

Local and large-scale climatic factors controlling tree-ring growth of *Pinus canariensis* on an oceanic island

Vicente Rozas^{1,*}, Ignacio García-González², Gonzalo Pérez-de-Lis²,
José Ramón Arévalo³

¹Misión Biológica de Galicia, Consejo Superior de Investigaciones Científicas (MBG-CSIC), Apdo. 28, 36080 Pontevedra, Spain

²Departamento de Botánica, Escola Politécnica Superior, Campus de Lugo, Universidade de Santiago de Compostela, 27002 Lugo, Spain

³Departamento de Ecología, Facultad de Biología, Universidad de La Laguna, 38206 La Laguna, Tenerife, Spain

ABSTRACT: Tree-ring growth of *Pinus canariensis* at high elevation on Tenerife, Canary Islands, is thought to be principally controlled by drought-induced stress. Aspect of mountain slopes on this oceanic island strongly influences local water input, with trade winds maintaining humid weather conditions on windward slopes, while leeward slopes remain much more arid. We tested whether *P. canariensis* tree-ring growth is controlled by local water availability and the large-scale climatic pattern of the North Atlantic Oscillation (NAO) along its elevation range on windward and leeward slopes on Tenerife. Wood cores were taken from 6 stands on windward and 6 on leeward slopes at elevations of 1120 to 1930 m. We found outstanding differences between windward and leeward slopes with regard to tree growth responses to local climate and NAO. Responsiveness to winter temperature was greater in windward stands, while tree growth in leeward stands was mainly controlled by total annual rainfall, which was strongly linked to NAO variation. Tree-ring growth was dependent on water input throughout the whole leeward slope, but elevation gradients were not relevant for tree growth dynamics. The unique exception was the lowest windward stand, located within the most humid environment on Tenerife, which experienced detrimental effects both of rainfall in late winter–spring and heat in summer. We conclude that slope aspect and exposure to trade winds are mostly driving *P. canariensis* growth. Prospects of growth of this species should consider that NAO-driven drought stress may affect populations on leeward slopes, where drier conditions could become limiting in the future.

KEY WORDS: Canary Islands pine · Dendrochronology · Drought stress · Elevation gradient · North Atlantic Oscillation · Subtropical mountain

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1. INTRODUCTION

At the alpine timberline, limiting conditions of high elevations determine the upper boundary of forests due to physiological stress, restricted photosynthesis, mechanical damage, growth limitation, or decreased reproduction (Körner 1998, Smith et al. 2003). In temperate, non-water-limited mountains, low air temperature is the main limiting factor for tree-ring growth in high elevation forests (Carrer et al. 2007), and an

increase in climatic sensitivity of trees with increased elevation can be expected (Liang et al. 2010, Zhang & Wilmking 2010). However, this is not the case for tropical and subtropical regions, where low water availability is the principal limit on tree growth at upper timberlines of continental mountains (Morales et al. 2004, González-Elizondo et al. 2005, Barichivich et al. 2009). Climate regimes in these dry timberlines contrast with those on subtropical oceanic islands, whose regional atmospheric circulation pat-

*Email: vrozas@mbg.csic.es

terns are markedly different from continental regions (Leuschner 1996).

Pinus canariensis is a mountain tree species that constitutes monospecific forests at elevations of 1000 to 2000 m on the subtropical, oceanic islands of the Canary archipelago. It is adapted to dry environments, showing traits related to fire resistance, e.g. thick bark, tall growth habit, sprouting capability, and serotiny, as well as further adaptations to xeric conditions, such as a deep root system, xeromorphic needles, and xeriscent cone opening (Climent et al. 2004, Grill et al. 2004). Despite these adaptations, *P. canariensis* is sensitive to 'intense' drought stress, which has been suggested as the major limiting climatic factor for this species at its upper timberline on Tenerife (Jonsson et al. 2002, Gieger & Leuschner 2004), the highest and largest island of the Canary archipelago.

In addition to elevation, the aspect of mountain slopes on Tenerife creates outstanding environmental differences between windward and leeward, which can differentially modulate the effects of climatic stress on tree performance. Orographic lifting of moist trade winds produces adiabatic cooling, condensation, and fog formation on northern and northeastern slopes, resulting in humid weather conditions due to both a high fog frequency and precipitation, that is mostly due to horizontal interception by plant canopies (Fernández-Palacios & de Nicolás 1995, Aboal et al. 2000). However, drought stress can be very pronounced on southern and western slopes, where the climate is drier because of protection from the trade winds.

Precipitation in the Canary Islands strongly depends on the high-pressure system over the Azores (Fernández-Palacios 1992), as a consequence of their location in the eastern margin of the North Atlantic Ocean, near the subtropical coast of north-western Africa. The North Atlantic Oscillation (NAO) has a significant influence on the winter–spring hydrological regime in southern Europe and northern Africa (Knippertz et al. 2003, Trigo et al. 2004). Similar to what has been recently shown for some Iberian tree species (Roig et al. 2009, Rozas et al. 2009b, Pasho et al. 2011), inter-annual variation in the large-scale NAO system could influence *Pinus canariensis* growth by determining local water input. The responses of tree-ring growth to local climatic variation of this species have been previously studied at particular sites on Tenerife (Jonsson et al. 2002, Pérez-de-Lis et al. 2011, Rozas et al. 2011a). However, there is no information on the joint influence of elevation and contrasting exposure to trade winds on the climatic

responsiveness of *P. canariensis* growth throughout its complete altitudinal distribution.

