

Contrasting effects of water availability on *Pinus pinaster* radial growth near the transition between the Atlantic and Mediterranean biogeographical regions in NW Spain

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Abstract Summer water stress is the main limiting factor for *Pinus pinaster* growth under Mediterranean climate, but no information on limiting physiographic and climatic factors under Atlantic conditions is available for this species. We hypothesize that water availability during the active period limits *P. pinaster* growth, with stands nearby the Atlantic–Mediterranean boundary being more sensitive to summer drought stress. We analyzed the inter- and intra-annual climatic response of this species at ten monospecific stands in a transitional area between the Atlantic and Mediterranean biogeographical regions in Galicia, NW Spain. Mean sensitivity of radial growth consistently decreased with increasing elevation, and growth variation was quite similar for the earlywood, latewood or total ring widths, suggesting a strong intra-annual coherency of radial growth. Growth patterns were site dependent and geographically structured, with three groups of stands showing different climatic responses. As expected for sites suffering from summer drought stress, water availability enhances growth in western and southern Galicia, showing negative responses to maximum temperatures and positive to water availability. In northern Galicia, away from the Atlantic–Mediterranean boundary, water surplus in the rainy seasons negatively influenced growth. This was probably due to the

combined effects of seasonal water-logging stress and the reduction of solar radiation associated with cloudiness, which would limit photosynthetic rates in winter and spring. Local variations of water availability strongly controlled the physiological processes that determine growth dynamics of *P. pinaster* in NW Spain, contributing to its geographical structure and contrasting sensitivity.

Keywords Tree rings · *Pinus pinaster* · Climate–growth relationship · Water balance · Drought · Atlantic climate

Introduction

Within the geographical range of a tree species, environmental features vary along physiographic and ecological gradients at different scales, creating heterogeneity in the spatial distribution of limiting factors for the species performance (Dittmar et al. 2003; Fekedulegn et al. 2003). Variation in growth patterns among tree populations reflects ecological and climatic variation within a given region, and can be used to detect main limiting factors and geographical gradients for tree growth and forest productivity (Mäkinen et al. 2002). Knowledge of the main climatic factors limiting tree growth is not only vital for estimating forest productivity in a particular region, but can also be very helpful to anticipate future patterns of wood productivity under changing climatic conditions (Case and Peterson 2005). This is particularly true near the boundaries between biogeographical regions, where limiting conditions can differentially affect the growth of species with distinct origin.

Dendrochronological methods are appropriate to describe tree-growth patterns on an annual basis and their dependence on physiographic and climatic factors at

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multiple spatial scales (Cook et al. 2001). Detailed studies of tree-ring networks at regional and stand scales are becoming more used to detect geographical patterns of tree responses to limiting environmental factors (Bogino and Bravo 2008; Mäkinen et al. 2002), but most of them focused on the inter-annual growth variation, which integrates the effects of weather conditions operating at multiple time scales along the entire growing season and preceding periods (Fritts 2001). However, the anatomical distinction between early- and latewood is prominent in many tree species, can lead to a higher temporal resolution and thus provide a better understanding of the mechanisms responsible for seasonal cambial activity and intra-annual growth dynamics (Lebourgeois 2000; Zweifel et al. 2006). But detailed studies on the climatic sensitivity of intra-annual growth chronologies are generally focused on environmental gradients, or on comparing growth sensitivity in contrasted environmental conditions (Parker et al. 2001; Splechtna et al. 2000; Watson and Luckman 2002).

Near the limit between the Atlantic and Mediterranean biogeographical regions in NW Spain, climate is characterized by an abundant annual rainfall, but a strong seasonality of precipitation causes a water deficit during summer, especially in those areas with more Mediterranean influence (Martínez Cortizas et al. 1994). However, the climatic sensitivity of radial growth for Mediterranean tree populations near the species range boundary, where climatic and ecological limiting conditions may substantially differ from those in the range core, has seldom been assessed. *Pinus pinaster* is a native tree species from the west-Mediterranean basin, i.e. the Italian and Iberian peninsulas, southern France, Corsica, Sardinia and northern Africa (Alía et al. 1997). Its distribution range is strongly fragmented, and the isolated populations typically show strong adaptations to local environmental conditions. Water stress and cold hardiness are probably some of the main factors driving population divergence (Chambel et al. 2007).

Within the Iberian range, *P. pinaster* lives on a wide variety of soil types, physiographic and climatic conditions. Thus, it grows under warmer and drier Mediterranean conditions at altitudes up to 2,000 m in central, east and southern Spain, where summer water stress constitutes the main limiting factor (Bogino and Bravo 2008). In contrast, it only spreads up to 900 m toward the north-western Atlantic coast under a colder and moister climate (Alía et al. 1997). Results from different palaeobotanical and genetic studies suggest that *P. pinaster* spread northwards from glacial refuges in southeastern Iberia and the Atlantic coast of Portugal since 7,500–6,500 year BP (Bucci et al. 2007; Figueiral 1995). In Galicia, NW Spain, it has been extensively cultivated since the nineteenth century for productive purposes, but no formal studies have explored

which the main climatic factors limiting *P. pinaster* growth under Atlantic conditions are. The pronounced genetic and physiological differences between Atlantic and Mediterranean populations (Alía et al. 1997; Bucci et al. 2007; Correia et al. 2008) suggest that the main limiting climatic factors may differ in these two regions.

In this work, we analyze tree-ring growth of *P. pinaster* in Galicia, NW Spain, at inter- and intra-annual time scales, near the transition between the Atlantic and Mediterranean biogeographical regions, as defined on the basis of botanical and climatic criteria (Rivas Martínez and Loidi Arregui 1999). Based on previous evidences (Rozas et al. 2009), we hypothesize that water availability during the active period limits growth in our study area, and that stands nearby the Atlantic-Mediterranean boundary are more sensitive to summer drought stress. In order to test these hypotheses, we aim at responding the following questions: (1) How do inter-annual growth patterns of *P. pinaster* vary along its range in Galicia, NW Spain? (2) What are the main limiting climatic factors for radial growth throughout the region, and specifically under Atlantic climate and near the transition to a Mediterranean climate?

