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**Effects of thinning intensity on radial growth patterns and  
temperature sensitivity in *Pinus canariensis* afforestations on  
Tenerife Island, Spain**

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**Short title:** Thinning effects on Canary pine afforestations

24 **Abstract**

25 ❖ The suitability of thinning to prevent forest growth decline from global warming has been  
26 scarcely tested in the Macaronesian Canary pine (*Pinus canariensis* Sweet ex Spreng.).

27 ❖ We used tree-ring series from dominant, codominant, and overtopped trees to study the  
28 effects of thinning intensity on basal area increments (BAI) and climate sensitivity on windward  
29 (wet) and leeward (dry) slopes on Tenerife, Canary Islands. Three replicated blocks of control,  
30 light thinning, and heavy thinning stands were set on each slope in 1988, and cores were  
31 extracted in 2007.

32 ❖ Heavy thinning induced growth release and increased BAI, mainly on dominant and  
33 codominant trees, whereas light thinning effects were negligible; their impacts were more intense  
34 on windward. Temperature sensitivity was hardly affected by thinning on leeward, where climate  
35 control was stronger. On windward, thinning enhanced the influence of summer temperatures.  
36 Upper crown classes were overall more sensitive, but overtopped trees responded better in  
37 summer.

38 ❖ Thinning intensity and aspect greatly influence growth on Canary pine afforestations, but  
39 individual responses are highly dependent on crown classes. In addition, thinning may be less  
40 effective to modify growth conditions on leeward slopes, at least if it is not intense.

41

42 **dendroecology / tree ring / climate-growth relationships / growth release / forest restoration**

43

44

45 **1. INTRODUCTION**

46 According to global warming predictions, a generalised raise in temperatures and a  
47 potential decline in annual rainfall are expected in the Mediterranean area for the current century  
48 (IPCC, 2007). These predictions can also be applied to the Macaronesian region, although

49 changes might be weaker due to its oceanic character. Deterioration of growth conditions will  
50 arise for many Mediterranean species if heat and water stress are intensified (Andreu et al.,  
51 2007). As Linares et al. (2009) reported, drought stress is probably the main reason for the  
52 current growth decline of coniferous woodlands in southern Europe.

53 Drought effects on tree growth and performance can be aggravated in densely-stocked  
54 stands, since trees suffer from a long-term stress by sustained intense competition, which  
55 incorporates more sensitivity to short-term stresses such as severe drought events (Linares et al.,  
56 2010). Therefore, reducing competition by thinning should enhance growing conditions, and thus  
57 alleviate water stress that constrains photosynthetic activity and growth (McDowell et al., 2003).  
58 Thinning also provides more growing space and a higher amount of light on the soil surface,  
59 which results in a greater carbon gain and a faster mineralization of the litter, yielding an  
60 increase in nutrient availability. However, advantages from thinning on growth may not be the  
61 same for trees of different crown classes, mainly due to a different duration of the growing  
62 period (Bréda et al., 1995).

63 Radial growth responses to climate considerably vary according to local tree density and  
64 crown class in areas where water is limiting (Linares et al. 2009; Martín-Benito et al., 2008). A  
65 reduction in the influence of precipitation, and an enhancement of temperature influence, is  
66 generally reported for non-dominant trees suffering from intense competition. In the  
67 Mediterranean area, this change in the response to temperature was also observed after thinning  
68 in dense stands, because it is obscured by inter-tree competition before thinning (Linares et al.  
69 2010). In general, a reduction of drought sensitivity usually results from thinning practices, but  
70 without increasing the intrinsic water use efficiency (Martín-Benito et al., 2010), which can be  
71 interpreted as a reduced competition for the available water after thinning.

72 Canary pine (*Pinus canariensis* Sweet ex Spreng.), endemic species of the western Canary  
73 Islands, can be vulnerable to global warming processes, because water availability is already a

74 key limiting resource in most forests where it occurs. Despite its morphological and  
75 physiological adaptations to cope with drought and heat (Jonsson et al., 2002; Peters *et al.*,  
76 2008), tree line in the Canary Islands may be modified by the effects of heat and drought on pine  
77 establishment (Gieger and Leuschner, 2004). On the other hand, the additional stress provided by  
78 inter-tree competition should also be considered for Canary pine afforestations established on  
79 Tenerife Island during the 20th century. Under the absence of a subsequent management, most  
80 stands attained excessive densities in comparison to natural stands, being more prone to growth  
81 decline, decay and intense wildfires. Nonetheless, public forest managers have been recently  
82 reconsidering the usefulness of these plantations, aiming the restoration of natural pine forest by  
83 means of silvicultural practices (Arévalo and Fernández-Palacios, 2005). Additionally,  
84 environmental conditions are remarkably different throughout narrow geographic ranges in the  
85 Canary Islands, because moisture provided by trade winds almost exclusively affects windward  
86 (northern) slopes, remaining leeward (southern) ones much drier (Fernández-Palacios and de  
87 Nicolás, 1995). However, no previous studies compared the effects of thinning on growth and  
88 climate sensitivity at windward and leeward stands, although thinning should not affect them in  
89 the same way.

90       There are previous studies dealing with thinning effects on Canary pine plantations, which  
91 were based on an experiment performed in 1988 in northeastern Tenerife Island to evaluate the  
92 impacts of several management practices on the regeneration of this species (Madrigal et al.,  
93 1989). Aboal et al. (2000) monitored throughfall to study fog entrapment nine years after  
94 thinning, and found that it was optimized by intermediate thinning intensities. Arévalo and  
95 Fernández-Palacios (2005) assessed the effects of thinning on the naturalization of pinewoods,  
96 and reported that intense thinning considerably increased tree size and promoted a more natural  
97 stand structure.

98 Dendroecological methods are widely used for studying both thinning and climate effects  
99 on the radial growth of trees (e.g. Misson et al., 2003), but have hardly been applied on Canary  
100 pine. The difficulty of this species to be used in dendrochronology has been highlighted by  
101 Jonsson et al. (2002), who mainly reported the abundance of missing rings and other growth  
102 anomalies. In our study, we used dendrochronological methods to assess the short-term impact of  
103 thinning intensity on Canary pine radial growth. Additionally, we performed an analysis of  
104 climate-growth relationships to assess the climatic influence on growth of trees of different  
105 crown class on both slopes on Tenerife Island, and the possible effects of thinning on the  
106 climatic response of this species. For this, we based on previous experimental stands set by  
107 Madrigal et al. (1989) to answer the following questions: (1) Are tree growth patterns (BAI)  
108 modified by the intensity of thinning and aspect? (2) Is the sensitivity to climate modulated by  
109 thinning? (3) Do trees of different crown classes respond differentially to thinning intensity and  
110 climate?

