C. Lawson can show

70 both tree-ring growth increases and reductions after surface fires of varying frequency  
71 (Peterson et al. 1994). Fires caused growth reductions in *P. strobus* L. and *P. taeda* L.  
72 (Elliott et al. 2002; McInnis et al. 2004). On the contrary, abrupt tree-ring growth  
73 increases were found on the surviving *P. monophylla* Torr. & Frém. following intense  
74 fires (Py et al. 2006).

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

84 *P. canariensis* also shows adaptations to xeric conditions, such as very deep root  
85 system, tight regulation of transpirational water loss, drought-induced xeromorphic  
86 adaptations of the needles, and xeriscent cone opening (Climent et al. 2004; Grill et al.  
87 2004). In spite of these adaptations, however, it is sensitive to prominent water stress, a  
88 limiting factor at the upper altitudinal timberline of the species in the Canary archipelago  
89 (Gieger and Leuschner 2004; Jonsson et al. 2002). There are prevailing environmental  
90 differences between windward and leeward slopes in the Canary Islands that may  
91 differentially modulate the effects of fire severity and climatic stress on tree performance  
92 and growth. On windward slopes, orographic lifting of moist oceanic trade winds  
93 produces adiabatic cooling, condensation, and fog formation, leading to the accumulation  
94 of clouds known as ‘cloud sea’, with precipitation mostly occurring by horizontal

95 interception by plant canopies (Aboal et al. 2000). By contrast, leeward slopes are  
96 protected from trade winds, and the climate is drier and more arid. While it seems  
97 reasonable to expect that *P. canariensis* responsiveness to fire and climate can be different  
98 on windward and leeward slopes in the Canary Islands, no investigation has been made to  
99 demonstrate the differences

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

107

## 108 **Materials and methods**

### 109 Study area

110 Tenerife is the largest island of the Canary archipelago with an area of 2,036 km<sup>2</sup>. The  
111 island has a steep relief dominated by the volcano Teide (3,718 m) and the Cordillera  
112 Dorsal, which splits the island into two main slopes at the south and north sides, causing  
113 significant differences in their weather regime (Fernández-Palacios 1992). Climate is  
114 Mediterranean, with a mean annual temperature of 12.6 °C, maximum amplitude between  
115 -4.2 and 31.2 °C, and an annual precipitation ranging from 460 to 930 mm (Aboal et al.  
116 2000). Soils associated to humid Canary pine woodlands on Tenerife were classified as  
117 Andisols, whereas Inceptisols dominate in xeric areas (Armas et al. 2007).

118 Altitude and wind-exposure are major determinants of the distribution of well-  
119 defined vegetation belts (Fernández-Palacios and de Nicolás 1995). Pine forests round the

120 highest part of the island with a distribution between 1,300-2,000 m, on windward slopes  
121 and 700-2,200 m on leeward slopes (Fernández-Palacios and de Nicolás 1995). On  
122 windward areas, pines form a high canopy over a dense understorey of shrubs and  
123 frequent laurel-like broadleaves, while leeward pinewoods contain sparse shrubs, and very  
124 often only a thick layer of needle litter covers the ground. The study plots are plantations  
125 established in 1948 and 1952 on windward and leeward slopes, respectively, located on  
126 the Cordillera Dorsal (Fig. 1a) near the north-eastern boundary of the Corona Forest  
127 Natural Park, at elevations ranging between 1,390 and 1,560 m (Table 1).

128

#### 129 Sampling

130 In June 1995, a big fire affected 2,709 ha in Tenerife during three days, burning both at  
131 low severity in surface fuels, and at high-severity fires in the crowns of trees. In a  
132 previous study assessing the effects of fire severity on pinewood understorey composition,  
133 27 study plots subjected to three different fire treatments –control not burnt, surface fire,  
134 crown fire– from the 1995 fire were selected (Arévalo et al. 2001). In our study, we  
135 selected six of these plots on the windward slope and six on leeward, two plots per  
136 treatment on both slopes (Fig. 1b, Table 1). We measured DBH (bole diameter at 1.30 m  
137 above ground), recorded the presence of epicormic sprouts and took two wood cores per  
138 tree using an increment borer from 22 trees per plot.

139

#### 140 Sample processing and tree-ring measurement

141 The cores were air-dried, glued onto wooden mounts, mechanically surfaced and then  
142 manually polished with successively finer grades of sandpaper, until the xylem cellular  
143 structure was visible in the transverse plane. Tree-ring series were absolutely dated by  
144 assigning calendar years to the rings. Total ring widths were measured under

145 magnification to the nearest 0.001 mm with a sliding-stage micrometer (Velmet Inc.,  
146 Bloomfield NY, USA) interfaced with a computer.

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

156

157 Assessing fire effects on growth patterns

158 Ring widths were used to calculate mean radial growth rates in order to assess the effects  
159 of 1995 fire on tree growth. Due to the great similarity between growth patterns of plot  
160 replicates for each treatment and aspect (correlations between plot replicates varied from  
161 0.766 to 0.938, all of them significant at a  $P < 0.001$  level), we used tree-ring data from  
162 each fire treatment, irrespective of the plot, both on windward and leeward slopes. A  
163 modified version of the percentage growth change (PGCs) filter of Nowacki and Abrams  
164 (1997) was applied to identify abrupt and sustained growth suppressions (Rozas 2004):  
165  $PGCs = [(M_1 - M_2) / M_2] \times 100$ , where  $M_1$  and  $M_2$  are, respectively, the preceding and  
166 subsequent 7-year ring-width means. PGCs chronologies were calculated by applying this  
167 formula to the individual tree-ring series, and mean PGCs chronologies for each fire  
168 treatment were separately calculated for windward and leeward slopes. Abrupt growth  
169 suppressions were recognized as peaks  $> 200\%$  in the average PGCs chronologies. In

170 addition, the number of absent rings identified by crossdating on the individual tree-ring  
171 growth series was summarized at an annual basis. Rings were considered as absent only if  
172 identified by crossdating on both cores of each tree.