Materials and methods

Study area

The study area comprises the region of Galicia, NW Spain, at the NW range boundary of *Pinus pinaster* (Fig. 1a), where this species covers over 47% of the forest area in pure or mixed stand, and represents one of the most important commercial woods. It has been extensively planted for the last century, and the resulting even-aged stands are typically managed through rotations of 40–50 years.

Regional climate is rather heterogeneous as a result of the interaction between the prevalence of Atlantic winds and an irregular orography (Martínez Cortizas et al. 1994). Thus, the coastal area has a strong oceanic influence, with a high annual precipitation (1,500–2,500 mm), a mean annual temperature ca. 10°C, and a short annual thermal oscillation (10–11°C). In contrast, the southern inland area shows a proper Mediterranean climate with a remarkable summer drought, a lower annual precipitation (<1,000 mm), higher mean temperature ca. 14.5°C, and a pronounced annual thermal oscillation (13–14°C) with a greater continental influence (De la Mata and Zas 2010a). Though weaker, this Mediterranean influence spreads toward transitional areas, mainly during summer, affecting the whole inland and the western Atlantic coast, while keeping moist and mild conditions in the north of the region (Martínez Cortizas et al.

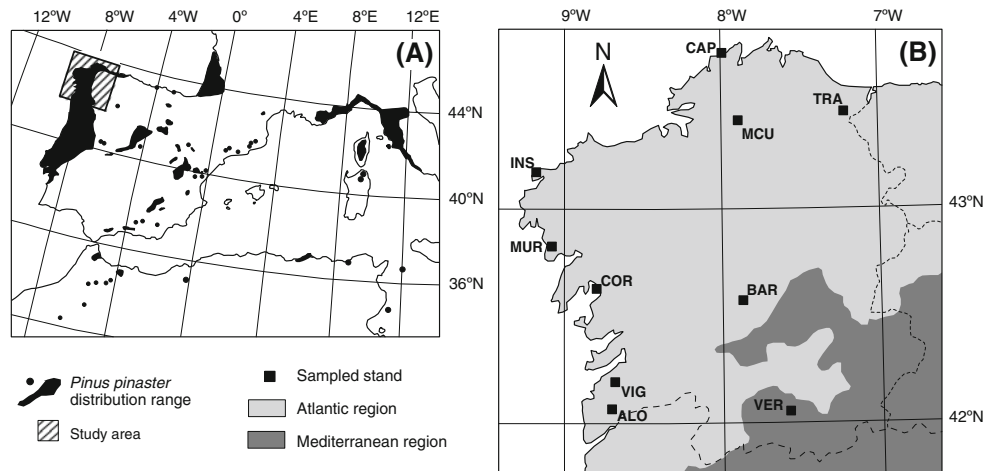


Fig. 1 a Location of the study area within the range of *Pinus pinaster* (Alía et al. 1997). b Location of the sampled stands in Galicia, NW Spain, and boundary between the Atlantic and Mediterranean

biogeographical regions (Rivas Martínez and Loidi Arregui 1999). Site codes are shown in Table 1

Table 1 Stand and tree characteristics for the sampled *Pinus pinaster* stands in Galicia, NW Spain

Stand name	Code	North latitude (°)	West longitude (°)	Elevation (m)	Soil type	DBH ± SD (cm)	Age ± SD (yr)
Monte Aloia	ALO	42.06	8.68	530	Regosol	46.2 ± 9.3	33 ± 6
A Barrela	BAR	42.53	7.85	620	Cambisol	66.7 ± 15.4	45 ± 4
A Capelada	CAP	43.67	7.98	340	Cambisol	45.0 ± 9.0	42 ± 3
Illa de Cortegada	COR	42.62	8.77	20	Regosol	54.4 ± 9.5	52 ± 6
Monte Insua	INS	43.13	9.15	10	Regosol	52.8 ± 11.8	34 ± 9
Marco da Curra	MCU	43.37	7.88	590	Podzol	29.6 ± 3.7	44 ± 1
Muros	MUR	42.80	9.05	155	Regosol	56.6 ± 5.9	54 ± 3
Trabada	TRA	43.40	7.22	640	Cambisol	45.7 ± 6.8	50 ± 5
Verín	VER	42.07	7.55	855	Luvisol	41.6 ± 3.5	43 ± 4
Vigo	VIG	42.20	8.65	365	Regosol	59.6 ± 8.3	55 ± 7

The stand name, code, geographical latitude and longitude, elevation, soil type (Guitián Ojea 1974), mean DBH, and age values are shown DBH diameter at breast height (130 cm), age estimated number of rings in the longest tree-ring series per tree, SD standard deviation

1994). Soils in the study area were mainly Regosols, Cambisols and Podzols, typical of humid conditions on acidic parent materials as schist, granite and gneiss, while Luvisols, typical of climate with a marked dry season, dominate in more xeric areas (Table 1, Guitián Ojea 1974).

Sampling and tree-ring data

We sampled ten monospecific stands located both in the coastal and inland areas of Galicia along the full elevation range of *P. pinaster* in the region, from sea level to 855 m (Table 1). The stands were located in the Atlantic biogeographical region, with the unique exception of VER, within the Mediterranean region (Fig. 1b). We measured DBH (bole diameter at breast height, 1.30 m) and took at least two increment cores per tree from 15 to 24 dominant

trees per stand. The cores were air-dried, glued onto wooden mounts and polished with successively finer grades of sandpaper, until the xylem cellular structure was visible in the transverse plane. The tree-ring series were absolutely dated by assigning calendar years to the rings following standard procedures (Speer 2010). Tree age was estimated based on the oldest core per tree, and no correction for the number of missing rings due to coring height was performed. Earlywood (EW) and latewood (LW) widths were measured under magnification to the nearest 0.001 mm with a sliding-stage micrometer (Velmex Inc., Bloomfield NY, USA) interfaced with a computer, and total ring (TR) widths were obtained as the sum of EW and LW on a year-by-year basis. Early- to latewood transition was defined according to a more or less gradual qualitative contrast in darkening, originated by a change in wood density. The

software COFECHA (Grissino-Mayer 2001) was used to quantitatively check for crossdating errors in the ring width series. All series with potential errors or weakly correlated with the master site chronology were corrected when possible or discarded.

