

Differential tree-growth responses to local and large-scale climatic variation in two *Pinus* and two *Quercus* species in northwest Spain¹

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Abstract: We assessed the seasonal climatic response of 2 *Pinus* and 2 *Quercus* tree species in a littoral island in northwest Spain, analyzing earlywood, latewood, and total ring widths. We used bootstrapped response functions to identify the variables controlling growth, and we estimated the pure and shared effects of local climate components (temperature and water balance) and a large-scale atmospheric pattern (North Atlantic Oscillation, NAO) on tree growth using a variance partitioning approach. For all species, the response functions showed stronger climatic signals in latewood and total ring than in earlywood. The pure effects of temperature, water balance, and NAO on tree growth were significant. However, a null shared effect between local climate and NAO was evidenced due to the absence of a direct link between NAO in the previous autumn and the other significant climatic variables. *Pinus pinaster* was the species most sensitive to local climate, mainly to water availability during its active period as a consequence of higher water use efficiency. *Quercus* growth was negatively influenced by winter temperature, and growth of *P. pinea* and both *Quercus* species was inversely related to NAO in the previous autumn. The obtained results suggest that *Q. robur* and *Q. pyrenaica* have similar growth behaviour and climatic sensitivity. However, both *P. pinea* and *P. pinaster* showed contrasting growth dynamics and sensitivity in this Atlantic littoral island, despite their common Mediterranean origin.

Keywords: dendroecology, NAO, RDA, tree rings, variation partitioning, water balance.

Résumé : Nous avons évalué la réponse climatique saisonnière de 2 espèces d'arbres du genre *Pinus* et 2 du genre *Quercus* sur une île du littoral du nord-ouest de l'Espagne, en analysant le bois initial, le bois final et les largeurs des cernes complets. Nous avons utilisé une fonction de réponse bootstrap pour identifier les variables régissant la croissance et nous avons évalué les effets purs et partagés de composantes du climat local (température et bilan hydrique) et d'un patron atmosphérique de grande échelle (Oscillation nord-atlantique, ONA) sur la croissance des arbres en utilisant une approche de partition de la variance. Pour toutes les espèces, les fonctions de réponse démontraient des signaux climatiques plus forts pour le bois final et le cerne complet que pour le bois initial. Les effets purs de la température, du bilan hydrique et de l'ONA sur la croissance des arbres étaient significatifs. Cependant, un effet nul partagé entre le climat local et l'ONA était mis en évidence par l'absence d'un lien direct entre l'ONA de l'automne précédent et les autres variables climatiques significatives. *P. pinaster* était l'espèce la plus sensible au climat local, principalement à la disponibilité en eau durant sa période active en raison de sa plus grande efficacité d'utilisation de l'eau. La croissance de *Quercus* était influencée négativement par la température hivernale alors que la croissance de *P. pinea* et des 2 espèces de *Quercus* était en relation inverse avec l'ONA de l'automne précédent. Les résultats obtenus suggèrent que *Q. robur* et *Q. pyrenaica* ont des comportements de croissance et une sensibilité climatique similaires. Cependant, *P. pinea* et *P. pinaster* présentent des dynamiques de croissance et des sensibilités contrastées dans cette île du littoral Atlantique, et ce, malgré leur origine méditerranéenne commune.

Mots-clés : analyse de redondance, bilan hydrique, cernes de croissance d'arbres, dendroécologie, ONA, partition de la variance.

Nomenclature : Castroviejo *et al.*, 1986–1989.

Introduction

Trees have often had to respond to changing climatic conditions, but the rate of change predicted in the 21st century is likely to be unprecedented (Saxe *et al.*, 2001). An increase of 1.8 to 4.0 °C in mean land surface temperature and more intense and longer droughts are expected over the next century (IPCC, 2007). Tree growth and forest productivity are major contributors to the terrestrial carbon sink

and its associated economic benefits (Canadell & Raupach, 2008). Moreover, the responses of forest ecosystems to climate change could be diverse at different spatial and temporal scales (Valladares, 2007). Thus, it would be desirable to know the relative effects of the different climatic components in determining potential shifts in forest productivity.

Study of the behaviour of tree species in the context of climate warming requires the application of appropriate methods. Dendrochronology can be used to analyze the relative responses of tree growth to climate, contributing to our understanding of the vulnerability of forest ecosystems

¹Rec. 2008-08-12; acc. 2009-04-27.

Associate Editor: Dominique Arseneault.

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DOI 10.2980/16-3-3212

to global warming and increasing drought risk. Analysis of tree rings is a useful tool for determining the variability of tree growth patterns and assessing what proportion of that variability is related to climate (Fritts, 2001). In conifers and ring-porous broadleaved trees, the intra-annual responses of growth to local climatic variation have been successfully assessed through the combined study of total ring width and early- and latewood widths with meteorological data (García-González & Eckstein, 2003; Lebourgeois, Cousseau & Ducos, 2004, Campelo *et al.*, 2006).

Some areas of the globe are more vulnerable than others to the consequences of global warming. Boundaries between biogeographic regions, where many species coexist at their limit of distribution, deserve special attention. This is the case in northwest Spain, where the climate is characterized by abundant annual rainfall, but a strong seasonality of precipitation causes a water deficit during summer. Several plant species reach their distribution boundaries in this area: Atlantic species are limited by summer drought, allowing the spread of Mediterranean species as conditions become more xeric.

In this study, we examine the responses of tree growth to local and large-scale climatic variation in 2 *Pinus* and 2 *Quercus* species in a littoral island on the Atlantic coast of Galicia, northwest Spain. We hypothesize that a negative water balance during late spring and summer strongly affects tree growth at this site, whereas earlywood growth

is related to conditions during the dormant season and during the beginning of cambial activity. Inter-annual rainfall variation in the study area is largely controlled by large-scale circulation patterns, mainly the winter North Atlantic Oscillation (NAO, Trigo *et al.*, 2004), so the NAO may influence growth by determining local water balance. Different timings and intensities of response are expected depending on species-specific physiological adaptations. The objectives of this study are 1) to assess the relationships between climate and radial growth of 4 coexisting tree species, focusing on the responses of earlywood, latewood, and total ring; and 2) to evaluate the separate and combined influence of local climate (temperature and water balance) and large-scale climatic components (NAO) on tree growth.

Methods

STUDY AREA

Cortegada island is located in the inner sector of the Arousa Bay, Pontevedra province, on the northwestern littoral of Spain (42° 37' N, 8° 47' W; Figure 1). The island belongs to the Spanish Atlantic Islands National Park since 2002 and has a total surface area of 54 ha, with a maximum altitude of 22 m. Soils are fluvisols with alluvial quaternary depositions in the northern sector of the island and sandy alumi-humic cambisols developed on granite and schist bedrock in the rest (Calvo & Macías, 2000). Cortegada was historically used for agricultural and livestock farming