173 To assess the short-term effects of fire severity on tree-ring growth, we considered  
174 three 5-year periods: pre-fire (1990–1994), post-fire (1996–2000), and recovery (2001–  
175 2005). Tree-ring growth data were square-root transformed to achieve requirements of  
176 normality and homocedasticity. The effects of plot, treatment, aspect and period on tree-  
177 ring growth were analyzed using repeated-measures ANOVA (Zar 2010), where plot was  
178 a random factor, treatment and aspect were between-subjects factors, and period was a  
179 within-subjects factor. The Huynh-Feldt corrected test was applied for within-subjects  
180 effects analysis due to the lack of data sphericity. Comparisons among periods, for each  
181 treatment and aspect, were carried out using one-way ANOVA and tested with the  
182 Tukey's HSD *post hoc* test. Statistical analyses were performed with the SPSS v15.0 for  
183 Windows package (SPSS Inc., Chicago IL, USA).

184

#### 185 Tree-ring standardization and chronology computation

186 Intra- and inter-annual responses of growth to climate were investigated after  
187 standardizing the raw EW, LW and TR series with the ARSTAN computer program  
188 (Cook and Holmes 1996). Asynchronous growth changes such as disturbance signals were  
189 unusual within our tree-ring series, and only 50 years of tree-ring data were available.  
190 This is why we used for standardization a flexible spline function, which guarantees the  
191 removal of most non-climatically related variance, such as the biological trends, by  
192 preserving high-frequency climatic information (Cook and Peters 1981). We used a spline  
193 function with a 50% frequency response of 32 years and pre-whitened the obtained  
194 residuals by autoregressive modeling. The resulting indices for the individual series were



195 averaged by biweight robust mean. The statistical quality of chronologies was assessed for  
196 the common interval 1967–2006 using standard basic statistics to measure the common  
197 signal (Briffa and Jones 1990): mean sensitivity (ms), first-order autocorrelation (Ac),  
198 mean correlation between trees (Rbt), within trees (Rwt), and between all cores (Rbar),  
199 signal-to-noise ratio (SNR), and expressed population signal (EPS).

200

201 Evaluating tree-ring growth responses to climate

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

211 We determined the climatic factors that significantly influenced radial growth, and  
212 total growth variance explained by climate on tree-ring chronologies, by redundancy  
213 analysis (RDA), a canonical multivariate method that seeks linear combinations of  
214 environmental factors correlated to linear combinations of response variables (Legendre  
215 and Legendre 1998). EW, LW and TR chronologies were considered as the response  
216 variables in RDA, while the climatic variables were environmental predictors. A forward  
217 selection procedure allowed excluding highly redundant and collinear predictors, which  
218 could have caused model instability and/or variance overestimation. Stepwise RDAs and  
219 Pearson's correlations were calculated to determine the explained tree-ring growth

220 variation for the retained predictors, as well as the sign of climate-growth relationships.  
221 The amount of growth variance explained in each RDA was calculated as the proportion  
222 of total variance given by the canonical eigenvalue  $\lambda$  (Legendre and Legendre 1998).  
223 Total explained variation in tree-ring chronologies for either windward or leeward slopes  
224 was obtained under a reduced RDA model including the significant predictors. For the  
225 described analyses, Monte Carlo tests with 9,999 random permutations were used to  
226 evaluate the significance of canonical eigenvalues. The sequence of several  
227 complementary RDAs was performed with the software CANOCO v4.0 for Windows (ter  
228 Braak and Smilauer 1998). A scatter plot of the weighting coefficients for the first two  
229 RDA axes under an overall canonical ordination displayed the relationships between the  
230 significant climatic predictors and chronologies for EW, LW and TR on both slopes.

231

## 232 **Results**

### 233 Fire impact on tree-ring growth patterns

234 Mean diameters of the sampled trees were quite similar on both slopes, ranging 26.3–31.2  
235 cm on windward and 25.1–31.0 on leeward (Table 1). The proportion of trees with  
236 epicormic sprouts greatly differed among fire treatments, with 0.0–17.4% in control plots,  
237 8.7–27.3% in surface fire plots, and 100% in crown fire plots. In control plots, only those  
238 trees overtopped or which suffered some mechanical damage showed sprouts. In surface  
239 fire plots, the same cases as in control plots were recorded, but additionally several trees  
240 showed basal sprouts due to fire damage in the lower part of the trunk. In crown fire plots,  
241 in contrast, crown and bark along the complete stems were scorched, with new sprouts  
242 densely and uniformly arranged in whorls with a general aspect of trees resembling  
243 ‘bottlebrushes’.

244 Growth patterns of control and surface fire treatments on the same slope were very  
245 similar, with no growth anomalies and the typical ring-width trend of a negative  
246 exponential decline with an associated decrease in inter-annual variability (Fig. 2). On  
247 both slopes, however, trees suffering from crown fire showed an abrupt decrease in ring  
248 width from 1995, and a new increase in mean growth rates and growth variability from  
249 2000 (Fig. 2).

250 Growth reductions in the crown fire treatment were evidenced as conspicuous peaks  
251 of PGCs with maxima in 1995 and 1994 on windward and leeward, respectively (Fig. 3).  
252 Reductions associated to the 1995 burn were more pronounced on windward (613% in  
253 mean PGCs) than on leeward (351%). Accordingly, absent rings were identified on both  
254 slopes, since 1996 on windward, and in 1975, 1983, 1987 and, 1995–2001 on leeward.  
255 Absent rings were mainly recorded for period 1996–2000, mostly from trees that  
256 experienced crown fire (Table 1 and Fig. 3).