Climate data

We used monthly gridded data from the datasets of the Climate Research Unit (CRU), University of East Anglia, UK, for maximum temperature (Tmax) and total precipitation (P) in the period 1967–2006, cloud-cover percentage in 1967–2002 (CRU TS 3, $0.5^\circ \times 0.5^\circ$), and for Palmer drought severity index (PDSI) in 1967–2002 (CRU self-calibrating PDSI, $0.5^\circ \times 0.5^\circ$). Data were taken from the Web site of the Royal Netherlands Meteorological Institute (<http://climexp.knmi.nl/>). The PDSI uses air temperature, cumulated rainfall and field water-holding capacity to compute a standardized measure of soil moisture ranging from -6 to 6 , which corresponds to extremely dry and wet soil conditions, respectively (Dai et al. 2004). Since maximum temperature is coupled to a minimum of rainfall during summer time, precipitation data were not directly used, but incorporated to water balance estimates (WB), calculated as $WB = P - PET$, where PET is the potential evapotranspiration estimated as a function of monthly mean temperatures and geographical latitude (Thornthwaite 1948). Mean monthly WB ranged between -75 mm in July and 145 mm in December–January, showing a tendency to water deficit from June to August.

The monthly climatic variables for Tmax, WB, and PDSI were averaged (Tmax, PDSI) or summed (WB) to seasonal values for winter (December–February), spring (March–May), summer (June–August), and autumn (September–November). The considered window for exploring the relations between climate and tree growth were from June of the previous year [Jun(-1)] to September of the current year (Sep) for monthly values; while for seasonal values, they ranged from summer of the previous year [Sum(-1)] to autumn of the current year (Aut). Additionally, annual values were also calculated by averaging or summing monthly values from previous October [Oct (-1)] to current September (Sep).

Chronology computation and assessment

The intra- and inter-annual responses of growth to climate were investigated after standardizing the raw EW, LW, and TR series with the ARSTAN computer program (Cook and Holmes 1996). Asynchronous growth changes such as disturbance signals due to natural canopy opening or logging were unusual within our tree-ring series, and only 39 years of tree ring data were available. Therefore, a

flexible spline function for standardization guarantees the removal of most non-climatically related variance, such as the biological trends, by preserving high-frequency climatic information (Cook and Peters 1981). A spline with a 50% frequency response of 32 years was fitted to the series, and the residuals obtained were pre-whitened by autoregressive modeling, yielding dimensionless indices that represent independent records of growth. The final chronologies were calculated as the robust biweight mean of the obtained stationary indices.

The statistical quality of the chronologies was assessed for 1967–2005, the common period of all chronologies, using standard basic statistics to measure the common signal. Mean sensitivity (MS) indicates the mean relative change between consecutive ring widths, signal-to-noise ratio (SNR) reveals the strength of the observed common signal among trees, and expressed populations signal (EPS) quantifies the degree to which the obtained chronology represents the theoretically perfect chronology (Briffa and Jones 1990; Fritts 2001). Moreover, the LW to TR ratio (LW/TR) in percent value, and the correlation between EW and LW chronologies (R_{EL}) indicating the intra-annual consistency of growth behavior, were also calculated.

Spatial variability in tree growth and climate responses

Common patterns of growth behavior within our tree-ring network were explored using principal component analysis (PCA) on the TR index chronologies of the ten stands for the common period 1967–2005. PCA transformed our collection of tree-ring chronology indices into a new set of principal components (PC), calculated on the covariance matrix of the original data. Orthogonal rotation of the PC axes was performed according to the Varimax criterion, which maximizes the spread of original PC loadings (Legendre and Legendre 1998). A scatter plot of the weighting coefficients for the first two PCs displayed the clusters of chronologies with similar growth variation. Principal component analysis was performed with the SPSS v15.0 package (SPSS Inc., Chicago, IL, USA).

Stands with similar growth behavior were grouped to calculate composite chronologies. All individual tree-ring series from stands belonging to the same cluster were pooled, standardized, and averaged with ARSTAN as previously described for the stand chronologies, giving a group chronology for each of EW, LW, and TR, composed of trees from several stands (Carrer et al. 2007). Descriptive statistics (MS, SNR, EPS, R_{EL} , and LW/TR) were also calculated for the composite chronologies in the common period 1967–2005.

In order to identify the main climatic variables that influenced growth at a local scale within the recognized groups, we calculated Pearson's correlations between EW,

LW and TR composite chronologies and climatic variables obtained after averaging the climatic series from the $0.5^\circ \times 0.5^\circ$ grid boxes corresponding to each group in the periods 1967–2005 for Tmax and WB, and 1967–2002 for cloud cover and PDSI.

The pure and shared effects of each climatic factor on the composite chronologies and the total variance explained by climate were assessed using redundancy analysis (RDA), which seeks linear combinations of environmental factors that are correlated to linear combinations of response variables (Legendre and Legendre 1998). A sequence of several complementary RDAs was performed with the software CANOCO v4.0 for Windows (ter Braak and Šmilauer 1998). The forward selection procedure after 9,999 Monte Carlo random permutations allowed excluding highly redundant and collinear climatic variables, which could have caused model instability and/or variance overestimation. Stepwise RDA was performed to know the explained tree-ring growth variation for the previously selected climatic predictors within each of the components Tmax, WB and PDSI. To assess the shared variation between Tmax, WB, and PDSI, the pure growth variance explained by each component was determined by RDA, while partial RDA (pRDA) determined the shared variation with each of the other components considered as covariables (Legendre and Legendre 1998). The amount of growth variance explained in each step was calculated as the proportion of total variance given by the canonical eigenvalue λ . The total explained variation in composite chronologies for the different recognized groups was obtained by RDA including all the significant predictors under a reduced model. For all described analyses, Monte Carlo tests with 9,999 random permutations were used to evaluate the significance of canonical eigenvalues. A scatter plot of the weighting coefficients for the first two RDA axes of an overall canonical ordination displayed the relationships between all composite chronologies for EW, LW, and TR, and the significant climate predictors at a regional scale.

