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Climate increases regional tree-growth variability in Iberian pine forests

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Abstract

Tree populations located at the geographical distribution limit of the species may provide valuable information about tree-growth response to changes on climatic conditions. We established nine *Pinus nigra*, 12 *P. sylvestris* and 17 *P. uncinata* tree-ring width chronologies along the eastern and northern Iberian Peninsula, where these species are found at the edge of their natural range. Tree-growth variability was analyzed using principal component analysis (PCA) for the period 1885–1992. Despite the diversity of species, habitats and climatic regimes, a common macroclimatic signal expressed by the first principal component (PC1) was found. Moreover, considering the PC1 scores as a regional chronology, significant relations were established with Spanish meteorological data. The shared variance held by the tree chronologies, the frequency of narrow rings and the interannual growth variability (sensitivity) increased markedly during the studied period. This shows an enhancement of growth synchrony among forests indicating that climate might have become more limiting to growth. Noticeably, an upward abrupt shift in common variability at the end of the first half of the 20th century was detected. On the other hand, moving-interval response functions showed a change in the growth–climate relationships during the same period. The relationship between growth and late summer/autumn temperatures of the year before growth (August–September, negative correlation, and November, positive correlation) became stronger. Hence, water stress increase during late summer previous to tree growth could be linked to the larger growth synchrony among sites, suggesting that climate was driving the growth pattern changes. This agrees with the upward trend in temperature observed in these months. Moreover, the higher occurrence of extreme years and the sensitivity increase in the second half of the 20th century were in agreement with an increment in precipitation variability during the growing period. Precipitation variability was positively related to tree-growth variability, but negatively to radial growth. In conclusion, a change in tree-growth pattern and in the climatic response of the studied forests was detected since the mid-20th century and linked to an increase in water stress. These temporal trends were in agreement with the observed increase in warmer conditions and in precipitation variability.

Keywords: climatic variability, dendroclimatology, global warming, growth pattern change, Iberian peninsula, *Pinus nigra*, *P. sylvestris*, *P. uncinata*, species distribution limit, water stress

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Introduction

Climate exerts a strong influence on the geographical distribution of plants through specific physiological thresholds of temperatures and water availability (Woodward, 1987). At the end of the 20th century many changes in phenology, distribution areas, ecological amplitude, community composition and dynamics were observed (Menzel & Fabian, 1999; Chapin *et al.*, 2000; Peñuelas & Filella, 2001; Walther *et al.*, 2002; Peñuelas & Boada, 2003). Significant links between

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these phenomena and the current climatic change have been established (Parmesan & Yohe, 2003; Root *et al*., 2003). Modeling efforts have been made to assess the impacts of global change on species distribution. Some calculations pointed out Spain as one of the regions with the most dramatic future species losses (Bakkenes *et al*., 2002). Moreover, special caution was recommended for species growing close to their distribution limits due to the failure of models to collect the complete suitable environmental range (Thuiller, 2003).

Frequently, climate becomes highly limiting to physiological processes for tree species at the edge of their natural range, because trees on these sites are particularly susceptible to climatic variations (Fritts, 1976). Our study was carried out in the Iberian Peninsula with three species located at the edge of their phytogeographical distribution area: *Pinus sylvestris* L., *P. uncinata* Ramond ex. DC and *P. nigra* Arnold subsp. *salzmannii*. The first two species, which are Eurosiberian, find in the Iberian Peninsula their southern and western distribution limit; while the latter, a typical Mediterranean pine, finds its western boundary. Distribution of the forests in the Iberian Peninsula is highly determined by the Atlantic and Mediterranean climatic influences. However, most forests are restricted to the mountainous areas where relief causes important variations to the regional climate (Blanco *et al*., 1997; Barbéro *et al*., 1998).

Annual temperatures over Europe have increased about 0.8 °C during the 20th century. A larger warming has been observed over the Iberian Peninsula (IPCC, 2001), where the 1980–1995 period was characterized by intense droughts, which produced severe damage to several woody species (Peñuelas *et al*., 2001). There has also been an increment in the mean of fire hazard indices and in the number of very high-risk days (Piñol *et al*., 1998). In general terms, exceptionally high temperatures and a great interannual climatic variability have characterized climate in the Iberian Peninsula during the second half of 20th century (Font Tullot, 1988; Romero *et al*., 1998; De Luis *et al*., 2000; IPCC, 2001; Giorgi *et al*., 2004).

We hypothesized that warming and climatic variability produced changes in tree-growth patterns, as well as in the climate response of Iberian pine forests. To answer this question, we established a network of 38 pine ring-width chronologies along eastern and northern Iberian Peninsula. Climate research generally encompasses much larger spatial and temporal scales than most ecological research studies which are local and short-term (Walther *et al*., 2002). In this context, dendroecological studies are valuable for examining long-term natural responses of plants because the length of tree-ring series provides an extended context to assess changes in tree growth (Knapp *et al*., 2001). The aims of this study were: (a) to detect the macroclimatic signal shared by all the chronologies; (b) to analyze temporal variability of radial growth and the possible climatic drivers; and (c) to assess growth–climate relationships and their stability throughout time.

Material and methods

Sampling sites and procedures

Sixty-one forest stands were initially sampled. At each site, a minimum of 15 trees were cored with an increment borer at 1.30 m high. At least two cores were taken from each tree. Sampling was focused on the oldest natural forest stands in the area. Isolated trees or trees growing in open forests were preferred to trees from dense forests. Site characteristics of the 38 selected sites (see below, chronology selection criteria) are described in Table 1A.

Chronology building

Cores were mounted and sanded until cells were clearly visible under a binocular microscope (Stokes & Smiley, 1968). All samples were visually cross-dated to avoid miscounting by missing (locally absent) or false (double) rings with the procedures described by Yamaguchi (1991). Afterwards, ring widths were measured with an accuracy of 0.01 mm using an ANIOL measuring device (Dendroware ANIOL, Schleswig, Germany) (Aniol, 1983). The resulting measured series underwent a cross-dating quality control with the statistical program COFECHA (Holmes, 1983).

