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

Abstract

- The suitability of thinning to prevent forest growth decline from global warming has been scarcely tested in the Macaronesian Canary pine (*Pinus canariensis* Sweet ex Spreng.).
- We used tree-ring series from dominant, codominant, and overtopped trees to study the effects of thinning intensity on basal area increments (BAI) and climate sensitivity on windward (wet) and leeward (dry) slopes on Tenerife, Canary Islands. Three replicated blocks of control, light thinning, and heavy thinning stands were set on each slope in 1988, and cores were extracted in 2007.
- Heavy thinning induced growth release and increased BAI, mainly on dominant and codominant trees, whereas light thinning effects were negligible; their impacts were more intense on windward. Temperature sensitivity was hardly affected by thinning on leeward, where climate control was stronger. On windward, thinning enhanced the influence of summer temperatures. Upper crown classes were overall more sensitive, but overtopped trees responded better in summer.
- Thinning intensity and aspect greatly influence growth on Canary pine afforestations, but individual responses are highly dependent on crown classes. In addition, thinning may be less effective to modify growth conditions on leeward slopes, at least if it is not intense.

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

1. INTRODUCTION

According to global warming predictions, a generalised raise in temperatures and a potential decline in annual rainfall are expected in the Mediterranean area for the current century (IPCC, 2007). These predictions can also be applied to the Macaronesian region, although changes might be weaker due to its oceanic character. Deterioration of growth conditions will arise for many Mediterranean species if heat and water stress are intensified (Andreu et al., 2007). As Linares et al. (2009) reported, drought stress is probably the main reason for the current growth decline of coniferous woodlands in southern Europe.

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

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

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

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

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

2. MATERIALS AND METHODS

2.1. Study area

The study area is located in the Cordillera Dorsal, near the northeastern boundary of the Corona Forestal Natural Park, Tenerife Island, Spain (Fig. 1A and B). The park extends over 46,613 ha, 25% of which was reforested with Canary pine from 1940 to 1960 at elevations between 1,000 and 2,000 m. Altitude and wind exposure are the major environmental factors affecting the distribution of vegetation types on Tenerife (Fernández-Palacios and de Nicolás, 1995). Thanks to the moisture occasionally provided as fog drip by trade winds, windward pine forests hold an abundant undergrowth cover, while leeward forests only show sparse shrubs. Climate is Mediterranean with a long dry season ranging from May to September (Figure 1C). Mean annual temperature showed a significant increasing trend in the period 1901-2006, while annual precipitation did not significantly change (Figure 1D). Soils are developed on deep horizons of volcanic scoria and are classified as Entisol, suborder Orthens (Fernández-Caldas et al., 1985).

2.2. Stand history and experimental design

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

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

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

2.3. Sampling, tree-ring measuring and crossdating

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

2.4. Thinning effects assessment

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

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

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

2.5. Calculation of the relationships between tree growth and climate

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

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

3. RESULTS

3.1. Radial growth responses to thinning

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

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

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

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

3.2. Common signal and climate-growth relationships

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

Correlations between standardized BAI chronologies and climate revealed that average temperature was the dominant climatic variable controlling growth, while rainfall nearly exerted no effects (data not shown). Temperature influence strongly differed between slopes, as control stands revealed, with positive significant correlations on windward only, and negative on leeward (Fig. 5). The effects of temperature on tree growth varied between both pre- and post-treatment periods for every treatment, shifting the months influencing growth. On windward, the positive effect of temperature in previous October-January shifted to current March, while on leeward, negative correlations in March-April changed to May-September (Fig. 5). Furthermore, we found an overall increment in the statistical significance of correlations after 1988 on both slopes.

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

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

4. DISCUSSION

4.1. Effects of thinning intensity and aspect on BAI

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

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

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

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

4.2. Variation in climate sensitivity

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

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

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

Dominant and codominant trees recovered faster after drought-induced narrow rings, corroborating the less plastic response of overtopped trees to the environmental variability (Linares et al., 2009), in which no retrieval occurred. Climate-growth correlations followed similar patterns among crown classes, namely for the upper ones. This suggests that aspect has more impact on climatic sensitivity than individual characteristics, such as the crown social status. However, the significance of correlations differed at specific seasons, being the upper classes more sensitive to climate. Suppressed trees were generally less sensitive except to previous and current summer temperatures, namely on the leeward control, which can be related to the major water stress suffered by overtopped trees in spring and summer (Martín-Benito et al., 2008).

