Drought-induced weakening of growth-temperature associations in a high-elevation pine network across the Pyrenees

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ABSTRACT

The growth/climate relationship of theoretically temperature-controlled high-elevation forests has been demonstrated to weaken over recent decades. This is likely due to new tree growth limiting factors, such as an increasing drought risk for ecosystem functioning and productivity across the Mediterranean Basin. In addition, declining tree growth sensitivity to spring temperature may emerge in response to increasing drought stress. Here, we evaluate these ideas by assessing the growth/climate sensitivity of 1500 tree-ring width (TRW) and 102 maximum density (MXD) measurement series from 711 and 74 *Pinus uncinata* trees, respectively, sampled at 28 high-elevation forest sites across the Pyrenees and two relictic populations of the Iberian System. Different dendroclimatological standardization and split period approaches were used to assess the high- to low-frequency behaviour of 20th century tree growth in response to temperature means, precipitation totals and drought indices. Long-term variations in TRW track summer temperatures until about 1970 but diverge afterwards, whereas MXD captures the recent temperature increase in the low-frequency domain fairly well. On the other hand summer drought has increasingly driven TRW along the 20th century. Our results suggest fading temperature sensitivity of Iberian high-elevation *P. uncinata* forest growth, and reveal the importance of summer drought that is becoming the emergent limiting factor of tree ring width formation in many parts of the Mediterranean Basin.

Key-words: climate change; drought; growth response; high-elevation forest; Pyrenees; summer temperature

46 *Highlights:*

- 47 • 1500 TRW and 102 MXD series were collected at 30 sites across the Pyrenees
- 48 • Growth/climate relationships were assessed on high- to low-frequency domains
- 49 • Summer temperatures and MXD increased after the 1970s, whereas TRW decreased
- 50 • Warming-induced drought constraints on TRW formation increased along the 20th
- 51 century

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1. Introduction

Trees growing in cold-limited environments such as high-latitude forests and the arctic and alpine ecotones can record temperature variations in their annual ring width (TRW) and maximum latewood density (MXD) (Fritts, 2001). In fact, temperature might be the main climatic driver of tree growth and thus it constrains wood formation during overall short growing seasons (Körner, 2012). Old growing treeline species, are therefore regarded as reliable proxy archives that enable annually resolved temperature reconstructions to be continuously developed for several centuries to millennia (Briffa et al., 1990; Esper et al., 2002). At the European-scale, several examples from the high-northern latitudes in Fennoscandia (Briffa et al., 1990; Grudd, 2008), and higher elevations along the Carpathian arc (Büntgen et al., 2007, 2013; Popa and Kern, 2008) and the Alps (Rolland et al., 1998; Büntgen et al., 2005, 2006; Corona et al., 2010) have demonstrated the palaeoclimatic potential of tree rings.

Mid-latitude areas are, however, affected by different climatic influences derived from tropical air-masses moving towards the poles and polar air-masses moving towards the equator; this causes most of the mid-latitude areas being alternately influenced by arid and humid conditions, with periodic droughts. Complex growth/climate relationships are therefore known for areas like the Mediterranean Basin or the Sierra Nevada in California (Tardif et al., 2003; Bunn et al., 2005; Carrer et al., 2010; Büntgen et al., 2012). In these ecosystems, daily to seasonal precipitation changes can mediate intra and inter-annual patterns of forest growth, and summer drought can be strong enough to even interrupt cell formation (Nicault et al., 2001; De Luis et al., 2007). It remains unknown if such drought-induced growth responses also occur in high-elevation forests of the Mediterranean mid-latitudes and may even affect water-

saturated upper treeline sites. If true, such hydroclimatic stressors would question the consistency of temperature reconstructions based on tree rings from high-elevation areas at mid-latitudes.

Spatiotemporal instability in growth/climate relationships, the so-called divergence phenomena (D'Arrigo et al., 2008), may indeed be magnified by predicted future drought across the Mediterranean Basin (Lebourgeois et al., 2012), which would dampen the temperature control of tree growth. Testing the hypothesis of recently more complex growth/climate relationships in Mediterranean mountain forest ecosystems is, however, complicated by the scarcity of high-elevation sites that were temperature-controlled in this area (Körner, 2012). The Pyrenees constitutes the only mountain system where undisturbed temperature-driven upper treelines can be found south of the Alpine arc.

Here we seek to assess if the growth/climate relationship in a high-elevation network of *Pinus uncinata* forest sites across the Pyrenees changed over the last century and, if so, to pinpoint the relevant drivers. We compile TRW chronologies from 30 sites and MXD measurements from six of these sites between 1750 and 2451 m asl. Various tree-ring detrending and chronology development techniques, together with split-period approaches and multiple intra-annual intervals are evaluated to assure that the observed associations between tree growth and climate are not artificially induced or spatiotemporally biased.

2. Materials and methods

2.1. Study species and sites

Pinus uncinata Ram. is a long-lived, slow-growing and shade-intolerant conifer with a large ecological amplitude concerning topography and soil type (Ceballos and Ruiz de la Torre, 1979). In this species ca. 80% of the annual width is formed during June and July and latewood formation lasts from July up to October (Camarero et al., 1998). Warm autumn and spring temperatures before and during ring formation enhance *P. uncinata* radial growth in Pyrenean forests (Tardif et al., 2003). We sampled 30 *P. uncinata* sites of which 27 sites are located in the Pyrenees, one site is in the Pre-Pyrenean Sierra de Guara and two southern relict populations are located in the Iberian System (Fig. 1). Data cover the whole geographical range of the species in the Iberian Peninsula and thus capture most of the ecological variability experienced by this species (Table 1). Most of the Pyrenean sites (18 sites) were located within or near protected areas, ensuring that these populations are not likely to have been logged for much of the 20th century. Specifically six sites were sampled within or near the Ordesa y Monte Perdido National Park (PNOMP; 42°40'N, 00°03'E; established in 1918), and twelve sites were sampled in the Aigüestortes i Estany de Sant Maurici National Park area (PNAESM; 42°35'N, 00°57'E; established in 1955). Pyrenean *P. uncinata* forests are usually low-density open-canopy stands located in steep and elevated sites forming isolated patches near the alpine treeline. The macroclimate of the Pyrenees is strongly influenced by east–west and north–south gradients with increasing Mediterranean conditions (e.g. warm and dry summers) eastwards and southwards, whereas continental conditions (e.g. cold winters) prevail in the Central Pyrenees. These diverse climatic influences explain the high climatic heterogeneity of this area (López-Moreno et al., 2008). Mediterranean summer drought is more prevalent at PNOMP than at PNAESM sites (Balcells and Gil-Pelegrín, 1992). Mean annual temperature and total precipitation

in the studied sites ranged from 2.0 to 4.9 °C and from 1200 to 2000 mm, respectively, with January and July as the coldest (mean -2.0 °C) and warmest (mean 12.5 °C) months respectively (Camarero, 1999). The relict populations of Teruel and Soria and the Prepyrenean site Guara are subjected to typically Mediterranean conditions such as warm and dry summers.

2.2. Field sampling and dendrochronological methods

We sampled 711 living trees between 1994 and 2011. At each site, five to 65 dominant (i.e. with crowns above the general level of the canopy) trees (mean $\pm$ SD = 24 ± 14 sampled trees per site) were randomly selected. The number of sampled trees per site depended on the availability of suitable trees within each site. All trees were cored with a Pressler increment borer taking two or three cores per tree ($n = 1500$ cores, mean $\pm$ SD = 47 ± 27 sampled cores per site). Each core was mounted and sanded with progressively finer grain until tree rings were clearly visible (Stokes and Smiley, 1968). Samples were then visually cross-dated and measured to a precision of 0.01 mm using a LINTAB measuring device (Rinntech, Germany). Cross-dating was evaluated using the program COFECHA (Holmes 1983), which calculates cross correlations between individual series of each core and a master chronology. For the MXD measurements, we cored a subsample ($n = 74$ trees) by taking cores perpendicular to the stem from 6 sites (4 sites located in PNAESM plus 2 sites from PNOMP) with a thicker Pressler increment borer (10 mm diameter); MXD cores were glued onto wooden supports and thin wooden laths (1.2 mm) were cut with a twin-bladed saw. Density was measured with an Itrax MultiScanner from Cox Analytical Systems (<http://www.coxsys.se>), where laths are scanned using a focused high-energy x-ray beam. The radiographic image is

analyzed with the software WinDendro (Regent Instruments, Canada), which performs a light calibration of the grey values using a calibration wedge (Grudd, 2008).