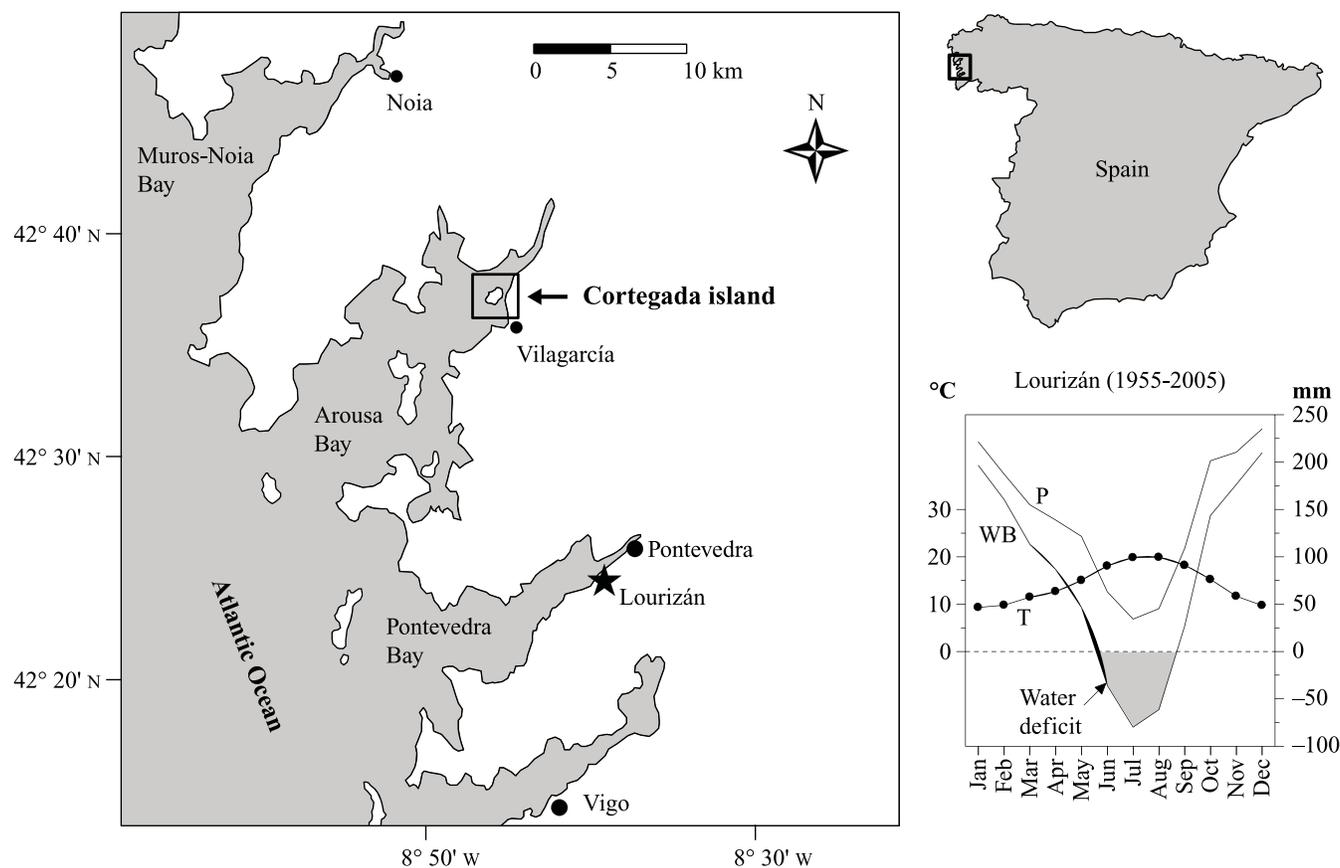


FIGURE 1. Location of Cortegada island and the Lourizán meteorological station in northwest Spain, along with climatic diagram of mean monthly temperature (T), monthly precipitation (P), and water balance (WB) for the period 1955–2005. The shaded area indicates negative WB.

purposes, but in 1907 human activities almost completely ceased. Tree ages and growth patterns suggest that a variety of native and introduced tree species colonized the abandoned land and grew spontaneously during the 20th century (Lamas & Rozas, 2007). Due to their dominance on the island and their conservational and productive importance in the region, the species *Pinus pinea*, *P. pinaster*, *Quercus pyrenaica* and *Q. robur* were selected for study.

CLIMATE

Local temperature (T) and precipitation (P) data were obtained from the Lourizán meteorological station, located ca. 26 km south of Cortegada, which has maintained a continuous record of meteorological data since 1955 (Figure 1). Regional climate is temperate and humid, with a mean yearly temperature of 14.2 °C and mean precipitation of 1721 mm·y⁻¹ for the period 1955–2005. Mean monthly temperature ranged between 9.3 °C in January and 19.9 °C in August, and monthly precipitation ranged between 34 mm in July and 235 mm in December. Since maximum temperature is coupled to a minimum of rainfall during summertime, precipitation data were not used directly, but were used to estimate water balance (WB), calculated as $WB = P - PET$, where PET is the potential evapotranspiration estimated as a function of monthly mean temperatures and geographical latitude (Thorntwaite, 1948). Mean monthly WB ranged between -80 mm in July and 210 mm in December, showing a tendency to water deficit from June to August (Figure 1). Monthly indices of the NAO based on the difference of normalized sea level pressures between Gibraltar and Reykjavik, Iceland (URL: <http://www.cru.uea.ac.uk/cru/data/nao.htm>) were used as an indicator of large-scale climatic variation.

STUDY SPECIES

The 4 tree species (*P. pinea*, *P. pinaster*, *Q. robur*, and *Q. pyrenaica*) belong to different functional groups and differ in their distribution areas. *Pinus pinea* is distributed along the northern margin of the Mediterranean basin, probably spread by cultivation from Lebanon and Turkey since the Roman Age; in contrast, *P. pinaster* is native to the west-Mediterranean basin, i.e., the Italian and Iberian peninsulas, southern France, Corsica, Sardinia and northern Africa (Blanco *et al.*, 2001). Both *Pinus* species are considered to be introduced in the study area, and *P. pinaster* has been extensively cultivated in the area since the 19th century for productive purposes. *Quercus robur* is considered a nemoral species (Corcuera, Camarero & Gil-Pelegrín, 2002) with a wide geographic and ecological range over Central and Atlantic Europe, whereas *Q. pyrenaica* is restricted to the west-central Iberian Peninsula, southwestern France, and northern Morocco (Blanco *et al.*, 2001), showing eco-physiological traits intermediate between nemoral and Mediterranean oaks (Corcuera, Camarero & Gil-Pelegrín, 2002).

FIELD AND LABORATORY PROCEDURES

Two opposite cores were taken from 15 to 22 dominant or codominant trees of each species using an increment borer at breast height. The site does not have a steep slope, and the presence of reaction wood was unusual. Cores were

air dried, glued onto wooden mounts, and sanded with progressively finer grades of sandpaper until the wood anatomical elements were visible in transverse section.

Tree-ring series were dated following standard procedures (Stokes & Smiley, 1996). Early- and latewood widths were measured under magnification to the nearest 0.001 mm with a Velmetx Unislide sliding-stage micrometer interfaced with a computer, and total ring width was calculated as the sum of both measurements for each ring. Early- to latewood transition in *Pinus* spp. can be more or less abrupt and was defined according to qualitative contrast in darkening, interpreted as a sharp change in wood density. In the ring-porous *Quercus* spp., the conspicuous larger vessels in the earlywood enabled us to recognize the transition to latewood. In order to detect dating and measurement errors, width series were checked with the COFECHA program (Holmes, 1983). We used those series that we could confidently crossdate to compute the chronologies of earlywood, latewood, and total ring for each species.

CHRONOLOGIES COMPUTATION

Chronology indices (Fritts, 2001) were calculated with the computer program ARSTAN (Cook & Holmes, 1996) after removing undesired growth trends using a double-detrending method. Thus, a negative exponential or straight line was fit to raw tree-ring series in order to remove the long-term trend related to tree ageing. Then, the obtained residuals were standardized with a spline function with a 50% frequency response of 32 y, which was flexible enough to reduce non-climatic variation by preserving high-frequency climatic information (Cook & Peters, 1981). Autoregressive modelling was also performed on the standardized series, and the final chronologies were calculated as the robust biweight mean of the obtained stationary residuals. These residual chronologies for earlywood, latewood, and total ring were used for all analyses of tree growth/climate relationships and variation partitioning. The statistical quality of the chronologies was assessed by means of the standard basic statistics (Briffa & Jones, 1990), both with respect to single series (autocorrelation [AR] and mean sensitivity [MS]) and to the common signal (trees intercorrelation [IC] and expressed population signal [EPS]). MS describes the mean percentage change from each measured annual ring value to the next, IC is the mean value of all possible correlations between individual series, and EPS indicates the extent to which the sample size is representative of a theoretical infinite population. The shared variation among residual chronologies in the period 1956–2005 (50 y) was evaluated by means of a principal component analysis (PCA) calculated from their correlation matrix.

ANALYSIS OF TREE GROWTH/CLIMATE RELATIONSHIPS

The relationships between tree growth and climatic variation were studied for the period 1956–2005 (50 y). The residual indices of earlywood, latewood, and total ring chronologies were taken as the dependent or response variables, which were compared to seasonal climatic variables, calculated as the mean (T and NAO) or the sum (WB) of 3 consecutive monthly variables as follows: winter (December–February); spring (March–May); summer

(June–August); and autumn (September–November). The seasonal T, WB, and NAO data from summer of the previous year ($t - 1$) to autumn of the current growth year (t) were taken as explanatory variables or environmental predictors. The relationships between climatic variables and the chronologies for each species were assessed by means of response function analysis using the software PRECON version 5.11 (Fritts *et al.*, 1991). We performed 9999 iterations of the bootstrap procedure to assess the statistical significance of regression coefficients in the response functions (Manly, 1997). Each regression coefficient was considered to be significant ($P < 0.05$) if it was at least twice, in absolute value, its bootstrapped standard deviation (Guiot, 1991).