The best series from each stand were selected after discarding: (a) series with abrupt growth changes in the raw data and (b) series poorly correlated with the master chronology. Then, individual series were standardized applying a spline function with a 50% frequency response of 32 years (Cook & Peters, 1981). Standardization involved transforming the ring-width value into a dimensionless index by dividing the observed by the expected values given by the spline function (Fritts, 1976). An autoregressive model was applied to remove the autocorrelation related to the previous year growth. A robust mean, which reduces the variance and bias caused by extreme values, was computed. As a result, an estimation of the common signal of all the series was obtained: the ring width chronology. Sixty-one residual chronologies were developed following this procedure using the program ARSTAN (Cook, 1985).

Chronology selection was based on two criteria: (1) reliability based on the expressed population signal criteria (EPS > 0.85, Wigley *et al*., 1984); and (2) lack of

Table 1 (A) Geographic features of the study sites. (B) Chronology characteristics*

(A) Sites				(B) Chronologies							
Site ID	Latitude	Longitude	Altitude (m)	Time span	Mean years	No. trees	No. radii	ms_x	r	Reliable time span	EPS 1885–1992
Pinus nigra											
n1	42°32′N	00°09′E	700	1819–1999	130.2	15	30	0.348	0.678	1862–1999	0.927
n2	40°07′N	01°05′W	1450	1585–1993	262	25	28	0.275	0.498	1751–1993	0.916
n3	37°48′N	02°57′W	1800	1331–2002	299.8	20	31	0.262	0.682	1602–2002	0.943
n4	40°35′N	01°47′W	1500	1817–1999	158.4	15	24	0.329	0.771	1822–1999	0.964
n5	40°17′N	00°32′W	1150	1856–1999	128.1	15	29	0.302	0.646	1866–1999	0.908
n6	37°15′N	02°30′W	1850	1653–1999	142.4	9	16	0.286	0.59	1884–1999	0.851
n7	40°40′N	00°03′W	1250	1844–1999	134.9	12	20	0.297	0.69	1853–1999	0.926
n8†	38°08′N	02°41′W	1620	1609–1994	282.4	16	23	0.292	0.514	1777–1994	0.832
n9	40°20′N	01°55′W	1370	1637–1995	260.5	16	20	0.269	0.569	1766–1995	0.879
P. sylvestris											
s1†	42°19′N	00°26′W	1450	1830–1999	102.8	16	32	0.317	0.647	1889–1999	0.801
s2†	40°48′N	00°21′E	1250	1800–2000	130.8	13	25	0.234	0.508	1897–1998	0.829
s3	42°28′N	00°29′E	1540	1786–1999	163.1	7	14	0.312	0.645	1885–1999	0.856
s4	42°48′N	00°22′W	1890	1713–1993	220.8	17	24	0.201	0.578	1798–1993	0.887
s5	43°04′N	05°15′W	1650	1633–2002	252.6	16	30	0.267	0.62	1767–2002	0.913
s6	40°14′N	00°20′W	1500	1844–2000	135.8	15	29	0.279	0.65	1855–2000	0.923
s7	41°20′N	01°01′E	950	1861–1999	78.1	18	31	0.35	0.682	1885–1992	0.857
s8	42°33′N	00°54′E	1888	1747–1995	141.6	17	36	0.27	0.624	1855–1995	0.902
s9	40°28′N	01°34′W	1645	1824–1999	123.3	14	26	0.34	0.723	1843–1999	0.917
s10	42°36′N	01°06′E	1450	1772–1999	113.2	15	37	0.294	0.643	1825–1999	0.853
s11	41°58′N	02°49′W	1750	1677–1999	196.3	14	24	0.21	0.571	1801–1999	0.865
s12	42°43′N	00°29′W	1750	1676–1993	242.3	12	16	0.257	0.578	1780–1993	0.853
P. uncinata											
u1	42°42′N	01°02′E	2390	1677–1996	170.1	14	24	0.177	0.638	1771–1996	0.921
u2	42°36′N	00°59′E	2334	1663–1995	206.7	13	25	0.186	0.616	1782–1995	0.899
u3	42°43′N	00°11′E	1890	1707–1996	197.8	9	18	0.265	0.632	1826–1996	0.862
u4	42°38′N	00°45′E	2160	1537–1994	213.8	19	32	0.192	0.546	1861–1994	0.864
u5	42°34′N	00°57′E	2210	1509–1995	252.2	21	42	0.198	0.575	1721–1995	0.923
u6	42°33′N	01°04′E	2078	1447–1996	344.5	11	20	0.182	0.533	1831–1996	0.851
u7	42°41′N	00°05′E	2000	1653–1993	218.5	17	24	0.202	0.55	1751–1992	0.885
u8	42°57′N	00°47′W	1750	1572–1999	266	16	31	0.235	0.558	1756–1999	0.899
u9	42°32′N	00°55′E	2135	1338–1997	249.7	31	59	0.167	0.581	1700–1995	0.929
u10	42°38′N	00°04′W	1900	1795–1998	156	17	34	0.22	0.583	1845–1998	0.891
u11	42°23′N	02°08′E	2075	1681–2001	177.5	20	37	0.176	0.541	1875–2001	0.884
u12	42°27′N	01°37′E	2350	1677–1997	195.5	20	39	0.193	0.602	1787–1997	0.916
u13	42°24′N	02°17′E	2080	1764–1999	150.5	11	19	0.199	0.568	1877–1998	0.851
u14	42°35′N	01°00′E	1933	1811–1996	163.7	20	40	0.221	0.7	1821–1996	0.946
u15	40°30′N	00°25′W	1890	1642–1996	242.4	22	33	0.214	0.588	1779–1996	0.897
u16	42°36′N	01°03′E	2290	1716–1995	187.2	17	19	0.17	0.537	1818–1995	0.911
u17	42°00′N	02°45′W	1950	1752–1999	189.9	17	32	0.177	0.571	1794–1994	0.896

*Time span; mean years is the average of the number of years measured in each core and gives an underestimated value of the mean age of the trees; number of trees; number of radii; interannual variability or mean sensitivity index (ms_x); mean correlation of all series with the master chronology (r); reliable time span ($\text{EPS} > 0.85$); and EPS value for the studied period (1885–1992).

