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5 Non-stationary influence of El Niño-Southern Oscillation and
6 winter temperature on oak latewood growth in NW Iberian
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Abstract The properties of El Niño-Southern Oscillation (ENSO), such as period, amplitude, and teleconnection strength to extratropical regions, have changed since the mid-1970s. ENSO affected the regional climatic regime in SW Europe, so that tree performance in the Iberian Peninsula could be affected by recent ENSO dynamics. We established four *Quercus robur* chronologies of earlywood and latewood widths in the NW Iberian Peninsula. The relationship between tree growth and the Southern Oscillation Index (SOI), the atmospheric expression of ENSO, showed that only latewood growth was negatively correlated with SOI of the previous summer–autumn–winter. This relationship was non-stationary, with significant correlations only during the period 1952–1980; and also non-linear, with enhanced latewood growth only in La Niña years, i.e. years with a negative SOI index for the previous autumn. Non-linear relationship between latewood and SOI indicates an asymmetric influence of ENSO on tree performance, biased towards negative SOI phases. During La Niña years, climate in the study area was warmer and wetter than during positive years, but only for 1952–1980. Winter temperatures became the most limiting factor for latewood growth since 1980, when mean regional temperatures increased by 1 °C in comparison to previous periods. As a result, higher winter respiration rates, and the extension of the growing season, would probably cause an additional consumption of stored carbohydrates. The influence of ENSO and winter temperatures proved to be of great importance for tree growth, even at lower altitudes and under mild Atlantic climate in the NW Iberian Peninsula.

Keywords Annual tree rings · Dendrochronology · ENSO · Climate warming · Latewood · *Quercus robur*

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48 **Introduction**

49 Dendroclimatologists focus on the impacts of locally measured climatic components on
50 radial growth dynamics of trees, but also on the effects of large-scale climatic patterns on
51 tree growth (Peterson and Peterson 2001; Schöngart et al. 2004). The productivity and
52 dynamics of aquatic and terrestrial ecosystems worldwide can be influenced by climatic
53 teleconnections, which account for major variations in local weather and climate (Stenseth
54 et al. 2002). The dominant teleconnections that affect weather and climate variability
55 worldwide (e.g., North Atlantic Oscillation (NAO), El Niño-Southern Oscillation
56 (ENSO)), provide a broad understanding of observed changes in the local physical
57 environment and the associated ecological processes (Stenseth et al. 2003). ENSO is the
58 strongest interannual variation of Earth's climate, affecting a wide range of geographic
59 areas (McPhaden et al. 2006), and it fluctuates between two phases with unusually warm
60 and cold conditions in the tropical Pacific Ocean, the so-called El Niño and La Niña,
61 respectively. The consequences of ENSO on the dynamics of vegetation and primary
62 productivity have been demonstrated over a wide range of terrestrial ecosystems, causing
63 their most important effects under arid and semiarid climates at tropical latitudes (Fichtler
64 et al. 2004; Holmgren et al. 2001).

65 ENSO also influences the climate of extratropical regions, with wet periods typically
66 associated with El Niño (positive SOI) phases, and droughts connected to La Niña
67 (negative SOI) episodes in southern and western North America (Cleaveland and Duvick
68 1992; Swetnam and Betancourt 1998). By contrast, El Niño events induce cooler surface
69 temperatures, reduced cloud cover, and reduced precipitation in northern New Zealand,
70 with opposite effects of La Niña phases (Fowler et al. 2000). As a consequence, important
71 ecological processes at regional scale in the extratropics, such as synchronic tree

establishment, vegetation productivity and dynamics, tree growth patterns, insect outbreaks, wildfires or tree dieback, are associated with the interannual wet-dry cycles derived from ENSO dynamics (Fowler et al. 2008; Schöngart et al. 2004; Swetnam and Betancourt 1998; Villalba and Veblen 1998). ENSO influence also appears in Southwest Europe and Northern Africa, with a significant impact on winter-spring rainfall, river discharge, and lake level variation in the Iberian Peninsula (Knippertz et al. 2003; Pozo-Vázquez et al. 2005; Rodó et al. 1997). Although ENSO influence on European climate could be considered stationary during the last centuries (Brönnimann et al. 2007), previous studies suggested that ENSO teleconnection to extratropical areas, and particularly to southern Europe, can vary from region to region, and can also change over time (Rodó et al. 1997; D'Arrigo et al. 2005; Pozo-Vázquez et al. 2005). We can expect negative sea-level pressure anomalies west of Spain and over southern Europe during El Niño events (Pozo-Vázquez et al. 2005; Brönnimann et al. 2007) which, in combination with other large-scale circulation patterns such as NAO, can significantly influence rainfall regimes in the Iberian Peninsula (Rodó et al. 1997; Zorita et al. 1992).