2.3. Tree-ring data and detrending

Since we only collected MXD data from the Pyrenees (Tables 1 and 2), we combined all the MXD series in one single chronology set called *Pyrenees*. For its part, TRW was assigned three different chronology subsets depending on the geographical location of the sampled sites: (i) the whole network of 30 sampled sites, (ii) the 27 Pyrenean sites, and (iii) the 15 PNAESM sites; hereafter called *AllSites*, *Pyrenees* and *Aigüestortes* subsets respectively. As explained before, PNOMP is more influenced by Mediterranean and drier conditions than PNAESM; therefore, and in order to assess possible Mediterranean drought influences, we used an additional TRW subset called *Ordesa*, derived from a compilation of the series coming from the six PNOMP sites. Apart from the geographical reason, the *Aigüestortes* subset was taken considering also the relative robust convergence of the principal components scores of the PNAESM sites in the two dimensional space of a principal component analysis, based on the covariance matrix of the chronologies of all sampled sites, and considering their common period 1901-1994 (see yellow symbols in Figure A1). The first and second principal components explained 47.2% and 8.1% of the whole site growth variability, respectively. Sites near the distribution limits of the species (e.g. GU, TE, CN, PA) are arranged at relatively lower altitudes (i.e. PC1 scores). Although the chronologies showed different loadings with the PC1, all of them had positive correlations within it, showing that they shared a common variance.

To remove tree-age related, non-climatic growth trends from the raw TRW and MXD measurement series (Cook and Kairiukstis, 1990), and to assess the effects of different standardization techniques on the final chronology shape, we applied several detrending methods using the ARSTAN program (Cook and Holmes, 1986). Specifically, we preserved variability at inter-annual to multi-decadal scales detrending each TRW and MXD individual series by means of cubic smoothing splines with 50% frequency-response cutoffs equal to 150 and 300 years (Cook and Peters, 1981). A negative exponential function detrending was also applied together with an alternative linear regression of slope of any sign (detrending called hereafter ‘negative exponential 1’) or with an alternative linear regression of negative slope (‘negative exponential 2’). We also applied the age-aligned regional curve standardization (RCS; Esper et al., 2003) for preserving inter-annual to centennial-scale variability.

For these different detrendings, dimensionless indices were calculated as residuals from the estimated growth curves after power transformation (pt) of the raw measurements (Cook and Peters, 1997), and as ratios after using the raw measurements without any transformation (nt). Summarizing, we applied ten different detrending methods (see table A1). We performed a variance stabilization technique to every chronology for minimizing the putative effects of changing sample size throughout time (Frank et al., 2007). Mean chronologies were then calculated using a bi-weight robust mean (Cook, 1985). We applied the Expressed Population Signal (EPS) calculated over 30-year windows lagged by 15 years to estimate signal strength of these records (Wigley et al., 1984). Throughout the paper, unless otherwise stated, we refer to TRW chronologies derived from the whole sampled network (i.e. *AllSites* TRW subset).

2.4. Instrumental target data and growth-climate response analyses

Monthly temperature (mean, maximum and minimum) and precipitation data (CRUTS3.10; Harris et al., 2013) were used for growth/climate response analysis. We considered 0.5° resolution grid-box data covering the different sampled sites. We also used the standardized precipitation evapotranspiration drought index (SPEI; Vicente-Serrano et al., 2010), calculated from the CRUTS3.20 dataset. Drought conditions are influenced by factors like temperature, relative humidity, evapotranspiration, wind speed, etc. The Standardized Precipitation Index (SPI) only takes on account the precipitation, thus neglecting the importance of other influential variables. The use of drought indices that include temperature data in their formulation, such as the Palmer Drought Severity Index (PDSI) seems to be preferable to identify warming-related drought impacts on ecological systems (Vicente-Serrano et al. 2010), specially taking on account the global temperature increase of recent decades. However, drought is a multi-scalar phenomenon since the time period from the arrival of water inputs until the water is available differs considerably (McKee et al. 1993). Thus, the time scale over which water deficits accumulate becomes important. The PDSI lacks the multi-scalar character of the SPI; the SPEI, first proposed by Vicente-Serrano et al. (2010) overcomes this limitation, combining in its formulation the sensitivity of PDSI to changes in evaporation demand caused by temperature with the multi-temporal nature of the SPI. Negative (positive) SPEI values correspond to dry (wet) conditions.

All the TRW and MXD chronologies (derived from the different detrendings and subsets) were correlated against monthly and seasonal means of maximum, mean, and minimum temperatures and totals of precipitation. We restricted the analyses to the period 1901-2009, which covers the available CRU data period. We used monthly data

from October of the previous year to September of the current year and seasonal means performed from March to September, including therefore the growing season. We also correlated the chronologies to the SPEI index for the 12 months of the year at different time scales from 1 to 24 accumulated months, covering the same period. In order to assess the temporal stability in the growth/climate relationships along the second half of the 20th century, we performed the correlations with climate in two independent 40-year subperiods: 1930-1969 and 1970-2009. We quantified spatial correlation fields between the tree-ring series and monthly and seasonal climatic variables for different periods using the web Climate Explorer (<http://climexp.knmi.nl>). We further evaluated instability in the growth/climate relationship by calculating 31-year moving correlations between growth (TRW, MXD) and climate variables (temperature, SPEI).

3. Results

3.1. Chronology characteristics

TRW (MXD) chronologies span from 1270 to 2010 AD (1407 to 2009 AD), with a mean length of 240 (192) years. TRW (MXD) series have a mean $\pm$ SD annual value of 0.66 ± 0.11 mm (0.77 ± 0.39 g cm⁻³) and a series inter-correlation of 0.44 (0.40). In both TRW and MXD, the eight different spline and exponential detrendings showed a very similar shape (Fig. A2); hence we averaged them in a single chronology, hereafter abbreviated as *TRWmean* and *MXDmean*. Raw and RCS TRW chronologies show the typical negative exponential trend until ~1450; from then on, RCS chronologies grow with a long and steady positive trend (Fig. 2a). From the 1950s onwards, all the TRW chronologies decline until the present. Raw and RCS MXD chronologies show a negative trend until ~1700, and then they rise up to the 1950s before decreasing again.

Since the 1970s all the MXD chronologies start trending upwards up to the present. (Fig. 2b). These results are essentially the same as the ones observed in the *Pyrenees* and *Aigüestortes* subsets (not shown). This MXD pattern is related to the temperature trends found over the 20th century in Europe: increasing temperatures until the 1950s followed by a decrease until the 1970s and a second increase from the 1970s until nowadays (IPCC 2013). These patterns are consequently observed in series of tree ring proxies (e.g. MXD) of temperature sensitive sites like the Alps, Scandinavia or the Pyrenees, and also in the temperature series of their subsequent climatic reconstructions (Corona et al. 2010; Büntgen et al. 2008a, 2011; Dorado-Liñán et al. 2012). The RCS chronologies highlight the decrease in TRW in the transition between the warm Medieval Climatic Anomaly and the cold Little Ice Age (LIA) starting in 1300 AD and lasting until 1850 AD, where temperatures started to increase again (Moreno et al., 2012). Both TRW and MXD chronologies display a valley shape in 1816 following the eruption of Mount Tambora in 1815, which caused the “year without summer” (Trigo et al., 2009). There is another sharp decrease in TRW and MXD around 1700 AD. The decrease in growth in the last 50 years is not unprecedented and lower growth rates occurred in some periods over the LIA, for instance during the fifteenth century (Fig. 2a). Expressed population signal (EPS) and signal-to-noise ratio (SNR) are very consistent among the 10 different detrendings (Table 3). TRW (MXD) chronology stays above the 0.85 EPS threshold since 1500 (1777) AD (Figs. A3 and A4). Mean segment lengths of the TRW site chronologies show how aging trees display a decreasing growth rate (Fig. A5), and proves the existence of a single biological-growth population portrayed by the sampled sites (Esper et al., 2003).

3.2. Growth-climate responses patterns

TRW and MXD are mainly influenced by previous-year November, May and September temperatures (Fig. 3). Similar results were found for the *Pyrenees*, *Aigüestortes* and *Ordesa* subsets (not shown). Among the different detrendings applied, RCS shows a smaller or even negative correlation between TRW chronologies and temperature. This indicates that a divergent behaviour in the recent decades between TRW and temperature is more evident when using RCS chronologies than with the other detrendings.

MXD displays higher correlations with temperature than those for the TRW. Monthly correlation analysis highlights the main influences of previous-year November and current-year May, June and September temperatures on MXD, with May being the most prominent month (Fig.3b). Contrary to the TRW, the different MXD detrendings display the same sign and behaviour in their climate correlation functions (Table 3), although RCS detrending brings the highest correlations with temperature for MXD in the second subperiod. This, and the fact that TRW RCS chronologies record a divergent behaviour with temperature more clearly than other detrendings, caused us to focus our analyses mainly on the RCS chronologies.