[†] See 'Methodology'.

EPS, expressed population signal.

evidence of past management practices. The EPS is a statistic that quantifies the common variability present in all tree-ring series at a particular site. It expresses the proportion between the common variance of the trees (signal) and the total variance (signal + noise). All the trees in a stand are affected by the same set of climatic variables, so common information could be regarded as climatic information (Cook & Briffa, 1990). Eventually,

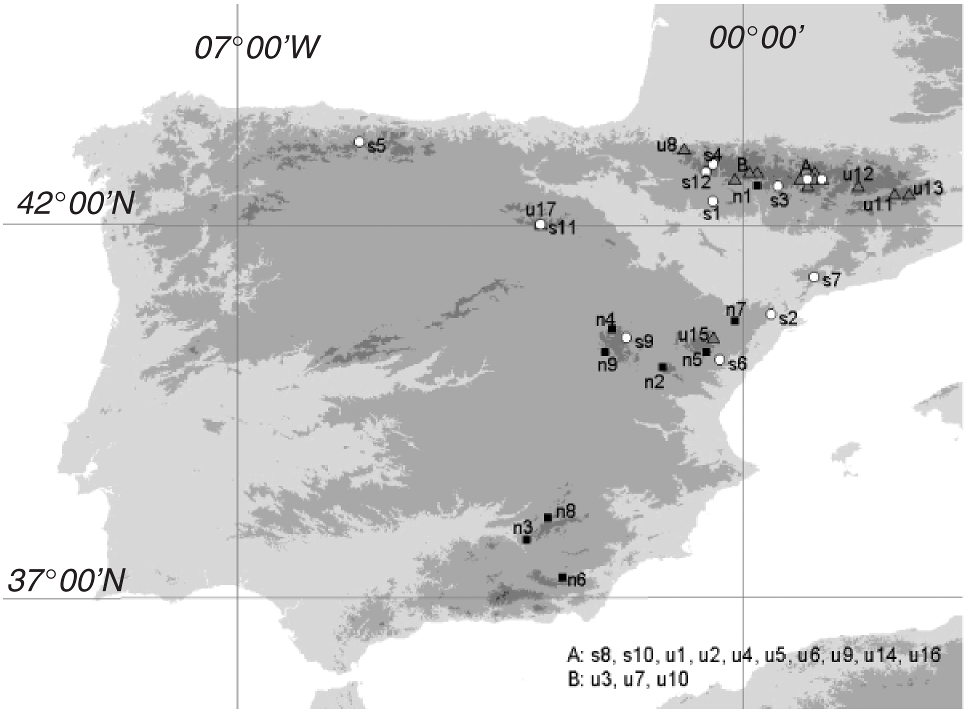

Fig. 1 Geographical position of the selected sites in the Iberian Peninsula. *Pinus nigra* stands are represented by black squares, *P. sylvestris* by white circles and *P. uncinata* by gray triangles. The A and B letters represent groups of chronology geographically closed.

38 chronologies were selected with a common timespan from 1885 to 1992 (Fig. 1). Three of them were chosen with an EPS between 0.80 and 0.85 because their quality was still good enough and all were reliable at least from 1897. These chronologies were kept due to the singularity of their location in order to achieve a better and more representative coverage of *P. nigra* and *P. sylvestris* distribution area. Descriptive statistics are presented (Table 1B) to allow comparisons among sites with other dendroclimatic data sets (Fritts, 1976; Cook & Briffa, 1990). A possible age effect was discarded in the temporal analyses of tree-growth variability and in the study of the radial growth–climate relationship stability following Carrer & Urbinati (2004) analyses procedures (results not shown).

Tree-growth variability

A principal component analysis (PCA) based on the correlation matrix was calculated for the common period 1885–1992 to evaluate the shared variance of the chronology network. PCAs also were computed separately by species: 9, 12 and 17 chronologies of *P. nigra*, *P. sylvestris* and *P. uncinata*, respectively. The broken stick test was performed to determine the significance of the components (Holmes, 1992). PCAs with all chronologies were computed for successive periods of 38 years lagged 5 years from 1885 to 1992 in order to evaluate the temporal changes of this shared variability. The use of 38-year periods was necessary because the number of observations (years) must be greater or equal to the number of variables (chronologies). The variance explained by the first principal component (PC1) was used as indicator of the similarity among the chronologies.

In order to analyze tree-growth variability, years with extreme growth values ($\pm 1.645\,\mathrm{SD}$, $P<0.1$) were identified and the annual sensitivity (s_x) was also calculated for each chronology. The s_x constitutes the relative difference from one ring-width index to the next. Sensitivity was calculated based on the formula $s_x = |I_{t+1} - I_t|\,2/(I_{t+1} + I_t)$, where I_t is the index value for the year t (Fritts, 1976). Next, all s_x series were averaged. To assess s_x trends, the mean (ms_x) and the standard deviation ($\mathrm{SD}s_x$) were computed for 38-year periods 5 years lagged. The frequency of chronologies showing extremely low ($<1.645\,\mathrm{SD}$) and high ($>1.645\,\mathrm{SD}$) indices and the temporal trends of s_x will reveal periods of lower or higher climatic influence (Tardif *et al.*, 2003).