VARIATION PARTITIONING

Response functions are able to statistically account for the collinearity within the large number of variables often considered (Fritts *et al.*, 1971), but they cannot provide a thorough assessment of the relative importance of each particular climatic component, or their shared effects on tree growth. The variation partitioning procedure breaks down the variation within dependent variables into several components, each reflecting the relative importance of a group of explanatory variables and their shared effects (Borcard, Legendre & Drapeau, 1992; Legendre & Legendre, 1998). Variation partitioning is done by using constrained and partial canonical ordination techniques (Legendre & Legendre, 1998). In particular, redundancy analysis (RDA) seeks linear combinations of environmental factors that are correlated to linear combinations of response variables (Borcard, Legendre & Drapeau, 1992). RDA has been previously used to assess tree growth/climate relationships, as an extension of multiple linear regression applied to several dependent variables (Beeckman, 1992; Trouet *et al.*, 2001; Tardif *et al.*, 2006). However, the variation partitioning approach has not been previously used to assess the relative importance of different climatic components for tree growth.

We used variation partitioning to break down variation in tree growth into 3 groups of explanatory variables: T, WB, and NAO. Variation was partitioned using a series of (partial) redundancy analyses as implemented in the program CANOCO version 4.0 (ter Braak & Smilauer, 1998). First, an RDA run with a forward selection procedure and the associated Monte Carlo permutation test (9999 random permutations) was performed for each of the 3 predictor variable groups to exclude seasonal variables that did not contribute significantly ($P > 0.05$) to tree-growth variation (Borcard, Legendre & Drapeau, 1992). All subsequent RDA and partial RDA analyses were performed considering only the climatic predictors retained in this forward selection procedure.

Variation partitioning with 3 explanatory groups of climatic variables produced 8 fractions (Legendre & Legendre, 1998): (a) pure effect of T, (b) pure effect of WB, (c) pure effect of NAO, (d) joint effect of T and WB, (e) joint effect of T and NAO, (f) joint effect of WB and NAO, (g) joint effect of T, WB, and NAO, and (h) unexplained variation. Fractions or groups of fractions, and their statistical significance, can be obtained directly by 3 RDA and 9 partial

RDA runs: (a) + (d) + (e) + (g) is the variation explained by T; (b) + (d) + (f) + (g) is the variation explained by WB; (c) + (e) + (f) + (g) is the variation explained by NAO; (a) is the variation explained by T, controlling for WB and NAO (partial RDA for T, with WB and NAO as covariables); (b) is the variation explained by WB, controlling for T and NAO; and so on. The total explained variation in the tree-growth data is the sum (a) + (b) + (c) + (d) + (e) + (f) + (g), obtained by RDA of the tree-ring chronologies including all the selected significant seasonal explanatory variables (reduced model). The variation in tree growth explained in each analysis was quantified by a canonical eigenvalue λ , with a total variation explained of 1.0. Negative values of λ were interpreted as zeros, because they correspond to cases where the explanatory variables explain less variation than random normal variables would (Legendre, 2008). The significance of each eigenvalue was tested using Monte Carlo permutation tests (9999 random permutations). The unexplained variation was obtained as $1 - [(a) + (b) + (c) + (d) + (e) + (f) + (g)]$. The analyses were performed for the complete set of response variables together (12 tree-ring chronologies) and for each separate set of response variables of each tree species (earlywood, latewood, and total ring chronologies).

Results

TREE-RING GROWTH CHARACTERISTICS AND COMMON VARIATION

Mean tree ages were 114 y in *P. pinea*, 52 y in *P. pinaster*, 86 y in *Q. pyrenaica*, and 88 y in *Q. robur* (Table 1), which significantly differed (Kruskal–Wallis test, $\chi^2 = 42.04$, $df = 3$, $P < 0.0001$). Mean growth rates reached more than $5 \text{ mm}\cdot\text{y}^{-1}$ in *P. pinaster* but less than $2 \text{ mm}\cdot\text{y}^{-1}$ in *Q. pyrenaica*, with intermediate values for both *P. pinea* and *Q. robur* ($\chi^2 = 265.43$, $df = 11$, $P < 0.0001$). Earlywood was wider than latewood in *Pinus* (earlywood was on average 60.6% of total ring width in *P. pinea* and 56.5% in *P. pinaster*), while it was considerably narrower than latewood in *Quercus* (latewood was on average 71.4% of total ring width in *Q. pyrenaica* and 79.9% in *Q. robur*). Some standard tree-ring chronologies displayed a high degree of autocorrelation (AC), suggesting persistence of the low-frequency signal, while others had low AC value as a result of efficient removal of the low-frequency signal. Mean sensitivity (MS) of all residual chronologies was consistently high, indicating a high-frequency variation. In the 4 species, MS was significantly higher for latewood chronologies ($\chi^2 = 188.53$, $df = 11$, $P < 0.0001$). Mean inter-tree correlation (IC) and expressed population signal (EPS) were higher for latewood and total ring than for earlywood (Table 1). This indicates a great amount of inter-annual growth variation shared among trees in the latewood and total ring widths but a smaller correspondence in earlywood.

The residual chronologies and the core sample sizes are shown in Figure 2a. In a PCA analysis, the first and second principal components (PC) shared 27.7% and 25.8% of the total tree-growth variation, respectively (Figure 2b). The scatterplot of the PCA loading coefficients showed that *Pinus* chronologies shared similar growth variation, while the *Quercus* chronologies for latewood and total ring

were grouped together. Earlywood chronologies of both *Quercus* species were closely associated, suggesting similar growth variation.

TREE GROWTH/CLIMATE RELATIONSHIPS

The coefficients of determination of the response functions were lower for earlywood than for latewood and total ring in all species, indicating lower climatic sensitivity (Table I). However, according to the *r*/*sd* ratios, all the response functions were globally significant (*P* < 0.001), even when the loss of degrees of freedom due to multiple

testing was accounted for. The order of tree species in descending value of *r*², *i.e.*, decreasing climatic sensitivity, was *P. pinaster*, *Q. robur*, *Q. pyrenaica*, and *P. pinea*. For *P. pinea*, only latewood and total ring had negative relationships with WB in autumn of the year of growth and with NAO in autumn of the previous year (Figure 3). The latewood and total ring chronologies of *P. pinaster* were significantly related to T, positively in winter and negatively in autumn of the year of growth. Positive relationships between WB and *P. pinaster* growth were evident from winter to summer. Also, significant negative relationships between total

TABLE I. Characteristics of the trees, the tree-ring series, the chronologies and climatic responses for the studied species in the period 1956–2005. MW (SD): mean width (standard deviation) of raw tree-ring series. AC: first-order autocorrelation of standard chronology. MS: mean sensitivity. IC: mean inter-tree correlation. EPS: expressed population signal. *r*²: coefficient of determination from the response function. *r*/*sd*: ratio between the coefficient of correlation and its standard deviation obtained after 9999 bootstrap iterations. When the ratio *r*/*sd* is ≥ 2, ≥ 2.58, or ≥ 3.3, the significance of the model is 0.05, 0.01, or 0.001, respectively.

Species	No. of trees (series)	Mean age ¹ (SD) (y)	Chronology ²	MW ¹ (SD) (mm)	AC	MS ¹	IC	EPS	<i>r</i> ²	<i>r</i> / <i>sd</i>
<i>P. pinea</i>	17 (30)	114 (24) ^a	EW	1.57 (0.59) ^c	0.306	0.214 ^a	0.264	0.843	0.223	5.425
			LW	1.03 (0.57) ^b	0.030	0.346 ^{de}	0.367	0.898	0.383	3.869
			TR	2.59 (1.09) ^{de}	0.301	0.224 ^a	0.338	0.884	0.358	6.229
<i>P. pinaster</i>	22 (34)	52 (6) ^c	EW	2.97 (0.73) ^e	0.034	0.305 ^{cd}	0.270	0.881	0.535	5.943
			LW	2.28 (0.72) ^d	0.172	0.378 ^e	0.325	0.906	0.625	5.992
			TR	5.26 (1.26) ^f	0.016	0.253 ^{abc}	0.349	0.915	0.664	8.232
<i>Q. pyrenaica</i>	16 (26)	88 (24) ^b	EW	0.47 (0.09) ^a	0.216	0.242 ^{ab}	0.169	0.726	0.385	8.267
			LW	1.15 (0.62) ^{bc}	0.265	0.361 ^e	0.334	0.867	0.429	4.172
			TR	1.61 (0.67) ^c	0.351	0.287 ^{bc}	0.368	0.883	0.437	5.650
<i>Q. robur</i>	15 (24)	86 (22) ^b	EW	0.55 (0.19) ^a	0.096	0.269 ^{abc}	0.134	0.669	0.410	8.205
			LW	2.19 (0.93) ^d	0.130	0.446 ^f	0.360	0.880	0.516	3.860
			TR	2.74 (1.07) ^{de}	0.184	0.378 ^e	0.380	0.888	0.524	5.171

¹Different superscript letters indicate significant differences (*P* < 0.001) according to the Kruskal–Wallis test.
²EW: Residual earlywood, LW: latewood and TR: total ring.