111

## 112 **2. MATERIALS AND METHODS**

### 113 **2.1. Study area**

114 The study area is located in the Cordillera Dorsal, near the northeastern boundary of the  
115 Corona Forestal Natural Park, Tenerife Island, Spain (Fig. 1A and B). The park extends over  
116 46,613 ha, 25% of which was reforested with Canary pine from 1940 to 1960 at elevations  
117 between 1,000 and 2,000 m. Altitude and wind exposure are the major environmental factors  
118 affecting the distribution of vegetation types on Tenerife (Fernández-Palacios and de Nicolás,  
119 1995). Thanks to the moisture occasionally provided as fog drip by trade winds, windward pine  
120 forests hold an abundant undergrowth cover, while leeward forests only show sparse shrubs.  
121 Climate is Mediterranean with a long dry season ranging from May to September (Figure 1C).  
122 Mean annual temperature showed a significant increasing trend in the period 1901-2006, while

123 annual precipitation did not significantly change (Figure 1D). Soils are developed on deep  
124 horizons of volcanic scoria and are classified as Entisol, suborder Orthens (Fernández-Caldas et  
125 al., 1985).

126

## 127 **2.2. Stand history and experimental design**

128 Windward and leeward stands were respectively planted in 1949 and 1953, introducing two  
129 seeds in each hole to ensure the success of plantation establishment. On windward, the removal  
130 of doubled trees in 1972, a moderate thinning from below in 1975 (removal of 40% of the  
131 previous density), and another in 1982 (removal of 33-40% with a low pruning) were carried out.  
132 On leeward, a light thinning from below in 1979 (removal of 20-28% and doubled-trees) and  
133 another in 1985 (removal of between 16-20% with a low pruning) were performed (Madrigal et  
134 al., 1989). Dead and overtopped trees were preferentially logged in these treatments.

135 In 1988, park managers selected 18 stands for study, which were representative of a larger  
136 area of over 1,500 ha of continuous Canary pine plantations (Madrigal et al., 1989). Three blocks  
137 composed by three 625 m<sup>2</sup> stands assigned to three respective thinning treatments (control  
138 stands: unthinned; light-thinned stands: removal of 6-18% of the total basal area; heavy-thinned  
139 stands: removal of 38-52%), were established on both windward and leeward slopes (Table 1,  
140 Fig. 1B). Thinning activities were carried out manually, and trees preferentially selected for  
141 thinning were those overtopped, small-sized or dying.

142 No significant differences in tree density existed among treatments within each slope before  
143 thinning (two-way ANOVA,  $F_{2,12} = 2.163$ ,  $p = 0.158$ ). However, tree density varied between  
144 slopes, either before ( $F_{1,12} = 34.839$ ,  $p < 0.001$ ) or after thinning ( $F_{1,12} = 29.981$ ,  $p < 0.001$ ).  
145 Similarly, windward stems showed a higher mean DBH than leeward ones (Student's  $t$  test,  $t =$   
146  $3.345$ ,  $p < 0.004$ ,  $df = 16$ ). Tree density, mean DBH, and further characteristics of the study  
147 stands are summarized in Table 1.

148

### 149 **2.3. Sampling, tree-ring measuring and crossdating**

150 The 18 study stands were newly located in May 2007, and 15 trees per stand were  
151 randomly selected for sampling, avoiding edge effects. Their DBHs were measured, the crown  
152 class (dominant, codominant, overtopped) was registered, and two increment cores were taken  
153 per tree from opposite sides of the bole. In heavy-thinned stands, only dominant and codominant  
154 trees were included in data analysis since overtopped trees were scarce. The cores were dried,  
155 mounted on wooden boards, and sanded. Tree rings were identified and dated under  
156 magnification following standard procedures (Stokes and Smiley, 1996). Total tree-ring widths  
157 were measured to the nearest 0.001 mm with a measuring device (Velmex Inc., Bloomfield, NY,  
158 USA). Tree-ring series were crossdated visually by comparison against series highly  
159 intercorrelated for each slope. Missing rings and other wood anomalies were detected and  
160 corrected when possible, and crossdating was verified quantitatively using COFECHA (Grissino-  
161 Mayer, 2001).

162

### 163 **2.4. Thinning effects assessment**

164 Series of annual basal area increments (BAI) were derived from raw tree-ring widths  
165 assuming a circular cross section, after averaging both series of each tree. We used BAI because  
166 it is less dependent on cambial age and stem size than tree-ring width (Biondi, 1999). We study  
167 the long-term responses of BAI to thinning using the percentage growth change (PGC) filter  
168 (Nowacki and Abrams, 1997). This method is a powerful technique for the identification of  
169 release events in tree-ring series based on the fact that trees surviving after natural disturbances  
170 or artificial thinning respond with a released growth (Copenheaver and Abrams, 2003).  
171 Individual PGC chronologies were calculated from BAI series by applying the formula:  $PGC =$   
172  $[(M_2 - M_1)/M_1] \times 100$ , where  $M_1$  and  $M_2$  are the preceding and subsequent nine-year mean BAI.

173 The nine-year span was chosen to keep consistency with periods used in other analyses in this  
174 work. The common period for comparison (1968-1997) was determined by the shortest series.  
175 We identified episodes of abrupt and sustained growth releases as peaks > 50% in the PGC  
176 chronologies averaged for each crown class, per thinning treatment and slope.

177 To evaluate the short-term responses of BAI to thinning, we applied a repeated measures  
178 analysis of variance. We selected periods of equal length, defined as pre-treatment (1979–1987),  
179 post-treatment (1989–1997), and stabilization (1998-2006) to calculate mean BAIs, which were  
180 used as within-subjects factors. Mean BAI within these periods was set as dependent variable,  
181 and aspect (windward and leeward), treatment (control, light thinning and heavy thinning), and  
182 the covariate block, were the inter-subjects factors. Significant differences among individual BAI  
183 means from each treatment were analyzed using the non-parametric Dunnett test since the  
184 equality of variances could not be assumed. The effects of thinning for each crown class was  
185 assessed by pairwise comparisons through of mean BAI between both treatments and control  
186 stands using *t* tests. All statistical analyses were performed using SPSS v.15.0 (SPSS Inc.,  
187 Chicago IL, USA).

188

### 189 ***2.5. Calculation of the relationships between tree growth and climate***

190 Mean BAI series were characterized for each treatment, aspect and crown class before  
191 (1970-1987) and after (1989-2006) the thinning treatment. Raw individual BAI series were  
192 detrended by fitting a cubic smoothing spline of 32 years and 50% cutoff, and the resulting  
193 indices were averaged into a chronology for each treatment per slope. We assessed chronology  
194 quality from the common signal among trees using the mean correlation between trees (Rbt), the  
195 expressed population signal (EPS), and the first-order autocorrelation (AC), whereas mean  
196 sensitivity (MS) served as a measure of year-to-year variability (Briffa and Jones, 1990).



