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

Gonzalo Pérez-de-Lis · Ignacio García-González · Vicente Rozas · José Ramón Arévalo

Abstract

· **Context** The suitability of thinning to prevent forest growth decline as a result of global warming has not been tested extensively in Macaronesian Canary pine (*Pinus canariensis* Sweet ex Spreng.).

· **Aims** This study aimed to answer the following questions: (1) are tree growth patterns modified by the aspect and thinning intensity? (2) Is sensitivity to climate modulated by thinning? (3) Do trees of different crown classes respond differentially to thinning intensity and climate?

· **Methods** 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.

· **Results** 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 the windward side. 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 more sensitive overall, 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 not intense.

Keywords Dendroecology · Tree ring · Climate-growth relationships · Growth release · Forest restoration

1 Introduction

According to global warming predictions, a generalised rise in temperatures and a potential decline in annual rainfall are expected in the Mediterranean area within the current century (IPCC 2007). These predictions can also be applied to the Macaronesian region, although such 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 long-term stress by sustained intense competition, which incorporates more sensitivity to short-term stresses such as severe drought events (Linares et al. 2010).

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Therefore, reducing competition by thinning should enhance growing conditions, and thus alleviate the water stress that constrains photosynthetic activity and growth (McDowell et al. 2003). Thinning also provides more growing space and a greater amount of light on the soil surface, which results in greater carbon gain and faster mineralization of the litter, yielding an increase in nutrient availability. However, the advantages of thinning for growth may not be the same for trees of different crown classes, due mainly to a different duration of the growing period (Bréda et al. 1995).

Radial growth responses to climate vary considerably 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 reduced competition for available water after thinning.

Canary pine (*Pinus canariensis* Sweet ex Spreng.)—a species endemic to 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), the tree line in the Canary Islands can 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 twentieth century. Under the absence of ongoing 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 recently been reconsidering the usefulness of these plantations, aiming to restore the natural pine forest by means of silvicultural practices (Arévalo and Fernández-Palacios 2005). Additionally, environmental conditions differ markedly throughout narrow geographic ranges in the Canary Islands, because moisture provided by trade winds affects windward (northern) slopes almost exclusively, with the leeward (southern) slopes being 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 9 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 naturalisation of pinewoods, and reported that intense thinning increased tree size considerably and promoted a more natural stand structure.