Results

Characteristics of trees and tree-ring chronologies

Mean DBHs of dominant trees in the sampled stands varied between 29.6 and 66.7 cm, and mean estimated ages between 33 and 55 years (Table 1). Earlywood was wider than latewood at all stands, with mean LW/TR ratios ranging between 30 and 45.6% (Table 2). The relative change between consecutive rings was higher in LW than EW series at all stands, as indicated by the MS values, which were lower for TR chronologies. MS values were

negatively correlated to elevation, but only significant for EW ($R = -0.64$, $P = 0.044$) and TR ($R = -0.72$, $P = 0.018$). The strength of the common signal within each stand was larger in TR than in EW and LW, as indicated by the SNR statistic, which ranged 2.91–19.11 for TR, 2.37–12.59 for EW, and 1.07–13.00 for LW. EPS values were mostly higher than 0.85 with few exceptions, suggesting that the amount of local year-to-year growth variation shared by trees was relatively high, especially for TR series. EW and LW growth variations were significantly correlated in all cases, with R_{EL} ranging between 0.45 ($P < 0.01$) and 0.72 ($P < 0.001$). Consequently, common signal among trees was site dependent, with the same sites showing high EPS values for EW, LW, and TR, but with a greater common signal for TR.

Geographical variation of tree-ring growth and its climatic response

The scatter plot for the two first PCs revealed three consistent groups of stands, with PC1 and PC2 explaining 36.6 and 29.7% of the total tree-ring growth variation, respectively (Fig. 2). A first group comprised three stands (COR, INS, MUR) in the west (W) of Galicia, a second group included four stands (ALO, BAR, VER, VIG) in the south (S), and a third group comprised three stands (CAP, MCU, TRA) in the north (N).

Composite chronologies of each of the three groups revealed a large amount of growth variation shared by the trees at a regional level. Thus, EPS values of the composite EW, LW, and TR chronologies were higher than 0.85 in all cases (Table 2), and chronologies of EW and LW were similar within each group (Fig. 3), with R_{EL} ranging between 0.64 and 0.69 ($P < 0.001$).

Correlations with climate indicated significant influences of Tmax, WB, and PDSI on tree growth, with similar patterns among EW, LW, and TR within each group, but contrasting signs and seasonality of the relationships among the three recognized groups (Fig. 4). Group W showed negative correlations for Tmax during January, spring and summer, and also for annual Tmax, and particularly pronounced in EW and TR (Fig. 4a). An even more remarkable response was found when considering water availability. Thus, positive responses to WB were strong, mainly for the whole year, but also from previous winter to summer, and to PDSI from previous autumn to spring, with EW being sensitive to PDSI in previous September–November, when water availability did not affect LW growth. As regards group S, the negative influence of Tmax and positive of WB was found in previous October for all tree-ring compartments, and only for LW and TR in July (Fig. 4b); response to PDSI was positive in previous

Table 2 Summary of descriptive statistics for earlywood, latewood, and total ring width chronologies of *Pinus pinaster* in the studied stands and the three recognized groups of stands in the common period 1967–2005

Stand or group	Number of trees/cores	Period	Earlywood					Latewood					Total ring						
			MW ± SD (mm)		MS	SNR	EPS	MW ± SD (mm)		MS	SNR	EPS	MW ± SD (mm)		MS	SNR	EPS	R _{EL}	LW/TR (%)
ALO	21/36	1967–2006	2.97 ± 1.49	2.97 ± 1.49	0.343	2.37	0.704	2.59 ± 1.32	0.373	1.07	0.516	0.268	2.91	0.744	0.51	45.1			
BAR	24/50	1959–2006	3.26 ± 1.39	3.26 ± 1.39	0.266	11.85	0.922	2.51 ± 1.33	0.348	13.00	0.929	0.244	19.11	0.950	0.72	41.2			
CAP	23/45	1965–2006	2.34 ± 1.34	2.34 ± 1.34	0.295	3.92	0.797	1.48 ± 0.88	0.336	4.33	0.812	0.245	6.60	0.868	0.65	40.7			
COR	22/34	1950–2005	2.97 ± 1.56	2.97 ± 1.56	0.312	7.60	0.884	2.28 ± 1.35	0.390	6.91	0.874	0.274	10.38	0.912	0.61	42.9			
INS	15/26	1964–2007	3.58 ± 1.72	3.58 ± 1.72	0.313	2.86	0.741	2.33 ± 1.27	0.380	3.32	0.769	0.270	3.11	0.756	0.64	37.5			
MCU	20/46	1961–2006	1.50 ± 0.86	1.50 ± 0.86	0.247	9.68	0.906	0.77 ± 0.46	0.349	8.31	0.893	0.225	11.92	0.923	0.69	33.8			
MUR	22/42	1950–2006	2.01 ± 1.26	2.01 ± 1.26	0.290	12.35	0.925	1.72 ± 1.10	0.337	7.21	0.878	0.243	11.34	0.919	0.45	45.6			
TRA	23/50	1949–2006	2.07 ± 0.94	2.07 ± 0.94	0.263	8.06	0.890	1.32 ± 0.73	0.372	8.10	0.890	0.242	11.45	0.916	0.51	36.3			
VER	23/49	1963–2006	2.19 ± 0.97	2.19 ± 0.97	0.216	12.59	0.926	0.95 ± 0.49	0.280	6.60	0.868	0.190	13.29	0.930	0.46	30.0			
VIG	19/33	1950–2007	2.84 ± 1.26	2.84 ± 1.26	0.332	6.32	0.863	1.38 ± 0.64	0.379	3.26	0.765	0.273	6.28	0.863	0.54	34.4			
Group W	59/102	1955–2007	2.73 ± 1.48	2.73 ± 1.48	0.303	9.59	0.905	2.06 ± 1.23	0.366	6.68	0.870	0.260	9.47	0.904	0.69	40.6			
Group S	87/168	1953–2007	2.80 ± 1.26	2.80 ± 1.26	0.281	8.84	0.898	1.85 ± 0.95	0.340	6.01	0.857	0.239	10.72	0.915	0.64	39.1			
Group N	66/141	1953–2006	1.97 ± 1.04	1.97 ± 1.04	0.268	10.54	0.913	1.19 ± 0.69	0.353	9.75	0.907	0.238	15.18	0.938	0.66	37.2			

MW ± SD mean width of the raw series ± standard deviation, MS mean sensitivity of the unstandardized series, SNR signal-to-noise ratio, EPS expressed population signal, R_{EL} correlation between EW and LW chronologies (all significant at the 0.01 level), LW/TR mean latewood width/total ring width ratio