Growth/precipitation correlations are found to be minor compared with those found for temperature, in both TRW and MXD data sets (not shown). Contrastingly, SPEI gives higher correlations than precipitation (Fig. 4). The main drought driver of TRW of Iberian *P. uncinata* forests is the SPEI for June and July accumulated at scales from one to two months, specially for the period 1901-2009 and the sub-period 1930-1969 (Fig. 4). As we pointed out before, PNOMP area has stronger Mediterranean influences than PNAESM area. Correspondingly, TRW from the *Ordesa* subset shows

this Mediterranean background in the TRW-SPEI relationship (using SPEI data covering the PNOMP area), where the influence of drought on growth extends until August and, in general, correlation coefficients with summer SPEI are stronger than in the case of *Aigüestortes* and *Pyrenees* subsets, consecutively (Fig. A6). These observations are consistent among the different detrending methods (Fig. A6 and Fig. A7).

In the case of MXD for the first subperiod, the highest negative (~ -0.4) and positive ($\sim 0.2-0.3$) correlations occur with the May SPEI for 4 to 5 months, and with July SPEI at 2-month scale, respectively. This greatly changes for the second subperiod, when the highest positive MXD/SPEI correlations (~ 0.4) are found in the period from previous September to current January (Fig. 4). Both TRW and MXD showed higher correlations with SPEI in the second than in the first subperiod, which indicates an increase in drought influence on growth in recent decades.

Finally, spatial correlations displayed between MXD values and temperature were stronger and more spatially coherent across SW Europe than those observed with TRW (Fig. A8).

3.3. Proxy-temperature divergence

Our results show a temporal instability of the growth/climate relationships of *P. uncinata* forests along the 20th century. In the low-frequency domain, divergent trends for TRW and maximum temperature are found since the 1970s (Fig. 5b), while TRW displays a convergent trend with SPEI (Fig. 5e). Similar results are observed for the *Pyrenees* and *Aigüestortes* subsets (not shown). For its part, MXD low-frequency trend

parallels with the low-frequency temperature warming, which started in the 1970s (Fig. 6b), but it diverges from SPEI (Fig. 6e).

A steady negative (positive) trend in the moving correlation record is displayed with temperature (SPEI) in the low-frequency range (Figs. 5b,e). In the high-frequency domain, stronger correlations with temperature are obtained after the 1950's (Fig. 5c), and a negative trend in the moving correlations with SPEI is found (Fig. 5f). MXD moving correlations display an increase with temperature and a decrease with SPEI in low-frequency domains (Fig. 6b,e). Low-frequency moving correlations in TRW seem more stable than in MXD, where we can observe cyclic increases and decreases in the moving correlations along the 20th century (Fig. 6b,e).

Focusing on the growing season, May temperature shows a direct correlation with TRW and MXD while summer months usually show a smaller or negative one (Fig. 3). To find out if the divergence phenomenon is due to a loss of temperature sensitivity or to an increase in this negative summer drought effect, we repeated the moving correlation analyses with summer (June-July) and May temperatures. Results are very similar to the ones obtained with the maximum temperature of May-September period (Fig. A9 and A10), again highlighting a TRW-temperature divergence and also a recent increase in the correlation between MXD and temperature.

To gain insight into potential differences in the divergence occurrence along the altitude we compared high- (>2150 m, 15 sites, 940 series) and low-elevation (< 2150 m, 15 sites, 572 series) TRW chronologies with June-July SPEI and MJJAS maximum temperature series. In both high- and low-elevation chronologies the divergence phenomenon with temperature in the low-frequency range is clear and the convergent trend with MXD in the low-frequency range too (Figures A11 and A12). In the high-

elevation chronology the low-frequency divergence with temperature seems to appear shortly delayed compared with the low-elevation chronology.

4. Discussion

Our results show low frequency trend offsets between the TRW series and temperature records since the second half of the 20th century (Fig. 5b). This suggests a weakening of the theoretically temperature-sensitive proxies (TRW) to capture recent warming trends such as those observed since the 1970s. Such ‘divergence’ phenomena between climatic and dendrochronological variables have also been displayed in other temperature-constrained high-elevation and boreal forests (Büntgen et al., 2006; Wilmking et al., 2004, 2005; D’Arrigo et al., 2004; Briffa et al., 1998). Nevertheless, this low-frequency offset between growth and temperature is not found in the high-frequency (i.e. year-to-year) climate sensitivity of our TRW series, which increasingly parallels temperature anomalies along the 20th century (Fig. 5c). Hence, the trend offset between the TRW series and temperature records is mainly restricted to the long-term trend, whereas coherency between productivity and temperature persists in the high-frequency (year-to-year) domain.

Spring cambial resumption in *P. uncinata* starts in May, and typically the tree growth is faster or slower depending mainly on the temperatures prevailing during this month. The moving correlations between May temperatures and TRW highlight that this spring temperature sensitivity is fading during recent decades (Fig. A9b). Contrary to TRW, MXD low-frequency positive trends follow the warming trend started in the 1970s. This is in agreement with data from the European Alps that suggest that the divergent behaviour is expected to occur in TRW more often than in MXD (Büntgen et

al., 2006). Furthermore, MXD shows higher correlations with temperature over the growing season compared to TRW, which is in agreement with former observations from the same area and species (Büntgen et al., 2010). This can be explained because TRW is more strongly autocorrelated, incorporating previous-year climatic and ecological conditions, together with ecological carryover effects and temperature forcing over a wider (seasonal or annual) time window (Fritts, 2001). In fact, our results show a significant correlation between TRW and previous November temperatures, which indicates that warmer conditions in late autumn might enhance carbohydrates storage and synthesis used for the formation of earlywood (i.e. increase of TRW) the following growing season.

The divergence phenomenon has been attributed to various causes including nonlinear growth-climate thresholds (Loehle, 2009), methodological issues techniques including “end effects” of chronology development (Esper and Frank, 2009; Briffa and Melvin, 2011; Briffa et al. 2013; Melvin et al. 2013), biases in instrumental data or additional anthropogenic influences (see D’Arrigo et al., 2007, and references therein), or temperature-induced drought stress (D’Arrigo et al., 2004). Our sampled sites are located within the drought-prone Mediterranean region, so we hypothesize a possible temperature-induced drought explanation of the TRW-temperature divergence observed.

The aforementioned TRW-temperature divergence of the second half of the 20th century is opposite to the relationship between TRW and SPEI trends, with low-frequency moving correlations steadily rising and reaching a maximum level after the 1970s (Fig. 5e). Mean temperatures during the growing season have increased during the last century and especially over the last decades, meantime precipitation regimes have not significantly changed (Figure A14). These results suggest that warming-

induced summer drought is increasingly influencing TRW in the 20th century in Pyrenean high-elevation forests, which agrees with observations from other Iberian mountain forests (Andreu et al., 2007; Macias et al., 2006). This can be due to a potential loss in the positive thermal response of trees when some temperature functional threshold is exceeded, leading to an increase in the influence of other potential factors like soil moisture or drought (D'Arrigo et al., 2004). This TRW-drought parallelism present in our high-elevation study disagrees with results from low-elevation drought sensitive tree-ring central European sites, where growth/drought or growth/precipitation relationships weaken after the 1970s (Wilson and Elling, 2004). Consequently, emerging elevation-specific factors influencing tree growth can be acting differently between high and low elevation sites or between central and southern European forests, producing these contrasting responses in recent decades. Contrastingly, our comparison between high- and low-elevation chronologies does not show important differences (Figs. A11 and A12).

Summer drought is becoming less influential on MXD instead, specifically since the 1970s, when low-frequency moving correlations between SPEI and MXD begin to fall and both trends diverge (Fig. 6e). In any case, the moving correlations of MXD-drought and MXD-temperature relationships show in general more instability than in the case of TRW along time (Fig. 6b,e). When it is too hot or dry for tracheid enlargement to occur, the rate of tracheid production decreases and a denser wood (higher MXD) is formed because of the formation of tracheids with thicker cell walls and narrower lumens (Jyske et al., 2009). This thickening and lignification of the cell walls, illustrated by latewood tracheids, improves the mechanical strength of stems but also allows tracheids to withstand higher xylem tension due to lower water potential

(Hacke et al., 2001). Specifically, MXD development is directly linked to climate conditions during spring and mainly during late summer to early autumn, when the latewood is formed (Briffa et al., 1998). During the first part of the growing season, when the earlywood is formed, climatic variations affect radial tracheid enlargement, whereas during the later part of the growing season climate mainly affects the cell wall thickening process of latewood (Camarero et al., 1998) (Fig. A13). For the subperiod 1930-1969, the strongest negative correlation (~ -0.4) of MXD with SPEI were found for May SPEI (Fig. 4). This means that wet and cool spring conditions could enhance earlywood formation potentially leading to more and wider tracheids with thinner cell walls and a subsequent delayed summer lignification producing a less dense latewood, i.e. lower MXD values. The strongest positive correlation ($\sim 0.2-0.3$) for the same period corresponds to July SPEI which suggests that wet late summers will entail denser latewood production through enhanced lignification and carbohydrates synthesis at the end of the growing season.