Dendroecological methods are used widely for studying both thinning and climate effects on the radial growth of trees (e.g. Misson et al. 2003), but have scarcely been applied to Canary pine. The difficulties of using this species in dendrochronology have been highlighted by Jonsson et al. (2002), who reported mainly 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. With this aim in mind, we based our study on previous experimental stands set by Madrigal et al. (1989) to answer the following questions: (1) are tree growth patterns [based on basal area increments (BAI)] modified by the aspect and thinning intensity? (2) Is 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,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 provided occasionally 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 (Fig. 1c). Mean
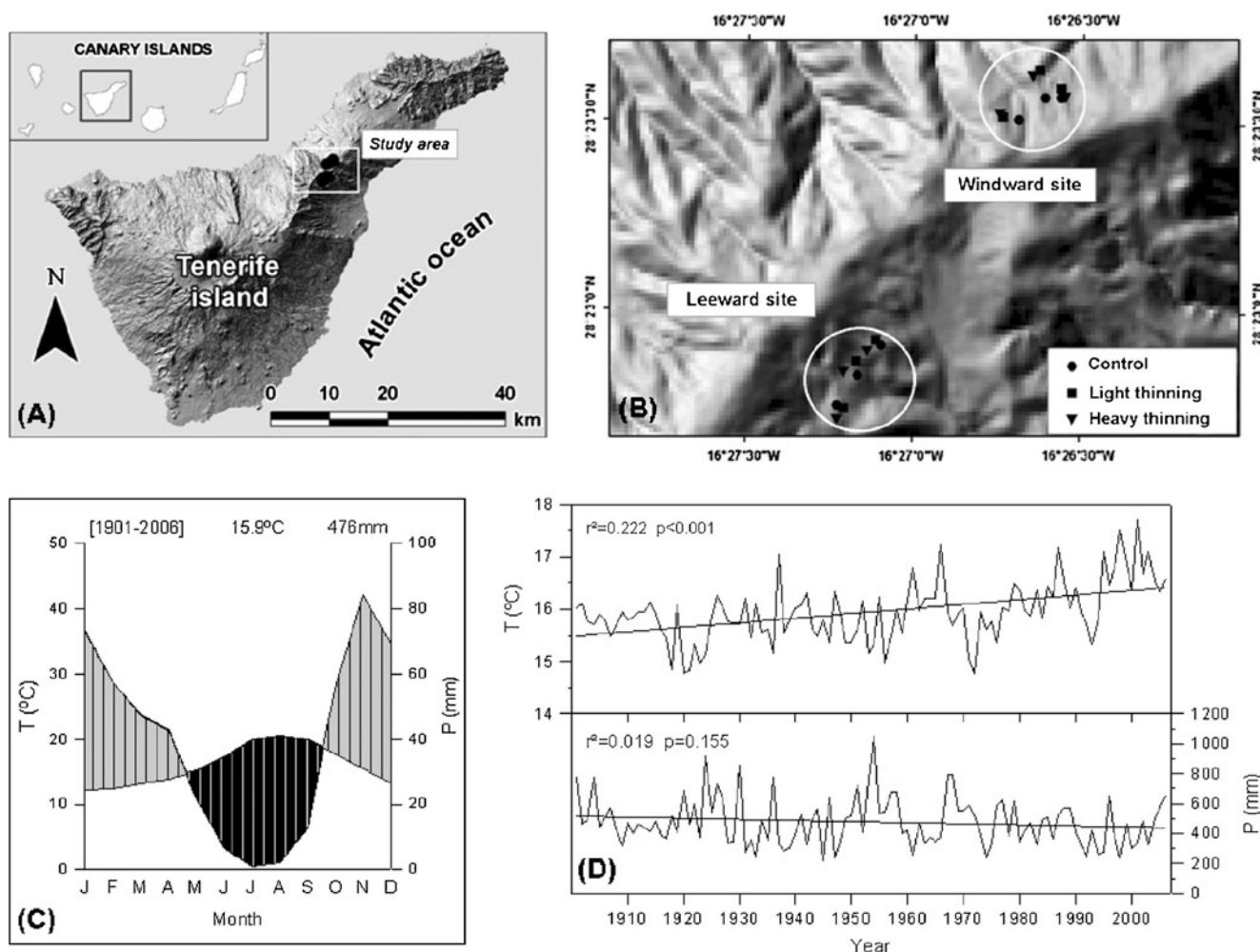
Fig. 1 **a** Location of the study area on Tenerife Island, Canary Islands, Spain. **b** Location of the study stands on the windward and leeward slopes. **c** Climate diagram of the study area for the period 1901–2006, showing the dry (*black area*) and wet (*grey area*) seasons.

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

annual temperature showed a significant increasing trend in the period 1901–2006, while annual precipitation did not change significantly (Fig. 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 planted in 1949 and 1953, respectively, 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 and 20% with a low pruning) were performed (Madrigal et

al. 1989). Dead and overtopped trees were logged preferentially 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 of 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 ($F_{1,12}=29.981$, $P<0.001$) thinning. Similarly,

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. *BA* Basal area, *DBH* diameter at breast high (1.30 m), *SD* standard deviation

Block [a]	Treatment	Elevation (m)	% BA removed	1988 before thinning			1988 after thinning		2007 [b]	
				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	1,650		1,072	62.4	27.2				30.7±7.7
	LT	1,640	7.68	752	53.4	30.1	656	49.3	30.9	34.2±7.9
	HT	1,643	52.02	800	52.1	28.8	352	25.0	30.1	39.9±5.3
W2	CO	1,654		1,232	67.0	26.3				27.8±4.8
	LT	1,652	14.45	1,312	69.9	26.0	912	59.8	28.9	29.8±7.4
	HT	1,659	40.31	704	45.9	28.8	368	27.4	30.8	40.4±5.9
W3	CO	1,671		992	56.6	26.9				31.6±7.1
	LT	1,671	6.35	752	50.4	29.2	656	47.2	30.3	37.5±8.8
	HT	1,670	46.57	928	49.6	26.1	352	26.5	31.0	37.3±4.8
L1	CO	1,701		1,456	59.8	22.9				24.6±4.5
	LT	1,699	13.57	1,504	58.2	22.2	1,216	50.3	22.9	26.7±4.2
	HT	1,686	45.55	1,312	55.1	23.1	528	30.0	26.9	34.5±2.9
L2	CO	1,698		1,664	65.5	22.4				26.1±5.6
	LT	1,704	13.66	1,600	52.7	20.5	1,280	45.5	21.3	23.0±3.9
	HT	1,697	38.13	1,605	43.8	18.7	800	27.1	20.8	23.9±4.3
L3	CO	1,719		2,224	71.8	20.3				24.4±5.6
	LT	1,718	18.10	2,000	68.5	20.9	1,360	56.1	22.9	24.3±6.2
	HT	1,704	51.58	1,488	60.1	22.7	544	29.1	26.1	35.6±5.9