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

Despite the potential masking effects arisen by an uneven stand management history and by the limitation of using short tree-ring series (Copenheaver and Abrams, 2003), our analyses demonstrated for the first time the impact of thinning treatments on growth patterns in young Canary pine plantations. Heavy thinning provides a more natural community structure and favours the establishment of new cohorts (Arévalo and Fernández-Palacios, 2005), improves growth rates, and modulates tree sensitivity to limiting climatic conditions. Therefore, management guidelines should take heavy thinning into consideration in order to improve growing conditions and self-maintenance in Canary pine plantations with focus on their restoration. This is especially true on leeward sites because: 1) more similar densities to those recorded by Blanco et al. (1989) for naturally regenerated stands are advisable (i.e. 130-440 stems ha^{-1}); and 2) the constraining climate conditions can swamp the impact of thinning if it is not intense enough, with a special concern to global warming. Nevertheless, to verify our supposition would be necessary to test more accurately how the contrasting climatic conditions, imposed by the topography and the circulation of trade winds, could modulate growth along the complete altitudinal range of Canary pine.

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

				1988 before thinning			1988 after thinning			2007 [b]
Block [a]	Treatment	Elevation (m)	% BA removed	Density (stems ha^{-1})	Mean BA (m^2 ha^{-1})	Mean DBH (cm)	Density (stems ha^{-1})	Mean BA (m^2 ha^{-1})	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

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

[a] W: blocks on windward slope. L: blocks on leeward slope.

[b] Calculations based on 15 sampled trees per stand.

Table 2.- Descriptive statistics of the standardized basal area increment chronologies for the periods 1970-1987 and 1989-2006 corresponding to the control (CO), light thinning (LT) and heavy thinning (HT) treatments.

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

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

Table 3.- Bootstrapped correlations between temperature variables and BAI chronologies for dominant (D), codominant (C), and overtopped (O) trees under control (CO), light thinning (LT), and heavy thinning (HT) treatments, for the periods 1970-1987 and 1989-2006.

			1970-1987			1989-2006		
Aspect	Treatment	Crown Class	Oct-1 Jan	Mar Apr	June	Jul-1 Aug-1	Mar Apr	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	-0.512*
		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**