In this study, we use dendrochronological techniques to assess the effects of local and large-scale climate variation on *Pinus canariensis* radial growth along its whole elevation range on Tenerife, Canary Islands. Our principal goals were (1) to determine the main limiting climatic factors for *P. canariensis* radial growth along 2 elevation gradients on windward and leeward slopes, and (2) to evaluate the influence of the NAO on both local climatic conditions and tree growth variation on this oceanic island. Specifically, we tested whether drought stress is the major limiting climatic factor for tree-ring growth of this species at its upper timberline, and whether climatic sensitivity of *P. canariensis* increases with elevation throughout its whole elevation range on Tenerife.

2. MATERIALS AND METHODS

2.1. Study area

Tenerife has an area of 2036 km² and a steep relief dominated by the volcano Teide (3718 m) and the Cordillera Dorsal, which splits the island into 2 main slopes at the windward and leeward sides. Natural pine woodlands are found in a band around the highest part of the island, with a lower limit at 1300 m on windward slopes and 700 m on leeward slopes, while their upper limits reach elevations over 2000–2200 m (Fernández-Palacios & de Nicolás 1995). In wet windward areas, pines form a high canopy over a dense understory with frequent laurel-like broadleaf trees. However, dry pinewoods at leeward sites contain sparse shrubs, and very often only a thick layer of needle litter covers the ground. The climate is Mediterranean, with a mean annual temperature of 12.6°C, ranging between 4.2 and 31.2°C, and an annual precipitation ranging from 460 to 930 mm (Aboal et al. 2000, Peters et al. 2008).

The study stands are plantations of *Pinus canariensis* established between 1950 and 1970 on the Cordillera Dorsal of Tenerife (Fig. 1a). Upper stands were located near the timberline, i.e. the upper limit of the close tall forest, although groups of trees and isolated individuals can occur up to 2000–2200 m. We used stands from even-aged artificial plantations because, in contrast to natural populations, they cover the complete range of elevations between 1000 and 2000 m. Moreover, exclusively juvenile trees were sampled. This avoids possible age-dependent differences in growth–climate relationships that can occur

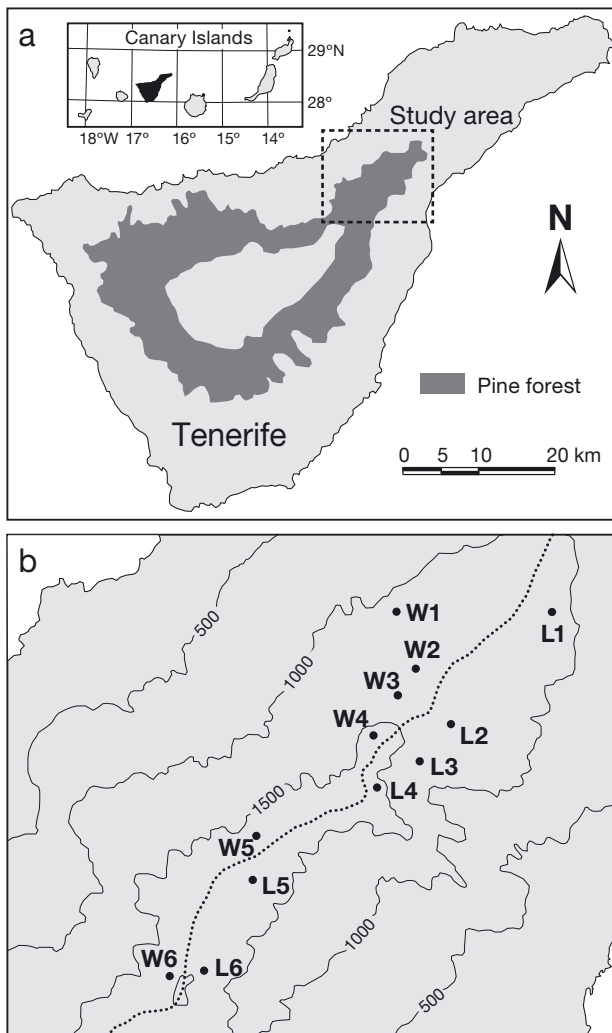


Fig. 1. (a) Study area within the range of *Pinus canariensis* forests on Tenerife Island, and (b) location of the study stands on the windward (W) and leeward (L) slopes. Contour lines indicate 500 m elevation intervals. The dotted line in (b) indicates the top of the Cordillera Dorsal mountain range

with trees of diverse ages (Carrer & Urbinati 2004). We also assumed that young *P. canariensis* trees should be more sensitive to limiting climatic conditions than older ones, as has been recently established for other Mediterranean conifers (Rozas et al. 2009a, Vieira et al. 2009). In addition, young trees have a low frequency of missing rings (Rozas et al. 2011a), a major limitation for the successful dating of tree-ring series of mature trees (Jonsson et al. 2002). Young trees also show poor development of the dense and resinous heartwood characteristic of older trees (Climent et al. 2002), which greatly hampers coring, core processing, and tree-ring analysis in this species.

2.2. Sampling, sample processing, and tree-ring measuring

We selected 6 stands both on windward and leeward slopes, at elevations ranging between 1120 and 1930 m (Fig. 1b, Table 1). We measured diameter at breast height (DBH, bole diameter at 1.30 m above ground) and took 2 wood cores per tree from 12 to 17 dominant and codominant trees at each stand. The cores were air-dried, glued onto wooden mounts, mechanically surfaced, and then manually polished until the xylem cellular structure was visible in the transverse plane. Tree-ring series were absolutely dated by assigning calendar years to the rings, and total ring widths were measured under magnification to the nearest 0.001 mm with a sliding-stage micrometer (Velmex). Quality control for the measured tree-ring width series was performed with the COFECHA software (Grissino-Mayer 2001), which was used to quantitatively check for crossdating and measuring errors.