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

[b] Calculations based on 15 sampled trees per stand

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 selected randomly 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, Bloomfield, NY). 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 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 9-year mean BAI. The 9-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 stabilisation (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 analysed 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, Chicago IL).

2.5 Calculation of the relationships between tree growth and climate

Mean BAI series were characterised for each treatment, aspect and crown class before (1970–1987) and after (1989–2006) 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 $0.5° \times 0.5°$, 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 the control only on windward, showing no declining trend. Likewise, dominant and codominant trees on windward differed significantly 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 influence growth significantly in any case ($P > 0.05$). Narrow tree rings were detected on leeward for 1975, 1983, 1991, 1995, and 2001, which occurred mostly 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 marked 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 $\times$ 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 sharp increase after heavy thinning, which was maintained or decreased roughly in the stabilisation period (Fig. 4).

3.2 Common signal and climate-growth relationships

The quality of standardised BAI chronologies was better on leeward, both before and after thinning (Table 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 decreased considerably on both slopes in the post-treatment period. Both thinning treatments caused a weaker reduction on windward, as did only the most intense treatment on leeward. On leeward, chronologies were autocorrelated only slightly before 1988 but not afterwards; no notable AC was observed on windward, except for the control in the most recent period.

Correlations between standardised BAI chronologies and climate revealed that average temperature was the dominant climatic variable controlling growth, while rainfall exerted nearly no effects (data not shown). Temperature influence differed strongly between slopes, as control stands revealed,
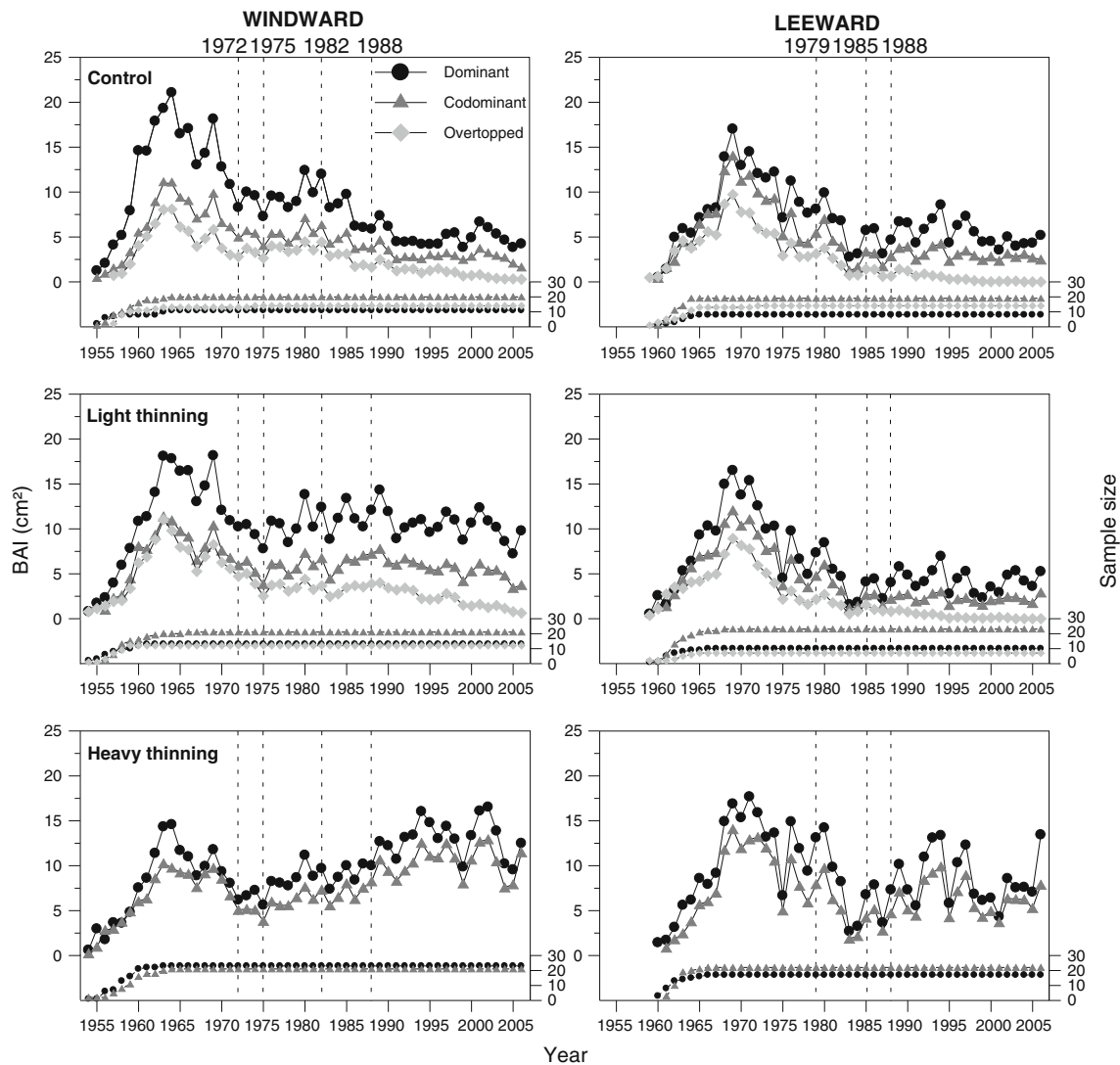
Fig. 2 Mean curves of basal area increment (BAI) chronologies for each canopy class, and sample size in number of trees, by treatment and slope. *Vertical dashed lines* Previous interventions and the 1988 thinning. Overtopped trees were not shown in either heavy thinning treatment