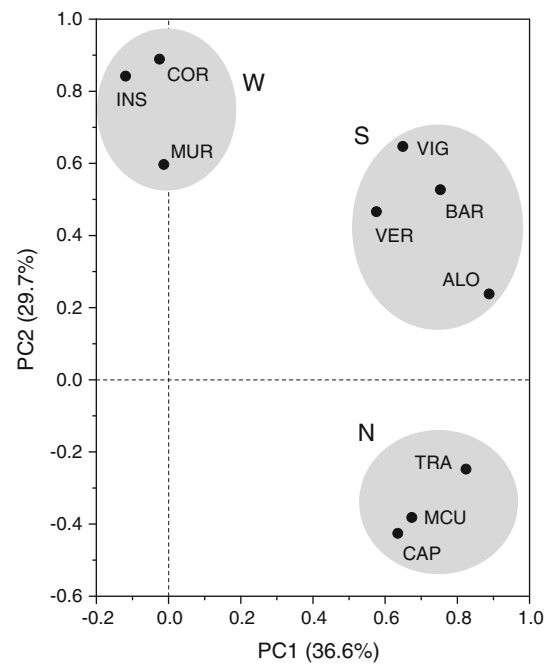


Fig. 2 Scatter plot of weighting coefficients for principal components (PC1 and PC2) calculated considering the TR indexed chronologies of *Pinus pinaster* in the period 1967–2005. The three recognized groups from the west (W), south (S), and north (N), stands are shown. Stand abbreviations are shown in Table 1

September, and from May to August, but mainly focused on LW and TR chronologies.

The results were different for group N, especially as regards the observed responses to water availability. Tmax influenced growth only negatively in previous October and positively for EW and TR in January (Fig. 4c). Responses to WB and PDSI were negative, and mainly concentrated in previous winter and spring. More specifically, EW was significantly correlated to WB in December–March, LW in February, and TR in February–March, while all three chronologies had significant correlations with PDSI from February to April.

Redundancy analysis and partial redundancy analysis models allowed excluding redundant and collinear climatic variables, assessing the pure growth variance explained by T, WB and PDSI, and estimating the shared variation between each of these components (Table 3). According to RDA models, the most important climatic variables for tree growth in group W were Tmax in spring and July, WB in July and the whole year, and PDSI in February, with WB explaining the greatest amount of growth variation; pRDA models showed a significant shared effect of Tmax with both WB and PDSI, but no shared effect between PDSI and WB. In group S, Tmax in previous October and July, WB in the same months and PDSI in previous September and June were the main climatic variables driving radial growth, with no significant pRDA models, which

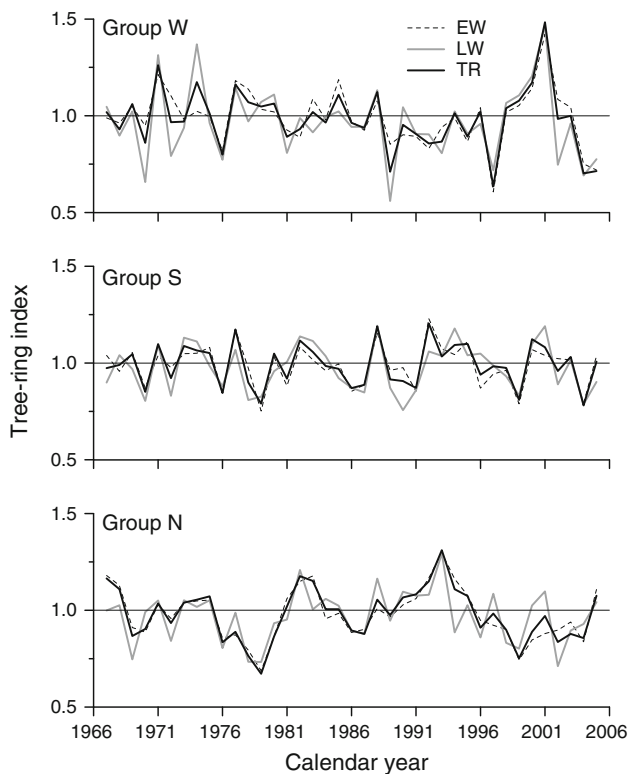


Fig. 3 Composite chronologies for *EW*, *LW*, and *TR*, derived from the groups for *Pinus pinaster* tree-ring chronologies corresponding to the west (*W*), south (*S*), and north (*N*) stands in the period 1967–2005

suggests non-shared variation between the climatic variables. In group *N*, *Tmax* in previous October and January and *WB* and *PDSI* in February significantly influenced tree

growth, but among them, only *PDSI* and *Tmax* showed a shared effect on growth variation. According to the reduced RDA models, 54.9, 42.4, and 42.0% of tree growth variation in groups *W*, *S*, and *N*, respectively, was explained by the considered climatic variables.

Climatic responses at a regional scale

According to an overall RDA model (F value = 4.84, $P < 0.001$), the climate variables with a significant effect on tree growth also showed significant correlations with the two first RDA axes (Table 4). Axis 1 explained 50% of the growth–climate relationships and was negatively correlated with July *Tmax*, while annual *WB* and June *PDSI* showed positive correlations with this axis. Axis 2 explained 44.5% of the growth–climate relationships and was positively correlated with *Tmax* in previous October and *PDSI* in February and April. The ordination obtained showed that tree-ring growth in group *W* was positively related to annual *WB* and negatively to July *Tmax* (Fig. 5). Group *S* was positively related to Jun *PDSI*, and group *N* negatively to February and April *PDSI*, while both groups were negatively related to *Tmax* in previous October. Among these, the most important predictors showing significant correlations with tree-ring growth were annual *WB* for group *W* (Fig. 6a), and June *PDSI* for group *S* (Fig. 6b), both of them with a positive relationship, and Feb *PDSI* for group *N*, with a negative relationship (Fig. 6c). Tree-ring growth in group *N* was also negatively related to cloud cover in February–April ($R = -0.52$, $P = 0.001$), while growth in other groups was independent of it.