2.3. Tree-ring standardizing and chronology computing

Inter-annual response of tree-ring growth to climate was investigated after standardizing the raw tree-ring width series with the ARSTAN software (Cook & Holmes 1996). Since only 50 yr of tree-ring data were available, a spline function with a 50 % frequency response of 32 yr was fitted to the series, which was flexible enough to minimize the variance related to ontogenetic trends and/or local disturbances, and to maximize the high-frequency climatic information (Helama et al. 2004). The obtained residuals were pre-whitened by autoregressive modeling, and the resulting indices for the individual series were averaged by biweight robust mean. The statistical quality of chronologies was assessed for 1967–2006, the common interval to all study stands, using mean sensitivity (MS), mean correlation between trees (RBT), signal-to-noise ratio (SNR), and expressed population signal (EPS; Briffa & Jones 1990).

2.4. Climate data

As the local network of meteorological stations on Tenerife is incomplete and mainly covers low-elevation areas, we took monthly gridded data from the datasets of the Climate Research Unit (CRU), University of East Anglia, UK, which were accessible

Table 1. *Pinus canariensis*. Site, tree, and tree-ring chronology characteristics for the sampled stands on Tenerife, Canary Islands. Stand or group code, elevation, number of sampled trees and cores, mean bole diameter at breast height (1.30 m, DBH), raw ring-width statistics, and statistics of residual tree-ring chronologies are shown. RW: mean ring width; MS: mean sensitivity of ring width series; RBT: mean between-trees correlation; SNR: signal to noise ratio; EPS: expressed population signal. W: stand on windward slope; L: stand on leeward slope. Group GrW includes stands W2, W3, W4, W5, and W6. Group GrL includes stands L1, L2, L3, L4, L5, and L6. Reliable period: period with ≥ 10 trees

Code	Elevation (m)	Trees	Cores	DBH \pm SD (cm)	Reliable period	RW \pm SD (mm)	MS	RBT ^a	SNR ^a	EPS ^a
W1	1120	12	24	35.9 \pm 6.9	1954–2006	1.7 \pm 1.1	0.302	0.459	10.20	0.911
W2	1400	15	30	27.6 \pm 6.9	1961–2006	1.6 \pm 1.2	0.298	0.518	12.87	0.928
W3	1460	17	34	28.6 \pm 6.6	1956–2006	1.7 \pm 1.5	0.345	0.458	5.08	0.835
W4	1540	15	30	29.2 \pm 6.1	1955–2006	1.8 \pm 1.1	0.284	0.473	9.88	0.908
W5	1650	17	34	29.3 \pm 6.4	1959–2006	1.9 \pm 1.8	0.300	0.462	5.16	0.838
W6	1910	12	24	37.9 \pm 4.5	1965–2006	2.6 \pm 1.6	0.287	0.468	9.66	0.906
GrW		76	152	29.7 \pm 6.9	1955–2006	1.9 \pm 1.5	0.304	0.291	18.85	0.950
L1	1130	12	24	41.9 \pm 5.5	1965–2006	2.0 \pm 1.4	0.378	0.545	14.35	0.935
L2	1390	16	32	31.0 \pm 5.8	1967–2006	2.5 \pm 2.2	0.497	0.575	14.87	0.937
L3	1490	16	32	31.0 \pm 6.8	1967–2006	2.4 \pm 1.5	0.423	0.543	11.90	0.922
L4	1530	17	34	25.3 \pm 6.0	1967–2006	2.4 \pm 1.6	0.416	0.715	25.13	0.962
L5	1700	17	34	25.3 \pm 5.1	1965–2006	2.2 \pm 2.1	0.367	0.572	12.04	0.923
L6	1930	12	24	36.7 \pm 3.8	1963–2006	2.5 \pm 2.0	0.265	0.542	14.19	0.934
GrL		90	180	29.6 \pm 7.0	1963–2006	2.3 \pm 1.8	0.386	0.390	40.89	0.976

^aCalculated from series of pre-whitened growth indices for the common period 1967–2006

from the web site of the Royal Netherlands Meteorological Institute (<http://climexp.knmi.nl/>). We used mean and maximum temperatures (T and T_{\max} , respectively), total precipitation (P), vapor pressure (VP), and mean sea-level pressure (SLP). The CRU time series showed significant correlations ($p < 0.05$) with available T and P records at elevations within or near the pine forest, suggesting a good correspondence between CRU and local datasets. However, we did not use local data sets due to the high proportion of missing data, especially on windward slopes. An index describing the monthly variation of the NAO was obtained from the web site of the US National Oceanic and Atmospheric Administration (www.cpc.ncep.noaa.gov/). NAO time series cover the period 1950–present, and were calculated as the differences in normalized SLPs between Stykkisholmur/Reykjavik, Iceland, and Lisbon, Portugal (Hurrell 1995). Monthly data from June of the previous year to September of the current growth year were combined in periods of 2 and 3 mo to identify their main effects on tree-ring growth at monthly, bimonthly, and seasonal scales. In addition, annual values were also calculated for each climatic variable from the previous October to the current September.

The joint effect of local and large-scale climate variation was expressed as the covariation among local climate time series and NAO, obtained by Pear-

son's correlations. The geographical variation of the NAO–local climate relationships for the Canary Islands and nearby areas of northwest Africa (latitude 24–36° N, longitude 4–20° W) was assessed by spatial field correlations between NAO and the selected climatic variables using the on-line Climate Explorer (<http://climexp.knmi.nl/>).