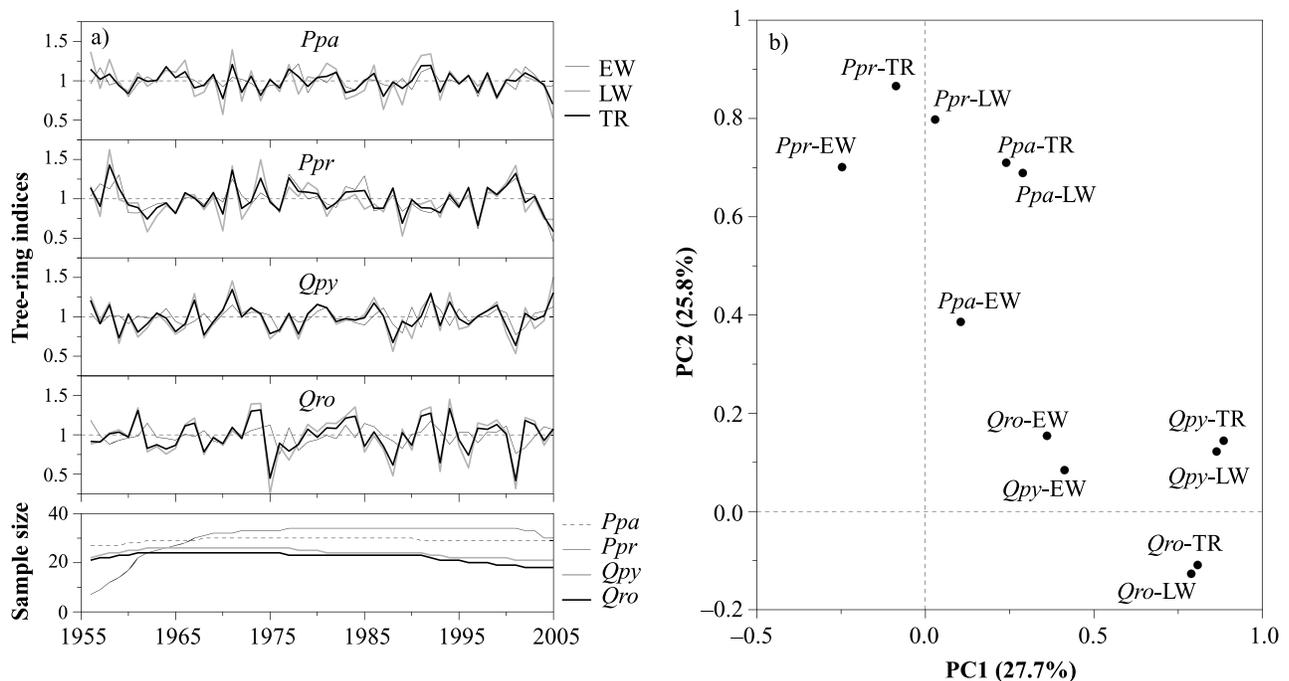


FIGURE 2. (a) Residual earlywood (EW), latewood (LW), and total ring (TR) tree-ring chronologies of *P. pinea* (*Ppa*), *P. pinaster* (*Ppr*), *Q. pyrenaica* (*Qpy*), and *Q. robur* (*Qro*) and their corresponding series sample sizes. (b) Scatter plot of principal component loadings obtained from a correlation matrix between tree-ring chronologies. The percentage of variance explained by the PC axes is shown.

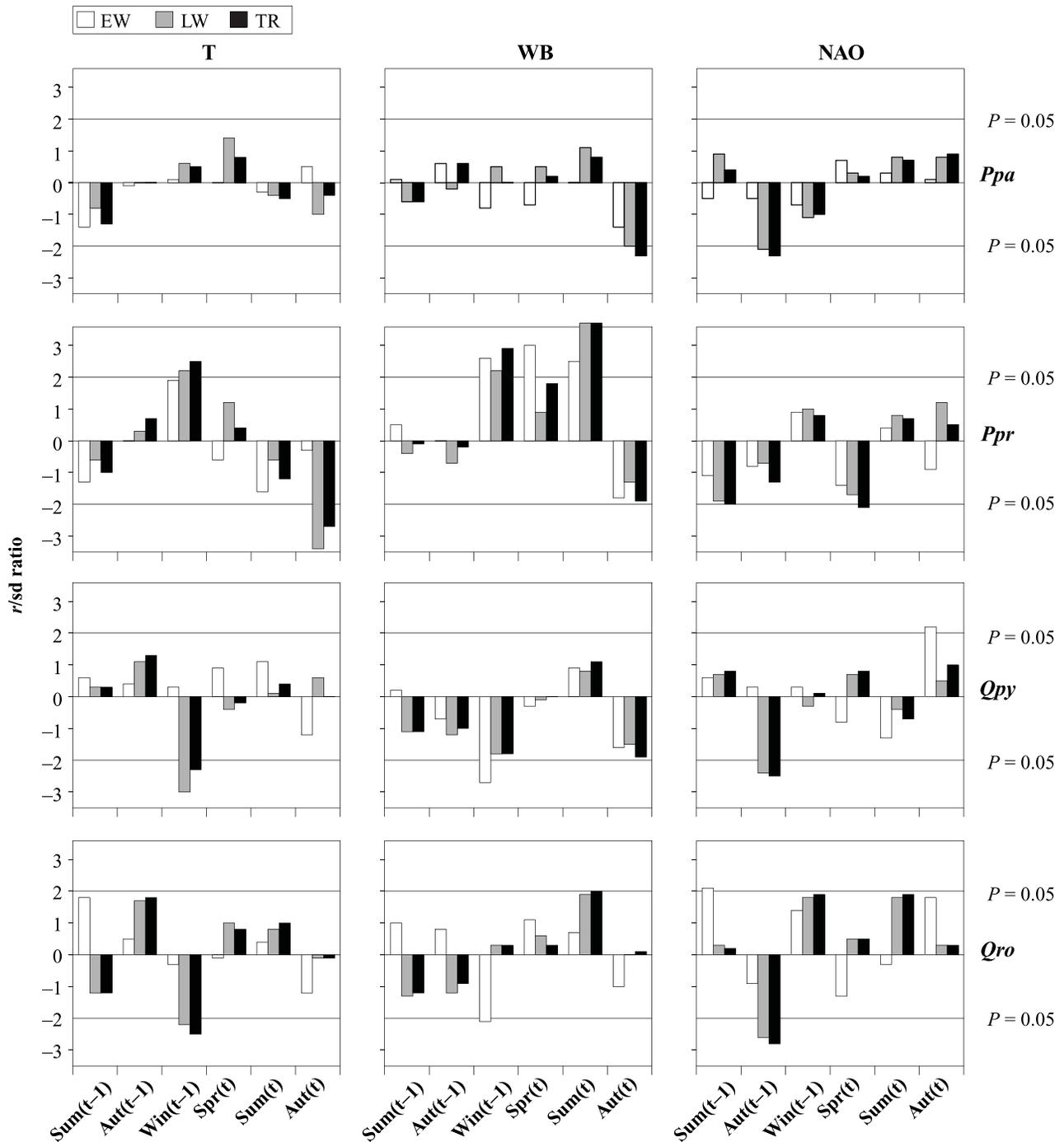


FIGURE 3. Response functions, expressed as the regression coefficients divided by their bootstrapped standard deviations (r/sd ratio), between the earlywood, latewood, and total ring indices and seasonal T, WB, and NAO indices. Horizontal lines indicate the significance limits ($P = 0.05$) for the r/sd ratio. Abbreviations: T, temperature; WB, water balance; *Ppa*, *Pinus pinea*; *Ppr*, *Pinus pinaster*; *Qpy*, *Quercus pyrenaica*; *Qro*, *Quercus robur*; EW, earlywood; LW, latewood; TR, total ring; Win, winter; Spr, spring; Sum, summer; Aut, autumn; (t - 1), year prior to tree growth; (t), current growth year.

ring growth of *P. pinaster* and NAO were observed in spring of the year of growth. The latewood and total ring chronologies of both *Quercus* species showed negative relationships with T in winter and NAO in the previous autumn. The earlywood of both *Quercus* species showed negative a relationship with winter WB. In addition, the earlywood of *Q. pyrenaica* was positively related with NAO in autumn of the year of

growth, whereas in *Q. robur* it was positively related with that of the previous summer (Figure 3).