Meteorological data

The meteorological data used were the monthly average temperature and total precipitation of Spain from TYN

CY 1.1 data set (Mitchell *et al.*, 2003). The country aggregation is based on the CRU TS 2.0 gridded data set. The gridded data were aggregated into countries using political boundaries (Mitchell *et al.*, 2001). A complete analysis of climate trends in mean values and in variability [using the variation coefficient (VC)] was done. The VC, the ratio between 100 SD and the mean (Sokal & Rohlf, 1969), is a standardized measure of data variability. Monthly temperature and precipitation VC series were calculated yearly, as well as using intervals of 38 years lagged 5 years in order to make these series comparable to the tree-growth variability results.

Tree growth–climate relationship

Correlation and response function analyses were performed using the program Dendroclim2002 (Biondi & Waikul, 2004) to quantify the climate–growth relationships between the regional chronology (PC1) and the Spanish climate series (monthly mean temperature and precipitation data) from 1902 to 2000. The same analyses were done for the PC1 scores of each species PCA.

In order to avoid the problem of multicollinearity, commonly found in multivariable sets of meteorological data, a stepwise multiple regression was computed on principal components to assess climate–growth relationships (response function; Fritts, 1976). The significances of the calculated partial regression coefficients were estimated based on 1000 bootstrapped estimates obtained by random extraction with replacement from the initial data set (Guiot, 1991). Climate–growth relationships were analyzed from the previous July up to October of the growth year.

Response functions were performed considering a 38-year fixed interval, increasing the initial and final years of the analyses by one for each iteration (Biondi, 1997, 2000). Because we used intervals of 38 years, the moving response functions had to be done separately for precipitation and temperature due to a lack of degrees of freedom corresponding to such a short period. Consequently, changes in the growth–climate relationship throughout time had to be assessed using bootstrapped correlation values. However, response function analyses were performed for two periods (1902–1949 and 1945–1992) to check that the change in the significance of the correlations was in agreement with the significance of the response function coefficients.

Results

The common variance

The PC1 and the second PC (PC2) of the chronology network PCA were significant, representing 32.5% and 13.6% of the total variance, respectively. The scatter plot of the PCA loading coefficients displayed groups of chronologies with similar growth patterns (Fig. 2). Although the chronologies showed different loadings with the PC1, all of them had positive correlations with it, showing that they shared a common variance. *P. sylvestris* chronologies were scattered, covering nearly all the range of the first axis values, most of them being in an intermediate position between *P. nigra* and *P. uncinata*. On the other hand, *P. sylvestris* and *P. nigra* chronologies were mainly positively correlated with the second PC, while most of *P. uncinata* chronologies were negatively correlated with it. When PCA was computed by groups of chronologies depending on species (*P. nigra*, *P. sylvestris* and *P. uncinata*), the first axes appeared significant (41%, 39.4% and 53.4%). In contrast, the second eigenvectors were not significant (13.5%, 14.8% and 8.7%; graphs not shown).

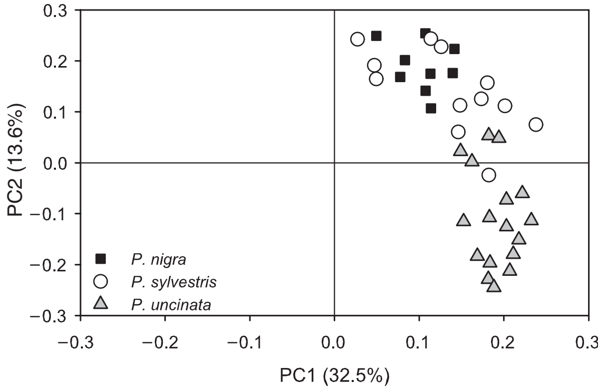

Fig. 2 Scatter plots of principal component analysis (PCA) loadings of the 38 chronologies for the period 1885–1992. Species symbols as in Fig. 1.

Temporal trends of the common variance

Figure 3 shows the evolution of the explained variance of the PC1 (i.e. the common variance among the chronologies involved in the PCA). The common variability of the chronologies showed a significant increase along the 20th century (as the fitted linear regression was highly significant, $P = 0.0001$). Moreover, an abrupt shift around the end of the first half of the century was observed. The variance explained by the PC1 increased from 28.73% in the '1925–1962' interval to 35.96% in the '1930–1967' interval (around 1949). This abrupt shift represented the maximum increment for all the studied period.

Tree-growth variability through time

The yearly relative frequency of chronologies with extreme growth indices is shown in Fig. 4. Since the

1950s, narrow tree-rings have been more frequently registered in comparison with the preceding period. This phenomenon was confirmed by sensitivity, which showed a sustained rise along the 20th century. Figure 5a shows a significant increase in ms_x and SDs_x trends along the 20th century, as the linear regressions fitted were significant. The SDs_x suffered an abrupt shift at the '1930–1967' period, showing a much greater variability of the sensitivity in the second half of the 20th century. The SDs_x shift occurred at the same period as the shift in the variance explained by PC1.

Trends in meteorological data

Figure 6 shows recent trends in monthly mean temperature and total precipitation, as well as in their VC. The slopes of the linear regressions fitted on the series (b in $y = a + bx$) were plotted to assess the significance of the trends. There were significant increases ($P < 0.01$) in annual and monthly mean temperature, but no significant trend in temperature VC series was detected (Fig. 6a). Concerning precipitation (Fig. 6b), although there was a significant ($P < 0.05$) decrement and increment in March and August precipitation, respectively, annual total precipitation did not present any trend. In contrast, significant increases in annual precipitation VC, as well as in September and October precipitation VC were found.

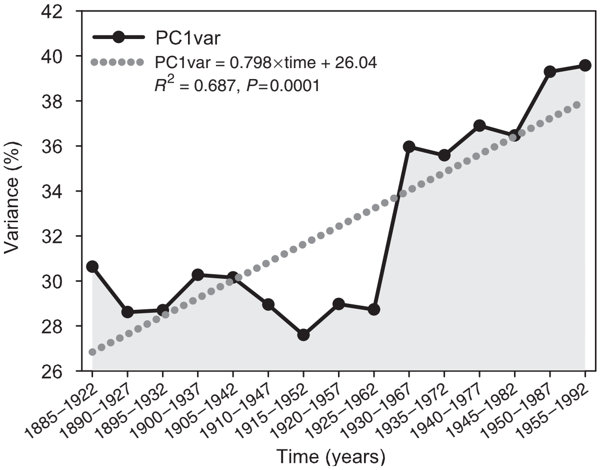

Fig. 3 Change of the variance explained by the first principal component (PC1var) using subintervals of 38 years lagged 5 years.