$^{*}p < 0.05$; $^{**}p < 0.01$, $^{***}p < 0.001$

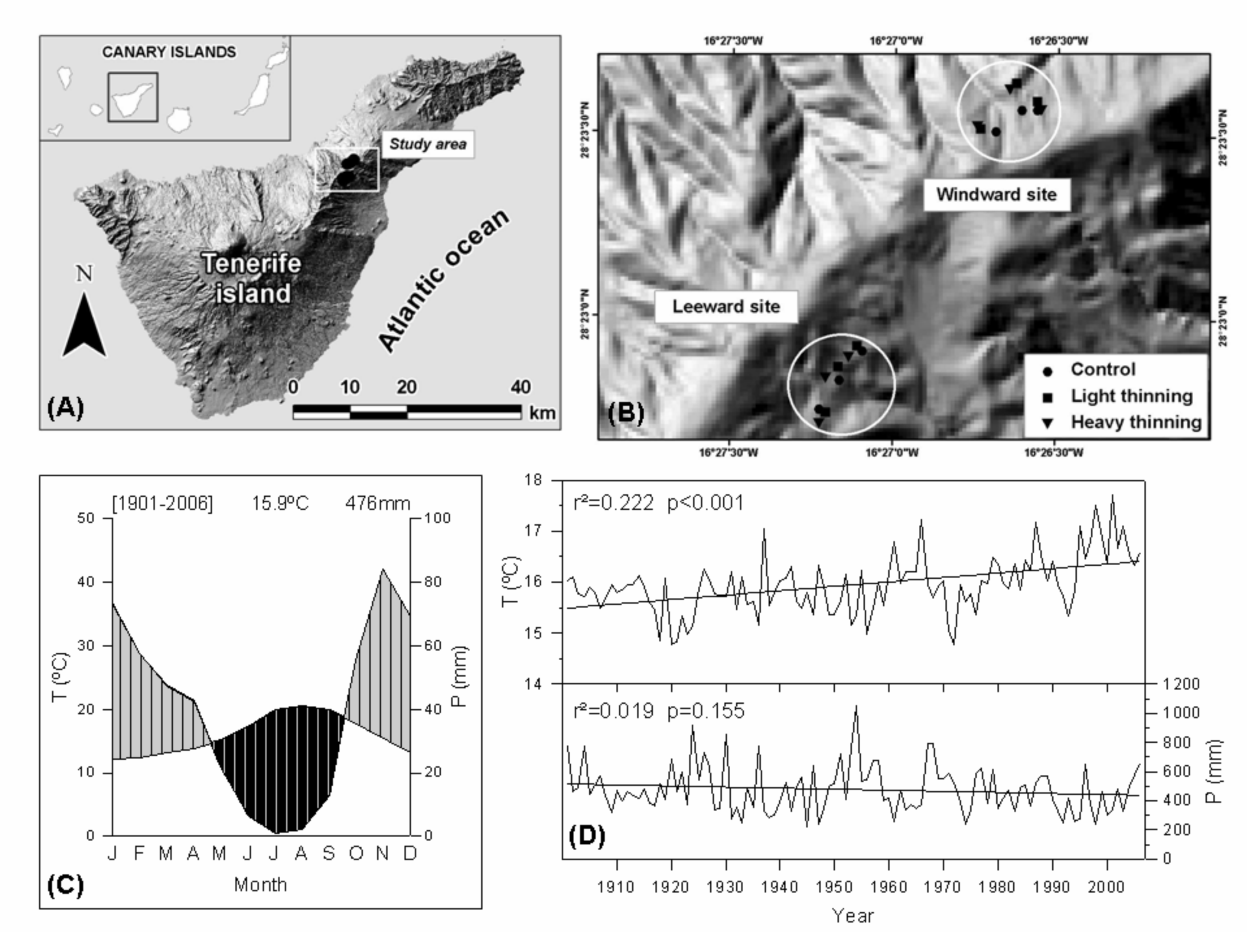

Figure 1.-A) Location of the study area on Tenerife Island, Canary Islands, Spain. **B)** Location of the study stands on the windward and leeward slopes. **C)** Climate diagram of the study area for the period 1901-2006, showing the dry (black area) and wet (grey area) seasons. **D)** Trends for mean annual temperature and precipitation in the study area in the period 1901-2006. Climate information is based on the CRU TS 3.0 dataset.

