Climate increases regional tree-growth variability in Iberian pine forests

LAIA ANDREU*, EMILIA GUTIÉRREZ*, MARC MACIAS†, MONTSE RIBAS*, ORIOL BOSCH* and J. JULIO CAMARERO
*Departament d’Ecologia, Universitat de Barcelona, Avinguda Diagonal 645, 08028 Barcelona, Spain, †Department of Geology, Faculty of Science, University of Helsinki, Gustaf Hallströminkatu, 2, 00014 Finland, ‡ARAID, Instituto Pirenaico de Ecología, CSIC Avda. Montan˜ana, 1005 Zaragoza 50192, Spain

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

Received 13 February 2006; revised version received 14 June 2006 and accepted 28 August 2006

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...
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 Arn 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 ( Penalva 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 the 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
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,
38 chronologies were selected with a common time-span 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 (±1.645 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

\[ s_x = \left| I_{t+1} - I_t \right| / \left( I_{t+1} + I_t \right) \]

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 (SDs~x~) were computed for 38-year periods 5 years lagged. The frequency of chronologies showing extremely low (<1.645 SD) and high (>1.645 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

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**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.
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).

**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 \( SD_x \) trends along the 20th century, as the linear regressions fitted were significant. The \( SD_x \) 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 \( SD_x \) 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 \( (b \text{ in } y = a + bx) \) 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.

### 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). \( P. \text{sylvestris} \) and \( P. \text{uncinata} \) responded negatively to September and positively to November temperature. Although \( P. \text{nigra} \) also had the same significant correlation values with those...
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
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.
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 in the '1930–1967' period denotes that not only the msx 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 (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. Treerowth 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 temperature 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* 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.

Acknowledgements

We are very grateful to Octavi Planells, Pete Fule and Salvador Puyo for the constructive and critical comments; to Elena Muntán for their help during fieldwork and chronology building and to José Creus for his contribution to the ForMAT database. Data were collected during the CICYT Spanish project (Contract AMB95-0160); EU ForMAT project (Contract ENV4-CT97-0641) and EU ISONET project (Contract EV K2-2001-00237). The authors acknowledge two anonymous referees for their suggestions that helped to improve the original version of the paper.

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