Measured climatic records during the last decades suggest that a warming trend in Western Europe is much stronger than predicted by climate models, despite such models already predict exceptionally high temperatures and a great climatic variability over SW Europe (IPCC 2007; van Oldenborgh et al. 2009). The phenology of temperate forests is mainly driven by temperature, affecting the start of the growing season, and thereby its duration (Kramer et al. 2000). Predictions for the end of the twenty-first century anticipate an average increase in the duration of the growing season of about 20 days for European oaks, with a predicted increase of up to 30 days in SW Europe (Lebourgeois et al. 2010). The observed extension of the growing season for European tree species during the last decades was mainly the result of an earlier onset of spring due to increased winter-spring

temperatures (Chmielewski and Rötzer 2001). In general, an increase in the length of the growing season increases tree growth in deciduous forest stands (Rötzer et al. 2004).

Quercus robur is a deciduous, long-living tree, which is dominant throughout a wide geographic and ecological range over Eastern, Central, and Atlantic Europe (Ducousso and Bordacs 2004). In general, the radial growth of this species in the Mediterranean region is negatively related to temperature during May-July of the active growing period (Tessier et al. 1994), while the response in northernmost locations is opposite, often showing a positive response to July temperature (Pilcher and Gray 1982). However, the positive impact of spring-summer rainfall on oak ring widths is a general feature throughout Europe (Friedrichs et al. 2009; Hiltunen and Berninger 2010; Tessier et al. 1994). Accordingly, previous studies of *Q. robur* in NW Spain showed that radial growth is mainly limited by water availability during the growing season, primarily during summer (García-González and Eckstein 2003), or by elevated winter temperatures (Rozas 2005; Rozas et al. 2009).

In this work, we study the influence of large-scale circulation patterns (ENSO, NAO), and regional climate on the inter- and intra-annual tree-growth variation in four populations of *Quercus robur* in the NW Iberian Peninsula, at the southwestern edge of its world range. The particular questions to be addressed are the following: Are tree-ring series sensitive to ENSO, NAO, and regional climate in the NW Iberian Peninsula? Has the sensitivity of the tree-ring growth to ENSO, NAO, and regional climate been changing for the last century? How do large-scale climatic patterns impact regional climate to induce a particular response on tree growth?

Materials and methods

Study sites

We selected four populations of *Q. robur* located at least 50 km apart in Galicia (42.19–43.58°N, 7.22–8.96°W), NW Spain (Fig. 1A). Two sites were located at low elevations (Table 1; Baio and Ribeiro do Bispo, below 300 m), whereas the others were at higher elevations (Estornín and San Mamede, above 800 m). The sites were relatively undisturbed by human management, at least during the last decades, without any other significant treatment than the occasional removal of dead trees for lumber. Regional climate is temperate and humid, with a mean yearly temperature ranging between 10.8 and 13.4°C, and yearly rainfall between 1,071 and 1,392 mm (averages for the period 1910–2006). A conspicuous elevation of the mean regional temperature was revealed by its general trend within the period 1910–2006, which significantly ($p < 0.001$) fitted to a rising quadratic line (Fig. 1B). Annual precipitation varied slightly among the considered period, though there was also a slight rising trend ($p = 0.026$; Fig. 1C).

Sampling, sample processing and tree-ring measurement

We took at least two 5 mm diameter cores per tree from 18 to 31 dominant trees at each site, using an increment borer at breast height. The cores were air dried, glued onto wooden mounts, mechanically surfaced, and then manually polished with successively finer grades of sandpaper, until the xylem cellular structure was visible in the transverse plane. The tree-ring series were absolutely dated by assigning calendar years to the rings through the identification of characteristic ring sequences. Earlywood (EW) and latewood (LW) widths were measured under magnification to the nearest 0.001 mm with a Velmex Unislide sliding-stage micrometer (Velmex Inc., Bloomfield NY, USA) interfaced with a computer; the conspicuously larger vessels in the EW, and its abrupt transition to the LW allowed an easy discrimination of both tree-ring compartments. Since both can be influenced by climate during different seasons, the development of separate EW and LW chronologies

can provide a more detailed assessment of intraannual climatic sensitivity (Rozas et al. 2009). The computer program COFECHA (Grissino-Mayer 2001) was used to quantitatively check for crossdating errors. We used the series that had been confidently dated to compute the chronologies of EW and LW for each site.