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

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

269 (Fig. 4b). Under control and surface fire, a significant reduction of tree growth was  
270 noticed in the post-fire, that was maintained for the recovery period ( $F_{2,95} = 6.22$ ,  $P =$   
271  $0.003$  for control;  $F_{2,101} = 12.63$ ,  $P < 0.001$  for surface fire). Under crown fire, a  
272 significant reduction of tree growth was also noticed for the post-fire period, but growth  
273 was significantly greater for the recovery period than for previous ones ( $F_{2,101} = 80.49$ ,  $P$   
274  $< 0.001$ ).

275

#### 276 High-frequency growth variation and climatic response

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

285 A large amount of growth variation was shared by EW, LW and TR at a local level,  
286 with very similar intra-annual variation patterns within each slope, but quite different  
287 between slopes (Appendix S2). The visual assessment was supported by statistical  
288 correlations among chronologies, which were highly significant within the same slope,  
289 especially between EW and TR; however, no significant correlations among chronologies  
290 from different slope were found (Appendix S3).

291 According to RDA models, climatic variables with a significant effect on tree-ring  
292 growth on the windward slope were  $T$  in previous December,  $P$  in July-August, and  $P$  in  
293 February, with both December  $T$  and July-August  $P$  explaining over  $17.7\%$  of growth

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

303       Based on an overall RDA model ( $F$ -value = 6.08,  $P < 0.001$ ), RDA axis 1 was  
304 positively correlated with P in previous November-December and July-August, and  
305 negatively with SLP in previous October-December (Appendix S4). RDA axis 2 was  
306 positively correlated with T in previous December, and P in July-August, but negatively  
307 with P in February. RDA axes 1 and 2 explained, respectively, 74.3% and 20.7% of the  
308 growth-climate relationships (Fig. 5). The ordination showed that tree-ring growth on  
309 windward was mainly positively related to T in previous December (correlation with TR,  
310  $R = 0.45$ ,  $P = 0.003$ ). On the leeward slope, the main factor affecting tree ring width  
311 negatively was SLP in previous October-December (correlation with TR,  $R = -0.66$ ,  $P <$   
312  $0.001$ ). The strong relationships between tree-ring growth and SLP in October-December  
313 can be also graphically verified (Fig. 6), with wider tree rings following years with low  
314 SLP values (i.e., 1990 and 2002), and narrower rings following years with high SLP  
315 values (i.e., 1975, 1983, 1987, and 1995).

316

## 317 **Discussion**

318 Climate-growth responses of *P. canariensis*

319 Even in a reduced geographical range, we found big differences in tree growth between  
320 windward and leeward slopes on Tenerife. This is in agreement with previous findings  
321 that Canary pine forests on windward and leeward are separate ecosystems, each with its  
322 own dynamics and environmental constraints (Fernández-Palacios and de Nicolás 1995).

323 The physiological effects of water inputs and reduced radiation caused by fog drip  
324 make climate less limiting on the windward slope. The amount of water captured by  
325 vegetation from the fog carried by trade winds implies that throughfall can account in  
326 average more than twice the incident rainfall (Aboal et al. 2000), therefore throughfall  
327 plays a fundamental role in the water relationships of *P. canariensis*. Fog alleviates water  
328 stress by reducing canopy transpiration or evaporation, and/or by improving plant water  
329 status by direct absorption through the foliage (Burgess and Dawson 2004). Reduced  
330 water stress on windward can explain the positive effects of elevated temperatures in  
331 previous December and the detrimental impact of February precipitation on *P. canariensis*  
332 growth. In Mediterranean pines, carbon assimilation occurs year round, and relatively  
333 high rates of winter photosynthesis can occur under warm conditions (Medlyn et al.  
334 2002). In fact, maximum daily net photosynthesis in *P. canariensis* can be higher during  
335 winter than in summer, due to a higher soil-water availability and a lower evaporative  
336 demand as compared to the warm and dry season (Peters et al. 2008). High winter  
337 photosynthetic rates and relatively elevated temperatures would result in a greater amount  
338 of carbohydrates stored to be used in the following active season (Zweifel et al. 2006).

339 The negative influence of February precipitation, mainly on latewood growth, may  
340 be related to reduced solar radiation modulated by cloudiness, which showed to be a  
341 primary factor limiting photosynthesis, carbon uptake and growth during the rainy season  
342 (Graham et al. 2003). Trees on windward show a positive response to precipitation in  
343 July-August, suggesting that summer water stress limits growth. Probably, summer

344 drought is mitigated by a high relative humidity of the air, and a high frequency of clouds  
345 due to trade winds influence. In this species, canopy transpiration is maintained at  
346 relatively high rates during the dry season (Luis et al. 2005), suggesting that water stress  
347 can negatively affect growth of *P. canariensis* during the warm and dry season, a  
348 generalized response of pine species under Mediterranean climate (Bogino and Bravo  
349 2008; Campelo et al. 2006).

350 On the leeward slope, the presence of narrow/wide rings produced during years of  
351 high/low sea-level pressure, suggested that annual growth was strongly limited by climatic  
352 factors depending on SLP, namely winter precipitation. In fact, precipitation in  
353 November-December is negatively correlated ( $R = -0.56$ ,  $P < 0.001$ ) with SLP in  
354 October-December. Wider rings were formed after rainy winters (1990 and 2002), while  
355 narrower and even absent rings occurred in years following lower winter precipitation  
356 (1975, 1983, 1987, and 1995). Narrow rings for these years were also identified by  
357 Jonsson et al. (2002) near the upper altitudinal timberline of *P. canariensis* (2,000-2,100  
358 m) on Tenerife, suggesting that they are characteristic of sites beyond the influence of the  
359 “cloud sea”. When the low-pressure system tends to be stronger, it causes moister and  
360 colder conditions than usual during November-December on Tenerife, so that soils are  
361 replenished with water before the summer drought. By contrast, high pressures in winter  
362 produce the reversed pattern, and lead to anomalous hot and dry winters on leeward.