TREE-GROWTH VARIATION PARTITIONING

In the RDA models, forward selection of the explanatory variables in the 3 components suggested that tree-growth variation was significantly related to the following

variables (Table II): (i) T of winter ($P = 0.012$) and summer ($P = 0.044$) of the year of growth, accounting for 10.7% of total tree-ring variation; (ii) WB of winter ($P = 0.015$) and summer ($P = 0.001$), accounting for 15.2% of tree-ring variation; and (iii) NAO of the previous autumn ($P = 0.024$), accounting for 6.0% of tree-ring variation. The reduced model considering only the significant seasonal variables indicated that 29.5% of tree-ring variation was related to climate. The RDA ordination obtained under this reduced model showed that axis 1, explaining 42.8% of growth/climate variation, was positively related to winter T and autumn NAO and negatively related to summer WB (Figure 4a). Axis 2 explained 33.5% of growth/climate variation and was positively related to winter WB and negatively related to summer T. Summer WB had positive relationships with tree growth, especially for *P. pinaster*. By contrast, T in winter and summer and NAO in the previous autumn showed negative effects on tree growth. According to this RDA ordination, latewood and total ring indices of *Quercus* showed negative relationships with T in winter and NAO in the previous autumn.

The RDA and partial RDA analyses performed to partition the variation of tree-growth in Cortegada were statistically significant, except for the partial RDA analysis of T when WB was considered a covariable, which revealed non-significant shared effects on tree growth (Table III). The pure and shared climatic components of tree-growth variation were obtained by means of the calculations described in Table IV. A summary of the variation partitioning results indicated that the pure effect of T explained 6.6%, the pure effect of WB explained 9.0%, and the pure effect of NAO explained 7.8% of tree-growth variation (Figure 4b). The shared effect between T and WB explained 6.1% of total growth variation, while the shared effect between local and large-scale climate accounted for only 0.3% of variation. In total, 70.4% of tree-growth variation remained unexplained by both local and large-scale climate.

RDA models obtained at the species level revealed the species-specific effects of the climatic components on tree growth (Table V). In *P. pinea* only the model for WB and the reduced model were statistically significant, and in *Q. pyrenaica* only the model for T and the reduced

TABLE II. Summary statistics of RDA models for the relationships between seasonal temperature (T), water balance (WB), and NAO indices (NAO) and the variation of tree growth in the period 1956–2005. The statistics of the seasonal variables retained through forward variable selection, the models for each component, and the reduced model (including all the significant seasonal variables) are shown. λ : eigenvalues for the variation of tree-ring indices explained by each model.

Components	Variables	Forward selection		RDA model statistics		
		F	P	λ	F	P
T	Win (t)	3.16	0.012	0.107	2.82	0.005
	Sum (t)	2.37	0.044			
WB	Win (t)	3.25	0.015	0.152	4.21	< 0.001
	Sum (t)	4.93	0.001			
NAO	Aut (t - 1)	3.08	0.024	0.060	3.08	0.018
Reduced model				0.295	3.34	< 0.001

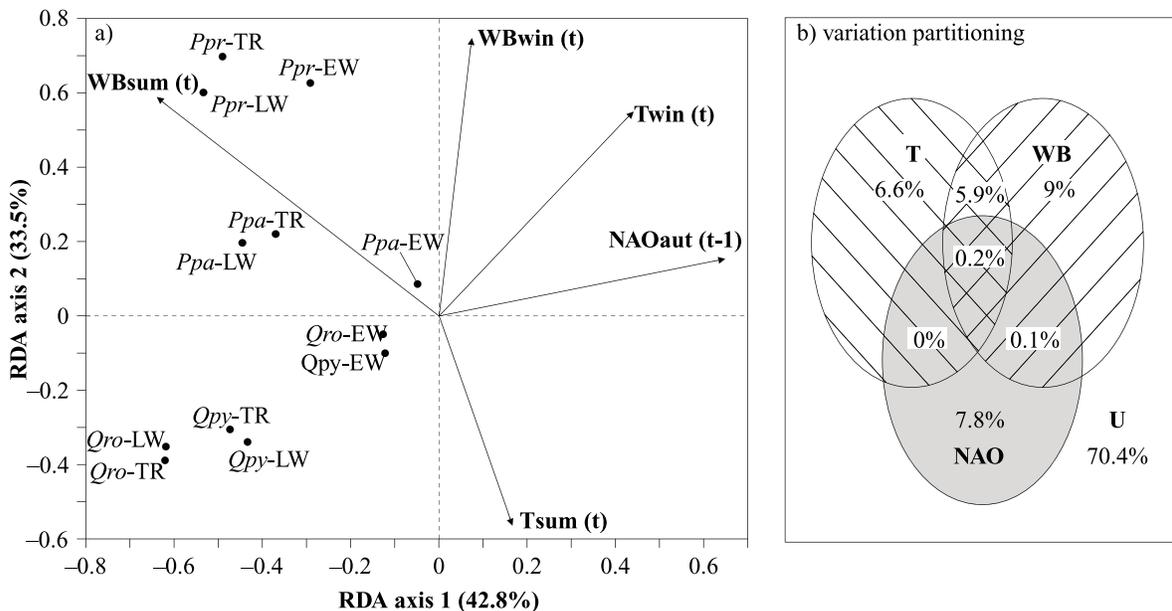


FIGURE 4. (a) RDA ordination obtained under the reduced model of Table II, showing the relationships between earlywood (EW), latewood (LW), and total ring (TR) indices and significant ($P < 0.05$) seasonal temperature (T), water balance (WB), NAO and unexplained (U). The percentage of variance explained by the RDA axes is shown. (b) Variation partitioning of the tree-ring chronologies derived from RDA and partial RDA analyses according to the calculations described in Table IV.

TABLE III. Summary statistics of RDA and partial RDA runs performed to partition the variation of tree growth into the pure and shared effects of seasonal temperature (T), water balance (WB), and NAO indices (NAO). λ : eigenvalues for the variation of tree-ring indices explained by each model.

Reference	Analysis	Variables	Covariables	λ	F	P
[1]	RDA	T		0.107	2.82	0.005
[2]	Partial RDA	T	WB	0.046	1.29	0.236
[3]	Partial RDA	T	NAO	0.125	3.93	0.001
[4]	Partial RDA	T	WB and NAO	0.066	1.99	0.044
[5]	RDA	WB		0.152	4.21	< 0.001
[6]	Partial RDA	WB	T	0.091	2.54	0.011
[7]	Partial RDA	WB	NAO	0.149	4.34	< 0.001
[8]	Partial RDA	WB	T and NAO	0.090	2.73	0.005
[9]	RDA	NAO		0.060	3.08	0.018
[10]	Partial RDA	NAO	T	0.078	4.42	0.002
[11]	Partial RDA	NAO	WB	0.058	3.36	0.013
[12]	Partial RDA	NAO	T and WB	0.078	4.71	0.002

 TABLE IV. Calculation of the 8 variation components resulting from the partition of tree growth among temperature, water balance, and NAO indices. λ : canonical eigenvalues for the variation of tree-ring indices explained by each fraction.

Growth variation explained by	Code	Calculation*	λ
Temperature	T	[4]	0.066
Water balance	WB	[8]	0.090
NAO	NAO	[12]	0.078
Temperature and water balance	T+WB	[7] – [8]	0.059
Temperature and NAO	T+NAO	[11] – [12]	0.000
Water balance and NAO	WB+NAO	[6] – [8]	0.001
Temperature and water balance and NAO	T+WB+NAO	[5] – [6] – [7] + [8]	0.002
Unexplained	U	1 – [sum of all other fractions]	0.704

*Numbers between brackets are the references of RDA and partial RDA runs indicated in Table III, from which eigenvalues were obtained to compute the canonical eigenvalues λ .

 TABLE V. Summary statistics of RDA models for the relationships between seasonal temperature (T), water balance (WB), and NAO indices (NAO) and the variation of tree growth by species. The statistics of the seasonal variables retained through forward variable selection, the models for each component, and the reduced model (including all the significant seasonal variables) are shown. λ : eigenvalues for the variation of tree-ring indices explained by each model. Asterisks indicate the significance level obtained in the forward selection procedure: * $P < 0.05$; ** $P < 0.01$.