Chronologies computation and assessment

Each raw ring-width series was standardized with the ARSTAN computer program (Cook and Holmes 1996). Both the ages of the sampled trees and the low-frequency variation of radial growth showed a high inter-individual variability, which could act as a relevant masking factor in the analysis of climate-growth relationships. Therefore, we used a flexible detrending, i.e., a spline function with a 50% frequency response of 32 years, in order to successfully remove the low-frequency trends and maximize the high-frequency climatic signal in our tree-ring index chronologies (Cook and Peters 1981). The residuals obtained were pre-whitened by autoregressive modelling, giving dimensionless indices that represent independent records of annual growth for each measured series. The indices for the individual series were averaged by biweight robust means, and the mean chronologies were truncated when the sample size was lower than five trees. The statistical quality of the chronologies was assessed in the optimum common period for each site using basic statistics to measure the common signal (Briffa and Jones 1990), i.e. signal-to-noise ratio (SNR), expressed populations signal (EPS), mean series intercorrelation (R_{bar}), and variance explained by the first principal component (PC1). SNR indicates the strength of the observed common signal among trees, EPS quantifies the degree to which the obtained chronology represents the theoretically perfect chronology, R_{bar} is the mean value of all possible correlations between the radial series, and PC1 indicates the percentage of year-

to-year growth variation shared by trees. Regional growth chronologies were obtained as the year-by-year mean of the local chronologies, for the common period to all sites.

Climatic data

We used the Southern Oscillation Index (SOI), the atmospheric expression of ENSO, to monitor its effects on tree growth and regional climate. SOI is calculated as the standardized difference of sea level pressure between Tahiti in the eastern Pacific and Darwin in northern Australia (Stenseth et al. 2003). Monthly SOI data for the period 1866–2008 were obtained from the Web site of the National Center for Atmospheric Research, USA (<http://www.cgd.ucar.edu/cas/catalog/limind/>). In addition we obtained monthly NAO data (Gibraltar-Iceland: <http://www.cru.uea.ac.uk/cru/data/nao/>) for the period 1821–2006, in order to test the effects of NAO on our tree-ring chronologies.

The growth of deciduous oaks has proved to be controlled by a complex combination of several climatic factors rather than by a single limiting factor (Friedrichs et al. 2009). Therefore, we used monthly gridded data (CRU TS 3 and CRU self-calibrating PDSI, $0.5^\circ \times 0.5^\circ$) for mean and maximum temperature (T and Tmax, respectively, period 1901–2006), total precipitation (P, period 1901–2006), Palmer Drought Severity Index (PDSI, period 1901–2002; Dai et al. 2004) and vapor pressure (VP, period 1901–2006), taken from the Web site of the Royal Netherlands Meteorological Institute (<http://climexp.knmi.nl/>). Annual values were calculated from monthly values on the basis of the hydrologic year, October 1st of the prior year (Oct (t-1)) to September 30th of the current year (Sep (t)). Regional values of T, Tmax, P, PDSI, and VP values were calculated as the year-by-year mean of these climatic series from the four 0.5° longitude $\times$ 0.5° latitude squares corresponding to the four study sites.

Climate-growth relationships

Correlations between monthly SOI and NAO records, and residual indices of EW and LW, were calculated for the common period 1952–2006. The temporal window for climatic variables was taken from June of the year before ring formation (Jun (t-1)) to September of the year of ring formation (Sep (t)). The effects of large-scale climatic fluctuations on tree growth may be difficult to ascertain because frequently the relationships between climate and local processes are non-stationary (i.e., time varying) and/or non-linear (Stenseth et al. 2003). For these reasons, we paid special attention to the detection of non-stationary and non-linear relationships among tree growth, SOI, NAO, and local climate indicators. To evaluate the stationarity and consistency of the relationships through time, we calculated moving 25-year correlation coefficients with the software DENDROCLIM2002 (Biondi and Waikul 2004), for 1910–2006. A bootstrap procedure was used for significance testing based on 1,000 iterations, and each correlation coefficient was considered to be significant ($p < 0.05$) if it was at least twice, in absolute value, its bootstrapped standard deviation ($|r/sd| \geq 2$).