363 Leeward populations of *P. canariensis* exhibit xeromorphic traits allowing a tight  
364 regulation of transpirational water loss (Grill et al. 2004). Accordingly, annual canopy  
365 transpiration lies significantly below the common values for other Mediterranean trees,  
366 suggesting a strong adaptation to low soil water availability during periods of great  
367 evaporative demand (Luis et al. 2005). The effect of winter precipitation can be due to the  
368 pronounced water deficit in the study area, with one-third of the annual precipitation

369 occurring in November-December. The positive influence of moist winters on growth is  
370 common in Mediterranean pines and can be attributed to soil water recharge during the  
371 wet season (Bogino and Bravo 2008; Martín-Benito et al. 2008).

372

373 Fire effects on tree growth

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

387 Most conspicuous effects of the 1995 fire on ring-width patterns were due to aspect  
388 and its interaction with fire treatment. Crown fire impacted tree growth considerably on  
389 both slopes, but more severely on windward. The reason for growth reduction in 1994 on  
390 leeward, as the PGCs filter revealed, is that the big fire in 1995 coincided with a  
391 climatically-caused narrow ring in the same year on leeward. Thus, the PGCs filter  
392 showed its maximum one year earlier than the actual date of fire. The harsh reduction of  
393 growth rates in the post-fire period, and the absent rings in all trees suffering from crown



394 fire on windward, suggested that fire impact on growth was greater than on leeward.  
395 Contrasting growth responses to fire observed on windward and leeward slopes are  
396 probably related to the different growth rates, stand structure, understory composition,  
397 fuel accumulation, and flammability on both slopes as a result of cloudiness influence.

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

414 The largest wildfires on Tenerife occurred in September 1983 (6,500 ha) and July  
415 1995 (2,700 ha) following dry winters with high sea-level pressure, which coincided with  
416 narrow and absent tree rings on leeward. Dry winters may desiccate coarse forest fuels  
417 enough to produce large fires, so that fire occurrence could be phase-locked with sea-level  
418 pressure. The relative predictability of fire events in the Canary Islands offers managers

419 and decision makers a useful alerting tool for planning preventive measures to mitigate  
420 the effects of large, high intensity wildfires when dry conditions occur in previous winter.  
421 Extensive reconstructions of past fire events in Canary pinewoods, based on dating  
422 abundant fire scars and analyzing tree-ring growth sequences from long-lived trees,  
423 should be performed to confirm this assumption.

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

431

432 **Acknowledgements** We thank Adrián González, Sonia Lamas, Pilar Manso, Irene  
433 Outeda, Beatriz Rodríguez-Morales, and Ana Soliño for laboratory assistance. The staff of  
434 Corona Forestal Natural Park of Tenerife facilitates access to field sites. V. Rozas  
435 benefited by a visiting fellowship to the University of La Laguna, funded by Consellería  
436 de Innovación e Industria, Xunta de Galicia, and research contracts by INIA-Xunta de  
437 Galicia and CSIC. This research was partially funded by Consellería de Innovación e  
438 Industria, Xunta de Galicia (PGIDIT06PXIB502262PR) and INIA, Spanish Ministry of  
439 Science and Innovation (RTA2006-00117).

440

#### 441 **References**

442 Aboal JR, Jiménez MS, Morales D, Gil P (2000) Effects of thinning on throughfall in  
443 Canary Islands pine forest - the role of fog. *J Hydrol* 238:218–230

444 Arévalo JR, Fernández-Palacios JM, Jiménez MJ, Gil P (2001) The effect of fire intensity  
445 on the understorey species composition of two *Pinus canariensis* reforested plots in  
446 Tenerife (Canary Islands). For Ecol Manage 148:21–29

447 Armas CM, Santana B, Mora JL, Notario JS, Arbelo CD, Rodríguez-Rodríguez A (2007)  
448 A biological quality index for volcanic Andisols and Aridisols (Canary Islands,  
449 Spain): Variations related to the ecosystem degradation. Sci Total Environ 378:238–  
450 244

451 Bogino SM, Bravo F (2008) Growth response of *Pinus pinaster* Ait. to climatic variables  
452 in central Spanish forests. Ann For Sci 65:506

453 Briffa KR, Jones PD (1990) Basic Chronology Statistics and Assesment. In: Cook ER,  
454 Kairiukstis LA (eds) Methods of Dendrochronology. Applications in the  
455 Environmental Sciences. Kluwer Academic Publishers, Boston, pp. 137–153

456 Brown PM, Wu R (2005) Climate and disturbance forcing of episodic tree recruitment in  
457 a southwestern ponderosa pine landcape. Ecology 86:3030–3038

458 Burgess SSO, Dawson TE (2004) The contribution of fog to the water relations of  
459 *Sequoia sempervirens* (D. Don): foliar uptake and prevention of dehydration. Plant  
460 Cell Environ 27:1023–1034

461 Campelo F, Nabais C, Freitas H, Gutiérrez E (2006) Climatic significance of tree-ring  
462 with and intra-annual density fluctuations in *Pinus pinea* from a dry Mediterranean  
463 area in Portugal. Ann For Sci 64:229–238

464 Climent JM, Gil L, Pardos JA (1998) Xylem anatomical traits related to resinous  
465 heartwood formation in *Pinus canariensis* Sm. Trees 12:139–145

466 Climent JM, Tapias R, Pardos JA, Gil L (2004) Fire adaptations in the Canary Islands  
467 pine (*Pinus canariensis*). Plant Ecol 171:185–196

468 Cook ER, Holmes RL (1996) Guide for computer program ARSTAN. In: Grissino-Mayer  
469 HD, Holmes RL, Fritts HC (eds) The International Tree-Ring Data Bank Program  
470 Library Version 2.0 User's Manual. Laboratory of Tree-Ring Research, University of  
471 Arizona, Tucson, pp 75–87