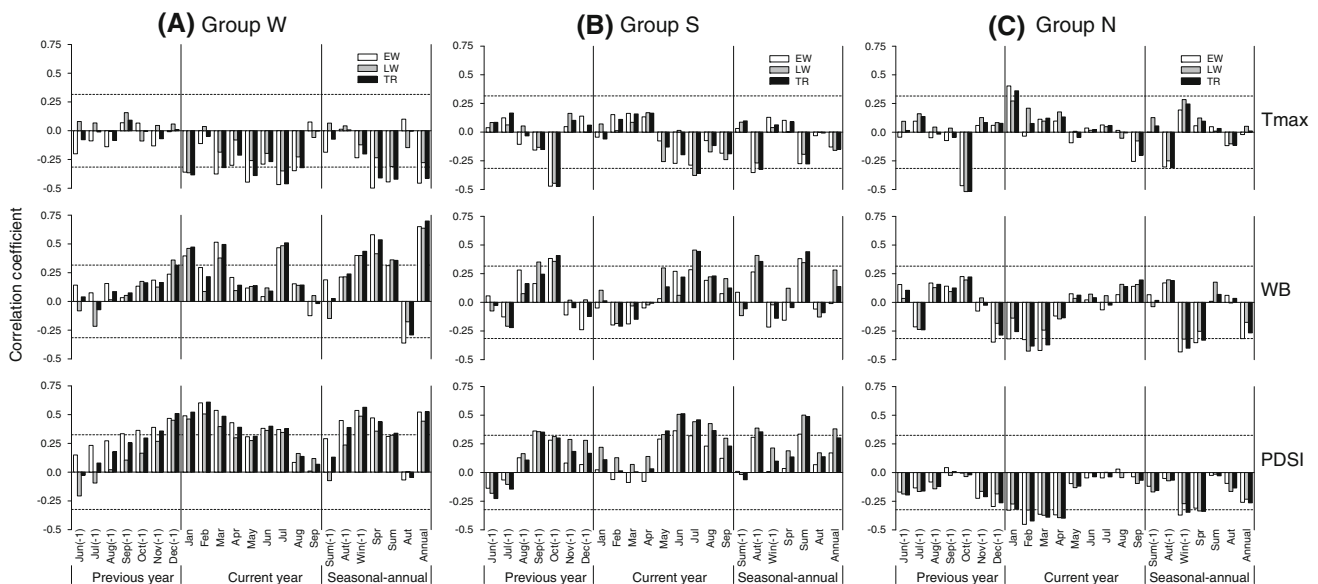


Fig. 4 Pearson’s correlations for the relationships between *EW*, *LW*, and *TR* chronologies of *Pinus pinaster* from the groups of stands *W*, *S* and *N*, and the monthly, seasonal and annual *Tmax*, *WB*, and *PDSI* variables. Horizontal dashed lines indicate the significance level ($P < 0.05$)

Table 3 Summary statistics of RDA and pRDA models for the relationships between the variation of *Pinus pinaster* tree-ring growth indices in the groups W, S, and N, and the climate predictors for maximum temperature (Tmax), water balance (WB), and Palmer drought severity index (PDSI)

Growth variables	Model	Constrained by	Predictors	Covariables	λ	F value	P value
Group W	RDA	Tmax	Spr, Jul		0.243	5.79	0.004
	RDA	WB	Jul, Annual		0.484	16.86	<0.001
	pRDA	WB	Jul, Annual	Tmax	0.304	11.40	<0.001
	RDA	PDSI	Feb		0.256	12.74	<0.001
	pRDA	PDSI	Feb	Tmax	0.129	7.22	0.007
	pRDA	PDSI	Feb	WB	0.001	0.07	0.919
	RDA	Reduced model			0.549	8.03	<0.001
Group S	RDA	Tmax	Oct(-1), Jul		0.296	7.58	<0.001
	RDA	WB	Oct(-1), Jul		0.220	5.06	0.004
	pRDA	WB	Oct(-1), Jul	Tmax	0.085	2.33	0.079
	RDA	PDSI	Sep(-1), Jun		0.230	5.39	0.005
	pRDA	PDSI	Sep(-1), Jun	Tmax	0.098	2.76	0.052
	pRDA	PDSI	Sep(-1), Jun	WB	0.075	1.79	0.160
	RDA	Reduced model			0.424	3.92	0.001
Group N	RDA	Tmax	Oct(-1), Jan		0.315	8.27	<0.001
	RDA	WB	Feb		0.147	6.37	0.013
	pRDA	WB	Feb	Tmax	0.023	1.19	0.279
	RDA	PDSI	Feb		0.153	6.70	0.012
	pRDA	PDSI	Feb	Tmax	0.098	5.86	0.017
	pRDA	PDSI	Feb	WB	0.061	2.77	0.090
	RDA	Reduced model			0.420	6.16	<0.001

The proportion of tree-ring growth variation accounted for by each model was quantified by the eigenvalue λ

Table 4 Correlations (*R*) and corresponding *P* values between the climatic variables that significantly influenced tree-ring growth of *Pinus pinaster*, and the first two RDA axes under the whole reduced model presented in Fig. 5

Climatic variables	RDA axis 1		RDA axis 2	
	<i>R</i>	<i>P</i> value	<i>R</i>	<i>P</i> value
Oct(-1) Tmax	-0.15	0.365	0.56	<0.001
Jul Tmax	-0.47	0.002	-0.02	0.906
Annual WB	0.65	<0.001	0.29	0.068
Feb PDSI	0.10	0.538	0.42	0.009
Apr PDSI	0.32	0.052	0.36	0.026
Jun PDSI	0.44	0.006	-0.06	0.707

Discussion

Despite the relatively reduced extension of the study area, we identified contrasting patterns of growth variability and climate sensitivity for *Pinus pinaster* related to the geographical gradients and differences in climatic regimes within our tree-ring network. The dependence of MS on stand elevation indicated that this is a main physiographic

factor controlling growth variability of *P. pinaster* in Galicia. Stands at a lower elevation had higher MS in both EW and TR, i.e., higher year-to-year variability in tree-ring chronologies, suggesting that the effects of environmental factors limiting inter-annual variations of cambial activity decrease with increasing elevation. The reduced MS at a higher elevation is also probably a consequence of a shorter growing season imposed by lower temperatures (Chhin et al. 2008; Leal et al. 2008; Lo et al. 2010). These results agree with previous studies that found strong differences in *P. pinaster* growth patterns between coastal (low elevation) and inland (high elevation) areas of Galicia (Álvarez González et al. 2005).