Radial growth response to climate

Considering the PC1 scores of the chronology network as a regional chronology for the studied area, climate–tree growth relationships were established between the PC1 and the Spanish climatic series (Fig. 7). The regional chronology showed significant responses to the climate conditions of the current summer, as well as to the late summer before the growth year. Tree growth showed significant ($P < 0.05$) response function coefficients to previous September (negative) and previous November (positive) temperatures. On the other hand, radial growth was positively correlated with July precipitation of current growth year. Correlation coefficients were also significantly negative and positive for prior August temperature and current June precipitation, respectively.

Correlation and response functions performed with the PC1 of each species showed that the three species shared the observed general pattern (Fig. 7), despite the own particular features of each one (results not shown). *P. sylvestris* and *P. uncinata* responded negatively to September and positively to November temperature. Although *P. nigra* also had the same significant correlation values with those

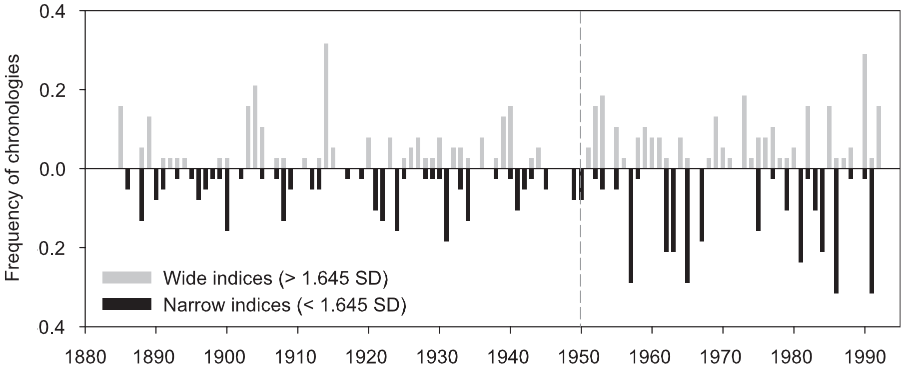

Fig. 4 Relative frequency of chronologies with wide (>1.65 SD) and narrow (<1.65 SD) ring-width residual chronology indices during the period 1885–1992.

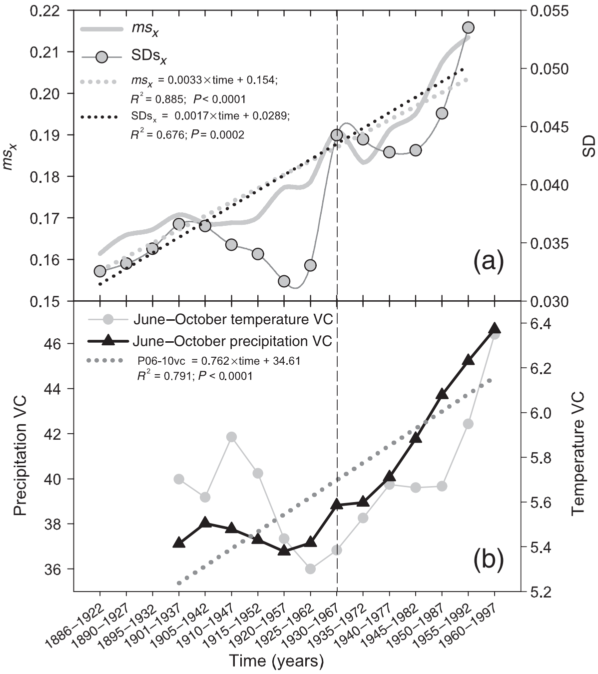

Fig. 5 (a) Temporal trends in the mean sensitivity (ms_x; gray line) and the standard deviation sensitivity (SDs_x; line with gray circles) using subintervals of 38 years lagged 5 years. (b) Temporal trends in precipitation variation coefficient (VC) from June to October (P06-10vc: black line with black triangles) and in temperature VC for the same period (gray line with gray circles).

months, the significant response function coefficients indicated that for this species growth was more affected by October temperature (negatively) and December and February temperature (positively). Concerning precipitation, July response function coefficients were significantly positive for the three species, while June was only significantly positive for *P. nigra* and *P. sylvestris*.

Radial growth response to climate through time

Figure 8 shows the evolution of the correlation values of three variables that were significant for both correlation and response function analyses (previous September and November temperature and current July precipitation). In addition, correlation values with prior August temperatures and current June precipitation (not significant for response function) are also displayed for a better understanding of changes in climate–growth relationship.

Our results indicate that the radial growth–climate relationship has varied across time. During the first half of the 20th century, correlation values between radial growth and September and November temperature previous to the growth year were negative and positive, respectively, but not significant. However, both became significant ($P<0.05$) at the '1930–1967' period (around 1949). Correlations with August temperatures became significant some years earlier than with September, but lost its significance at the end of the studied period. Conversely, radial growth correlation with current July precipitation remained stable throughout the century, while June precipitation was significant only at the beginning of the first half of the 20th century (Fig. 8c).

The three species shared the trends of prior August–September temperature and current July precipitation. However, positive correlation with summer precipitation (June and July) achieved higher values in the case of *P. nigra* and *P. sylvestris*. On the other hand, *P. uncinata* clearly showed the prior November temperature trend, while the other species did not (results not shown).

The change in the significance of the correlations along the 20th century (Fig. 8) was in agreement with the results of the response function analyses performed for two periods (1902–1949) and (1945–1992). Prior September and November temperature and current July precipitation only had significant response function values in the second period. In the first period, response coefficients of current July precipitation were also high, but very low values were found for prior September and November temperatures. In contrast, during the growth year high coefficients were found for June temperature and precipitation (results not shown).