In the sub-period 1970-2009 the highest positive MXD-SPEI correlations (~ 0.4) are found in January considering the cumulative drought since the previous September (5-month SPEI scale), which means that wet conditions in the previous autumn and winter of a specific year would imply the production of a dense latewood during the late summer of the next year. This is an unexpected observation since we unveil not only influences of late summer/early autumn conditions of the current year on MXD but also of lagged climatic conditions of the previous year as is usually the case in TRW (Tardif et al., 2003; Fritts, 2001). The interpretation may be the same as in TRW since previous wet conditions might enhance carbohydrates synthesis and storage later used for lignifying and thickening latewood cells the following growing season. Note that these

indirect influences of previous winter conditions on latewood production were also observed in xeric *Pinus halepensis* stands, which constitute typical lowland Mediterranean forests (Pasho et al., 2011). Overall, the SPEI drought index provided a superior signal of tree growth than precipitation data in the study forests. Differences in responses between sub-periods could be due to different drought stress intensities from one sub-period to the other, different temperature conditions or climatic variability (e.g. the first half of the 20th century was climatically less variable than the second half) or indirect effects of other global or local drivers like increasing atmospheric concentrations of CO₂ and rising N deposition.

Current data support the occurrence of climate warming and its effects on various forest ecosystem services in the Pyrenees during recent decades. From 1880 to 1980 AD at least 94 glaciers disappeared in the whole Pyrenees, 17 of them on the Spanish side since 1980 (Morellón et al., 2012). Camarero and Gutiérrez (2004) observed an increase in tree establishment and density within the treeline ecotone over the 20th century. In a European context there is a positive trend in temperatures (+0.90°C) from the beginning of the 20th century and, although lower than in central and northern Europe, the warming trend in the Mediterranean region has intensified since the 1970s (IPCC 2013). The Pyrenees are more likely to be vulnerable against climate warming and drying trends than other Mediterranean and European ranges (Schröter et al., 2005) due to two main ecological drawbacks. First, the Pyrenees are east-west arranged, i.e. perpendicularly to the expected northern (or upward) migratory routes. Second, they are influenced by Mediterranean climatic conditions characterized by a summer drought. The negative effects on forest growth under the forecasted scenarios of climate change

could be even worse than expected if drought stress plays a complementary role together with the rising temperatures.

Several dendrochronological studies have focused on growth-climate relationships at Pyrenean high-elevation forests (e.g. Gutiérrez 1991, Rathgeber and Roche 2003, Tardif et al. 2003, Andreu et al. 2007, Büntgen et al. 2008a, Esper et al. 2010). Our study constitutes a step forward in the sense that (i) we use a larger dataset covering a broad biogeographical gradient including the southern and western distribution limits of this species and that (ii) we find a weakening in the TRW-temperature relationships possibly connected to an increasingly important role of drought as a growth driver during recent decades. The divergence phenomenon here exposed should be considered in the assessment and performance of Pyrenean climate reconstructions from tree rings, which are based on short calibration periods. Trees are showing increasing drought and decreasing temperature sensitivities in recent decades even in these high-elevation ecosystems where we would expect a strong temperature response. This would imply that a Pyrenean climate reconstruction based on present-day growth-climate relationships should take on account the role of additional climatic factors that could be potentially limiting tree growth in an increasing degree. According to our results, temperature reconstructions performed in the Pyrenean range using MXD (Büntgen et al. 2008a, Dorado-Liñán et al. 2012) are reliable since they are based on MXD/temperature relationships where no divergence was found.

This divergence phenomenon has been mainly explained here in terms of temperature-induced drought stress, but we should not ignore additional factors potentially influencing the degree and intensity of the growth/climate offset. For instance, nitrogen fertilization or increasing atmospheric CO₂ concentrations may

enhance radial growth thus leading to the formation of a less dense earlywood (Lundgren, 2004). Our next research step would be a site-level study of the low- and high-frequency signals in the growth/climate correlations, which would allow us to draw conclusions for larger scales in a more accurate way (Büntgen et al., 2008b). A more exhaustive MXD sampling of several tree species should be also necessary to make a more accurate comparison between TRW and MXD responses.

5. Conclusions

This study comprises 1500 tree-ring width (TRW) and 102 maximum density (MXD) measurement series from 711 and 74 trees, respectively, which were sampled at 30 high-elevation *Pinus uncinata* forest sites across the Iberian range of the species. Rising temperatures led to an increase in drought stress of Pyrenean high-elevation forests as has been observed in other Mediterranean mountain forests (Jump et al., 2006; Piovesan et al., 2008). Therefore, these high-elevation forests, growing in typically temperature-limited conditions, are becoming more limited by water availability. This growth limitation driven by the amount of available water could be particularly strong in steep sites with rocky substrates where soil shows a poor water holding capacity. We may be witnessing how tree physiological thresholds in terms of optimal temperature for growth are surpassed, reinforcing the role of drought as a growth-limiting factor of high-elevation forests during recent decades.

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References

- Andreu, L., Gutiérrez, E., Macías, M., Ribas, M., Bosch, O., Camarero, J.J., 2007. Climate increases regional tree-growth variability in Iberian pine forests. *Global Change Biology* 13, 804–815.
- Balcells, E., Gil-Pelegrín, E., 1992. Consideraciones fenológicas de las biocenosis de altitud en el Parque Nacional de Ordesa y Monte Perdido, acompañadas y apoyadas mediante estudio preliminar de los datos meteorológicos obtenidos desde 1981 a 1989 en el observatorio de Góriz. *Lucas Mallada* 4, 71–162.
- Briffa, K.R., Bartholin, T.S., Eckstein, D., Jones, P.D., Karlén, W., Schweingruber, F.H., Zetterberg, P. 1990. A 1400-year treering record of summer temperatures in Fennoscandia. *Nature* 346, 434–439.
- Briffa, K.F., Schweingruber, F.H., Jones, P.D., Osborn, T. 1998. Reduced sensitivity of recent tree growth to temperature at high northern latitudes. *Nature* 391, 678–682.
- Briffa, K.R., Melvin, T.M., 2011. A closer look at Regional Curve Standardisation of tree-ring records: Justification of the need, a warning of some pitfalls, and suggested improvements in its application. In: Hughes, M.K., Diaz, H.F., Swetnam, T.W. (Eds.), *Dendroclimatology: Progress and Prospects*. Springer Verlag, pp. 113–145.
- Briffa, K.R., Melvin, T.M., Osborn, T.J., Hantemirov, R.M., Kirdyanov, A.V., Mazepa, V., Shiyatov, S.G., Esper, J., 2013. Reassessing the evidence for tree-growth and inferred temperature change during the Common Era in Yamalia, northwest Siberia. *Quaternary Science Reviews*, 72, 83–107.

- Bunn, A.G., Waggoner, L.A., Graumlich, L.J., 2005. Topographic mediation of growth in high elevation foxtail pine (*Pinus balfouriana* Grev. et Balf.) forests in the Sierra Nevada, USA. *Global Ecology and Biogeography* 14, 103–114.
- Büntgen, U., Esper, J., Frank, D.C., Nicolussi, K., Schmidhalter, M., 2005. A 1052-year tree-ring proxy for Alpine summer temperatures. *Climate Dynamics* 25, 141–153.
- Büntgen, U., Frank, D.C., Nievergelt, D., Esper, J., 2006. Summer temperature variations in the European Alps, AD 755-2004. *Journal of Climate* 19, 5606–5623.
- Büntgen, U., Frank, D.C., Kaczka, R.J., Verstege, A., Zwijacz-Kozica, T., Esper, J., 2007. Growth/climate response of a multi-species treering network in the western Carpathian Tatra Mountains, Poland and Slovakia. *Tree Physiology* 27, 687–702.
- Büntgen, U., Frank, D.C., Grudd, H., Esper, J., 2008a. Long-term summer temperature variations in the Pyrenees. *Climate Dynamics* 31, 615–631.
- Büntgen, U., Frank, D.C., Wilson, R., Carrer, M., Urbinati, C., Esper, J., 2008b. Testing for tree-ring divergence in the European Alps. *Global Change Biology* 14, 2443–2453.
- Büntgen, U., Frank, D.C., Trouet, V., Esper, J., 2010. Diverse climate sensitivity of Mediterranean tree-ring width and density. *Trees, Structure and Function* 24, 261–273.
- Büntgen, U., Raible, C.C., Frank, D., Helama, S., Cunningham, L., et al., 2011. Causes and Consequences of Past and Projected Scandinavian Summer Temperatures, 500–2100 AD. *PLoS ONE* 6(9): e25133. doi:10.1371/journal.pone.0025133

563

564 Büntgen, U., Frank, D.C., Neuenschwander, T., Esper, J., 2012. Fading temperature

565 sensitivity of Alpine tree growth at its Mediterranean margin and associated

566 effects on large-scale climate reconstructions. *Climatic Change* 114, 651–666.