472 Cook ER, Peters K (1981) The smoothing spline: a new approach to standardizing forest  
473 interior tree-ring width series for dendroclimatic studies. *Tree-Ring Bull* 41: 45–53

474 Drobyshev I, Niklasson M, Angelstam P (2004) Contrasting tree-ring data with fire record  
475 in a pine-dominated landscape in the Komi Republic (Eastern European Russia):  
476 recovering a common climate signal. *Silva Fenn* 38:43–53

477 Drury SA, Veblen TT (2008) Spatial and temporal variability in fire occurrence within the  
478 Las Bayas Forestry Reserve, Durango, Mexico. *Plant Ecol* 197:299–316

479 Elliott KJ, Vose JM, Clinton BD (2002) Growth of eastern white pine (*Pinus strobus* L.)  
480 related to forest floor consumption by prescribed fire in the southern Appalachians.  
481 *South J Appl For* 26:18–25

482 Fernández-Palacios JM (1992) Climatic responses of plant species on Tenerife, the  
483 Canary Islands. *J Veg Sci* 3:595–602

484 Fernández-Palacios JM, de Nicolás JP (1995) Altitudinal pattern of vegetation variation  
485 on Tenerife. *J Veg Sci* 6:183–190.

486 Gieger T, Leuschner C (2004) Altitudinal change in needle water relations of *Pinus*  
487 *canariensis* and possible evidence of a drought-induced alpine timberline on Mt.  
488 Teide, Tenerife. *Flora* 199:100–109

489 Graham EA, Mulkey SS, Kitajima K, Phillips NG, Wright SJ (2003) Cloud cover limits  
490 net CO<sub>2</sub> uptake and growth of a rainforest tree during tropical rainy seasons. *Proc Nat*  
491 *Acad Sci USA* 100:572–576

492 Grill D, Tausz M, Pollinger U, Jiménez MS, Morales D (2004) Effects of drought on  
493 needle anatomy of *Pinus canariensis*. *Flora* 199:85–89

494 Grissino-Mayer HD (2001) Assessing crossdating accuracy: A manual and tutorial for the  
495 computer program COFECHA. *Tree-Ring Res* 57:205–221

496 Jonsson S, Gunnarson B, Criado C (2002) Drought is the major limiting factor for tree-  
497 ring growth of high-altitude Canary Island pines on Tenerife. *Geogr Ann A* 84:51–71.

498 Kitzberger T, Swetnam TW, Veblen TT (2001) Inter-hemispheric synchrony of forest  
499 fires and the El Niño-Southern Oscillation. *Global Ecol Biogeogr* 10:315–326

500 Legendre P, Legendre I (1998) *Numerical Ecology*. Second edition. Elsevier, Amsterdam

501 Luis VC, Jiménez MS, Morales D, Kucera J, Wieser G (2005) Canopy transpiration of  
502 Canary Islands pine forest. *Agr Forest Meteorol* 135:117–123

503 Martín-Benito D, Cherubini P, del Río M, Cañellas I (2008) Growth response to climate  
504 and drought in *Pinus nigra* Arn. trees of different crown classes. *Trees* 22:363–373

505 Mast JN, Fulé PZ, Moore MM, Covington WW, Waltz AEM (1999) Restoration of a  
506 presettlement age structure of an Arizona ponderosa pine forest. *Ecol Appl* 9:228–239

507 McInnis LM, Oswald BP, Williams HM, Farrish KW, Unger DR (2004) Growth response  
508 of *Pinus taeda* L. to herbicide, prescribed fire, and fertilizer. *For Ecol Manage*  
509 199:231–242

510 Medlyn BE, Loustau D, Delzon S (2002) Temperature response of parameters of a  
511 biochemically based model of photosynthesis. I. Seasonal changes in mature maritime  
512 pine (*Pinus pinaster* Ait.). *Plant Cell Environ* 25:1155–1165

513 Mutch LS, Swetnam TW (1995) Effects of fire severity and climate on ring-width growth  
514 of giant sequoia after fire. In: Brown JK, Mutch RW, Spoon CW, Wakimoto RH  
515 (coords) *Proceedings Symposium on fire in wilderness and park management: past*

516 lessons and future opportunities. Gen. Tech. Rep. INT-GTR-320. Ogden, UT. US  
517 Department of Agriculture, Forest Service

518 Niklasson M, Granström A (2000) Numbers and sizes of fires: long-term spatially explicit  
519 fire history in a Swedish boreal landscape. *Ecology* 81:1484–1499

520 Nowacki GJ, Abrams MD (1997) Radial growth averaging criteria for reconstructing  
521 disturbance histories from presettlement-origin oaks. *Ecol Monogr* 67:225–249

522 Otto R, García-del-Rey E, Gil P, Fernández-Palacios JM (2010) The effect of fire severity  
523 on first-year seedling establishment in a *Pinus canariensis* forest on Tenerife, Canary  
524 Islands. *Eur J Forest Res* 129:499–508

525 Peterson DL, Sackett SS, Robinson LJ, Haase SM (1994) The effects of repeated  
526 prescribed burning on *Pinus ponderosa* growth. *Int J Wildland Fire* 4:239–247

527 Peters J, González-Rodríguez AM, Jiménez MS, Morales D, Wieser G (2008) Influence of  
528 canopy position, needle age and season on the foliar gas exchange of *Pinus*  
529 *canariensis*. *Eur J Forest Res* 127:293–299

530 Piñol J, Terradas J, Lloret F (1998) Climate warming, wildfire hazard, and wildfire  
531 occurrence in coastal eastern Spain. *Climatic Change* 38:345–357