197 Bootstrapped Pearson's correlations were calculated between standardized BAI  
198 chronologies and monthly records of temperature and precipitation for the defined periods, each  
199 out of 10,000 bootstrap iterations, and applying the correction proposed by Mason and Mimmack  
200 (1992) to compute the confidence intervals. Climate data, derived from the Climate Research  
201 Unit auto calibrated model (CRU TS 3.0) of the University of East Anglia, UK, were monthly  
202 time series of mean temperature and total precipitation interpolated with a geographical  
203 resolution of  $0.5^\circ \times 0.5^\circ$ , were obtained from the Web site of the Royal Netherlands  
204 Meteorological Institute (<http://climexp.knmi.nl/>).

205

### 206 **3. RESULTS**

#### 207 ***3.1. Radial growth responses to thinning***

208 For the upper crown classes, BAI showed increasing trends after heavy thinning on both  
209 slopes, lasting for a shorter time span on leeward (Fig. 2). By contrast, patterns after light  
210 thinning differed from control only on windward, showing no declining trend. Likewise,  
211 dominant and codominant trees on windward significantly differed from control after both  
212 thinning treatments (Student's *t*-tests,  $p < 0.001$ ), but not overtopped trees ( $t = -1.20$ ,  $p = 0.242$ ).  
213 On leeward, only heavy thinning diverged from control for both dominant ( $t = -2.82$ ,  $p = 0.01$ )  
214 and codominant trees ( $t = -4.89$ ,  $p < 0.001$ ), while light thinning did not significantly influence  
215 growth in any case ( $p > 0.05$ ). Narrow tree rings were detected on leeward for 1975, 1983, 1991,  
216 1995, and 2001, which mostly occurred after dry or during warm years. Wide rings formed  
217 following these depressions only in dominant and codominant trees of heavily thinned stands.

218 Mean PGC values above the minimum threshold of 50% occurred only after heavy  
219 thinning, which showed the greatest number of released trees, whereas light thinning released a  
220 low proportion of trees (Fig. 3). Most of the released trees were codominant or dominant in both  
221 treatments. The most remarkable release after heavy thinning occurred in 1988 on windward

222 (PGC = 57.73%), but in 1991 on leeward (PGC = 80.21%). Not only the 1988 thinning had a  
223 relevant effect on tree growth patterns, but also the treatments in 1975 and 1982 on windward,  
224 and 1985 on leeward, as suggested by the frequencies of released trees.

225 Aspect (repeated measures ANOVA,  $F_{1,261} = 54.401$ ,  $p < 0.001$ ), treatment ( $F_{2,261} = 78.445$ ,  
226  $p < 0.001$ ), period ( $F_{2,522} = 15.904$ ,  $p < 0.001$ ), and their interactions ( $p < 0.05$ ), except aspect  $\times$   
227 period ( $p > 0.05$ ), were significant predictors of BAI. In contrast, no differences arose among  
228 blocks ( $F_{1,261} = 1.425$ ,  $p = 0.234$ ). Short-term variations of BAI immediately prior and after the  
229 thinning treatment followed similar patterns of variation on both aspects, with gently-descending  
230 BAI trends for control and light thinning, and a harsh increase after heavy thinning, which was  
231 maintained or roughly decreased in the stabilization period (Fig. 4).

232

### 233 **3.2. Common signal and climate-growth relationships**

234 The quality of standardized BAI chronologies was better on leeward, both before and after  
235 thinning (Tab. 2), with a higher year-to-year variability (perceived by MS) and inter-tree  
236 synchrony of growth (Rbt and EPS). These values for common signal mainly decreased on both  
237 slopes for the post-treatment period. Both thinning treatments caused a weaker reduction on  
238 windward, and so did only the most intense treatment on leeward. On leeward, chronologies  
239 were only slightly autocorrelated before 1988 and no more afterwards; no remarkable AC was  
240 observed on windward, except for control in the most recent period.

241 Correlations between standardized BAI chronologies and climate revealed that average  
242 temperature was the dominant climatic variable controlling growth, while rainfall nearly exerted  
243 no effects (data not shown). Temperature influence strongly differed between slopes, as control  
244 stands revealed, with positive significant correlations on windward only, and negative on  
245 leeward (Fig. 5). The effects of temperature on tree growth varied between both pre- and post-  
246 treatment periods for every treatment, shifting the months influencing growth. On windward, the

247 positive effect of temperature in previous October-January shifted to current March, while on  
248 leeward, negative correlations in March-April changed to May-September (Fig. 5). Furthermore,  
249 we found an overall increment in the statistical significance of correlations after 1988 on both  
250 slopes.

251 On windward, thinning modified climate sensitivity of the windward as compared to the  
252 control, particularly for the most intense treatment (Fig. 5). Thus, the influence of temperature in  
253 late winter and spring decreased with increasing thinning intensity, being not significant for  
254 heavy thinning. Simultaneously, a strongly negative influence of temperatures in previous late  
255 summer-autumn and current June and September arose. By contrast, correlations were very  
256 similar among treatments on leeward, with the exception of the slightly enhanced negative  
257 correlations with May-September temperature for heavily thinned stands.

258 When comparing crown classes, responses to temperature were similar on each slope,  
259 although the significance of correlations occasionally differed (Tab. 3). Dominant and  
260 codominant trees were the most sensitive ones in control stands. On windward, they responded to  
261 October-January before 1988, and to March-April afterwards; on leeward, only correlations to  
262 March-April before 1988 were high. However, the positive influence of current June temperature  
263 on windward control before 1988 was higher for codominant and overtopped trees. Similarly,  
264 negative influence of previous July-August and current May-September in the post-treatment  
265 period was greater for overtopped trees on leeward control. Temperature responses of dominant  
266 and codominant individuals were similar for both thinning treatments.

267

## 268 **4. DISCUSSION**

### 269 ***4.1. Effects of thinning intensity and aspect on BAI***

270 Only the most intense thinning treatment was able to induce an evident growth release on  
271 both slopes, suggesting that BAI patterns are modified by thinning intensity. Our results are in

272 accordance to previous studies, which reported poor individual growth responses after light  
273 thinning in comparison to heavy thinning (Cañellas et al., 2004; Martín-Benito et al., 2010). Yet,  
274 no uniform responses arose through different crown classes. Codominant trees were the most  
275 benefited from thinning, followed by dominant trees, which could be explained by a lower effect  
276 of thinning from below on dominant crown class, subjected to a lower competition intensity  
277 (Mäkinen and Isomäki, 2004). Bréda et al. (1995) noted that overtopped and dominant trees take  
278 more advantage than codominant trees as a result of thinning from above. Nevertheless,  
279 overtopped trees were not favoured by light thinning in our study. This treatment was probably  
280 not intense enough to reduce the stress experienced by the lowest crown classes. Overtopped  
281 trees can be stagnated, losing the capacity to acquire enough vigour to significantly release, even  
282 if the competition intensity is greatly reduced (Linares et al., 2009).