567 Büntgen, U., Kyncl, T., Ginzler, C., Jacks, D.S., Esper, J., Tegel, W., Heussner, K.U.,

568 Kyncl, J., 2013. Filling the Eastern European gap in millennium-long

569 temperature reconstructions. *Proceedings of the National Academy of Science,*

570 USA doi: 10.1073/pnas.1211485110.

571 Camarero, J.J., 1999. Dinámica del límite altitudinal del bosque en los Pirineos y su

572 relación con el cambio climático. PhD Thesis, Universitat de Barcelona,

573 Barcelona.

574 Camarero, J.J., Guerrero-Campo, J., Gutiérrez, E., 1998. Tree-ring growth and

575 structure of *Pinus uncinata* and *Pinus sylvestris* in the Central Spanish Pyrenees.

576 *Arctic and Alpine Research* 30, 1–10.

577 Camarero, J.J., Gutiérrez, E., 2004. Pace and pattern of recent treeline dynamics:

578 response of ecotones to climatic variability in the Spanish Pyrenees. *Climatic*

579 *Change* 63, 181–200.

580 Carrer, M.P., Nola, P., Motta, R., Urbinati, C., 2010. Contrasting tree-ring growth to

581 climate responses of *Abies alba* toward the southern limit of its distribution area.

582 *Oikos* 119, 1515–1525.

583 Ceballos, L., Ruiz de la Torre, J., 1979. Árboles y arbustos de la España Peninsular.

584 Escuela Técnica Superior de Ingenieros de Montes, Madrid, Spain.

585 Cook, E.R., 1985. A Time Series Analysis Approach to Tree-Ring Standardization.

586 PhD Thesis, Lamont-Doherty Geological Observatory, New York.

- 587 Cook, E.R., Peters, K., 1981. The smoothing spline: a new approach to standardizing
588 forest interior tree-ring width series for dendroclimatic studies. *Tree-Ring*
589 *Bulletin* 41, 45–53.
- 590 Cook, E.R., Holmes, R.L., 1986. Program ARSTAN, Version 1. Laboratory of Tree-
591 Ring Research, The University of Arizona, Tucson, USA, 72 pp.
- 592 Cook, E.R., Kairiukstis, L.A., 1990. Methods of dendrochronology: applications in the
593 environmental sciences. International Institute for Applied Systems Analysis,
594 Boston, MA, USA: Kluwer Academic Publishers.
- 595 Cook, E.R., Peters, K., 1997. Calculating unbiased tree-ring indices for the study of
596 climatic and environmental change. *Holocene* 7, 359–368.
- 597 Corona, C., Guiot, J., Edouard, J.L., Chalié, F., Büntgen, U., Nola, P., Urbinati, C.,
598 2010. Millennium-long summer temperature variations in the European Alps as
599 reconstructed from tree rings. *Climate of the Past* 6, 379–400.
- 600 D'Arrigo, R., Kaufmann, R., Davi, N., Jacoby, G., Laskowski, C., Myneni, R.,
601 Cherubini, P., 2004. Thresholds for warming-induced growth decline at
602 elevational treeline in the Yukon Territory. *Global Biogeochemical Cycles* 18,
603 GB3021, doi: 10.1029/2004GB002249.
- 604 D'Arrigo, R., Wilson, R., Liepert, B., Cherubini, P., 2008. On the 'divergence
605 problem' in northern forests: a review of the tree-ring evidence and possible
606 causes. *Global and Planetary Change* 60, 289–305.
- 607 De Luis, M., Gričar, J., Čufar, K., Raventós, J., 2007. Seasonal dynamics of wood
608 formation in *Pinus halepensis* from dry and semi-arid ecosystems in Spain.
609 *IAWA Journal* 28, 389–404.

- Dorado-Liñán, I., Büntgen, U., González-Rouco, F., et al., 2012. Estimating 750 years of temperature variations and uncertainties in the Pyrenees by tree-ring reconstructions and climate simulations. *Climate of the Past* 8, 919–933.
- Esper, J., Cook, E.R., Schweingruber, F.H., 2002. Low-frequency signals in long tree-ring chronologies and the reconstruction of past temperature variability. *Science* 295, 2250–2253.
- Esper, J., Cook, E.R., Krusic, P.J., Peters, K., Schweingruber, F.H., 2003. Tests of the RCS method for preserving low-frequency variability in long tree-ring chronologies. *Tree-Ring Research* 59, 81–98.
- Esper, J., Frank, D.C., 2009. Divergence pitfalls in tree-ring research. *Climatic Change* 94, 261–266.
- Esper, J., Frank, D.C., Battipaglia, G., Büntgen, U., Holert, C., Treydte, K., Siegwolf, R., Saurer, M., 2010. Low-frequency noise in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ tree ring data: A case study of *Pinus uncinata* in the Spanish Pyrenees. *Global Biogeochemical Cycles* 24, doi:10.1029/2010GB0037772.
- Frank, D., Esper, J., Cook, E.R., 2007. Adjustment for proxy number and coherence in a large-scale temperature reconstruction. *Geophysical Research Letters* 34, doi: 10.1029/2007GL030571.
- Fritts, H.C., 2001. *Tree Rings and Climate*. Blackburn Press, Caldwell.
- Grudd, H., 2008. Torneträsk tree-ring width and density AD 500-2004: a test of climatic sensitivity and a new 1500-year reconstruction of northern Fennoscandian summers. *Climate Dynamics* 31, 843–857.
- Gutiérrez, E., 1991. Climate tree-growth relationships for *Pinus uncinata* Ram. in the Spanish pre-Pyrenees. *Acta Oecologica* 12, 213–225.

- Hacke, U.G., Sperry, J.S., Pockman, W.T., Davis, S.D., McCulloh, K.A., 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* 126, 457–461.
- Harris, I., Jones, P.D., Osborn, T.J., Lister, D.H., 2013. Updated high-resolution grids of monthly climatic observations – the CRU TS3.10 Dataset. In press, *International Journal of Climatology*, doi: 10.1002/joc.3711.
- Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin* 43, 68–78.
- IPCC 2013. *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 1535 pp
- Jump, A.S., Hunt, J.M., Peñuelas, J., 2006. Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. *Global Change Biology* 12, 2163–2174. doi: 10.1111/j.1365-2486.2006.01250.x
- Jyske, T., Hölttä, T., Mäkinen, H., Nöjd, P., Lumme, I., Spiecker, H., 2010. The effect of artificially induced drought on radial increment and wood properties of Norway spruce. *Tree Physiology* 30, 103–115.
- Körner, Ch., 2012. *Alpine Treelines*. Springer, Basel.
- Lebourgeois, F., Mérian, P., Courdier, F., Ladier, J., Dreyfus, P., 2012. Instability of climate signal in tree-ring width in Mediterranean mountains: a multispecies analysis. *Trees* 26, 715–729.

- Loehle, C., 2009. A mathematical analysis of the divergence problem in dendroclimatology. *Climatic Change* 94, 233–245.
- López-Moreno, J.I., Goyette, S., Beniston, M., 2008. Climate change prediction over complex areas: spatial variability of uncertainties and predictions over the Pyrenees from a set of regional climate models. *International Journal of Climatology* 28, 1535–1550.
- Lundgren, C., 2004. Microfibril angle and density patterns of fertilized and irrigated Norway spruce. *Silva Fennica* 38, 107–117.
- Macias, M., Andreu, L., Bosch, O., Camarero, J.J., Gutiérrez, E., 2006. Increasing aridity is enhancing silver fir (*Abies alba* Mill.) water stress in its south-western distribution limit. *Climatic Change* 79, 289–313.
- McKee, T.B.N., Doesken, J., Kleist, J., 1993. The relationship of drought frequency and duration to time scales. In *Proceedings of the 8th Conference of Applied Climatology, 17-22 January, Anaheim, CA*. American Meteorological Society, Boston, MA. 179-184.
- Melvin, T.M., Grudd, H., Briffa, K.R., 2013. Potential bias in “updating” tree-ring chronologies using Regional Curve Standardisation: re-processing the Torneträsk Maximum-Latewood-Density data. *The Holocene*, 23, 364–373.
- Morellón, M., Pérez-Sanz, A., Corella, J.P., et al., 2012. A multi-proxy perspective on millennium-long climate variability in the Southern Pyrenees. *Climate of the Past* 8, 683–700.
- Moreno, A., Pérez, A., Frigola, J., et al., 2012. The Medieval Climate Anomaly in the Iberian Peninsula reconstructed from marine and lake records. *Quaternary Science Reviews* 43, 16–32.