532 Py C, Bauer J, Weisberg PJ, Biondi F (2006) Radial growth responses of singleleaf  
533 pinyon (*Pinus monophylla*) to wildfire. *Dendrochronologia* 24:39–46

534 Rodríguez A, Durán J, Fernández-Palacios JM, Gallardo A (2009) Short-term wildfire  
535 effects on the spatial pattern and scale of labile organic-N and inorganic-N and P  
536 pools. *For Ecol Manage* 257:739–746

537 Rozas V (2004) A dendroecological reconstruction of age structure and past management  
538 in an old-growth pollarded parkland in northern Spain. *For Ecol Manage* 195:205–219

539 Smith KT, Sutherland EK (2001) Terminology and biology of fire scars in selected central  
540 hardwoods. *Tree-Ring Res* 57:141–147

541 ter Braak CJF, Šmilauer P (1998) CANOCO reference manual and user's guide to Canoco  
542 for Windows: software for canonical community ordination (Version 4). Center for  
543 Biometry Wageningen and Microcomputer Power, Ithaca, New York

544 Veblen TT, Kitzberger T, Villalba R, Donnegan J (1999) Fire history in northern  
545 Patagonia: the roles of humans and climatic variation. *Ecol Monogr* 69:47–67

546 Westerling AL, Hidalgo HG, Cayan DR, Swetnam TW (2006) Warming and earlier  
547 spring increase western U.S. forest wildfire activity. *Science* 313:940–943

548 Yermakov Z, Rothstein DE (2006) Changes in soil carbon and nitrogen cycling along a  
549 72-year wildfire chronosequence in Michigan jack pine forests. *Oecologia* 149:690–  
550 700

551 Zar JH (2010) *Biostatistical Analysis*. 5th edition. Pearson Prentice Hall, Inc. Upper  
552 Saddle River, NJ

553 Zweifel R, Zimmermann L, Zeugin F, Newbery DM (2006) Intra-annual radial growth  
554 and water relations of trees: implications towards a growth mechanism. *J Exp Bot*  
555 57:1445–1459

556

557

558

559

560

561 **Table 1** Characteristics of the studied *Pinus canariensis* plots and trees at windward and  
 562 leeward slopes on Tenerife based on 22 sampled trees per plot. Plot numbers refer to plot  
 563 designations from Arévalo et al. (2001)

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

564

565



566

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

Source of variation	SS	DF	MS	<i>F</i> value	<i>P</i> 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 (*)					
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		

570 (\*) The Huynh-Feldt corrected test was applied due to the lack of data sphericity.

571 SS: sum of squares; DF: degrees of freedom; MS: mean square

572

573

574

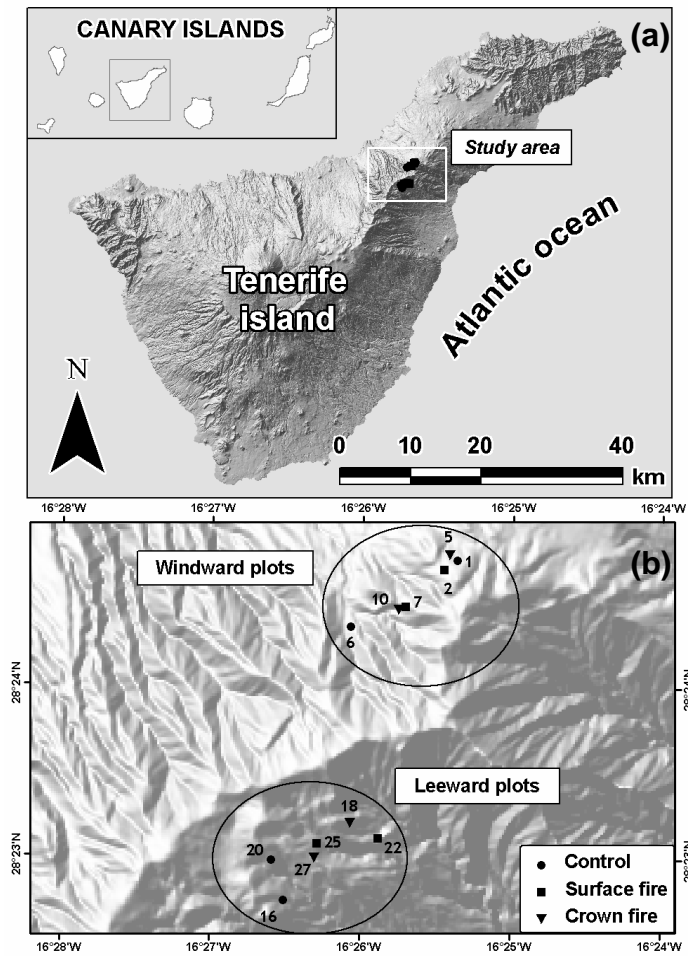
575 **Table 3** Summary statistics of RDA models and Pearson's correlations for the  
 576 relationships between the variation of tree-ring growth indices on the windward and  
 577 leeward slopes, and climate predictors for mean temperature (T), precipitation (P), and  
 578 sea-level pressure (SLP). The proportion of tree-ring growth variation accounted for by  
 579 each variable and by reduced models was quantified by the eigenvalue  $\lambda$

Aspect	Climatic predictors	RDA models			Pearson's correlations (*)		
		$\lambda$	<i>F</i> value	<i>P</i> 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			

580 (\*) significance levels: \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$