283 Aspect exerted a modulation on thinning effects, since the impacts of thinning intensity on  
284 BAI were more limited on leeward than on windward, as shown by our results. We suggest that  
285 the modulation exerted by aspect was likely due to the facts that: 1) thinning effects were masked  
286 by the higher stem density on leeward with the consequently smaller stem-sized trees, whose  
287 growth after thinning is less in absolute terms than larger ones (Cañellas et al., 2004; Mäkinen  
288 and Isomäki, 2004); and 2) thinning is less effective at dry sites if it is not intense enough,  
289 because inter-tree competition for water is stronger, so that site conditions cannot support high-  
290 density stands (Cotillas et al., 2009; Linares et al., 2009; Moreno and Cubera, 2008). Thus, a still  
291 high competition level not sufficiently removed by thinning, coupled with the more limiting  
292 climatic conditions, should have somehow obscured the advantages of thinning on leeward  
293 (Misson et al., 2003). Thus, besides the effects of the treatment in 1988, the impact of treatments  
294 performed in 1975 and 1982 also showed to be relevant, which probably preconditioned  
295 differential responses in the post-treatment period, more evident on windward.

296 Despite the more limited effects of thinning on leeward, the reduction of tree density still  
297 contributed to increase BAI, presumably due to a more pronounced drought tolerance of Canary  
298 pine on this slope, since growth recovered from the drought-induced depressions, mainly those in  
299 1992-1993 and 1996. Similar results were found for trees suffering from different intensities of  
300 competition, or as a result of thinning experiences, either under Mediterranean (Linares et al.,  
301 2009; Martín-Benito et al., 2008) or temperate climates (Kohler et al., 2010; Misson et al., 2003).

302 Increased growth rates by heavy thinning are usually linked to the simultaneous  
303 enhancement of tree water status and illumination within the stand as inter-tree competition is  
304 reduced (Aussenac, 2000). A higher water supply allows a better stomatal conductance and  
305 carbon assimilation, which encourage tree growth (McDowell et al., 2003), and extend the  
306 growing season (Linares et al., 2009). Besides, more dramatic detrimental effects of drought can  
307 be expected in the heliophytic Canary pine in shaded environments (Climent et al., 2006). Heavy  
308 thinning would be more favourable in this case, because it generates larger canopy gaps and  
309 greater irradiance, leading to the release of surviving trees (Stan and Daniels, 2010). As shown  
310 by Blanco et al. (2008), thinning can also alter nutrient return via needle litterfall in Scots pine,  
311 but not proportionally to its intensity, suggesting the existence of thresholds in the ecological  
312 response to thinning from below. Nonetheless, additional measurements on water input, solar  
313 radiation, and nutrient return would allow us to verify these hypotheses for Canary pine woods.

314

#### 315 ***4.2. Variation in climate sensitivity***

316 As shown by the higher common signal and year-to-year variability, climatic control of  
317 BAI appears to be more intense on leeward. Besides, common signal decreased after 1988 in  
318 whatever treatment, likely due to the increasing competition among trees as they become larger.  
319 But this reduction was less intense for the thinning treatments, mainly on windward, indicating  
320 that thinning affected climate sensitivity.

321 Our findings indicate that aspect modulated the impact of thinning on climate sensitivity.  
322 Increasing temperatures within the stands as a consequence of a higher exposure to radiation  
323 after thinning (Moreno and Cubera, 2008), would counteract the positive effect of temperatures  
324 in previous winter and highlight their negative impact in current summer (Martín-Benito et al.,  
325 2010), as occurred on windward only after the heavy thinning. This could also be linked to the  
326 fact that fog entrapment in Canary pine woods is lower after heavy thinning than after light  
327 thinning (Aboal et al., 2000), which probably magnified the negative effects of warm previous  
328 autumn and current summer on windward after heavy thinning. On the contrary, leeward stands  
329 were homogeneous in their response in whatever period, which does not agree with the increased  
330 temperature sensitivity that frequently occurs in dry sites after thinning (Gea-Izquierdo et al,  
331 2009; Linares et al., 2010). Since thinning appears to affect growth rates of trees, but not their  
332 temperature sensitivity, we suggest that the stronger climatic control on leeward causes that year-  
333 to-year variation of growth is mainly determined by climate, regardless of local tree density. This  
334 fact verifies that the limited thinning effects on leeward can be attributed not only to the higher  
335 tree density but also to the more constraining climate conditions.

336 Climate-growth relationships for Canary pine proved to be unstable through time also in  
337 control stands. There was an increase of the negative influence of temperatures for the most  
338 recent period, mainly on leeward. Although climate responses are sometimes age-dependent  
339 (Carrer and Urbinati, 2004), similar processes reported for other pine species in southwestern  
340 Europe since the late 80's were mostly related to climate warming (Andreu et al., 2007; Bogino  
341 and Bravo, 2008; Martín-Benito et al., 2010), which was also the case of mean annual  
342 temperature in our study area.

343 Dominant and codominant trees recovered faster after drought-induced narrow rings,  
344 corroborating the less plastic response of overtopped trees to the environmental variability  
345 (Linares et al., 2009), in which no retrieval occurred. Climate-growth correlations followed

346 similar patterns among crown classes, namely for the upper ones. This suggests that aspect has  
347 more impact on climatic sensitivity than individual characteristics, such as the crown social  
348 status. However, the significance of correlations differed at specific seasons, being the upper  
349 classes more sensitive to climate. Suppressed trees were generally less sensitive except to  
350 previous and current summer temperatures, namely on the leeward control, which can be related  
351 to the major water stress suffered by overtopped trees in spring and summer (Martín-Benito et  
352 al., 2008).

353 The negligible influence of precipitation had not been reported before for other  
354 Mediterranean pines (Andreu et al., 2007; Bogino and Bravo, 2008), although it can be related to  
355 the relative influence of rainfall in the Canary Islands in comparison to other water sources, such  
356 as fog drip. As shown Aboal et al. (2000) on windward, mean annual throughfall can account for  
357 up to two times the incident rainfall. Furthermore, in areas with nearly no precipitation during  
358 summer, growth regulation by water stress can be controlled by high temperatures rather than  
359 local and erratic rainfall (Martín-Benito et al., 2008).