Precipitation variability

Figure 5b shows the precipitation VC during the growing period (from June to October, according to the correlation and response function results, Fig. 7). A significant increase in the precipitation VC was detected along the 20th century, shown by the significance ($P<0.0001$) of a fitted linear regression. The temperature VC during the growing period, one order of magnitude below precipitation VC, presented a slight increase since the second half of the 20th century. However, this increase was not significant.

The relationship between the growing period precipitation VC and the annual sensitivity (s_x) is shown in Fig. 9a, whereas Fig. 9b shows its relationship with the regional chronology (PC1 scores). PC1 was significant and negatively related to June–October precipitation VC, while s_x was significant and positively related to it.

Discussion

The macroclimatic signal

Our chronologies were built from a wide range of forests considering that three different species were

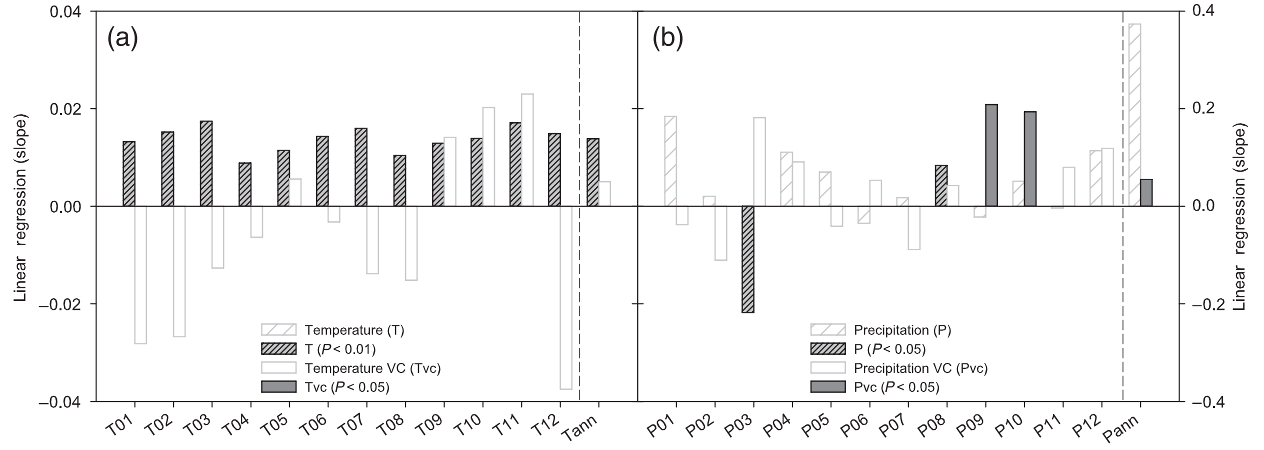

Fig. 6 Recent trends (slope of the linear regression; *b* in $y = a + bx$) in annual and monthly mean temperature and total precipitation, as well as in temperature variation coefficient (VC) and precipitation VC series.

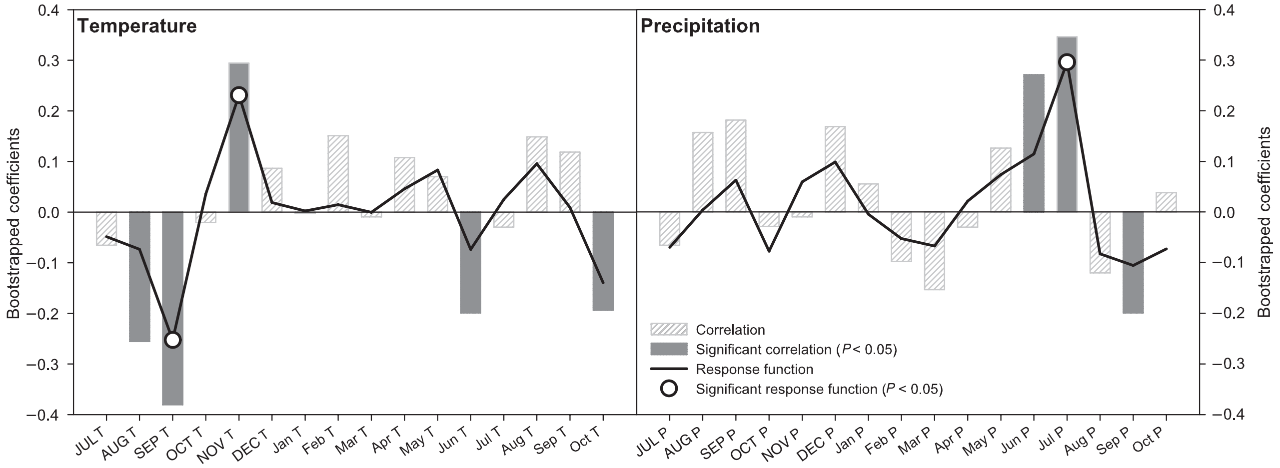

Fig. 7 Bootstrapped correlations (bars) and response functions (lines) performed between the first principal component (PC1) and monthly climate data from prior July to current October. Capitals: prior year months; lowercase: current year months. Significant correlation and response function coefficients ($P < 0.05$) are indicated with gray bars and white circles, respectively.

sampled in sites with different features and under different climatic influences. Despite all those factors, the PC1 contained a significant percentage of common variance shared by all the chronologies (Fig. 2). One of the main dendrochronological principles is the assumption that common information shared among trees in a stand could be regarded as climatic information. On a broader scale, the common variability shared by the 38 chronologies across the Iberian Peninsula should be caused by climate. Macroclimate seems the only reliable factor that could be influencing all these chronologies spread along the north and east of the Peninsula. Although our main result was the finding of a common climatic signal, tree-growth similarities among chronologies of the same species also were observed, as well as dissimilarities among chronologies of different species. Other authors have reported similar results (Gutiérrez, 1990; Schweingruber *et al*., 1991 in Tessier *et al*., 1997).