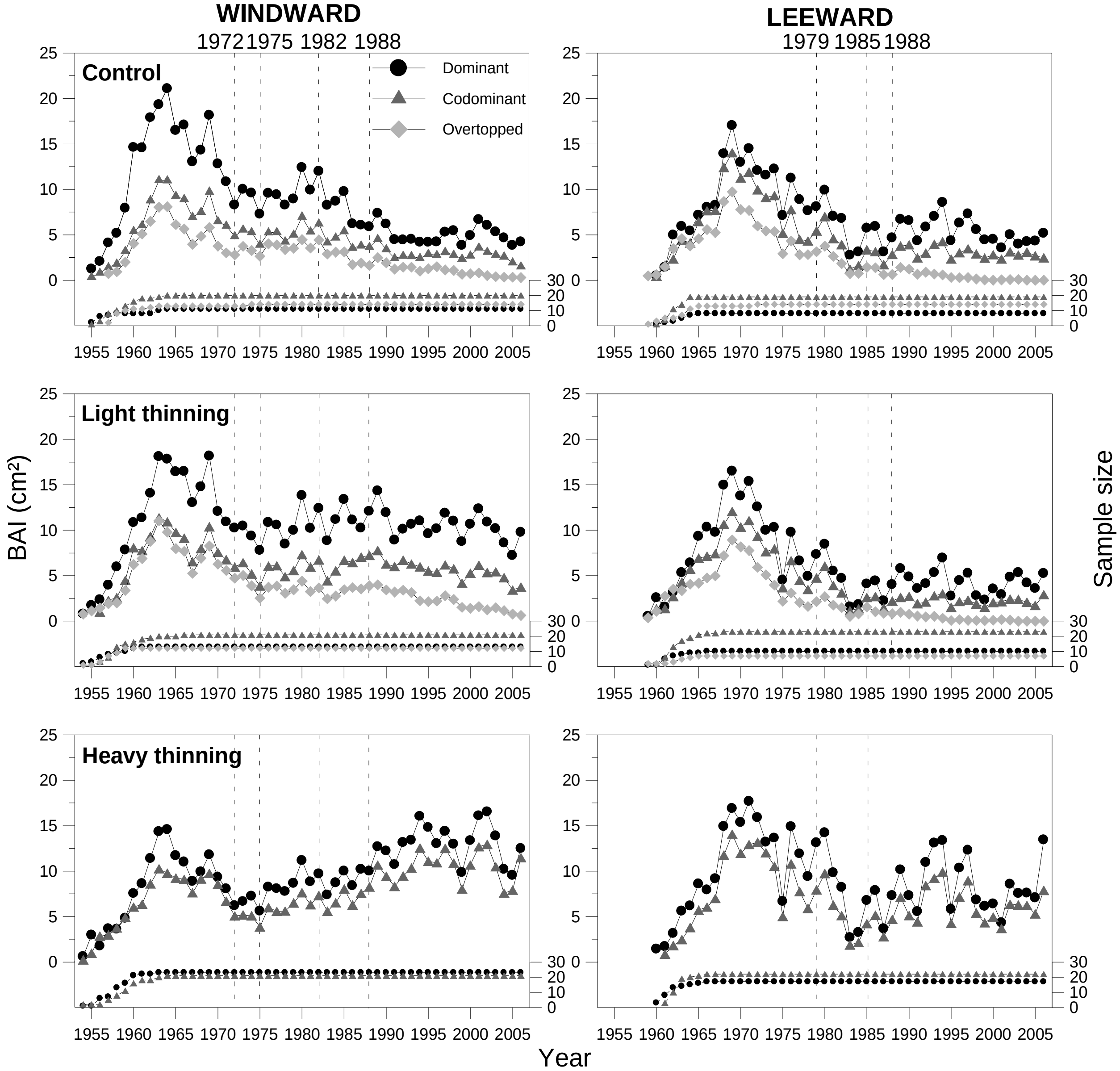

Figure 2.- Mean curves of basal area increment chronologies for each canopy class, and sample size in number of trees, by treatment and slope. Vertical dashed lines correspond to previous interventions and the 1988 thinning. Overtopped trees were not shown in both heavy thinning treatments.