360 Despite the potential masking effects arisen by an uneven stand management history and  
361 by the limitation of using short tree-ring series (Copenheaver and Abrams, 2003), our analyses  
362 demonstrated for the first time the impact of thinning treatments on growth patterns in young  
363 Canary pine plantations. Heavy thinning provides a more natural community structure and  
364 favours the establishment of new cohorts (Arévalo and Fernández-Palacios, 2005), improves  
365 growth rates, and modulates tree sensitivity to limiting climatic conditions. Therefore,  
366 management guidelines should take heavy thinning into consideration in order to improve  
367 growing conditions and self-maintenance in Canary pine plantations with focus on their  
368 restoration. This is especially true on leeward sites because: 1) more similar densities to those  
369 recorded by Blanco et al. (1989) for naturally regenerated stands are advisable (i.e. 130-440  
370 stems ha<sup>-1</sup>); and 2) the constraining climate conditions can swamp the impact of thinning if it is

371 not intense enough, with a special concern to global warming. Nevertheless, to verify our  
372 supposition would be necessary to test more accurately how the contrasting climatic conditions,  
373 imposed by the topography and the circulation of trade winds, could modulate growth along the  
374 complete altitudinal range of Canary pine.

375

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479

480 **Table 1.-** General characteristics of the study stands on windward and leeward slopes in  
 481 Tenerife, for control (CO), light thinning (LT) and heavy thinning (HT) treatments. Stand  
 482 elevation, the percentage of basal area removed, the structural characteristics of the stands in  
 483 1988, before and after thinning treatment, and mean tree diameter of the sampled trees in 2007  
 484 are shown.  
 485

Block <sup>a</sup>	Treatment	Elevation (m)	% BA removed	1988 before thinning			1988 after thinning			2007 <sup>b</sup>
				Density (stems ha <sup>-1</sup> )	Mean BA (m <sup>2</sup> ha <sup>-1</sup> )	Mean DBH (cm)	Density (stems ha <sup>-1</sup> )	Mean BA (m <sup>2</sup> ha <sup>-1</sup> )	Mean DBH (cm)	Mean DBH (cm) ± SD
W1	CO	1650		1072	62.4	27.2				30.7 ± 7.7
	LT	1640	7.68	752	53.4	30.1	656	49.3	30.9	34.2 ± 7.9
	HT	1643	52.02	800	52.1	28.8	352	25.0	30.1	39.9 ± 5.3
W2	CO	1654		1232	67.0	26.3				27.8 ± 4.8
	LT	1652	14.45	1312	69.9	26.0	912	59.8	28.9	29.8 ± 7.4
	HT	1659	40.31	704	45.9	28.8	368	27.4	30.8	40.4 ± 5.9
W3	CO	1671		992	56.6	26.9				31.6 ± 7.1
	LT	1671	6.35	752	50.4	29.2	656	47.2	30.3	37.5 ± 8.8
	HT	1670	46.57	928	49.6	26.1	352	26.5	31.0	37.3 ± 4.8
L1	CO	1701		1456	59.8	22.9				24.6 ± 4.5
	LT	1699	13.57	1504	58.2	22.2	1216	50.3	22.9	26.7 ± 4.2
	HT	1686	45.55	1312	55.1	23.1	528	30.0	26.9	34.5 ± 2.9
L2	CO	1698		1664	65.5	22.4				26.1 ± 5.6
	LT	1704	13.66	1600	52.7	20.5	1280	45.5	21.3	23.0 ± 3.9
	HT	1697	38.13	1605	43.8	18.7	800	27.1	20.8	23.9 ± 4.3
L3	CO	1719		2224	71.8	20.3				24.4 ± 5.6
	LT	1718	18.10	2000	68.5	20.9	1360	56.1	22.9	24.3 ± 6.2
	HT	1704	51.58	1488	60.1	22.7	544	29.1	26.1	35.6 ± 5.9

486  
 487 BA: basal area. DBH: diameter at breast high (1.30 m). SD: standard deviation.

488 <sup>a</sup> W: blocks on windward slope. L: blocks on leeward slope.

489 <sup>b</sup> Calculations based on 15 sampled trees per stand.

490

491

492 **Table 2.-** Descriptive statistics of the standardized basal area increment chronologies for the  
 493 periods 1970-1987 and 1989-2006 corresponding to the control (CO), light thinning (LT) and  
 494 heavy thinning (HT) treatments.  
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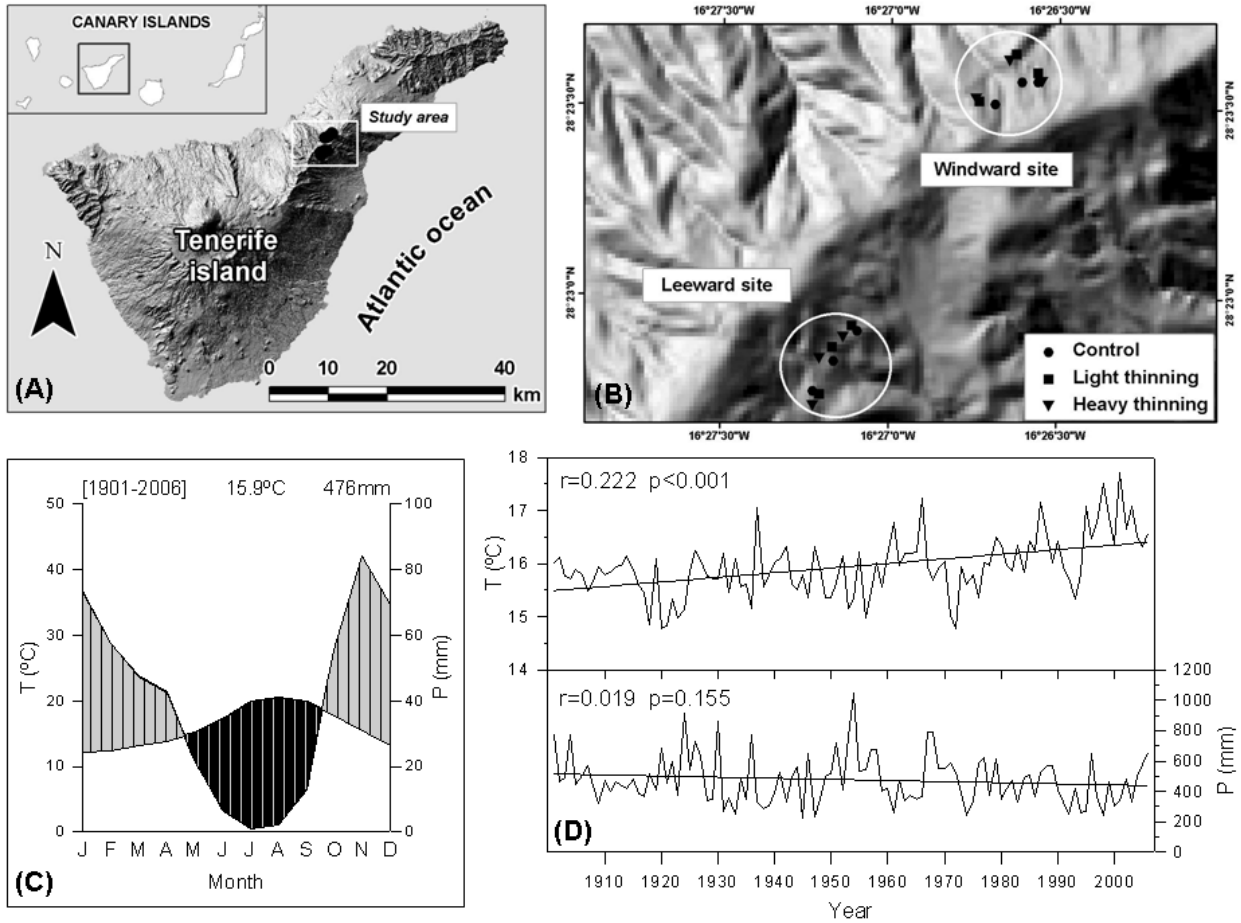
Aspect	Treatment	Rbt		EPS		MS		AC	
		1970-1987	1989-2006	1970-1987	1989-2006	1970-1987	1989-2006	1970-1987	1989-2006
Windward	CO	0.456	0.298	0.973	0.903	0.200	0.138	0.229	0.520
	LT	0.278	0.286	0.945	0.925	0.177	0.144	0.205	0.137
	HT	0.304	0.296	0.952	0.949	0.175	0.144	0.141	0.362
Leeward	CO	0.647	0.290	0.987	0.904	0.291	0.190	0.484	0.096
	LT	0.616	0.334	0.987	0.929	0.348	0.233	0.555	0.021
	HT	0.768	0.568	0.993	0.982	0.352	0.307	0.520	0.216