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, and was not significant for heavy thinning. Simultaneously, a strongly negative influence of temperature in the previous late summer–autumn

and current June and September arose. In 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 differed occasionally (Table 3). Dominant and codominant trees were the most sensitive 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, the negative influence of the previous July–August and current May–September in the post-treatment period was greater for overtopped trees
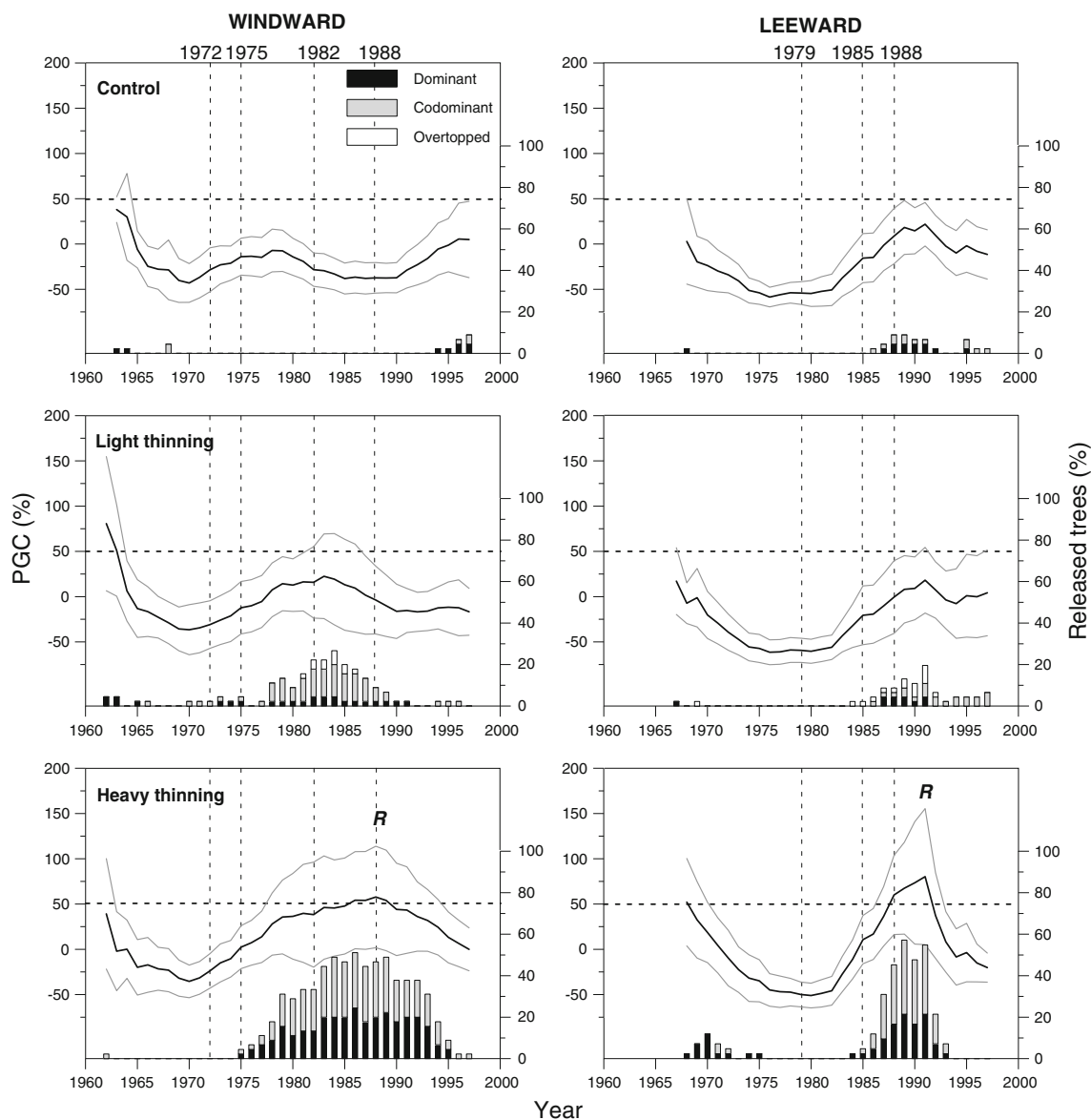
Fig. 3 Mean (*black lines*) and standard deviation (*grey lines*) of percentage growth change (PGC) for BAI of trees by treatment and slope. *Horizontal dashed lines* Minimum threshold (50% PGC) for release detection, *R* highest PGC above the threshold, *bars* percentage of released trees (>50% PGC) in each crown class per treatment, *vertical dashed lines* previous interventions and the 1988 thinning. Central years of the 9-year intervals used to calculate PGC values are in the *abscise axes*

on the 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 with those of previous studies that reported poor individual growth responses after light thinning in comparison to heavy thinning (Cañellas et