2.5. Evaluating tree-ring growth responses to climate

Common patterns of climatic sensitivity within our tree-ring data set were assessed with Pearson's correlations, which quantify the relationships between growth variation and climatic predictors, and also between all possible pairs of stand tree-ring chronologies. Monthly, bimonthly, seasonal, and annual climatic time series with the strongest correlations to stand tree-ring chronologies were selected as predictors of tree growth. Stands with a similar climatic response were grouped to calculate composite chronologies, so that all individual tree-ring series from stands belonging to the same group were pooled, standardized, and averaged with ARSTAN as previously described for stand chronologies (Carrer et al. 2007). Descriptive statistics (MS, RBT, SNR, EPS) were also calculated for group chronologies in the common period.

We determined the growth variance explained by climate on tree-ring chronologies by means of redundancy analysis (RDA), a canonical multivariate method that seeks linear combinations of environmental predictors correlated to linear combinations of response variables (Legendre & Legendre 1998). Stand index chronologies were considered as the response variables in RDA, while the climatic variables were environmental predictors. A forward selection procedure was performed for each identified group of chronologies to exclude those predictors that did not contribute significantly ($p > 0.05$) to tree-growth variation. Stepwise RDAs were calculated to determine the amount of growth variance explained by each selected predictor, which was given by the canonical eigenvalue λ (Legendre & Legendre 1998). Total explained variation in tree-ring chronologies was obtained under reduced RDA models including the shared effects of all significant climatic predictors. Monte Carlo tests with 9999 random permutations were used to evaluate the significance of canonical eigenvalues. The sequence of complementary RDAs was performed with the software CANOCO v4.0 for Windows (ter Braak & Šmilauer 1998). A scatterplot of the weighting coefficients for the first 2 RDA axes under an overall canonical ordination displayed the relationships between the significant climatic predictors and stand chronologies.

3. RESULTS

In general, leeward trees showed higher growth rates and values for all descriptive statistics of the site chronologies (MS, RBT, SNR, EPS) than windward trees (Table 1), indicating a better common signal.

EPS values were >0.85 , with the exceptions of stands W3 and W5, and the values of all other statistics were in general elevated, especially on the leeward side, suggesting a satisfactory replication and an optimum common signal for the majority of stand chronologies.

Pearson's correlations to climatic variables revealed 3 groups of stands with inter-correlated tree-ring chronologies, mainly determined by stand location (windward or leeward) (Table 2). Group W included stands W2, W3, W4, W5, and W6, with Pearson's correlations among stand chronologies ranging between $r = 0.386$ ($p = 0.007$) and 0.811 ($p < 0.001$); climatic predictors with a significant positive correlation with tree-ring were T_{max} and VP in the previous December, and T of the current November. Group L comprised all leeward stands, with correlations among chronologies between $r = 0.481$ and 0.806 ($p < 0.001$ in all cases); SLP and NAO in the previous October–December revealed a negative correlation with tree-ring growth, mostly at intermediate elevations (1300 to 1600 m), while a more abundant annual P enhanced growth. A third group included a single stand, W1, the lowest on windward, which was not significantly correlated to any other stand chronology (r ranged between -0.145 and 0.202 , with $p > 0.05$ in all cases); tree-ring growth was negatively affected by late winter–spring P and summer T, but positively affected by high SLP in the previous summer.

An overall RDA revealed that 45.1 % of tree growth variation in the study area was explained by the climatic variables considered ($\lambda = 0.451$, $F = 2.094$, $p < 0.001$), and the ordination confirmed the groups of stands we obtained and the role of the main climatic variables. Tree-ring growth in group W was positively related to T_{max} and VP in the previous Decem-

Table 2. *Pinus canariensis*. Correlations between tree-ring chronologies at the studied stands and the climatic variables that controlled growth for the common period 1967–2006. W: stand on windward slope; L: stand on leeward slope; T (T_{max}): mean (maximum) temperature; VP: vapor pressure; SLP: sea level pressure; NAO: North Atlantic Oscillation index; P: total precipitation. **Bold**: significant correlations ($p < 0.05$). '(–1)' indicates the time period of the previous year

Climatic variable	W1	W2	W3	W4	W5	W6	L1	L2	L3	L4	L5	L6
T_{max} Dec(–1)	0.122	0.404	0.330	0.420	0.460	0.388	0.107	–0.051	0.002	0.071	0.131	0.194
VP Dec(–1)	0.062	0.400	0.356	0.352	0.390	0.403	0.185	0.079	0.044	0.095	0.195	0.249
T Nov	0.014	0.376	0.390	0.342	0.332	0.106	0.102	–0.123	–0.036	0.003	–0.103	–0.001
SLP Oct–Dec(–1)	0.039	0.016	–0.007	0.211	–0.098	0.092	–0.355	–0.670	–0.533	–0.637	–0.468	–0.434
NAO Oct–Dec(–1)	0.143	0.093	0.037	0.184	–0.034	0.197	–0.366	–0.531	–0.471	–0.616	–0.356	–0.346
P annual	–0.180	–0.074	0.108	–0.082	–0.104	–0.110	0.332	0.555	0.456	0.478	0.390	0.328
P Oct–Dec(–1)	0.074	–0.293	–0.041	–0.167	–0.154	–0.134	0.126	0.476	0.378	0.428	0.369	0.275
P Mar–May	–0.438	0.245	0.134	0.130	0.123	0.131	0.480	0.312	0.187	0.332	0.141	0.114
SLP Jun–Jul(–1)	0.429	–0.250	0.077	0.063	–0.074	–0.124	–0.026	–0.084	0.288	0.129	0.002	0.029
T Jun–Aug(–1)	–0.410	0.236	–0.099	–0.162	–0.021	–0.088	0.247	0.194	–0.057	–0.014	0.086	–0.181
T_{max} Jul	–0.338	0.121	–0.017	–0.055	0.115	0.065	–0.032	–0.040	–0.013	0.016	0.063	–0.096