496  
 497 Rbt: Mean correlation between trees. EPS: Expressed population signal. MS: Mean sensitivity.  
 498 AC: First-order autocorrelation coefficient.  
 499

500 **Table 3.-** Bootstrapped correlations between temperature variables and BAI chronologies for  
 501 dominant (D), codominant (C), and overtopped (O) trees under control (CO), light thinning (LT),  
 502 and heavy thinning (HT) treatments, for the periods 1970-1989 and 1989-2006.  
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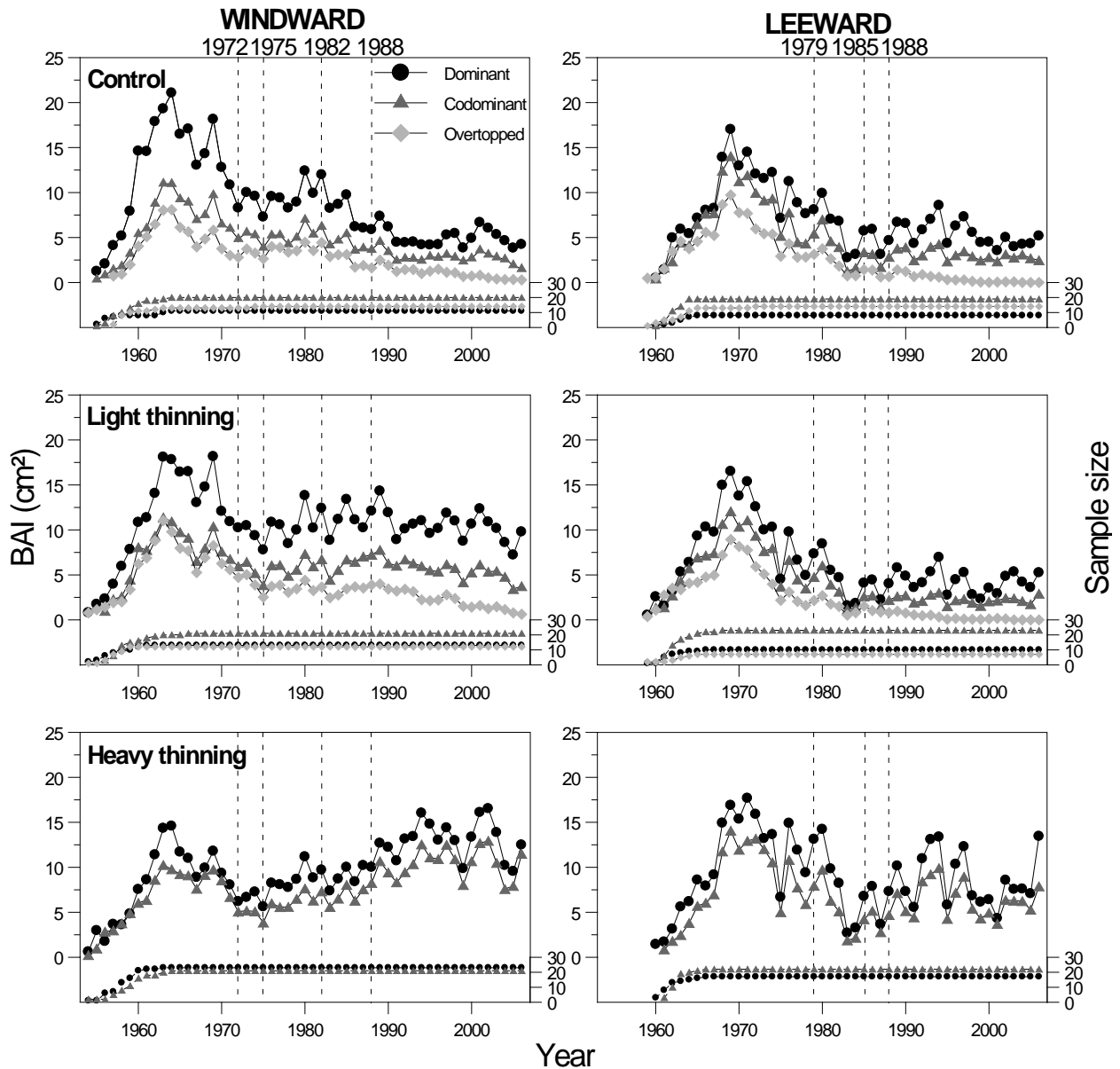
Aspect	Treatment	Crown Class	1970-1987			1989-2006		
			T Oct-1 Jan	T Mar Apr	T June	Jul-1 Aug-1	T Mar Apr	T May Sep
Windward	CO	D	0.590**	0.012	0.594**	0.032	0.689***	0.250
		C	0.568**	0.026	0.626***	0.114	0.602***	0.296
		O	0.501*	0.080	0.569***	-0.066	0.584*	-0.068
	LT	D	0.599**	0.035	0.385	-0.190	0.477***	-0.126
		C	0.589**	0.116	0.402	-0.135	0.438*	-0.127
		O	0.615**	0.179	0.429	-0.042	0.201	-0.107
	HT	D	0.488*	0.172	0.488*	-0.447**	0.257	-0.346
		C	0.384	0.039	0.407	-0.413*	0.335	-0.376
	Leeward	CO	D	-0.251	-0.548**	-0.315	-0.384	-0.256
C			-0.294	-0.542**	-0.257	-0.380	-0.369	-0.499*
O			-0.297	-0.458*	-0.123	-0.568**	-0.176	-0.635***
LT		D	-0.187	-0.547**	-0.261	-0.397*	-0.317	-0.532*
		C	-0.222	-0.545**	-0.269	-0.557**	-0.007	-0.412
		O	-0.290	-0.498**	-0.416*	-0.450*	-0.173	-0.306
HT		D	-0.213	-0.541**	-0.302	-0.502*	-0.351	-0.617***
		C	-0.283	-0.485*	-0.289	-0.541**	-0.360	-0.636**