The spatial coherency of climate sensitivity within the identified groups supports previous evidences from other conifers that similar growth responses may be expected within climatically homogeneous areas (Carrer et al. 2007; Littell et al. 2008). The multivariate analyses of our tree-ring chronologies generated three groups of stands characterized by their geographical distance to the littoral, and to the boundary between the Atlantic and Mediterranean biogeographical regions, which is coherent with the described patterns of water regime throughout the year (Martínez Cortizas et al. 1994). Groups W and S are similar

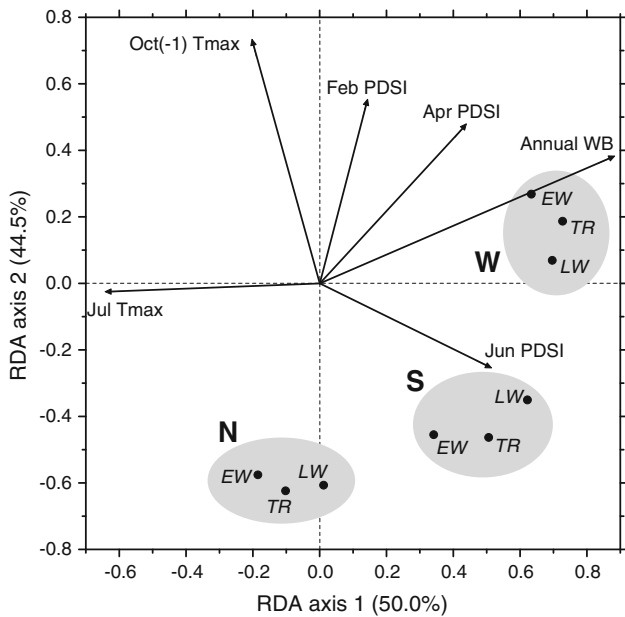


Fig. 5 Ordination diagram from RDA scores showing the relationships between *Pinus pinaster* tree-ring index chronologies for the west (W), south (S), and north (N) groups of stands and the significant ($P < 0.05$) climatic variables, according to a whole reduced RDA model. The percentage of variance accounted for by the RDA axes is shown

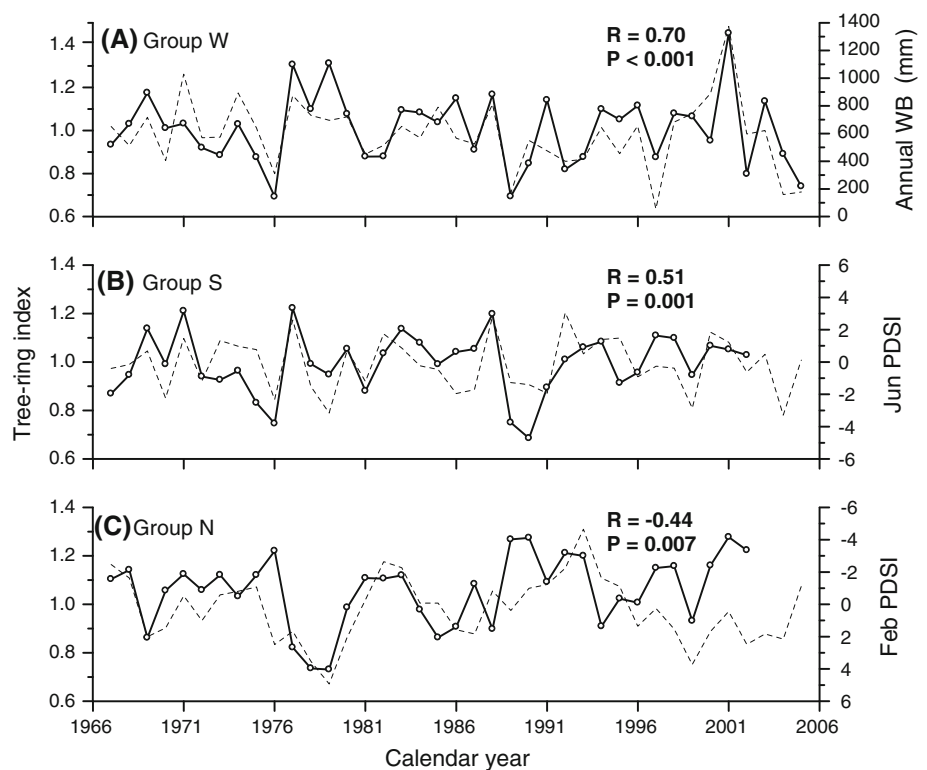
to each other, and comprise sites located close to the western Atlantic coast or southern Galicia where, respectively, higher temperatures due to low elevation or the

more Mediterranean conditions of the southern inland can lead to periods of low water availability, though less remarkable than under a proper Mediterranean climate. In contrast, group N clearly separates from these stands, and includes sites in northern Galicia, where water deficit is considerably reduced as a result of the combination of lower temperatures, recurrent fog, and abundant precipitation.

Trees in groups W and S show generalized negative responses to Tmax and positive responses to WB and PDSI, suggesting that water stress limits *P. pinaster* growth in western and southern Galicia. This result confirms previous expectations that radial growth of *P. pinaster* is mainly limited by water deficit prior to and during the active period, with characteristic positive effects of moister winter, spring and summer (Bogino and Bravo 2008; Rozas et al. 2009; Vieira et al. 2009). This situation is particularly clear in group W, where pine growth was dependent on annual water balance and soil water availability in spring, and also showed a stronger climatic signal than the other groups. The positive effect of moist previous autumns on EW growth in group W, and on TR in group S, could be a consequence of sustained photosynthetic activity at the end of the active season, resulting in a greater amount of carbohydrates stored to be used in the following active season (Zweifel et al. 2006).