ber, and to T in November (Fig. 2), and these significant climatic predictors accounted for 34.2% of the inter-annual growth variance (Table 3). Group L was related to conditions in the previous October–December, namely positively to P, and negatively to SLP and NAO, and also positively to annual P; all of these variables explained 44.4% of growth variance (Fig. 2, Table 3). Finally, tree-ring growth in stand W1 clearly differed from all others, as it was positively related to SLP in the previous June–July, and negatively to T in the previous June–August, P in March–May, and T_{\max} in July; the shared effect on growth variance was 37.9% (Fig. 2, Table 3). The most important predictors showing significant correlations with group tree-ring chronologies were T_{\max} in the previous December for group W, with a positive relation (Fig. 3a). Both SLP in the previous October–December for group L (Fig. 3b), and P in March–May for stand W1 (Fig. 3c), showed a negative relation with tree growth (note the different orientation on y-axes).

In the study area, the positive association between VP and T_{\max} in the previous December was highly significant (Fig. 4a), and related to their positive influence on tree-ring growth in group W. Moreover, the inverse association between annual P and SLP (Fig. 4b), and positive associations between SLP and NAO (Fig. 4c), both in October–December, were also highly significant, and revealed a negative correlation between annual P and NAO for these months ($r = -0.438$, $p = 0.005$). Spatial field correlations showed this widespread negative association between annual P and NAO in October–December across the Canary archipelago and nearby regions of the north-west coast of Africa (Fig. 5). There was also a highly significant inverse association between June–July SLP and T in June–August in the study area (Fig. 4d), which is related to the opposite relationships of tree-ring growth at stand W1 to these variables in the previous year.

4. DISCUSSION

Climate was a key factor driving *Pinus canariensis* tree-ring growth on Tenerife Island, but was modulated by site factors determining the exposure to trade winds. Thus, we found outstanding differences in the responsiveness of tree-ring growth to climate between windward and leeward slopes. The contrasting climatic sensitivity of growth according to slope aspect is probably due to physiological effects of water inputs and reduced radiation caused by fog

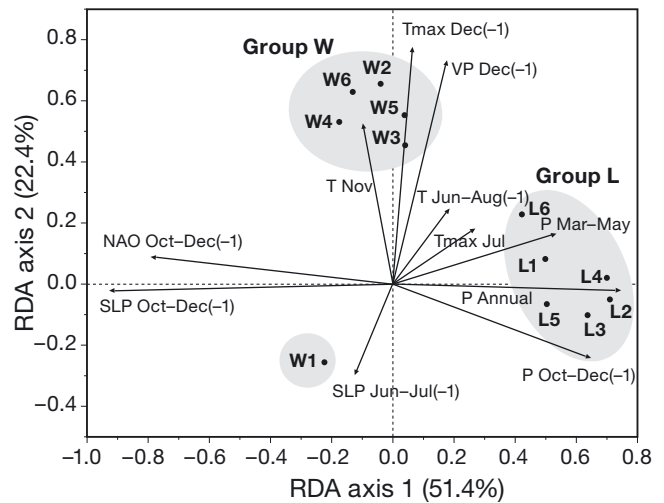


Fig. 2. *Pinus canariensis*. Biplot scores from the redundancy analysis (RDA) model for the relationships of tree-ring growth on windward (W) and leeward (L) slopes with the climatic predictors significantly ($p < 0.05$) related to tree-ring growth variation for the period 1967–2006. The percentage of variance accounted for by each RDA axis is shown. Stand codes are shown in Table 1; other abbreviations as in Table 2

Table 3. Summary statistics of redundancy analysis (RDA) models for the relationships between tree-ring growth variation in the recognized groups (W, L, and W1) of chronologies, and the significant climatic predictors for the common period 1967–2006. The effects of each individual climatic predictor retained through forward selection, and the combined effects of all significant predictors for each group of chronologies, indicated by reduced RDA models, are shown. λ : eigenvalues for the variation of tree-ring indices explained by each climatic predictor, or shared by all predictors in the case of reduced RDA models. Abbreviations as in Table 2

Predictor	λ	F	p
W			
T_{\max} Dec(-1)	0.255	13.01	<0.001
VP Dec(-1)	0.230	11.37	0.001
T Nov	0.156	7.04	0.009
Reduced model	0.342	6.22	0.001
L			
SLP Oct-Dec(-1)	0.422	27.73	<0.001
NAO Oct-Dec(-1)	0.297	16.02	<0.001
P annual	0.246	12.39	0.002
P Oct-Dec(-1)	0.193	9.07	0.004
Reduced model	0.444	6.98	<0.001
W1			
P Mar-May	0.192	9.03	0.005
SLP Jun-Jul(-1)	0.184	8.58	0.006
T Jun-Aug(-1)	0.168	7.69	0.007
T_{\max} Jul	0.114	4.89	0.032
Reduced model	0.379	5.35	0.002