Temporal variability of radial growth

The variance held in common by the tree chronologies (macroclimatic signal) was not stable throughout time: it increased markedly during the studied period (Fig. 3). A maximum upward increment around the end of the first half of the 20th century ('1930–1967' interval) drew a clear shift between the two halves of the century. Up to a certain threshold, similarities among chronologies should increase under more limiting climatic conditions

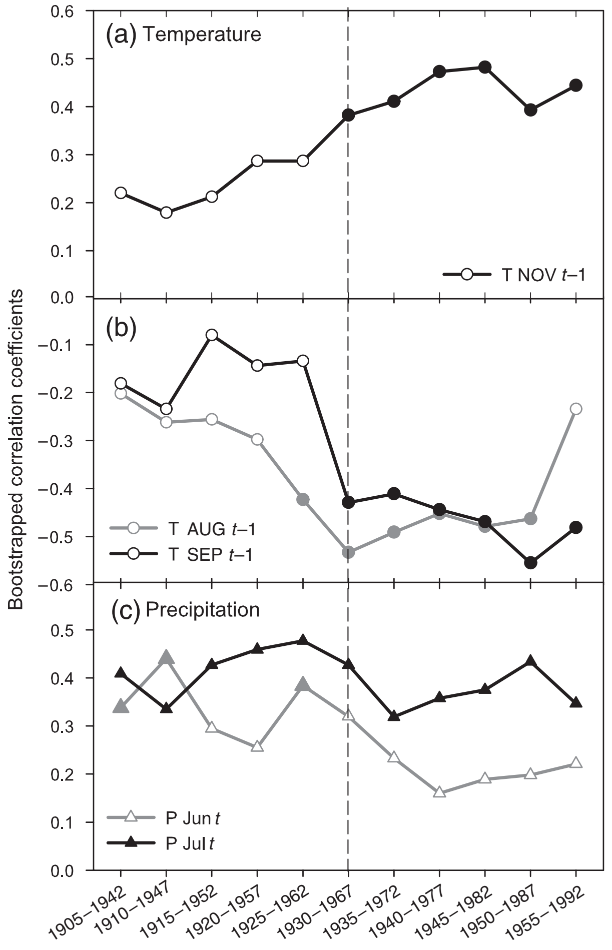

Fig. 8 Temporal changes in bootstrapped correlation coefficients using intervals of 38 years lagged 5 years of previous November temperature (a); August and September temperature before ring formation (b); and current June and July precipitation (c). Filled symbols: significant correlation coefficients ($P < 0.05$).

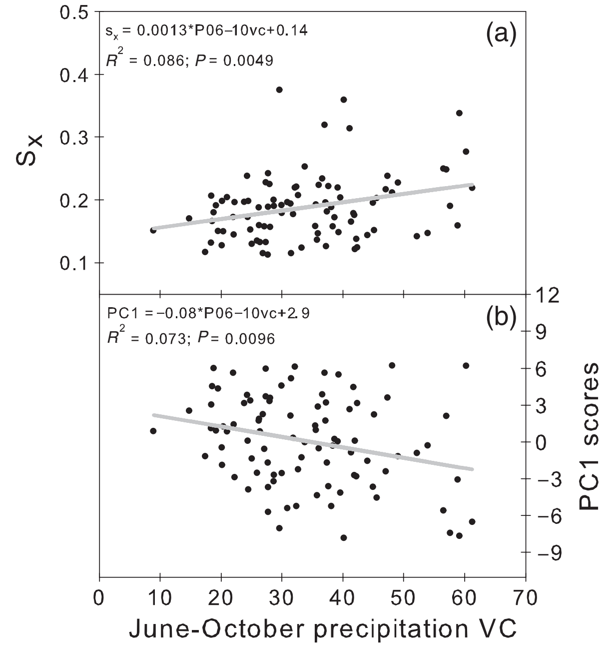

Fig. 9 (a) Relationship between annual sensitivity (s_x) and June to October precipitation variation coefficient (VC) (P06-10vc). (b) Relationship between PC1 scores and June to October precipitation VC (P06-10vc).

(Tardif *et al.*, 2003). Shared growth variability can be interpreted as a common response to regional climatic signals (Tardif *et al.*, 2003; Macias *et al.*, 2004), and its changes along the 20th century as a signal of climatic changes which have affected the growth of the forests (Macias *et al.*, 2006). Therefore, a higher common variance indicates that the sampled forests were growing more synchronously in the second half of the 20th century, suggesting that climate has become more limiting to growth.

Similarly, the frequency of narrow rings (Fig. 4), as well as interannual growth variability (Fig. 5a) also rose along the 20th century. The increment in the frequency of extremely narrow rings suggests that during the second half of the 20th century there were more years in which climatic conditions limited tree growth. As a consequence, narrower rings were produced in more forests during these years of unfavorable growing conditions. The dramatic increment of the SDs_x in the '1930–1967' period denotes that not only the ms_x stepped up along the 20th century, but also its variability in the second half was appreciably superior.

Climate conditions might have become more limiting to growth since the mid-20th century, as suggested by increasing similarity among the tree chronologies. Yearly climatic variability has also increased as illustrated by the higher sensitivity and extreme growth indices recorded by the trees. Thus, growth pattern changes of three different species have been detected in the Iberian Peninsula supporting the idea that climate is the main cause because nonclimatic explanations decline at increasing spatial scale and species number (Parmesan & Yohe, 2003). The significant increases observed in monthly mean temperatures and in annual precipitation variability (Fig. 6) could have been some of the climatic factors limiting growth in the second half of the 20th century. However, the establishment of climate–growth relationships is essential to set up a significant link between the growth pattern change and climate.