Species	RDA model statistics components	Variables from forward selection	λ	F	P
<i>P. pinea</i>	WB	Aut (t) *	0.078	4.03	0.037
	NAO	Aut (t – 1) *	0.070	3.59	0.052
	Reduced model		0.164	4.34	0.012
<i>P. pinaster</i>	T	Win (t) * Sum (t) *	0.161	4.52	0.008
	WB	Win (t) * Spr (t) ** Sum (t) **	0.416	10.93	< 0.001
	Reduced model		0.445	7.06	< 0.001
<i>Q. pyrenaica</i>	T	Win (t) *	0.132	7.31	0.007
	NAO	Aut (t – 1) *	0.068	3.48	0.054
	Reduced model		0.288	7.58	0.001
<i>Q. robur</i>	T	Aut (t – 1) * Win (t) *	0.155	2.82	0.038
	NAO	Aut (t – 1) * Win (t) *	0.163	4.57	0.011
	Reduced model		0.309	3.94	0.003

model were significant. In *P. pinaster* and *Q. robur* all the RDA models performed were statistically significant. The obtained results suggested a pure effect of local climate on growth in *P. pinaster* (T and WB) and a combined effect of local and large-scale climatic variation (T and NAO) on growth in *Q. robur*. According to the reduced models, the overall proportion of tree-ring growth variation explained by climate was 44.5% in *P. pinaster*, 30.9% in *Q. robur*, 28.8% in *Q. pyrenaica*, and 16.4% in *P. pinea*.

A summary of the variation partitioning results indicated that the species most sensitive to T were *Q. pyrenaica* and *Q. robur*, whereas *P. pinea* and especially *P. pinaster* were the species most sensitive to WB (Table VI). *Pinus pinea*, *Q. pyrenaica*, and especially *Q. robur* were the species most sensitive to NAO. The shared effect between T and WB was only found in *P. pinaster*. No shared effects between the local climatic variables and NAO on tree growth were evidenced for the study species.

TABLE VI. Variation partitioning for the tree-ring indices of the 4 species among T, WB, and NAO derived from RDA and partial RDA analyses. The percentage of tree-growth variation explained by each component is shown. The combinations not shown (T+NAO, WB+NAO, and T+WB+NAO) displayed zero values for all species. The significance of the reduced models for the individual components T, WB, and NAO is shown in Table V.

Code	<i>P. pinea</i>	<i>P. pinaster</i>	<i>Q. pyrenaica</i>	<i>Q. robur</i>
T	0.0	2.9	17.6	14.6
WB	8.6	28.4	0.0	0.0
NAO	7.8	0.0	11.2	16.3
T+WB	0.0	13.2	0.0	0.0
U	83.6	55.5	71.2	69.1

Discussion

In this study, we partitioned the variation of tree-ring growth into local and large-scale climatic components, which proved to be a valuable procedure that supports techniques ordinarily used in dendroclimatology. The results obtained by means of the traditional response function were corroborated by using RDA and partial RDA to estimate the pure and shared effects of seasonal T, WB, and NAO on tree growth. According to the variation partitioning, the local effect of T and WB explained 21.8% of growth variation, while 8.1% can be related to the large-scale NAO effect. The percentages of variance explained by the reduced RDA models were considerably lower than those obtained in the response functions. Similar results were obtained by Trouet *et al.* (2001) when comparing RDAs and response functions of tree-ring series and 3 climatic data sets (monthly P, maximum T, and the Southern Oscillation Index) in eastern Africa. This difference arises because the response function includes all the climatic variables in the model, while the RDA includes only those significant variables selected in the forward selection procedure (Legendre & Legendre, 1998).

NAO is a secondary climatic component influencing tree growth in Cortegada, explaining a small proportion of growth variation and being significant only for *Q. robur*. Tree-ring chronologies from Europe, North Africa, and North America often show significant relationships with NAO variation, being used as proxy records to reconstruct the winter NAO index of recent centuries (Glueck & Stockton, 2001; Cook *et al.*, 2002). Tree growth in northern Europe is positively correlated to the large-scale variation of autumn–winter NAO, while in southern Europe this relation with NAO is negative (Piovesan & Schirone, 2000; Linderholm, Solberg & Lindholm, 2003). Accordingly, our study revealed a negative response to autumn NAO in *P. pinea*, *Q. pyrenaica*, and *Q. robur*. The negative response can be explained by the spatial structure of NAO, which determines that mild and rainy winters in northern Europe are related to positive NAO indices, while in southern Europe winter precipitation is inversely correlated with NAO (Hurrell & van Loon, 1997).

The shared effect of local climate and NAO on tree growth was negligible in Cortegada, suggesting that there was no joint effect of local and large-scale climatic variation on tree growth. However, the assumption that tree

growth does not respond directly to the variability of large-scale atmospheric circulation but responds to its influence through local climatic effects (Mäkinen *et al.*, 2003; Mysterud *et al.*, 2003) cannot be refuted by the obtained results. Because the effects of stochastic fluctuations are impossible to quantify by means of the variation partitioning procedure (Borcard, Legendre & Drapeau, 1992), we suspect that other local variables not included in this study may partially explain a significant amount of tree-growth variation. The NAO exerts a dominant influence on precipitation, surface air temperature, intensity and number of storms, moisture transport, ocean heat content, and atmospheric pressure in Europe (Pozo-Vázquez *et al.*, 2001; Hurrell *et al.*, 2003), which together could play a relevant role in controlling the physiological processes that determine tree growth. Moreover, the absence of a direct link between the local climatic records and the large-scale climatic indices that significantly influenced tree growth can be explained by the lag between the occurrence of the different NAO phases and their effects in coastal north-west Spain (Trouet *et al.*, 2001). In the study area, winter NAO is significantly correlated to summer T ($r = 0.369$, $P = 0.004$) and winter WB ($r = -0.453$, $P < 0.001$). By contrast, autumn NAO is not significantly correlated to the local variables that controlled tree growth, which explains the null shared variation between local climate and NAO. For a more complete understanding of the relative effects of local and large-scale climatic variation on tree growth, further studies based on regional networks of tree-ring chronologies are needed.

We expected that the radial growth of *Pinus* would be mainly limited by summer water stress (Richter, Eckstein & Holmes, 1991; Andreu *et al.*, 2007). However, *P. pinea* growth was mostly independent from WB in Cortegada. Growth of *P. pinea* is favoured by wet winter–summer under more limited annual precipitation than in the study area, *e.g.*, 538–581 mm·y⁻¹ in Portugal (Campelo *et al.*, 2006) or 827 mm·y⁻¹ in Turkey (Akkemik, 2000). Water availability in Cortegada is probably not limiting for growth of *P. pinea*, a species that may be adapted to more pronounced seasonal fluctuations in soil water content. *Pinus pinaster* was the most climatically sensitive species, with a percentage of growth variance related to climate similar to those reported in previous studies: 42.6% to 64.9% in central Spain (Bogino & Bravo, 2008) and 56% to 65% in the Atlantic littoral of Portugal (Vieira, Campelo & Nabais, 2009). As in other localities in the Iberian Peninsula, water availability in spring and summer are the main predictors of *P. pinaster* growth (Bogino & Bravo, 2008; Vieira, Campelo & Nabais, 2009); in Cortegada, winter WB also had a significant effect on growth.

A common feature in tree rings of both *Pinus* species is the formation of intra-annual density fluctuations due to sudden changes of water availability during the growth period (Campelo *et al.*, 2006; De Micco *et al.*, 2007; Vieira, Campelo & Nabais, 2009). However, *P. pinaster* has higher water use efficiency in comparison to other *Pinus* species, and this efficiency seems to be more pronounced in the mesic genotypes in humid environments, where relatively high levels of rainfall guarantee vigorous growth (Tognetti

et al., 2000; Martínez-Vilalta & Piñol, 2002). Atlantic populations of *P. pinaster* showed higher water use efficiency and growth potential than Mediterranean ones, being able to maintain high growth rates while experiencing moderate water stress (Correia *et al.*, 2008). Moreover, greater growth of *P. pinaster* can result from winter photosynthesis stimulated by elevated temperatures (Schaberg *et al.*, 1998); carbon gain in winter can be allocated to growth of fine roots, increasing their absorptive capacity at the onset of the water deficit in summer. By contrast, high temperatures in autumn seem to be detrimental for growth of this species, probably causing earlier cessation of the growth period.