al. 2004; Martín-Benito et al. 2010). However, no uniform responses arose through different crown classes. Codominant trees benefited most from thinning, followed by dominant trees, which could be explained by a lower effect of thinning from below on dominant crown class, which are subject to lower competition intensity (Mäkinen and Isomäki 2004). Bréda et al. (1995) noted that overtopped and dominant trees gain more advantage than codominant trees as a result of thinning from above. Nevertheless,

Fig. 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* Pre-treatment period, *POST* post-treatment period, *STB* stabilisation period
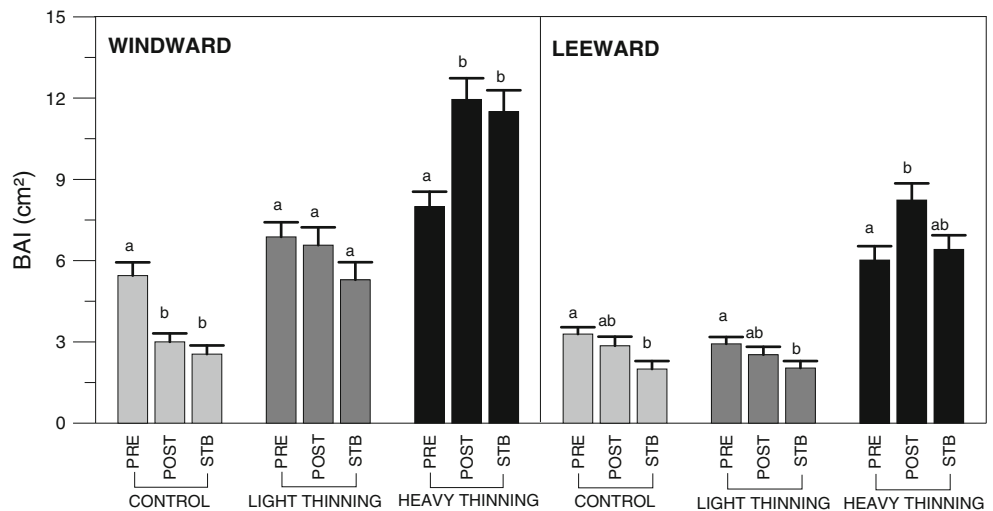
overtopped trees were not favoured by light thinning in our study. This treatment was probably not intense enough to reduce the stress experienced by the lowest crown classes. Overtopped trees can become stagnated, losing the capacity to acquire enough vigour to significantly release, even if competition 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 for larger trees (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 that is 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 proved to be relevant, which probably preconditioned differential responses in the post-treatment period that were more evident on windward.