- Nicault, A., Rathgeber, C.B.K., Tessier, L., Thomas, A., 2001. Intra-annual variations of radial growth and ring structure. *Annals of Forest Science* 58, 769–784.
- Pasho, E., Camarero, J.J., De Luis, M., Vicente-Serrano, S.M., 2011. Spatial variability in large-scale and regional atmospheric drivers of *Pinus halepensis* growth in eastern Spain. *Agricultural and Forest Meteorology* 151, 1106–1119.
- Piovesan, G., Biondi, F., Di Filippo, A., Alessandrini, A., Maugeri, M., 2008. Drought-driven growth reduction in old beech (*Fagus sylvatica* L.) forests of the central Apennines, Italy. *Global Change Biology* 14, 1265–1281. doi: 10.1111/j.1365-2486.2008.01570.x
- Popa, I., Kern, Z., 2008. Long-term summer temperature reconstruction inferred from tree-ring records from the Eastern Carpathians. *Climate Dynamics* 32, 1107–1117 doi:10.1007/s00382-008-0439-x
- Rathgeber, C., Roche, P., 2003. Spatio-temporal growth dynamics of a subalpine *Pinus uncinata* stand in the French Alps. *Comptes Rendus Biologies* 326, 305–315.
- Rolland, C., Petitcolas, V., Michalet, R., 1998. Changes in radial tree growth for *Picea abies*, *Larix decidua*, *Pinus cembra* and *Pinus uncinata* near the alpine timberline since 1750. *Trees* 13, 40–53.
- Schröter, D., Cramer, W., Leemans, R., et al., 2005. Ecosystem service supply and vulnerability to global change in Europe. *Science* 310, 1333–1337.
- Stokes, M.A., Smiley, T.L., 1968. *An Introduction to Tree-ring Dating*. The University of Chicago Press, Chicago, IL.

- Tardif, J., Camarero, J.J., Ribas, M., Gutiérrez, E., 2003. Spatiotemporal variability in tree growth in the Central Pyrenees: climatic and site influences. *Ecological Monographs* 73, 241–257.
- Trigo, R.M., Vaquero, J.M., Alcoforado, M-J., Barriendos, M., Taborda, J., García-Herrera, R., Luterbacher, J., 2009. Iberia in 1816, the year without a summer. *International Journal of Climatology* 29, 99–115.
- Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2010. A Multiscalar Drought Index Sensitive to Global Warming: The Standardized Precipitation Evapotranspiration Index. *Journal of Climate* 23, 1696–1718.
- Wigley, T.M.L., Briffa, K.R., Jones, P.D., 1984. On the average of correlated time series, with applications in dendroclimatology and hydrometeorology. *Journal of Climate and Applied Meteorology* 23, 201–213.
- Wilmking, M., Juday, G., Barber, V., Zald, H., 2004. Recent climate warming forces contrasting growth responses of white spruce at treeline in Alaska through temperature thresholds. *Global Change Biology* 10, 1724–1736.
- Wilmking, M., D'Arrigo, R., Jacoby, G., Juday, G., 2005. Divergent growth responses in circumpolar boreal forests. *Geophysical Research Letters* 32, L15715.
- Wilson, R.J.S., Elling, W., 2004. Temporal instability in tree-growth/climate response in the Lower Bavarian Forest region: implications for dendroclimatic reconstruction. *Trees, Structure and Function* 18, 19–28.

SUPPORTING INFORMATION LEGENDS

Figure A1. (a) Principal Components Analysis based on 30 TRW chronologies showing the scores of the first two principal components PC1 and PC2 (sites codes are as in Table 1; analysed period is 1901-1994, covered by chronologies from all sites). PC1 and PC2 scores change as a function of altitude (a) and longitude (b), respectively. Stands with special characteristics or located near the distribution limit of the species are indicated. Different symbols correspond to sites from different geographical areas (PNOMP, black circles; PNASM, yellow circles; western and central Pyrenees, downward blue triangle; Iberian System, red square; eastern Pyrenees, white circle; Pre-Pyrenees, upward white triangle). The continuous line in (c) indicates the regression line without considering the red outlier on the left.

Figure A2. Upper and lower graphs show the different TRW (blue) and MXD (green) chronologies, respectively, coming from the 10 different detrendings applied. Dark blue and dark green indicate the TRW and MXD RCS chronologies, in that order. Light blue and light green indicate the eight different chronologies coming from exponential and spline detrendings. Continued and dotted lines refer to chronologies derived from non-transformed and power-transformed data, correspondingly.

Figure A3. Temporal distribution of (a) 101 MXD and (b) 1500 TRW core samples of *Pinus uncinata*, ordered by calendar age of their innermost ring, and EPS statistic (calculated over 30 years lagged by 15 years) of the whole set (i.e. 6 MXD sites and 30 TRW sites) of raw chronologies. The vertical black lines show the temporal limit of the signal strength acceptance ($EPS > 0.85$): 1777 AD for MXD and 1500 AD for TRW.

The grey horizontal dashed lines denote the 0.85 EPS criterion for signal strength acceptance (Wigley et al. 1984).

Figure A4. (a) EPS statistic (calculated over 30 years lagged by 15 years) of each site raw chronology without variance adjustment. (b) Temporal distribution of the 1500 *Pinus uncinata* TRW cores, grouped by site (from bottom West to top East) and ordered by calendar age of their innermost ring. Vertical lines show the limit of the signal strength acceptance ($\text{EPS} > 0.85$; see Wigley et al. 1984).

Figure A5. Relationships between mean segment length (MSL) vs. mean TRW growth rate (AGR) (a) and MXD (b). Different symbols correspond to sites as in Fig. S1.

Figure A6. Contour plots summarizing the Pearson correlation coefficients (r) calculated between TRW chronologies and June-July SPEI index for the 12 months of the year (y axis) at different time scales from one to 24 accumulated months (x axis), covering the period 1901-2009. For the SPEI index we used averaged data from 0.5°-gridded data covering the sampled sites from *Ordesa*, *Aigüestortes* and *Pyrenees* subsets. *TRW mean* refers to the mean chronology averaging the eight different standard chronologies derived from spline and negative exponential detrendings (from power transformed and non transformed raw data); *TRW RCS_{pt}* and *TRW RCS_{nt}* refer to the TRW standard RCS chronologies from power transformed and non transformed raw data, respectively. Legends in the right side show the correlation coefficients from negative values in blue to positive values in orange and red. Significant values ($p < 0.05$) correspond to $r > 0.19$ or $r < -0.19$.

Figure A7. Contour plots summarizing the Pearson correlation coefficients (r) calculated between (a) TRW and (b) MXD standard chronologies and the SPEI index for the 12 months of the year (y axis) at different time scales (1-24 months, x axis), considering the period 1901-2009 and two subperiods: 1930-1969 and 1970-2009. For SPEI index we used averaged data from 0.5° grids covering (a) the 30 TRW sampled sites and (b) the 6 MXD sampled sites. Legends in the right side show the correlation coefficients from negative values in blue to positive values in red. Significant values ($p < 0.05$) are those with $r > 0.19$ or $r < -0.19$ for the period 1901-2009, and $r > 0.35$ or $r < -0.35$ for both subperiods (1930-1969 and 1970-2009). *TRW/MXDmean* refers to the mean chronology coming from averaging the 8 different standard chronologies derived from spline and exponential detrendings; *RCSpt* and *RCSnt* refer to the RCS chronologies derived from power transformed and non transformed raw data, respectively.

Figure A8. Comparison between the highest spatial field correlations of TRW and MXD RCS chronologies against April-May maximum temperatures for the period 1950-2009 (climate data were derived from the CRUTS3.10 dataset). The asterisk indicates the approximate location of the centroid of the study area in NE Spain.

Figure A9. Comparison between May (left column; subfigure a) and June-July (right column; subfigure d) CRUTS3.10 maximum temperature record (red) for the period 1901-2009, and TRW RCSnt (dark blue) and TRW RCSpt chronologies (light blue). Upper graphs indicate 31-year moving correlations between the temperature records and

the chronologies. Each moving correlation point refers to the central year of a 31-year window. Subfigures (a), (b) and (c) show the standard, 20-year low- and high-pass (anomalies) filtered datasets, respectively, for May temperature. Subfigures (d), (e) and (f) show the same for June-July maximum temperature.