504 \* $p < 0.05$ ; \*\* $p < 0.01$ , \*\*\* $p < 0.001$   
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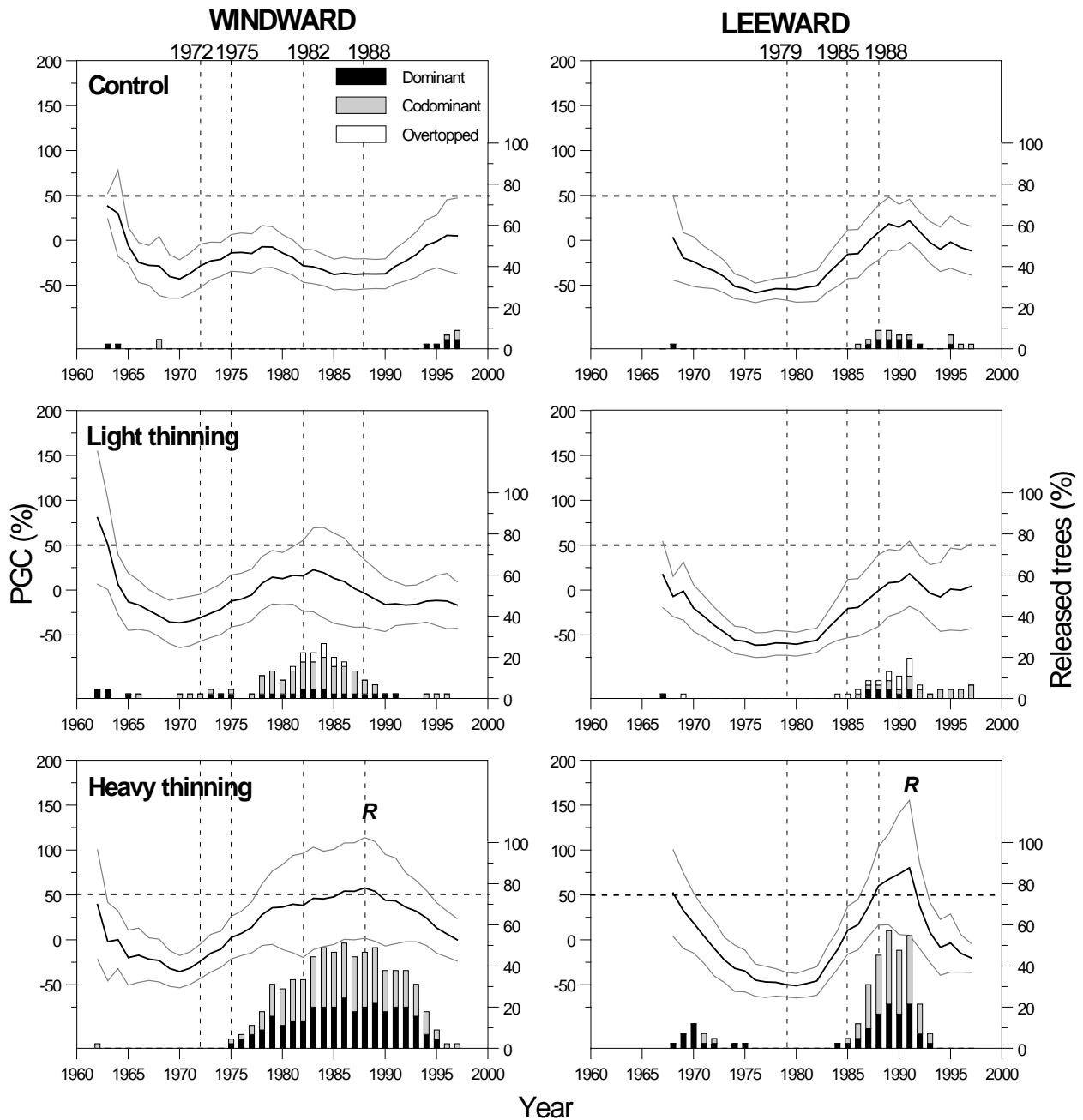
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 509 **Figure 1.-A)** Location of the study area on Tenerife Island, Canary Islands, Spain. **B)** Location  
 510 of the study stands on the windward and leeward slopes. **C)** Climate diagram of the study area  
 511 for the period 1901-2006, showing the dry (black area) and wet (grey area) seasons. **D)** Trends  
 512 for mean annual temperature and precipitation in the study area in the period 1901-2006. Climate  
 513 information is based on the CRU TS 3.0 dataset.  
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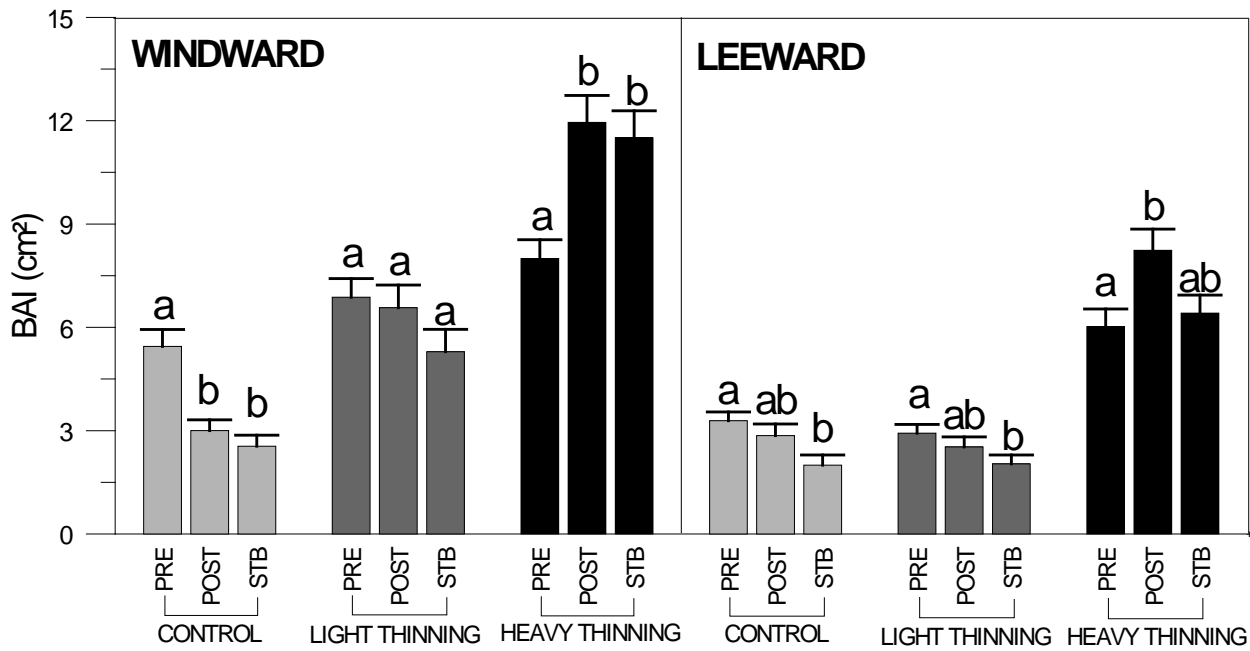
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**Figure 2.-** Mean curves of basal area increment chronologies for each canopy class, and sample size in number of trees, by treatment and slope. Vertical dashed lines correspond to previous interventions and the 1988 thinning. Overtopped trees were not shown in both heavy thinning treatments.