Despite the more limited effects of thinning on leeward, the reduction in tree density still contributed to increased BAI, presumably due to a more pronounced drought tolerance of Canary pine on this slope, since growth recovered from 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 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

Table 2 Descriptive statistics of the standardised basal area increment (BAI) chronologies for the periods 1970–1987 and 1989–2006 corresponding to the control (CO), light thinning (LT) and heavy thinning (HT) treatments. *Rbt* Mean correlation between trees, *EPS* expressed population signal, *MS* mean sensitivity, *AC* first-order autocorrelation coefficient

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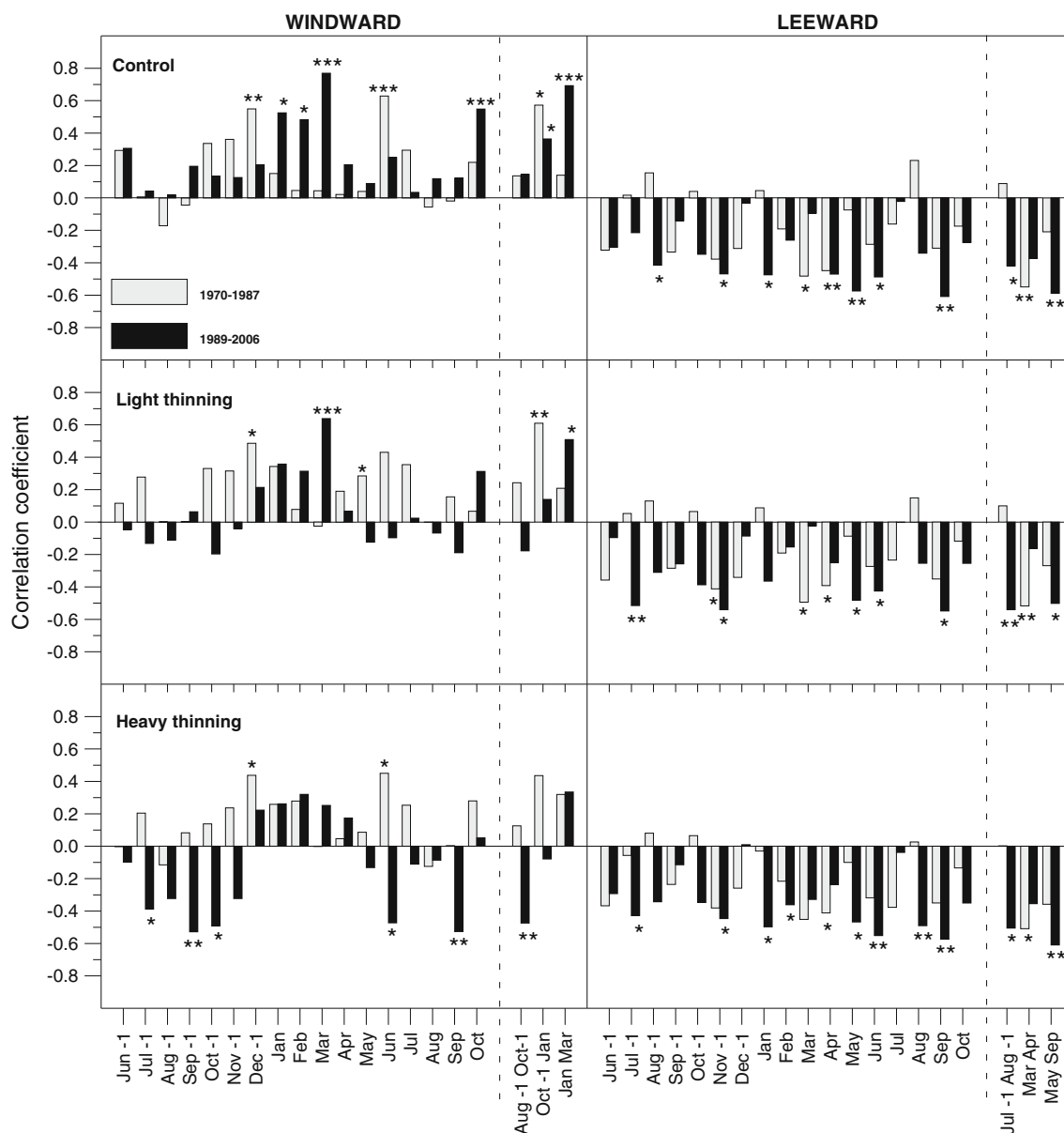
Fig. 5 Bootstrapped correlations between mean temperatures and standardised BAI series per thinning treatment, in the pre-treatment (1970–1987) and post-treatment (1989–2006) periods. Significance levels (*$P<0.05$, ** $P<0.01$, ***$P<0.001$) were obtained by 10,000 bootstrap iterations