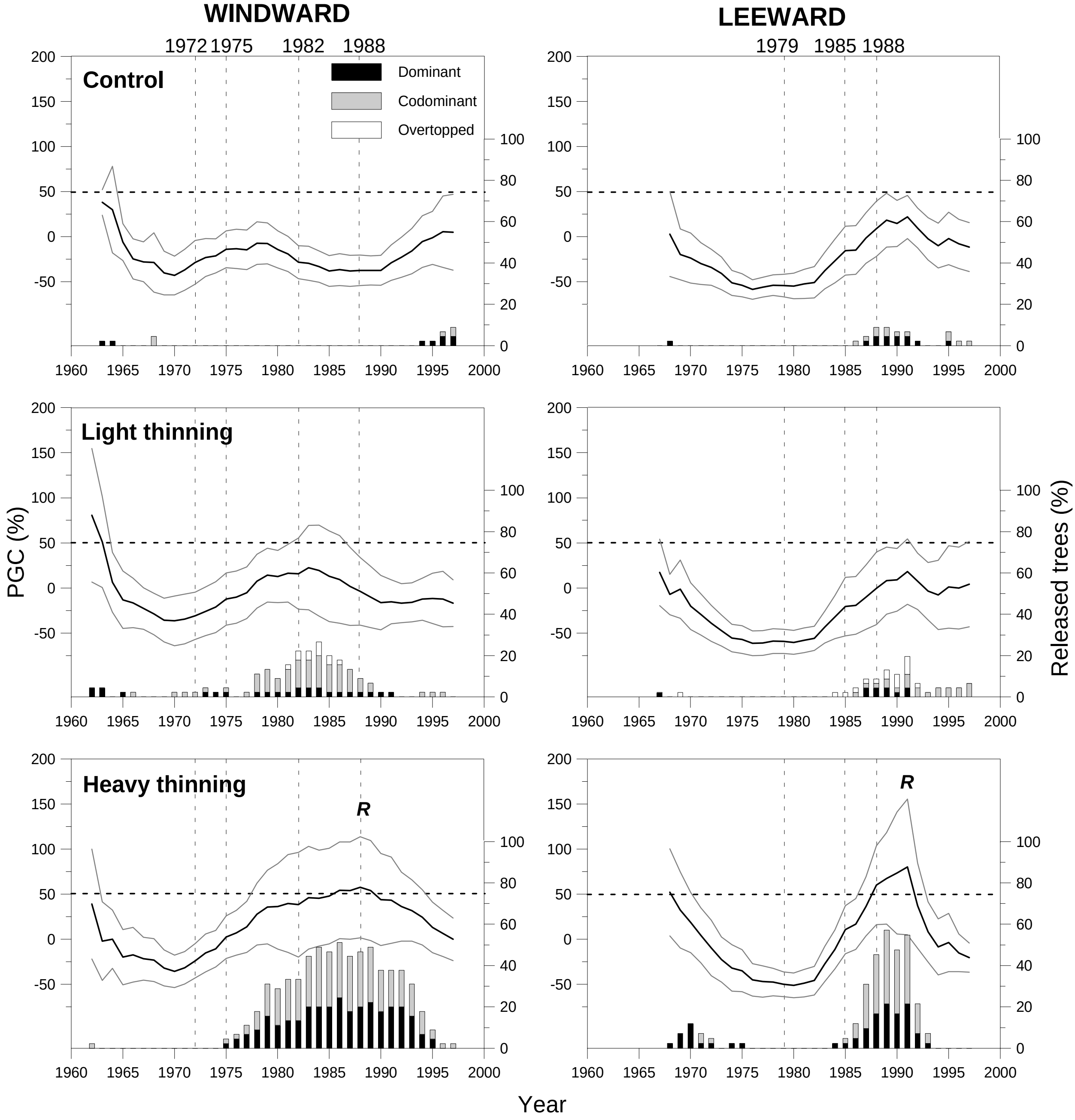

Figure 3.- Mean (black line) and standard deviation (grey line) of percentage growth change (PGC) for BAI of trees by treatment and slope. Horizontal dashed line indicates the minimum threshold (50% PGC) for release detection, and *R* the highest PGC above the threshold. Bars represent the percentage 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.

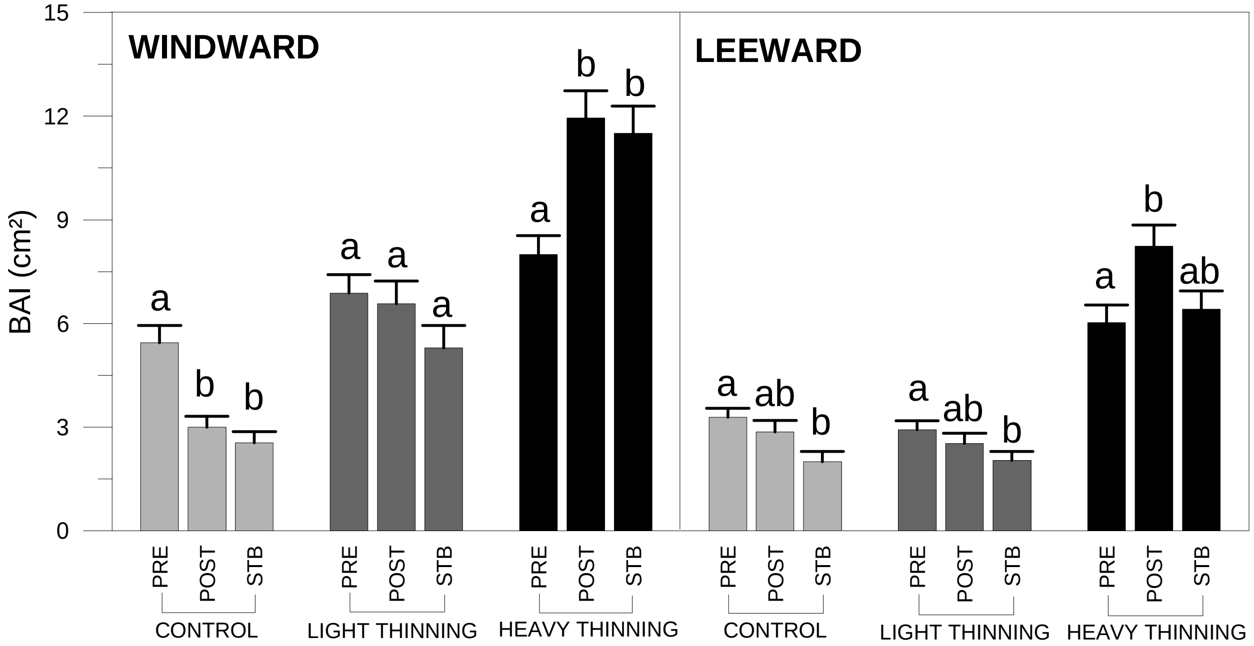

Figure 4.- Mean BAI (+ 1 standard error) for each period, treatment and slope. Different letters within a treatment indicate significantly different mean BAI, according to *post hoc* non-parametric Dunnett test. PRE is pre-treatment period, POST is post-treatment period, and STB is stabilization period.