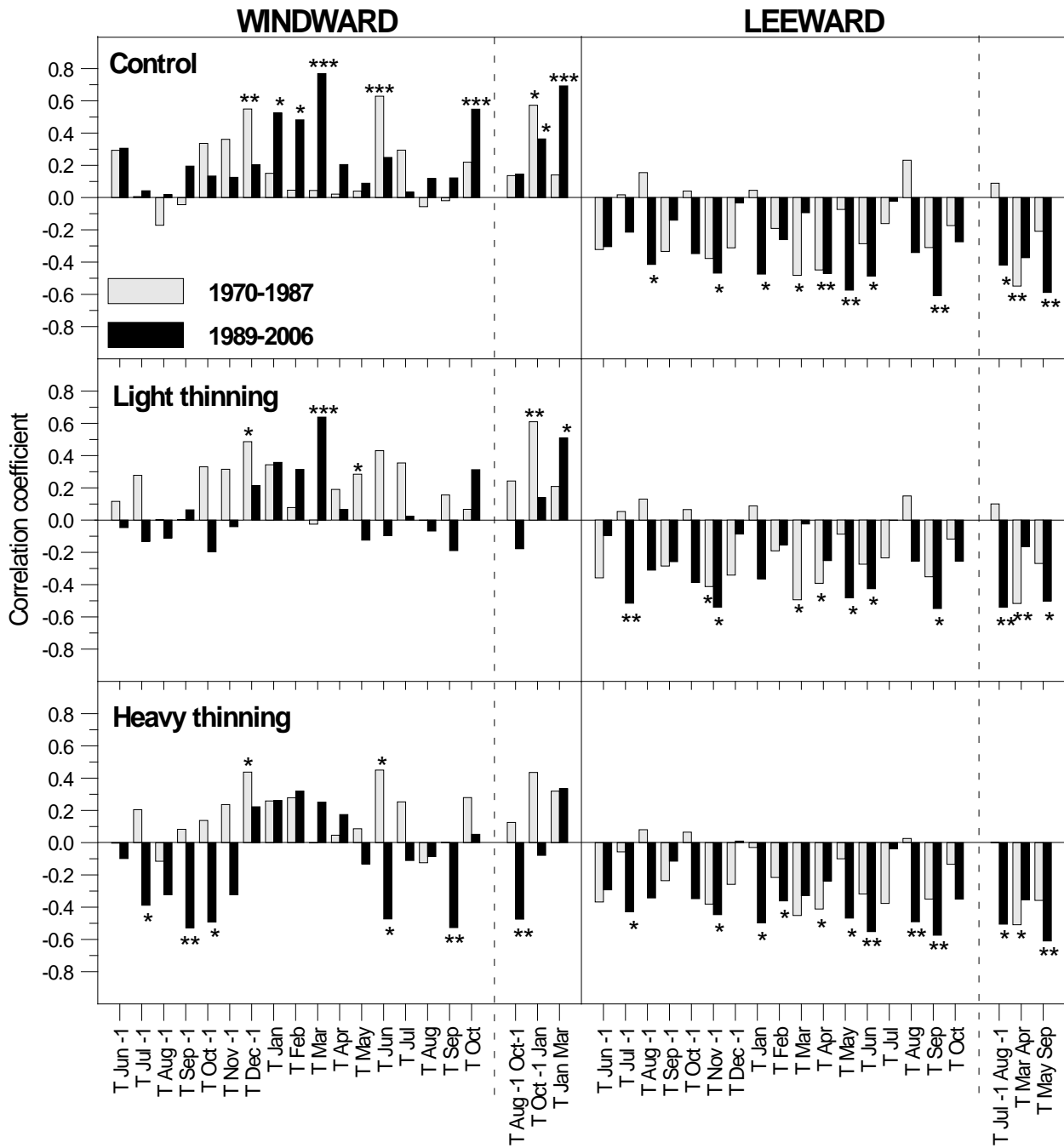


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**Figure 3.-** Mean (black line) and standard deviation (grey line) of percentage growth change (PGC) for BAI of trees by treatment and slope. Horizontal dashed line indicates the minimum threshold (50% PGC) for release detection, and *R* the highest PGC above the threshold. Bars represent the percentage of released trees (>50% PGC) in each crown class per treatment. Vertical dashed lines indicate previous interventions and the 1988 thinning. Central years of the 9-year intervals used to calculate PGC values are in the abscise axes.



535  
 536 **Figure 4.-** Mean BAI (+ 1 standard error) for each period, treatment and slope. Different letters  
 537 within a treatment indicate significantly different mean BAI, according to *post hoc* non-  
 538 parametric Dunnett test. PRE is pre-treatment period, POST is post-treatment period, and STB is  
 539 stabilization period.  
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**Figure 5.-** Bootstrapped correlations between mean temperatures (T) and standardized BAI series per thinning treatment, in the pre-treatment (1970-1987) and post-treatment (1989-2006) periods. Significance levels ( $*p < 0.05$ ,  $** p < 0.01$ ,  $***p < 0.001$ ) were obtained by 10,000 bootstrap iterations.