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 proportional 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 the leeward side. Besides, common signal decreased after 1988 regardless of treatment, likely due to 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 can modulate the impact of thinning on climate sensitivity. Increasing temperatures within stands as a consequence of a higher exposure

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	October(-1)-January	March–April	June	July(-1)-August(-1)	March–April	May–September
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**

*$P<0.05$; **$P<0.01$, ***$P<0.001$

to radiation after thinning (Moreno and Cubera 2008), would counteract the positive effect of temperatures in the previous winter and highlight their negative impact in the 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 a warm previous autumn and current summer on windward after heavy thinning. On the contrary, leeward stands were homogeneous in their response regardless of period, which does not agree with the increased temperature sensitivity that occurs frequently in dry sites after thinning (Gea-Izquierdo et al. 2009; Linares et al. 2010). Since thinning appears to affect the growth rates of trees, but not their temperature sensitivity, we suggest that the stronger climatic control on leeward that causes year-to-year variation of growth is determined mainly by climate, regardless of local tree density. This fact confirms that the limited thinning effects on leeward can be attributed not only to 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 in 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 1980s were related

mostly to climate warming (Andreu et al. 2007; Bogino and Bravo 2008; Martín-Benito et al. 2010), which was also the case for 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 environmental variability (Linares et al. 2009), in which no retrieval occurred. Climate-growth correlations followed similar patterns among crown classes, especially 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 in specific seasons, the upper classes being 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 has 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 twice 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 demonstrate 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) densities more similar 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, which is particularly concerning with regards to global warming. Nevertheless, to verify our supposition, it 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.

References

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

Andreu L, Gutiérrez E, Macias M, Ribas M, Bosch O, Camarero JJ (2007) Climate increases regional tree-growth variability in Iberian pine forests. Glob Chang Biol 13:804–815

Arévalo JR, Fernández-Palacios JM (2005) From pine plantations to natural stands. Ecological restoration of a *Pinus canariensis* Sweet, ex Spreng forest. Plant Ecol 181:217–226

Aussenac G (2000) Interactions between forest stands and microclimate: Ecophysiological aspects and consequences for silviculture. Ann For Sci 57:287–301

Biondi F (1999) Comparing tree-ring chronologies and repeated timber inventories as forest monitoring tools. Ecol Appl 9:216–227

Blanco A, Castroviejo M, Fraile JL, Gandullo JM, Muñoz LA, Sánchez O, (1989) Estudio ecológico del pino canario. Serie Técnica No. 6. MAPA

Blanco JA, Imbert JB, Castillo FJ (2008) Nutrient return via litterfall in two contrasting *Pinus sylvestris* forests in the Pyrenees under different thinning intensities. For Ecol Manage 256:1840–1852

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

Bréda N, Granier A, Aussenac G (1995) Effects of thinning on soil and tree water relations, transpiration and growth in an oak forest (*Quercus petraea* (Matt.) Liebl.). Tree Physiol 15:295–306