Figure A10. Comparison between May (left column; subfigure a) and June-July (right column; subfigure d) CRUTS3.10 maximum temperature records (red) for the period 1901-2009, and MXD RCSnt (dark green) and MXD RCSpt chronologies (light green). The rest of explanations are as in figure A8.

Figure A11. Comparison between low- (left column) and high-elevation (right column) chronologies. In (a) and (b) May-September maximum temperature (red) is compared with the TRW RCSnt chronology (dark blue). Upper graph indicates 31-year moving correlations between the 1901-2009 May-September maximum temperature and the RCSnt chronology. Each moving correlation point refers to the central value of a 31-year window. Subfigures (c, d) and (e, f) show the same for 20-year low-, and high-pass (anomalies) series, respectively.

Figure A12. Comparison between low- (left column) and high-elevation (right column) chronologies. In (a) and (b) June-July SPEI (orange) is compared with TRW RCSnt chronology (dark blue). Upper graph indicates 31-year moving correlations between the 1901-2009 May-September maximum temperature and the RCSnt chronology. Each moving correlation point refers to the central value of a 31-year window. Subfigures (c,

d) and (e, f) show the same for 20-year low-, and high-pass (anomalies) series, respectively.

Figure A13. Example of a densitometric profile covering seven annual rings (period 1927-1933) showing intra-annual MXD and wood-anatomical variability for a *Pinus uncinata* tree from Gerber site (PNAESM). MXD reaches the maximum values during the late growing season, usually from August up to September, when cell-walls are thickening.

Figure A14. CRUTS3.10 mean May-September precipitation (in blue) and mean May-September temperature (in red) trends from 1901 to 2013. We found significant (Mann-Kendall $P < 0.05$) positive mean May-September temperature trends for the period 1901-2013 and also for the subperiod 1970-2009 (solid and broken red lines, respectively). Instead, no significant trend was found for the mean May-September precipitation trends.

TABLES

Table 1. Geographical, topographical and ecological characteristics of the sampled *P. uncinata* sites. Stands are arranged from East to West. Sites' codes are as in Figure 1. Values are means $\pm$ SD. In bold, sites where samples for maximum density (MXD) were obtained. Superscripts ^o and ^a indicate the sites located in PNOMP and PNAESM respectively. Dbh = diameter at breast height

Site (code)	Latitude (N)	Longitude (E / W)	Altitude (m a.s.l)	Aspect	Slope (°)	Dbh (cm)	Height (m)	Age at 1.3 m (years)
Estans de la Pera (EP)	42° 27'	1° 35' E	2360	SW	30 ± 0	65.2 ± 11.0	7.8 ± 2.0	339 ± 117
Mata de València (MA) ^a	42° 38'	1° 04' E	2019	N-NW	19 ± 10	43.2 ± 3.6	12.0 ± 3.1	237 ± 72
Estany de Lladres (LA) ^a	42° 33'	1° 03' E	2120	NW	35 ± 12	52.1 ± 9.8	8.3 ± 1.6	313 ± 123
Airoto (AI)	42° 42'	1° 02' E	2300	W	37 ± 29	58.5 ± 13.5	7.4 ± 1.6	288 ± 100
Tessó de Son (TS) ^a	42° 35'	1° 02' E	2239	N-NE	42 ± 14	74.5 ± 18.8	9.3 ± 3.8	346 ± 202
Estany Negre (NE)^a	42° 33'	1° 02' E	2451	SE	35 ± 18	71.0 ± 26.0	6.6 ± 1.9	411 ± 182
Estany Gerber (GE)^a	42° 37'	0° 59' E	2268	W	15 ± 15	53.5 ± 14.6	6.9 ± 1.4	426 ± 147
Estany d'Amitges (AM)^a	42° 35'	0° 59' E	2390	S-E	40 ± 21	69.0 ± 26.0	9.3 ± 3.8	355 ± 106
Mirador (MI)^a	42° 35'	0° 59' E	2180	SE	33 ± 18	55.1 ± 25.8	7.6 ± 2.3	401 ± 132
Ratera (RA) ^a	42° 35'	0° 59' E	2170	N	40 ± 5	28.3 ± 8.1	10.4 ± 2.0	380 ± 146
Sant Maurici (SM) ^a	42° 35'	0° 59' E	1933	S-SE	16 ± 15	38.2 ± 5.7	11.5 ± 1.7	204 ± 23
Monestero (MO) ^a	42° 34'	0° 59' E	2280	SE	28 ± 13	64.4 ± 16.1	9.3 ± 2.1	346 ± 110
Cortícels (CO) ^a	42° 34'	0° 56' E	2269	W-NW	24 ± 17	83.1 ± 28.8	10.7 ± 3.8	509 ± 177
Barranc de Llacs (LL) ^a	42° 32'	0° 55' E	2250	N-NW	44 ± 38	71.7 ± 20.0	10.5 ± 2.5	616 ± 175
Atxerito (AT)	42° 53'	0° 45' E	1875	N	57 ± 22	64.7 ± 27.2	7.7 ± 2.4	422 ± 159
Conangles (CG)	42° 37'	0° 44' E	2106	S-SW	43 ± 15	56.0 ± 14.5	6.4 ± 2.7	318 ± 117
Vall de Mulleres (VM)	42° 37'	0° 43' E	1800	N-NE	34 ± 13	69.0 ± 26.0	9.8 ± 1.8	437 ± 184
Bielsa (BI)	42° 42'	0° 11' E	2100	E	60 ± 4	45.1 ± 9.4	7.7 ± 3.0	270 ± 67
Sobrestivo (SB) ^o	42° 40'	0° 06' E	2296	S	38 ± 2	61.7 ± 17.5	7.6 ± 1.7	341 ± 97
Foratarruego (FR)^o	42° 37'	0° 06' E	2031	W	37 ± 11	49.5 ± 18.3	8.3 ± 2.9	433 ± 50
Senda Cazadores (SC)^o	42° 38'	0° 03' W	2247	N	39 ± 12	60.9 ± 16.5	9.4 ± 1.6	357 ± 145
Ordesa-Cara Norte (ON) ^o	42° 38'	0° 03' W	2270	N	40 ± 12	50.2 ± 12.5	9.8 ± 1.7	311 ± 45
Mirador del Rey (MR) ^o	42° 38'	0° 04' W	1980	SW	25 ± 10	53.3 ± 15.3	10.9 ± 4.6	117 ± 18
Las Cutas (CU) ^o	42° 37'	0° 05' W	2150	S-SW	20 ± 5	33.3 ± 8.3	9.9 ± 2.5	129 ± 16
Guara (GU)	42° 17'	0° 15' W	1790	N-NW	35 ± 5	44.5 ± 8.1	9.0 ± 1.7	149 ± 36
Respomuso (RE)	42° 49'	0° 17' W	2350	S	30 ± 19	49.5 ± 15.1	7.6 ± 1.5	280 ± 83
Pic d'Arnousse (PA)	42° 48'	0° 31' W	1940	NW	32 ± 4	65.4 ± 5.1	9.4 ± 0.7	248 ± 83
Valdelinares-Teruel (TE)	40° 23'	0° 38' W	1800	SW-W	10 ± 5	63.8 ± 12.4	10.2 ± 1.8	214 ± 107
Larra-La Contienda (CN)	42° 57'	0° 46' W	1750	SW	38 ± 24	46.4 ± 14.0	7.8 ± 2.2	350 ± 108
Castillo de Vinuesa (VI)	42° 00'	2° 44' W	2050	W	21 ± 1	85.6 ± 23.0	9.4 ± 2.9	368 ± 148

Table 2. Statistical characteristics for each site TRW chronology. Variables of raw tree-ring series for the time span analyzed: SD, standard deviation; AC, first-order autocorrelation. Variables of residual chronologies: ms_x , mean sensitivity, a measure of year-to-year growth variability; r_{bt} , mean correlation between trees which evaluates the similarity in growth among trees; E1, variance explained by the first principal component. The reliable time span was defined as the period with $EPS > 0.85$, where the EPS (Expressed Population Signal) is a measure of the statistical quality of the mean site chronology as compared with a perfect infinitely replicated chronology (Wigley et al. 1984). $N\ trees$ is the number of trees needed to reach the EPS threshold for each site. The mean length was calculated for the time span, while tree-ring width, AC, ms_x , r_{bt} and E1 are calculated from 1901 to 1994. In bold, sites where MXD sampling was also carried out. Superscripts ^o and ^a indicate the sites located in PNOMP and PNAESM respectively.