Furthermore, negative relationships between Tmax and growth were generalized for group W, and in July for LW

Fig. 6 Tree-ring index chronologies of *Pinus pinaster* for total ring width (dashed lines) in the west (a), south (b), and north (c) groups of stands with the water-availability indicators (continuous lines). The correlation coefficient (R) and its significance level (P) are shown. Note the descending scale of the Feb PDSI axis in c



and TR in group S, probably due to water deficit generated by elevated temperatures in spring and summer. *P. pinaster* has a high water use efficiency in comparison with other pine species, especially mesic genotypes under humid environments, where relatively high levels of rainfall guarantee vigorous growth (Martínez-Vilalta and Piñol 2002; Tognetti et al. 2000). Common garden experiments have revealed that Atlantic populations of *P. pinaster* have a better water use efficiency and growth potential than Mediterranean ones, being able to maintain high growth rates even under moderate water stress (Correia et al. 2008). This, together with the characteristic high growth plasticity of *P. pinaster* Atlantic populations (Chambel et al. 2007), can explain the observed negative growth responses to Tmax, and positive to WB and PDSI in previous autumn, winter, spring, and summer for both groups.

As regards group N, prolonged cloudiness, frequent fogs and abundant precipitation in northern Galicia (Martínez Cortizas et al. 1994) can explain the positive effects of elevated Tmax in January, and the detrimental effects of WB, PDSI and cloud cover in winter and spring. Positive influence of high winter temperatures on pine growth has been previously interpreted as a consequence of the damage produced by freezing embolism and ice formation within the buds, with enhanced growth if they do not occur (Chhin et al. 2008; Parker et al. 2001). However, such freeze events are not expected in the study area, and snow typically occurs only at higher elevations, above the upper limit of *P. pinaster* in Galicia. In this case, the larger growth of *P. pinaster* can result from winter photosynthesis stimulated by elevated temperatures (Medlyn et al. 2002); carbon gain in winter can be allocated for growth in the following active season, which can partially explain the negative influence of water availability as an indirect effect of lower daily temperatures. The observed negative effect of water availability in late winter-spring has been previously noticed in other conifers under wet climates, such as in north-central Europe and north-western North America (Chhin et al. 2008; Mäkinen et al. 2002; Peterson and Peterson 2001; Watson and Luckman 2002). *P. pinaster* is a Mediterranean species adapted to harsh summer droughts (Martínez-Vilalta and Piñol 2002), and may be susceptible to soil water saturation and oxygen deprivation in the rhizosphere that could negatively impact nutrient uptake. However, to our knowledge, the effects of water-logging on its physiology and growth have not been studied yet; but the known adverse effects of water-logging stress on the growth and survival of *P. elliotii* var. *densa* in Florida, USA (Ford and Brooks 2002), support this interpretation. Additionally, cloudiness associated with rainy periods can notably reduce solar radiation, photosynthetic rates and the amount of photosynthates assimilated, as seems to be the case for February–April in northern Galicia. This

interpretation is supported by previous evidence that reduced solar radiation, modulated by cloudiness frequency and duration, was a primary factor limiting photosynthesis, carbon uptake, and growth during the rainy season in a tropical tree (Graham et al. 2003).

Our results suggest that conditions modulating growth activity in autumn controlled the amount of carbohydrate reserves at the end of the growing season. Climatic conditions in previous October influenced growth in groups S and N, manifested as negative response to Tmax in both groups and positive to WB in group S. Similar results on the detrimental effects of elevated temperatures in previous autumn were found in other conifers, such as *Picea abies* in northern Europe (Mäkinen et al. 2002) and *Pinus nigra* in southwest Europe (Lebourgeois 2000; Martín-Benito et al. 2010). This suggests an additional preconditioning effect related to the amount of reserves stored for the following growing season. Carbon assimilation in *P. pinaster* can occur year round, and changes in the response of stomatal conductance to vapor pressure can cause a seasonal acclimation in photosynthetic temperature response (Medlyn et al. 2002); this acclimation allows relatively high rates of photosynthesis under warm conditions. In pine species, non-structural carbohydrates and lipids built up in autumn, when radial growth has already ceased, are stored throughout the winter to be used in the following active season (Hoch et al. 2003). A warm-moist October would increase respiration rates and/or delay the end of the growing season and therefore reduce the amount of stored reserves (Lebourgeois 2000).

Although the different ecological and physiological mechanisms causing a link between environmental variability and tree growth or directly modulating tree growth behavior may be strongly site dependent (Loehle and LeBlanc 1996; Rathgeber et al. 2005), the results presented here indicate a clear and robust geographical structure of the sensitivity of *P. pinaster* growth to climate variation within the studied region. Climate appears as a main factor driving tree growth, although other site and stand factors have been shown to be also very relevant in controlling tree growth under temperate conditions (Leonelli et al. 2009; Lo et al. 2010). *P. pinaster* has very plastic physiological responses to particular combinations of climatic factors, which can largely vary among (Alía et al. 1997; Chambel et al. 2007) and within populations (Zas et al. 2004). In addition, most *P. pinaster* stands in Galicia derive from plantations established by the Forest Administration in the 1940s to 1970s, which were performed with different seed-sources from a wide variety of Iberian provenances (De la Mata and Zas 2010a). Consequently, some of the study stands could include genotypes presumably not adapted to the local climatic conditions, i.e., with a higher drought tolerance, a lower growth potential and/or a lower water

use efficiency than local mesic Atlantic provenances (Correia et al. 2008; De la Mata and Zas 2010b; Tognetti et al. 2000). Unfortunately, we were not able to determine the origin of the genetic material in these stands, and then further studies are necessary in which the role of the genetic variation is accounted for.

Conclusion

Growth responses of *Pinus pinaster* to climatic variation showed a clear geographically structured pattern, with three groups of closed sites showing different climate sensitivities. This suggests that the variability of climate regimes is important for *P. pinaster* growth within the study region near the transition between the Atlantic and Mediterranean regions. The combination of elevated maximum temperatures and reduced soil water availability is detrimental for tree performance in western and southern Galicia, where summer water deficit is more pronounced. This is a similar response to those previously described for other pine species growing at low elevations under temperate climates (Lebourgeois 2000; Parker et al. 2001). On the other hand, conditions related to water surplus during winter and early spring cause growth reduction in areas where a period of summer drought, typical of Mediterranean climate, is absent. Further investigations on the climate sensitivity of tree-ring growth combined with the characterization of population genetics and studies performed on common garden genetic trials would inform us about the adaptive value of the observed responses to the ecological conditions existing in NW Spain.

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