581

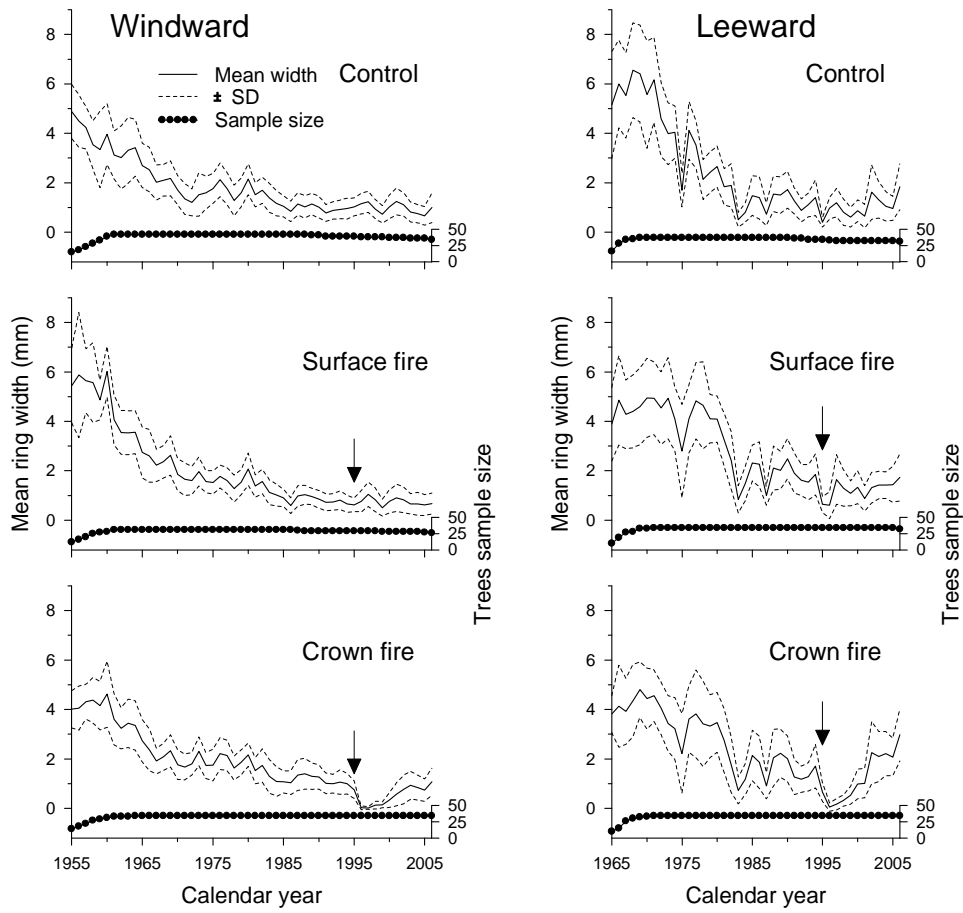
582



584

585 **Fig. 1 a)** Location of the study area. **b)** Location of the windward and leeward study plots  
 586 with their corresponding fire treatments. Plot numbers refer to plot designations from  
 587 Arévalo et al. (2001)

588

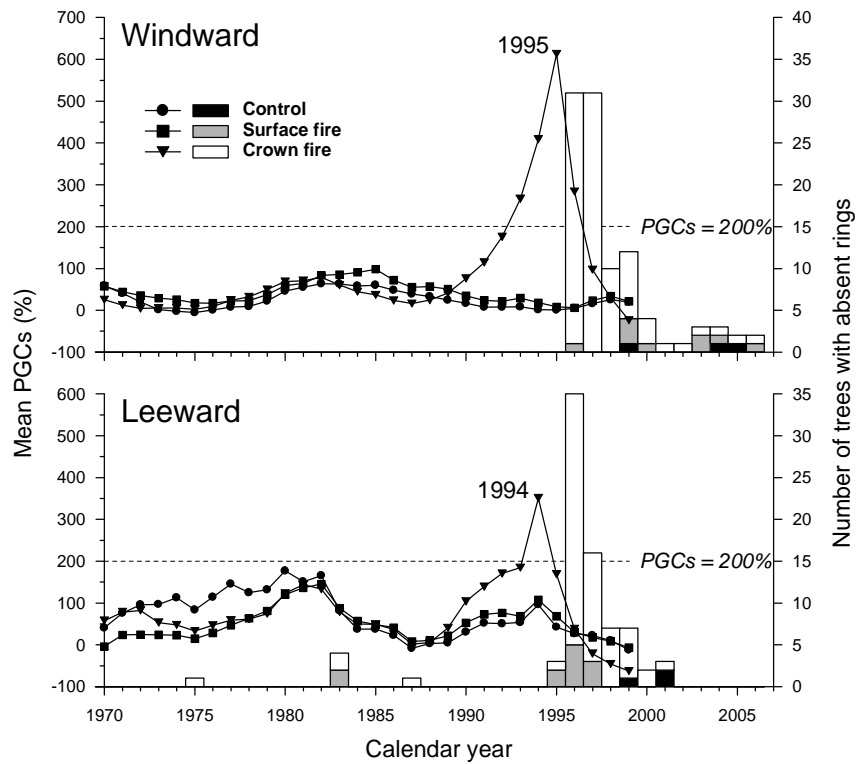


590

591 **Fig. 2** Radial growth patterns of *P. canariensis* (mean ring width  $\pm$  SD) per fire treatment  
 592 on windward and leeward slopes, with their corresponding sample sizes. Arrows indicate  
 593 the 1995 fire