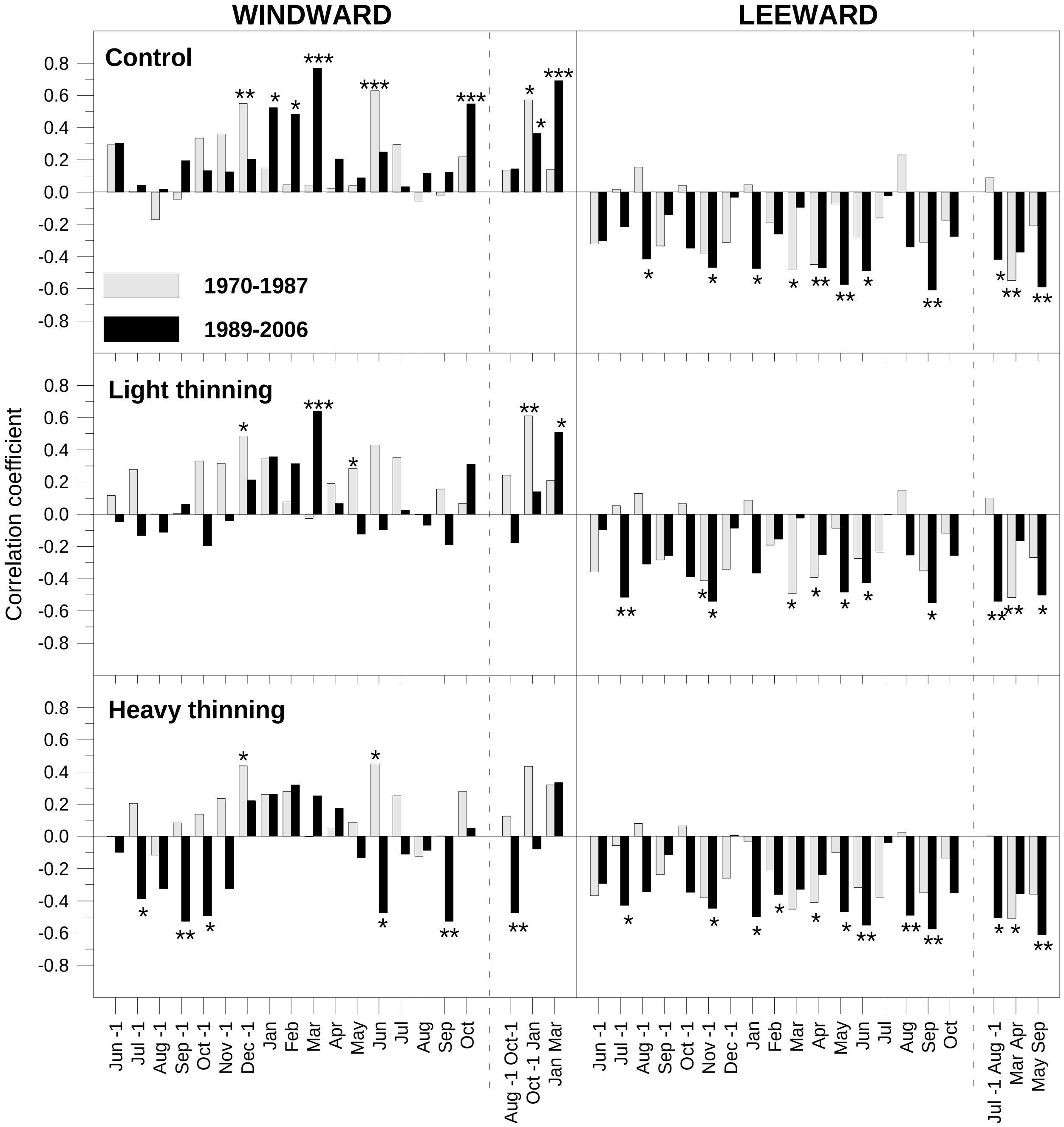

Figure 5.- Bootstrapped correlations between mean temperatures and standardized BAI series per thinning treatment, in the pre-treatment (1970-1987) and post-treatment (1989-2006) periods. Significance levels (*p < 0.05, ** p < 0.01, ***p < 0.001) were obtained by 10,000 bootstrap iterations.