Site	No. trees / radii	Time span	Raw data			Residual chronology				
			Mean length (years)	Tree-ring width $\pm$ SD (mm)	AC	Reliable time span ($EPS > 0.85$)	N trees	ms_x	r_{bt}	E1 (%)
EP	20 / 39	1586-1997	198	0.95 ± 0.36	0.77	1775-1997	10	0.15	0.35	37.84
MA ^a	10 / 20	1668-1997	175	0.92 ± 0.51	0.85	1785-1997	9	0.18	0.40	47.19
LA ^a	36 / 74	1390-2009	243	0.80 ± 0.40	0.85	1390-2009	13	0.13	0.27	32.34
AI	16 / 31	1651-1996	194	1.02 ± 0.35	0.77	1748-1996	7	0.14	0.45	49.00
TS ^a	10 / 17	1537-1995	252	0.88 ± 0.38	0.84	1773-1995	13	0.12	0.32	38.43
NE^a	46 / 86	1393-2009	242	0.74 ± 0.33	0.79	1652-2009	11	0.14	0.36	38.34
GE^a	41 / 79	1270-2010	278	0.59 ± 0.26	0.81	1423-2010	11	0.12	0.43	50.06
AM^a	25 / 56	1592-2009	229	0.83 ± 0.33	0.77	1665-2009	7	0.15	0.48	51.79
MI^a	33 / 85	1390-2009	252	0.59 ± 0.32	0.83	1596-2009	12	0.16	0.34	37.25
RA ^a	5 / 13	1818-2009	192	1.07 ± 0.70	0.88	1856-2009	5	0.17	0.40	50.36
SM ^a	20 / 40	1811-1996	164	0.94 ± 0.68	0.89	1819-1996	9	0.18	0.48	50.57
MO ^a	30 / 76	1481-2009	246	0.92 ± 0.50	0.87	1691-2009	13	0.12	0.31	34.24
CO ^a	25 / 43	1509-1995	274	0.64 ± 0.25	0.78	1594-1995	15	0.14	0.34	37.51
LL ^a	17 / 17	1338-1997	435	0.59 ± 0.29	0.88	1548-1997	17	0.11	0.33	38.51
AT	17 / 43	1317-2010	339	0.59 ± 0.21	0.75	1474-2010	16	0.13	0.28	31.52
CG	25 / 54	1510-1994	215	0.82 ± 0.36	0.82	1700-1994	14	0.15	0.26	30.37
VM	12 / 23	1476-1994	234	0.77 ± 0.37	0.83	1816-1994	12	0.14	0.29	34.34
BI	11 / 20	1707-1996	196	0.80 ± 0.53	0.82	1766-1996	10	0.21	0.40	46.27

SB ^o	53 / 95	1512-2009	285	0.84 ± 0.51	0.85	1617-2009	16	0.15	0.30	32.1
FR^o	12 / 25	1438-1947	305	0.50 ± 0.29	0.82	1582-1947	5	0.16	0.30	47.41
SC^o	65 / 119	1421-2010	256	0.72 ± 0.41	0.85	1571-2010	27	0.12	0.28	29.51
ON ^o	14 / 27	1531-1998	234	0.76 ± 0.36	0.81	1716-1998	6	0.21	0.28	33.43
MR ^o	17 / 34	1795-1998	156	0.77 ± 0.44	0.86	1836-1998	12	0.15	0.31	34.39
CU ^o	10 / 20	1871-1997	98	1.71 ± 0.65	0.74	1892-1997	10	0.22	0.39	47.56
GU	27 / 42	1800-2011	122	1.85 ± 1.00	0.81	1873-2011	11	0.23	0.39	42.26
RE	20 / 47	1572-2010	202	0.84 ± 0.42	0.81	1742-2010	18	0.15	0.26	31.40
PA	8 / 16	1755-1994	170	1.14 ± 0.62	0.84	1778-1994	5	0.18	0.32	40.58
TE	35 / 68	1730-2008	157	1.33 ± 0.74	0.83	1741-2008	13	0.14	0.41	46.57
CN	25 / 57	1364-2010	252	0.68 ± 0.42	0.82	1670-2010	13	0.16	0.33	36.93
VI	24 / 42	1561-2010	238	0.99 ± 0.49	0.81	1731-2010	14	0.18	0.31	42.10

Table 3. Statistical characteristics of TRW and MXD chronologies (from the whole dataset) resulting from the 10 different detrending methods applied. Variables of standard tree-ring series for the period 1901-2009: *corr*, correlation coefficient with the maximum temperature of the period MJJAS; EPS, Expressed Population Signal, a measure of the statistical quality of the mean site chronology as compared with a perfect infinitely replicated chronology (Wigley et al. 1984); SNR, signal-to-noise ratio, the statistical size of the common variance between the trees; PC1, variance explained by the first principal component; ms_x , mean sensitivity, a measure of year-to-year growth variability.

	Data transformation method	Detrending method	<i>corr</i>	EPS	SNR	PC1 (%)
TRW	non-transformed	neg exp1	0.013	0.995	23.666	28.35
		neg exp2	0.087	0.994	23.365	30.56
		150-yr spline	0.213	0.994	23.365	27.42
		300-yr spline	0.219	0.995	23.366	28.07
		RCS	-0.066	0.995	23.366	22.58
	power-transformed	neg exp1	-0.012	0.995	23.366	27.42
		neg exp2	0.064	0.994	23.365	32.14
		150-yr spline	0.180	0.995	23.366	28.03
		300-yr spline	0.119	0.995	23.366	26.52
		RCS	-0.149	0.996	23.367	25.86
MXD	non-transformed	neg exp1	0.244	0.919	11.381	37.07
		neg exp2	0.277	0.919	11.381	36.16
		150-yr spline	0.336	0.920	11.490	55.31
		300-yr spline	0.301	0.919	11.381	42.59
		RCS	0.247	0.918	11.274	46.27
	power-transformed	neg exp1	0.246	0.921	11.599	33.32
		neg exp2	0.274	0.921	11.599	31.76
		150-yr spline	0.339	0.923	11.820	37.87
		300-yr spline	0.306	0.921	11.599	45.07
		RCS	0.198	0.920	11.490	47.96

FIGURE LEGENDS

Figure 1. Network of the 30 Iberian *Pinus uncinata* sampled sites (white areas indicate high-elevation sites). The left lower 3D graph emphasizes the sampled sites located at high altitudes, mostly in the Spanish Pyrenees. The right lower map shows the location of the study area (red box, NE Spain) within the Mediterranean Basin (blue box).

Figure 2. Comparison between the RCS chronologies (dark lines) and the mean standard chronology derived from the 8 different spline and negative exponential detrendings (light lines), for (a) TRW and (b) MXD. Upper insets show the chronologies comparison for the period 1850-2009 for MXD and 1850-2010 for TRW (areas delimited by the black rectangles). Similar results are displayed in the *Pyrenees* and *Aigüestortes* subsets. Continued and dotted lines refer to chronologies derived from non-transformed and power-transformed data, correspondingly.

Figure 3. Correlation coefficients between maximum temperatures and (a) TRW or (b) MXD RCS chronologies. Monthly correlations are computed from previous-year October (o) to current-year September (Sep), and seasonal correlations are computed from current-year March to September, over the common period 1901-2009 and two subperiods: 1930-1969 and 1970-2009. Significant correlations are indicated with asterisks ($p < 0,05$) and dots ($p < 0,001$).

Figure 4. Contour plots summarizing the Pearson correlation coefficients (r) calculated between (a) TRW and (b) MXD RCS standard chronologies derived from power transformed raw data and the SPEI index for the 12 months of the year (y axis) at different time scales (1-24 months, x axis), considering the period 1901-2009 and two subperiods: 1930-1969 and

1970-2009. For SPEI index we used averaged data from 0.5° grids covering (a) the 30 TRW sampled sites and (b) the 6 MXD sampled sites. Legends in the right side show the correlation coefficients from negative values in blue to positive values in red. Significant values ($p < 0.05$) are those with $r > 0.19$ or $r < -0.19$ for the period 1901-2009, and $r > 0.35$ or $r < -0.35$ for both subperiods (1930-1969 and 1970-2009).

Figure 5. (a) May-September maximum temperature (red lines) and (d) June-July SPEI series (orange lines) compared with TRW RCSnt (dark blue lines) and RCSpt chronologies (light blue lines) for TRW. Upper graph indicates 31-year moving correlations between the climatic series and the RCSnt and RCSpt chronologies, coloured in dark and light blue lines respectively. Each moving correlation point refers to the central value of a 31-year window. For May-September maximum temperature, the same analyses for (b) 20-year low- and (c) high-pass (anomalies) series are displayed. For June-July SPEI, the same analyses are also displayed for (e) 20-year low- and (f) high-pass series.

Figure 6. (a) May-September maximum temperature (red lines) and (b) June-July SPEI series (orange lines) compared with MXD RCSnt (dark green lines) and RCSpt chronologies (light green lines) for MXD. The rest of explanations are as in Figure 5.