594

595

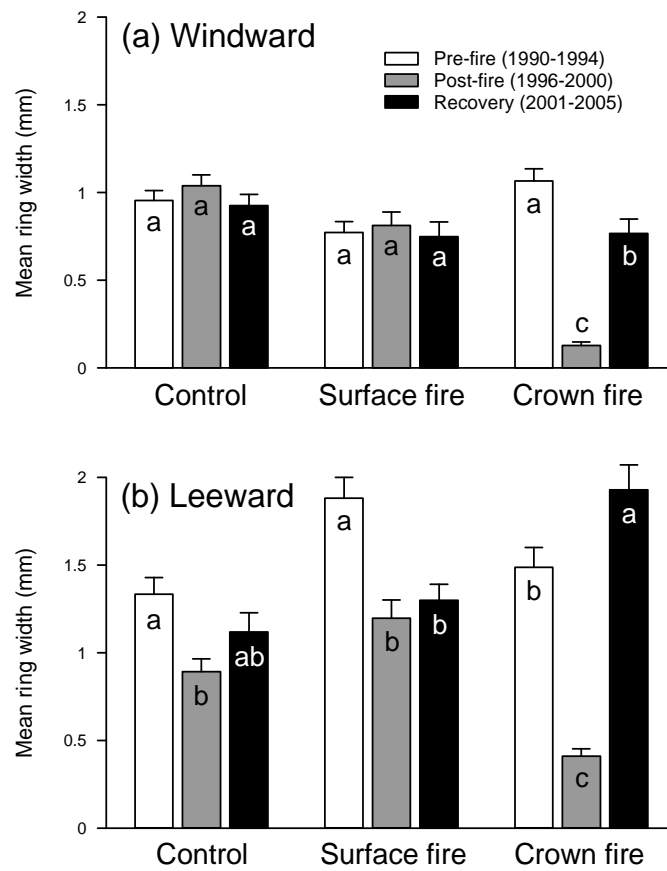


597

598 **Fig. 3** Mean PGCs chronologies (lines) and number of trees with absent rings (bars) per  
 599 fire treatment on windward and leeward slopes. The years of maximum PGCs values and  
 600 the considered threshold for 200% PGCs are shown

601

602



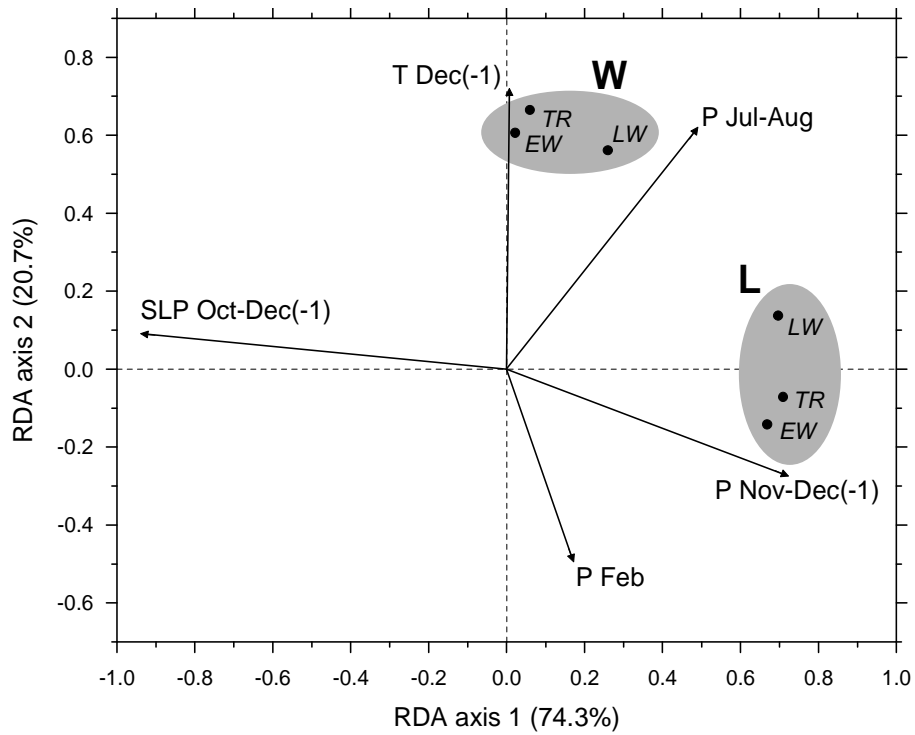
604

605 **Fig. 4** Comparison of mean ring widths (+1 SE) per period and fire treatment on **a**  
 606 windward and **b** leeward slopes. Different letters within each treatment indicate  
 607 significant differences ( $P < 0.05$ ) among periods according to Tukey's HSD *post hoc* test

608

609

610



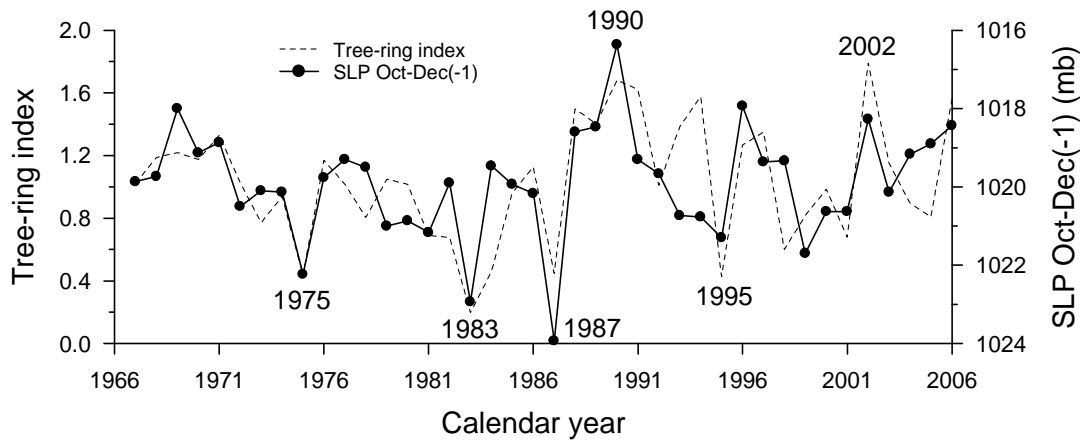
611

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

617

618

619



620

621 **Fig. 6** Comparison of tree-ring growth indices on leeward slope with SLP in October-  
622 December of the previous year. Note the inverted scale in the vertical axis for SLP. Years  
623 with maximum (1990, 2002) and minimum (1975, 1983, 1987, 1995) growth are shown

624

625