The results of this study are consistent with previous findings showing that radial increment variation of *Quercus* trees is inversely related to winter temperature in Atlantic Europe (Pilcher & Gray, 1982; Rozas, 2005). Warmer winters stimulate respiration and consequent use of stored carbohydrates, when losses cannot be replaced by photosynthesis (Hamerlynck & Knapp, 1996). But such conditions negatively affected latewood growth of *Quercus* in Cortegada, while *a priori* it could be expected that early- and latewood formation would be supported by previous- and current-year photosynthates, respectively (Robertson *et al.*, 1996). In ring-porous trees, large earlywood vessels, which are responsible for more than 90% of water transport (Ellmore & Ewers, 1985), remain functional only during a single growing season (Cochar & Tyree, 1990). As a consequence, early production of large vessels is necessary for the recovery of hydraulic conductivity and usually occurs before leaf expansion (Suzuki, Yoda & Suzuki, 1996). Since expanding leaves are strong carbon sinks, stored carbohydrates are at their minimum after leaf expansion in spring and at their maximum just before leaf fall in autumn (Barbaroux & Bréda, 2002; Hoch, Richter & Körner, 2003). This process of storage during the previous growing season is notably affected by climatic conditions (Gallé *et al.*, 2007); Yang and Midmore (2005) state that a great proportion of these reserves is used to build the photosynthetic apparatus in the following spring.

We hypothesize that the mild winters on this island due to the Atlantic climate cause significant consumption of stored reserves in *Quercus* as compared with colder climates. As a result, winter temperatures mediate latewood production, since they affect the reserves available for leaf flushing. In addition, a trade-off between carbohydrate investments for latewood growth and those stored for use in the following active period is expected during summer. However, the positive effects of spring–summer water availability on *Quercus* growth, which have been observed for several European sites (Pilcher & Gray, 1982; García-González & Eckstein, 2003; Lebourgeois, Cousseau & Ducos, 2004; Rozas, 2005; Drobyshev *et al.*, 2008), are not significant in Cortegada. Notwithstanding the negative water balance in summer, the sizable annual precipitation in the study area ($> 1700 \text{ mm}\cdot\text{y}^{-1}$) probably means that water availability is not limiting for *Quercus* growth.

Our results suggest that tree-ring growth is not very sensitive to climate at our study site and that in the near future we can expect a moderate response of growth to

the predicted climate changes. However, *P. pinaster* and *Q. robur* are the most climatically sensitive species, and also the most important species in the area from a productive and conservational perspective. *Pinus pinaster* shows the greatest sensitivity to water availability, and *Quercus robur* is susceptible to high winter temperatures. Over the long term, we can expect that the capability of these species to provide forest-derived products and act as carbon sinks will be significantly reduced along the Atlantic littoral of north-west Spain. Further studies of climatic sensitivity based on classic dendrochronological research, stable isotopes in wood, and quantitative anatomical features (Ferrio *et al.*, 2003; García-González & Eckstein, 2003) are needed at the interface between the Atlantic and Mediterranean climates to assess the potential consequences for coexisting tree species of temperature increments and longer drought periods.

Acknowledgements

We gratefully acknowledge the financial support of Xunta de Galicia, research project PGIDT06PXIB502262PR. V. Rozas benefited from a contract from INIA-Xunta de Galicia, partially funded by the European Social Fund, and S. Lamas benefited from a fellowship from Consellería de Medio Ambiente, Xunta de Galicia. We also thank D. Arseneault and two anonymous referees for suggestions that improved the article. L. Sampedro and S. Viehmann helped us during field work.

Literature cited

- Akkemik, U., 2000. Dendroclimatology of umbrella pine (*Pinus pinea* L.) in Istanbul, Turkey. *Tree-Ring Bulletin*, 56: 17–20.
- Andreu, L., E. Gutiérrez, M. Macías, M. Ribas, O. Bosch & J. J. Camarero, 2007. Climate increases regional tree-growth variability in Iberian pine forests. *Global Change Biology*, 13: 1–12.
- Barbaroux, C. & N. Bréda, 2002. Contrasting distribution and seasonal dynamics of carbohydrate reserves in stem wood of adult ring-porous sessile oak and diffuse-porous beech trees. *Tree Physiology*, 22: 1201–1210.
- Beeckman, H., 1992. Redundancy analysis of tree rings and meteorological data in a Nelder design poplar plantation. Pages 22–26 in T. S. Bartholin, B. E. Berglund, D. Eckstein & F. H. Schweingruber (eds.). *Tree Rings and Environment*. Ludqua Report 34. University of Lund, Ystad, Sweden.
- Blanco, E., M. A. Casado, M. Costa, R. Escribano, M. García, M. Génova, A. Gómez, F. Gómez, J. C. Moreno, C. Morla, P. Regato & H. Sáinz, 2001. Los bosques ibéricos: una interpretación geobotánica. Editorial Planeta, Madrid.
- Bogino, S. M. & F. Bravo, 2008. Growth response of *Pinus pinaster* Ait. to climatic variables in central Spanish forests. *Annals of Forest Science*, 65: 506.
- Borcard, D., P. Legendre & P. Drapeau, 1992. Partialling out the spatial component of ecological variation. *Ecology*, 73: 1045–1055.
- Briffa, K. & P. D. Jones, 1990. Basic chronology statistics and assessment. Pages 137–152 in E. Cook & L. Kairiukstis (eds.). *Methods of Dendrochronology: Applications in the Environmental Sciences*. Kluwer Academic Publishers, Dordrecht.
- Calvo, R. & F. Macías, 2000. Mapa de suelos de Galicia, E. 1:50.000. Vilagarcía de Arousa. Consellería de Medio Ambiente, Xunta de Galicia.