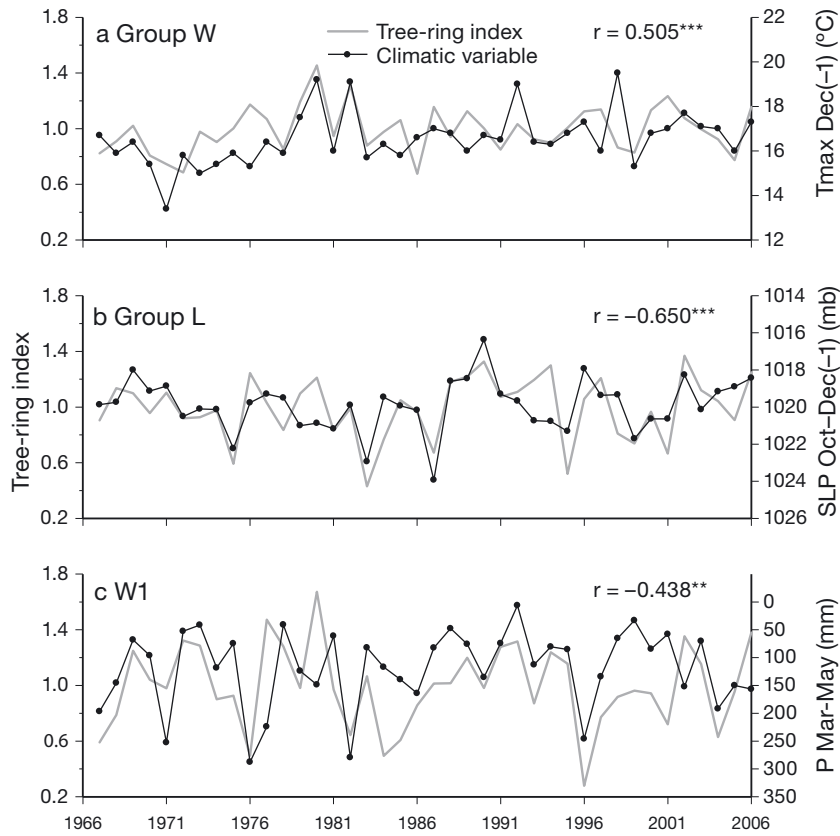


Fig. 3. *Pinus canariensis*. Comparison of tree-ring growth indices in (a) group W, (b) group L, and (c) stand W1 with those climatic variables that explained a large amount of growth variance. P: total precipitation, SLP: sea level pressure, T_{\max} : maximum temperature. Note the inverted scales in the vertical axes for climatic variables in (b) and (c). ** $p < 0.01$; *** $p < 0.001$

drip on windward slopes, where climate is less limiting (Rozas et al. 2011a). This interpretation agrees with previous considerations of windward and leeward pine forests as separate ecosystems in the Canary Islands, each with its own floristic composition and environmental constraints (Fernández-Palacios & de Nicolás 1995). Our findings support previous results on contrasting climatic responses on opposite mountain slopes, attributed to strong differences in microclimatic conditions between them (Liang et al. 2006). However, elevation gradients do not have a marked influence on the local variation of climatic responses of *P. canariensis* growth on Tenerife; this finding is contrary to the expected increase of climatic sensitivity with elevation (Nakawatase & Peterson 2006, Liang et al. 2010, Zhang & Wilmking 2010), and also to previous evidence of the combined effect of elevation and aspect in controlling climatic responsiveness (Dang et al. 2007).

The unique exception to the homogeneous within-slope response was stand W1, which had a particular

growth pattern and climatic sensitivity. Trees in stand W1 showed a general negative effect of water availability in late winter–spring, which has been previously observed for other conifers under non-water-limited climates, such as in north-central Europe, northwestern North America, and the northern Iberian Peninsula (Peterson & Peterson 2001, Mäkinen et al. 2002, Rozas et al. 2011b). This stand is located under the direct influence of the ‘cloud sea’ within the domain of the laurel forest, which extends at elevations between 600 and 1200 m on the windward slope, and constitutes the most humid environment in the Canary Islands (Fernández-Palacios 1992). Rainy conditions and cloudiness considerably reduce solar radiation, photosynthetic rates, and the amount of assimilates, as seems to be the case for March–May at lower elevation in northern Tenerife. In fact, reduced solar radiation, modulated by frequency and duration of cloudiness, is a primary factor limiting photosynthesis, carbon uptake, and tree growth (Graham et al. 2003). We believe that these conditions probably delayed the onset of xylogenesis, leading to narrower rings, as has been

observed by Gričar et al. (2006) in *Picea abies*. But the observed negative response to warm summers suggests that summer temperature at a lower elevation is high enough to diminish growth despite the milder conditions within the laurel-forest belt. This result is in agreement with evidences that pine radial growth under a Mediterranean climate is limited by elevated temperatures during the active period, with characteristic negative effects of warm summers (Vieira et al. 2009, Martín-Benito et al. 2010, Rozas et al. 2011b), which may be due to a loss of photosynthetic efficiency or increased respiration rates (Medlyn et al. 2002). Moreover, trade winds providing moisture at intermediate altitudes can occasionally be blocked in summer by a low-pressure system located over the Sahara, leading to a drop in the inversion layer, and extremely warm conditions at these sites (Marzol Jaén 1987).