Climate–growth relationship

Pine forests response to summer drought seems to be general for the three species as inferred from the response functions. Radial growth was constrained by water stress during summer previous to growth, as suggested by the negative relationship with previous September temperature, and to a lesser degree, by a positive relationship with precipitation at the end of the summer (Fig. 7). Our results reveal that warm late summers can prolong the growing season, limiting the formation of metabolic reserves and consequently affecting radial growth in the following year (Fritts, 1976). These results have been corroborated by a previous study of tree-ring phenology and structure in Pyrenees (Camarero *et al*., 1998). On the other hand, July precipitation of current year was positively associated with radial growth, showing that precipitation is crucial during the year of ring formation. *P. sylvestris* and *P. nigra* presented a stronger positive relationship with current June–July precipitation than *P. uncinata*, suggesting that they may be more susceptible to deficits in the water balance. In agreement with these findings, the former species are located in drier sites than *P. uncinata*, which lives at higher elevations, where evapotranspiration is lower. The obtained climate–growth relationships using regional climate series agree with those performed using local climatic series in the Pyrenees (Camarero, 1999; Tardif *et al*., 2003) and the east of Spain (Gutiérrez, 1989; Richter & Eckstein, 1991).

Change in climatic response

Moving interval response functions suggest an extension of the water-stress period from mid-summer to late summer (from August to September temperature) and a strengthening of the climate–growth relationship. Tree-growth has increased its negative correlation with prior September temperature and its positive correlation with prior November temperature along the 20th century (Fig. 8). Moreover, the most remarkable result was that correlation values became significant in the '1930–1967' period (around 1949). This change in the climatic response was produced at the same time that the change in the tree-growth pattern described above. While the evolution of the correlation coefficients with prior August–September temperature was common for the three species, the November temperature correlation trend was particular for *P. uncinata*. Therefore, excluding November temperature, late summer temperatures previous to growth may be the climatic driver of the observed tree-growth pattern change among forests in the Iberian Peninsula, indicating an increase in water stress effects on radial growth during the last half of the 20th century. These findings were in agreement with the significant temperature increases observed in these months (Fig. 6a). Similarly, enhanced *Abies alba* water stress has been reported in northern Spain (Macias *et al*., 2006). Another study in Alaska also pointed out that temperature explained more variability in white spruce radial growth after 1950, suggesting that a true climatic control was involved (Wilmking *et al*., 2004).

Precipitation variability

In agreement with the observed tree-growth pattern (Figs 3, 4 and 5a), precipitation variability during the growing period presented an increasing trend along the 20th century (Fig. 5b). Consistent with our results, Font Tullot (1988) reported in the Iberian Peninsula an increase in the frequency of extreme climatic events (high temperatures, frosts, droughts) in the second half of the 20th century. Other authors have found an increase in climatic anomalies during the last 50 years (Manrique & Fernández-Cancio, 2000). The increment in precipitation variability may induce an increase in common tree-growth variation among the forests, as well as in the tree-growth variability through time. According to this, s_x values were positively related to the precipitation VC of the growing period (Fig. 9a). On the other hand, it is noteworthy the negative effect that precipitation variability may have over tree growth (Fig. 9b), suggesting that climatic variability could also be a factor limiting tree growth. Therefore, our results highlight that two factors could have been limiting radial growth during the second half of the 20th century: (1) an underlying upward trend of mean temperatures that enhances water stress during previous late summer; and (2) an increase in precipitation variability during the growing period. These results agree with the increase in warmer conditions (IPCC, 2001; Giorgi *et al*., 2004) and climatic variability (Font Tullot, 1988; Romero *et al*., 1998; De Luis *et al*., 2000) described in Spain.

Increases in temperature and in the frequency of extreme climatic events are expected in Europe (IPCC, 2001). In this context, the intensification of warming in a longer term could lead to the elimination of drought-susceptible trees (Barber *et al*., 2000) through stress-related mortality (Wilmking *et al*., 2004). On the other hand, extreme weather and climate events have been linked to biological changes (Easterling *et al*., 2000), like for example, a severe drought in 1994 that caused important damages and even mortality in Spanish forests (Martínez-Vilalta & Piñol, 2002; Lloret *et al*., 2004). Considering that we showed that our forests are highly sensitive to warming and climatic variability, new climatic conditions could bring serious consequences for Iberian forests growth dynamics.

Finally, the stability of the significant relationship between current July precipitation and growth highlights the possibility of realistic reconstructions of summer precipitation in Iberian Peninsula using a network of tree-ring width chronologies. However, special caution is recommended for temperature reconstruction due to the instability of its relationship with radial growth. Similarly, other authors also pointed out that some climate reconstructions based on ring width could miscalibrate past climate (Tardif *et al.*, 2003; Wilmking *et al.*, 2004).

Conclusions

Despite the diversity of species, habitats and climatic regimes, our chronologies shared a common macroclimatic signal expressed by the first PC. The shared variance held by the tree chronologies and the interannual growth variability increased markedly during the studied period. This enhancement of growth synchrony among forests indicates that climate might have become more limiting to tree ring formation. Noticeably, the upward abrupt shift in common variability at the end of the first half of the 20th century happened at the same time as an enhancement of the prior August–September temperature influence over radial growth. Consequently, the greater similarity in tree-growth may be linked to a strengthening of water stress during late summer previous to the ring formation that agrees with the temperature increasing trend observed in these months. Moreover, the higher occurrence of extremely narrow rings and the sensitivity increase coincided with an increment of the precipitation variability during the growing period. Precipitation variability was positively related to tree-growth variability, but negatively to radial growth. Therefore, at least two climatic factors could have been limiting tree growth and driving the observed changes in growth pattern and in climatic response of the studied forest during the second half of the 20th century: the increasing trends observed in mean temperatures and the increment detected in precipitation variability during the growing period.

The absence of temporal stability in some growth–climate relationships may be critical and should be considered for reconstructions of past climatic conditions using tree-ring widths. The analysis of the temporal trends of shared variance among chronologies, as well as other tree ring characteristics should be taken into account to improve the reliability of the reconstructions.

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