- Campelo, F., C. Nabais, H. Freitas & E. Gutiérrez, 2006. Climatic significance of tree-ring width and intra-annual density fluctuations in *Pinus pinea* from a dry Mediterranean area in Portugal. *Annals of Forest Science*, 64: 229–238.
- Canadell, J. G. & M. R. Raupach, 2008. Managing forests for climate change mitigation. *Science*, 320: 1456–1457.
- Castroviejo, S., M. Laínz, G. López-González, P. Montserrat, F. Muñoz-Garmendia, J. Paiva & L. Villar (eds.), 1986–1989. *Flora Ibérica Volumes I and II*. Real Jardín Botánico, C.S.I.C., Madrid.
- Cochard, H. & M. T. Tyree, 1990. Xylem dysfunction in *Quercus*: Vessel sizes, tyloses, cavitation and seasonal changes in embolism. *Tree Physiology*, 6: 393–407.
- Cook, E. R., R. D. D'Arrigo & M. E. Mann, 2002. A well-verified, multiproxy reconstruction of the winter North Atlantic oscillation index since A.D. 1400. *Journal of Climate*, 15: 1754–1764.
- Cook, E. R. & R. L. Holmes, 1996. Guide for computer program ARSTAN. Pages 75–87 in H. D. Grissino-Mayer, R. L. Holmes & H. C. Fritts (eds.). *The International Tree-Ring Data Bank Program Library Version 2.0 User's Manual*. Laboratory of Tree-Ring Research, University of Arizona, Tucson, Arizona.
- Cook, E. R. & K. Peters, 1981. The smoothing spline: A new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. *Tree-Ring Bulletin*, 41: 45–53.
- Corcuera, L., J. J. Camarero & E. Gil-Pelegrín, 2002. Functional groups in *Quercus* species derived from the analysis of pressure–volume curves. *Trees*, 16: 465–472.
- Correia, I., M. H. Almeida, A. Aguiar, R. Alía, T. S. David & J. S. Pereira, 2008. Variations in growth, survival and carbon isotope composition ($\delta^{13}\text{C}$) among *Pinus pinaster* populations of different geographic origins. *Tree Physiology*, 28: 1545–1552.
- De Micco, V., M. Saurer, G. Aronne, R. Tognetti & P. Cherubini, 2007. Variations of wood anatomy and $\delta^{13}\text{C}$ within-tree rings of coastal *Pinus pinaster* showing intra-annual density fluctuations. *IAWA Journal*, 28: 61–74.
- Drobyshev, I., M. Niklasson, O. Eggertsson, H. Linderson & K. Sonesson, 2008. Influence of annual weather on growth of pedunculate oak in southern Sweden. *Annals of Forest Science*, 65: 512.
- Ellmore, G. S. & F. W. Ewers, 1985. Hydraulic conductivity in trunk xylem of elm, *Ulmus americana*. *IAWA Bulletin*, 6: 303–307.
- Ferrio, J. P., A. Florit, A. Vega, L. Serrano & J. Voltas, 2003. $\Delta^{13}\text{C}$ and tree-ring width reflect different drought responses in *Quercus ilex* and *Pinus halepensis*. *Oecologia*, 137: 512–518.
- Fritts, H. C., 2001. *Tree Rings and Climate*. Blackburn Press, Caldwell.
- Fritts, H. C., T. J. Blasing, B. P. Hayden & J. E. Kutzbach, 1971. Multivariate techniques for specifying tree-growth and climate relationships and for reconstructing anomalies in paleoclimate. *Journal of Applied Meteorology*, 10: 845–864.
- Fritts, H. C., E. A. Vaganov, I. V. Sviderskaya & A. V. Shashkin, 1991. Climatic variation and tree-ring structure in conifers: Empirical and mechanistic models of tree-ring width, number of cells, cell size, cell-wall thickness and wood density. *Climate Research*, 1: 97–116.
- Gallé, A., P. Haldimann & U. Feller, 2007. Photosynthetic performance and water relations in young pubescent oak (*Quercus pubescens*) trees during drought stress and recovery. *New Phytologist*, 174: 799–810.
- García-González, I. & D. Eckstein, 2003. Climatic signal of earlywood vessels of oak on a maritime site. *Tree Physiology*, 23: 497–504.
- Glueck, M. F. & C. W. Stockton, 2001. Reconstruction of the North Atlantic Oscillation, 1429–1983. *International Journal of Climatology*, 21: 1453–1465.
- Guiot, J., 1991. The bootstrapped response function. *Tree-Ring Bulletin*, 51: 39–41.
- Hamerlynck, E. & A. K. Knapp, 1996. Photosynthetic and stomatal responses to high temperature and light in two oaks at the western limit of their range. *Tree Physiology*, 16: 557–565.
- Hoch, G., A. Richter & C. Körner, 2003. Non-structural carbon compounds in temperate forest trees. *Plant, Cell and Environment*, 26: 1067–1081.
- Holmes, R. L., 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin*, 43: 69–78.
- Hurrell, J. W. & H. van Loon, 1997. Decadal variations in climate associated with the North Atlantic Oscillation. *Climatic Change*, 36: 301–326.
- Hurrell, J. W., Y. Kushnir, G. Ottersen & M. Visbeck, 2003. An overview of the North Atlantic Oscillation. Pages 1–35 in J. W. Hurrell, Y. Kushnir, G. Ottersen & M. Visbeck (eds.). *The North Atlantic Oscillation: Climate Significance and Environmental Impact*. Geophysical Monograph Series, 134. American Geophysical Union, Washington DC.
- IPCC, 2007. *Climate Change 2007: The Physical Science Basis*. Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.
- Lamas, S. & V. Rozas, 2007. Crecimiento radial de las principales especies arbóreas de la isla de Cortegada (Parque Nacional de las Islas Atlánticas) en relación con la historia y el clima. *Investigación Agraria: Sistemas y Recursos Forestales*, 16: 3–14.
- Lebourgeois, F., G. Cousseau & Y. Ducos, 2004. Climate–tree–growth relationships of *Quercus petraea* Mill. stand in the Forest of Bercé (“Futaie des Clos”, Sarthe, France). *Annals of Forest Science*, 61: 361–372.
- Legendre, P., 2008. Studying beta diversity: Ecological variation partitioning by multiple regression and canonical analysis. *Journal of Plant Ecology*, 1: 3–8.
- Legendre, P. & L. Legendre, 1998. *Numerical Ecology*. 2nd English edition. Elsevier, Amsterdam.
- Linderholm, H. W., B. O. Solberg & M. Lindholm, 2003. Tree-ring records from central Fennoscandia: The relationships between tree growth and climate along a west–east transect. *Holocene*, 13: 887–895.
- Mäkinen, H., P. Nöjd, H.-P. Kahle, U. Neumann, B. Tveite, K. Mielikäinen, H. Röhle & H. Spiecker, 2003. Large-scale climatic variability and radial increment variation of *Picea abies* (L.) Karst. in central and northern Europe. *Trees*, 17: 173–184.
- Manly, B. F. J., 1997. *Randomization, Bootstrap and Monte Carlo Methods in Biology*. Chapman & Hall, London.
- Martínez-Vilalta, J. & J. Piñol, 2002. Drought-induced mortality and hydraulic architecture in pine populations of the NE Iberian Peninsula. *Forest Ecology and Management*, 161: 247–256.
- Mysterud, A., N. C. Stenseth, N. G. Yoccoz, G. Ottersen & R. Langvatn, 2003. The response of terrestrial ecosystems to climate variability associated with the North Atlantic Oscillation. Pages 235–262 in J. W. Hurrell, Y. Kushnir, G. Ottersen & M. Visbeck (eds.). *The North Atlantic Oscillation: Climate Significance and Environmental Impact*. Geophysical Monograph Series, 134. American Geophysical Union, Washington DC.
- Pilcher, J. R. & B. Gray, 1982. The relationships between oak tree growth and climate in Britain. *Journal of Ecology*, 70: 297–304.
- Piovesan, G. & B. Schirone, 2000. Winter North Atlantic oscillation effects on the tree rings of the Italian beech (*Fagus sylvatica* L.). *International Journal of Biometeorology*, 44: 121–127.
- Pozo-Vázquez, D., M. J. Esteban-Parra, F. S. Rodrigo & Y. Castro-Diez, 2001. A study of NAO variability and its possible non-linear influences on European surface temperature. *Climate Dynamics*, 17: 701–715.

- Richter, K., D. Eckstein & R. L. Holmes, 1991. The dendrochronological signal of pine trees (*Pinus* spp.) in Spain. *Tree-Ring Bulletin*, 51: 1–13.
- Robertson, I., A. M. Pollard, T. H. E. Heaton & J. R. Pilcher, 1996. Seasonal changes in the isotopic composition of oak cellulose. Pages 617–628 in J. S. Dean, D. M. Meko & T. W. Swetnam (eds.). *Tree Rings, Environment and Humanity*. Radiocarbon, Tucson, Arizona.
- Rozas, V., 2005. Dendrochronology of pedunculate oak (*Quercus robur* L.) in an old-growth pollarded woodland in northern Spain: Tree-ring growth responses to climate. *Annals of Forest Science*, 62: 209–218.
- Saxe, H., M. G. R. Cannell, O. Johnsen, M. G. Ryan & G. Vourlitis, 2001. Tree and forest functioning in response to global warming. *New Phytologist*, 149: 369–400.
- Schaberg, P. G., J. B. Shane, P. F. Cali, J. R. Donnelly & G. R. Strimbeck, 1998. Photosynthetic capacity of red spruce during winter. *Tree Physiology*, 18: 271–276.
- Stokes, M. A. & T. L. Smiley, 1996. *An Introduction to Tree-Ring Dating*. University of Arizona Press, Tucson, Arizona.
- Suzuki, M., K. Yoda & H. Suzuki, 1996. Phenological comparison of the onset of vessel formation between ring-porous and diffuse-porous deciduous trees in a Japanese temperate forest. *IAWA Journal*, 17: 431–444.
- Tardif, J. C., F. Conciatori, P. Nantel & D. Gagnon, 2006. Radial growth and climate responses of white oak (*Quercus alba*) and northern red oak (*Quercus rubra*) at the northern distribution limit of white oak in Québec, Canada. *Journal of Biogeography*, 33: 1657–1669.
- ter Braak, C. J. F. & P. Smilauer, 1998. *CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (Version 4)*. Center for Biometry Wageningen, Wageningen and Microcomputer Power, Ithaca, New York.
- Thornthwaite, D. W., 1948. An approach toward a rational classification of climate. *Geographical Review*, 38: 55–94.
- Tognetti, R., M. Michelozzi, M. Laureti, E. Brugnoli & R. Giannini, 2000. Geographic variation in growth, carbon isotope discrimination, and monoterpene composition in *Pinus pinaster* Ait. provenances. *Canadian Journal of Forest Research*, 30: 1682–1690.
- Trigo, R. M., D. Pozo-Vázquez, T. J. Osborn, Y. Castro-Díez, S. Gámiz-Fortis & M. J. Esteban-Parra, 2004. North Atlantic Oscillation influence on precipitation, river flow and water resources in the Iberian Peninsula. *International Journal of Climatology*, 24: 925–944.
- Trouet, V., K. Haneca, P. Coppin & H. Beeckman, 2001. Tree ring analysis of *Brachystegia spiciformis* and *Isoberlinia tomentosa*: Evaluation of the ENSO-signal in the Miombo woodland of eastern Africa. *IAWA Journal*, 22: 385–399.
- Valladares, F., 2007. A mechanistic view of the capacity of forests to cope with climate change. Pages 11–35 in F. Bravo, V. Le May, R. Jandl & K. von Gadow (eds.). *Managing Forest Ecosystems: The Challenge of Climate Change*. Springer Verlag, Berlin.
- Vieira, J., F. Campelo & C. Nabais, 2009. Age-dependent responses of tree-ring growth and intra-annual density fluctuations of *Pinus pinaster* to Mediterranean climate. *Trees*, 23: 257–265.
- Yang, Z. & D. J. Midmore, 2005. Modelling plant resource allocation and growth partitioning in response to environmental heterogeneity. *Ecological Modelling*, 181: 59–77.