On the windward slope, water stress is not limiting for *Pinus canariensis* growth at higher elevations (1400–2000 m). Summer drought is probably miti-

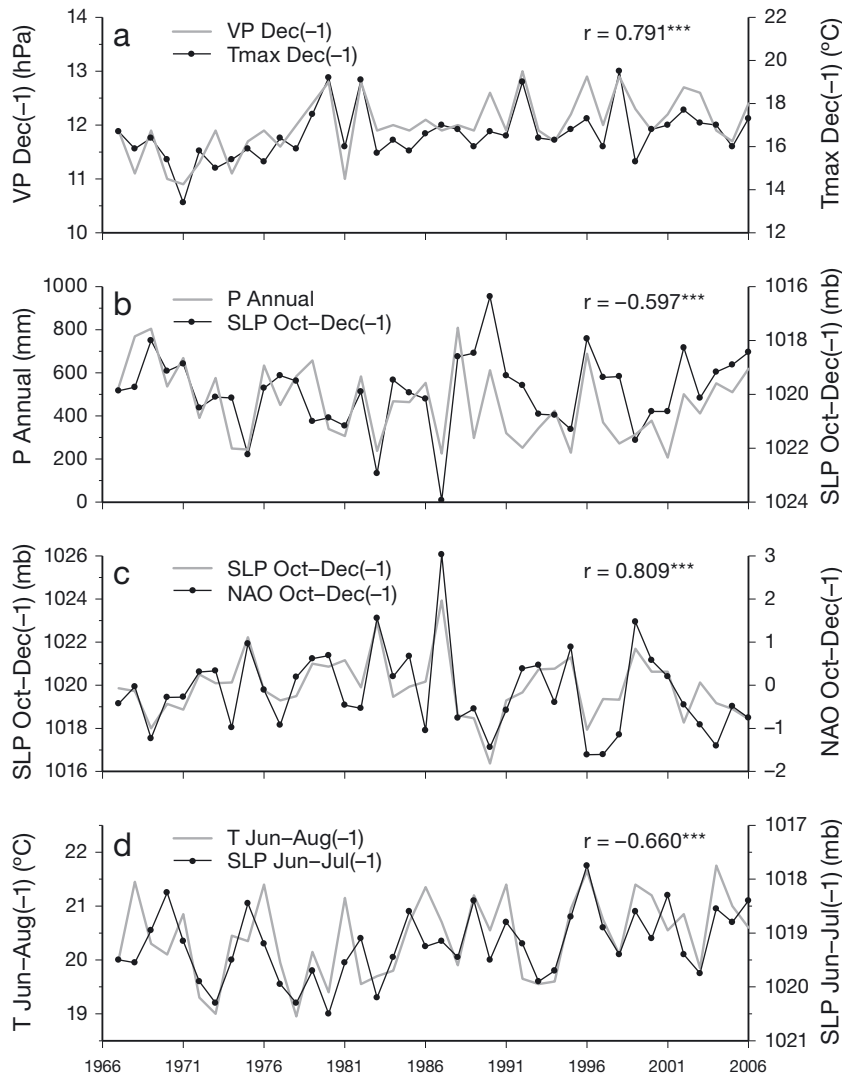


Fig. 4. *Pinus canariensis*. Covariation of climatic variables that explained a large amount of growth variance. VP: vapor pressure, P: total precipitation, SLP: sea level pressure, T (T_{\max}): mean (maximum) temperature, NAO: North Atlantic Oscillation index. Note the inverted scales in the vertical axes for SLP in (b) and (d). *** $p < 0.001$

gated by a high relative humidity in the air, and by frequent fog formation due to the influence of trade winds. Fog alleviates water stress by decreasing transpiration, and it may be the only source of water input at sites where deep soil water is unavailable (Burgess & Dawson 2004). Reduced water stress on the windward slope explains the positive effects of elevated winter temperatures, both in the previous December and the current November. The positive influence of high winter temperatures on growth of Mediterranean pines has been interpreted as a consequence of winter photosynthesis stimulated by elevated VP and increased transpiration under non-water-limiting conditions (Medlyn et al. 2002). In fact, maximum

daily net photosynthesis of *P. canariensis* can be higher during winter than in summer, due to a higher soil-water availability and a lower evaporative demand as compared to the warm and dry season (Peters et al. 2008). Thus, high photosynthetic rates due to a relatively elevated winter temperature would result in a greater amount of carbohydrates stored to be used in the following active season. Cambial activity of pine species under wet subtropical and tropical climates may span most of the year, from February–April to October–November (Biondi et al. 2005, Dhirendra Singh & Venugopal 2011), with a warm November probably resulting in a longer growing season. We hypothesize that a high temperature in the current November may delay the end of cambial activity, and extend the active growing period, leading to the formation of wider rings when carbon reserves are not limiting, but this hypothesis should be tested through studies on xylogenesis.

On the leeward slope, positive responses of tree-ring growth to previous October–December rainfall, and especially to annual P, suggest that annual growth is strongly limited by water availability. These results agree with those by Jonsson et al. (2002) at the upper leeward treeline of *Pinus canariensis* (2000–2100 m) on Tenerife, and indicate that water availability limits growth not only at a high elevation, but along the whole elevation range on the leeward slope. Leeward popu-

lations of *P. canariensis* exhibit xeromorphic traits, allowing a tight regulation of water loss by transpiration (Grill et al. 2004). Accordingly, annual canopy transpiration lies significantly below the common values for other Mediterranean trees, suggesting a strong adaptation to low soil water availability during periods of great evaporative demand (Luis et al. 2005). The beneficial effect of winter and annual P can be due to the pronounced water deficit in the study area, with one-third of the annual P occurring in November–December. This positive influence of annual P and moist winters on growth is common for Mediterranean pines (Martín-Benito et al. 2010, Pasho et al. 2011, Rozas et al. 2011b), and for moun-