Briffa KR, Jones PD (1990) Basic chronology statistics and assessment. In: Cook ER, Kairiukštis LA (eds) Methods of dendrochronology. Applications in the environmental sciences. Kluwer, Boston, pp 137–153

Cañellas I, del Río M, Roig S, Montero G (2004) Growth response to thinning in *Quercus pyrenaica* Willd. coppice stands in Spanish central mountain. Ann For Sci 61:243–250

Carrer M, Urbinati C (2004) Age-dependent tree-ring growth responses to climate in *Larix decidua* and *Pinus cembra*. Ecology 85:730–740

Climent JM, Aranda I, Alonso J, Pardos JA, Gil L (2006) Developmental constraints limit the response of Canary Island pine seedlings to combine shade and drought. For Ecol Manage 231:164–168

Copenheaver CA, Abrams MD (2003) Dendroecology in young stands: case studies from jack pine in northern lower Michigan. For Ecol Manage 182:247–257

Cotillas M, Sabaté S, Gràcia C, Espelta JM (2009) Growth response of mixed Mediterranean oak coppices to rainfall reduction: Could selective thinning have any influence on it? For Ecol Manage 258:1677–1683

Fernández-Caldas E, Tejedor M, Quantin P (1985) Los suelos volcánicos de Canarias. Servicio de Publicaciones de la Universidad de La Laguna, la Laguna. p 250

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

Gea-Izquierdo G, Martín-Benito D, Cherubini P, Cañellas I (2009) Climate-growth variability in *Quercus ilex* L. west Iberian open woodlands of different stand density. Ann For Sci 66:802

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

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

IPCC (2007) CoreWriting Team, Pachauri RK, Reisinger A (eds) Climate change 2007: Synthesis report. Contribution of working groups I, II and III to the fourth assessment report of the intergovernmental panel on climate change. IPCC, Geneva, Switzerland

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

Kohler M, Sohn J, Nägele G, Bauhus J (2010) Can drought tolerance of Norway spruce (*Picea abies* (L.) Karst.) be increased through thinning? Eur J For Res 129:1109–1118

Linares JC, Camarero JJ, Carreira JA (2009) Plastic responses of *Abies pinsapo* xylogenesis to drought and competition. Tree Physiol 29:1525–1536

Linares JC, Camarero JJ, Carreira JA (2010) Competition modulates the adaptation capacity of forests to climatic stress: insights from recent growth decline and death in relict stands of the Mediterranean fir *Abies pinsapo*. J Ecol 98:592–603

Madrigal A, Domínguez ML, Peraza M, Barber JR, Herrero J, Rodríguez-Solano R (1989) Estudio de la selvicultura de las masa artificiales de *Pinus canariensis* Sweet ex Spreng. Gobierno de Canarias, Dirección General del Medio Ambiente; Fundación General de la Universidad Politécnica de Madrid, Departamento de Silvopascicultura. Santa Cruz de Tenerife y Madrid

Mäkinen H, Isomäki A (2004) Thinning intensity and long-term changes in increment and stem form of Scots pine trees. For Ecol Manage 203:21–34

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

Martín-Benito D, del Río M, Heinrich H, Helle G, Cañellas I (2010) Response of climate-growth relationships and water use efficiency to thinning in a *Pinus nigra* afforestation. For Ecol Manage 259:967–975

Mason SJ, Mimmack GM (1992) The use of bootstrap confidence intervals for the correlation coefficient in climatology. Theor Appl Climatol 45:229–233

McDowell N, Brooks JR, Fitzgerald SA, Bond BJ (2003) Carbon isotope discrimination and growth response of old *Pinus ponderosa* trees to stand density reductions. Plant Cell Environ 26:631–644

Misson L, Nicault A, Guiot J (2003) Effects of different thinning intensities on drought response in Norway spruce (*Picea abies* (L.) Karst.). For Ecol Manage 183:47–60

Moreno G, Cubera E (2008) Impact of stand density on water status and leaf gas exchange in *Quercus ilex*. For Ecol Manage 254:74–84

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

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

Stan AB, Daniels LD (2010) Growth releases of three shade-tolerant species following canopy gap formation in old-growth forests. J Veg Sci 21:74–87

Stokes MA, Smiley TL (1996) An introduction to tree-ring dating and measurement. University of Arizona Press, Tucson