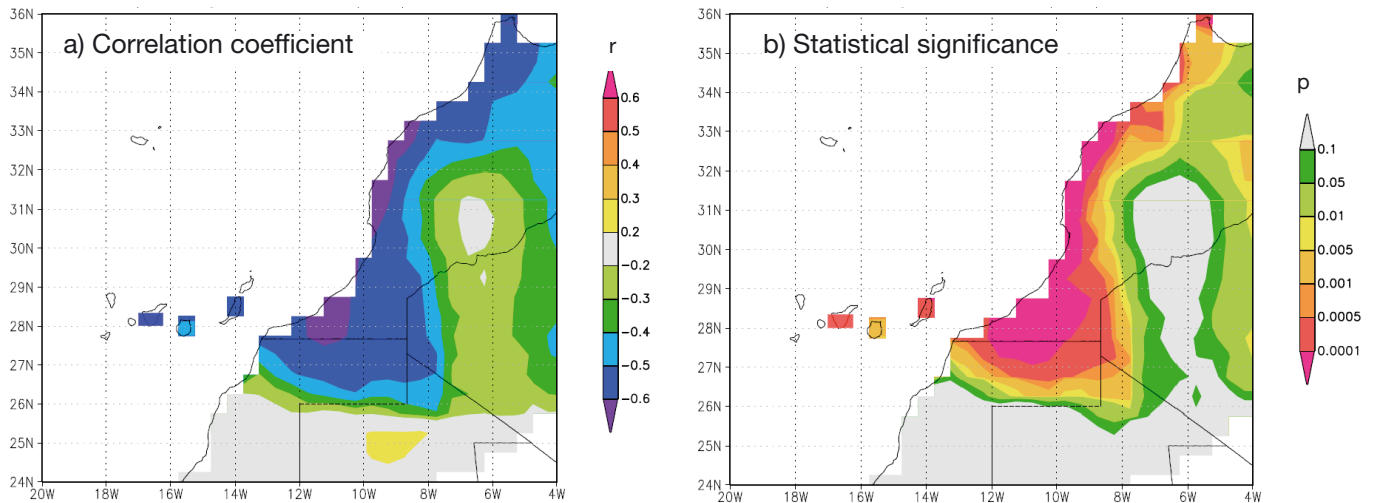


Fig. 5. (a) Spatial field correlations and (b) their statistical significance between annual precipitation and NAO in the previous October–December, in the Canary archipelago and the northwest coast of Africa

tain conifers suffering from seasonal drought (Wang et al. 2005, Nakawatase & Peterson 2006, Littell et al. 2008), and can be attributed to soil water recharge during the wet season.

The strong negative correlations of annual P to SLP and NAO in the previous October–December suggest that water availability in the Canary archipelago is strongly linked to autumn–winter SLP variation and NAO dynamics. When the low-pressure system over the North Atlantic Ocean tends to be stronger, moister and colder conditions probably occur on Tenerife, so that soils are replenished with water before the summer drought. By contrast, a high pressure during winter produces the reverse pattern, and leads to anomalous hot and dry winters on leeward slopes (Rozas et al. 2011a). Our results corroborate previous findings that tree growth responds indirectly to the variability of large-scale climatic patterns through their influence on local climate conditions (Nakawatase & Peterson 2006, Barichivich et al. 2009). The observed detrimental effect of the NAO on leeward *Pinus canariensis* agrees with previous evidence that tree growth in southern Europe is negatively correlated to the large-scale variation of autumn–winter NAO indices (Piovesan & Schirone 2000, Roig et al. 2009, Rozas et al. 2009b, Pasho et al. 2011), while this relation is positive in northern Europe (Lindholm et al. 2001, Linderholm et al. 2003, Macias et al. 2004). This pattern can be explained by the spatial structure of the NAO, which determines that mild and rainy winters in northern Europe are related to positive NAO indices, while winter precipitation is inversely correlated to NAO in southern Europe (Hurrell 1995).

Our results confirm a negligible effect of elevation gradients on the climatic responsiveness of *Pinus canariensis*. The fact that tree-ring growth is strongly dependent on precipitation throughout the whole leeward slope invalidates the hypothesis of a drought-induced timberline on Tenerife, so that explanations other than drought stress should be considered. In addition, no evidence of physiological stress or reduced vitality is exhibited by isolated trees located above the upper timberline on Tenerife (Gieger & Leuschner 2004). Therefore, a causal explanation for timberline on this oceanic island could be related to limitations for seedling establishment and survival, instead of limited growth of adult trees due to severe climatic conditions. Seed germination capacity and seedling survival sharply decline at higher altitudes, where seedling establishment may depend on small-scale substrate properties and neighboring plants that alter microclimate and create favorable conditions for plant growth (Germino et al. 2002, Smith et al. 2003). In the particular case of *P. canariensis*, optimum seedling establishment is linked to both surface fire occurrence and an intermediate density of mature trees, which guarantee enough seed abundance and favorable micro-environmental conditions for seed germination and seedling survival (Otto et al. 2010). Above the timberline, these conditions are lacking, which in conjunction with harsh microclimatic conditions of the upper elevation on Tenerife, probably cause severe physiological stress to seedlings (Gieger & Leuschner 2004). Our results showed that growth of *P. canariensis* trees at their upper timberline is not strongly limited by low water availability, although this regulation

occurs throughout the complete leeward slope, and particularly at mid-elevation. Prospects of growth and vitality of this species should consider that drought stress can affect populations on leeward slopes where drier conditions, controlled by NAO dynamics, can become limiting in the future.

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