Tree growth-climate relationships were analyzed using stepwise multiple linear regression in three consecutive periods selected a posteriori within 1910–2006, by taking the monthly, seasonal and annual SOI, NAO, T, Tmax, P, PDSI, and VP values as climatic predictors. Stepwise procedure allowed excluding redundant and collinear climatic predictors, which could have caused variance overestimation. The total variation of tree growth explained by climate at each site was quantified from the coefficients of determination adjusted for the loss of degrees of freedom (r^2_{adj}) derived from the regression models. Statistical analyses were performed with the software SPSS v15.0 (SPSS Inc., Chicago IL, USA).

Pearson's correlations between SOI and climatic variables were calculated in the same consecutive periods. To describe the temporal variation of geographic patterns for SOI-regional climate correlations in these consecutive periods, we performed spatial-field correlations between SOI and selected climatic variables of the CRU database for the Iberian Peninsula (latitude 35°N–45°N, longitude 10°W–4°E) using the Climate Explorer (<http://climexp.knmi.nl/>).

Results

Tree-ring chronologies assessment

Mean ages of the sampled trees varied between 48 and 129 years, and their standard deviations between 8 and 35 years (Table 1). All LW chronologies surpassed the frequently applied minimum threshold of 0.85 for EPS, and showed high values for SNR, Rbar and PC1, indicating that the trees shared a large amount of inter-annual LW growth variation. By contrast, EW had a rather low quality for dendrochronological analyses, according to their values of chronology statistics. Site chronologies (Fig. 2) were significantly correlated to each other for the common period 1952–2006 ($p < 0.01$), ranging between 0.316 and 0.528 for EW, and between 0.399 and 0.685 for LW, as a result of a shared inter-site variation.

Teleconnection of ENSO on latewood growth

No significant correlations between EW tree-ring indices and monthly SOI values were observed for the common period 1952–2006. In contrast, LW indices were significantly correlated to SOI values between July and December before tree growth, depending on the site, and in January and March of the current year in only EST (Fig. 3). However, no

consistent patterns of significant correlations were found between NAO indices and EW or LW chronologies at any of the four study sites; only LW at EST showed a significant correlation with previous December NAO ($r = 0.296$, $p = 0.025$). Moreover, the observed relationships between seasonal SOI and LW indices were non-stationary, as moving bootstrapped correlations revealed a significant negative relationship just within the period 1952–1980 (Fig. 4), and mainly for the previous autumn.

Besides its non-stationarity, the relationship between LW growth and SOI was non-linear within the period 1952–1980. LW growth indices and autumn SOI were statistically independent for 1910–1951 and 1981–2006, whereas both variables showed a highly significant ($p < 0.001$) non-linear relationship at the four sites in 1952–1980 (Appendix S1); and so did the mean LW growth chronology at a regional scale (Fig. 5A), indicating an asymmetrical effect of SOI on latewood growth. The non-linear models showed that SOI accounted for 35–49% of LW growth variance in 1952–1980, but only 19–33% using linear models. Accordingly, SOI of previous September–November explained 64.8% of mean LW growth according to the exponential model, while the linear model accounted for 41.9% of LW growth variance, which is considerably lower. LW indices were higher in years with negative SOI values during the autumn before tree growth, whereas positive SOI values did not influence LW.

Climate-growth relationships

The climatic response of LW growth was non-stationary, with the increasing amount of variance explained by climate (r^2_{adj} model values) increasing along time (Table 2). It did not reach 35% for 1910–1951, and there were no climatic variables with comparable effects that were common to all four sites. For 1952–1980, climate accounted for 45.3–48.4% of LW growth variance, and SOI in previous autumn was the most significant

variable controlling LW growth at all sites, explaining 23.6–35.5% of growth variance. The greatest climatic sensitivity was reached for 1981–2006, with 58.1–73.1% of latewood growth variance related to climate; in this period, the negative effect of winter temperatures explained the largest amount of growth variance, between 21.2% at the highest site, and 46.8% at the lowest site. The period 1981–2006 was the warmest, with mean T increasing from 11.8°C in 1910–1951, to 12.0°C in 1952–1980, and to 12.9°C in 1981–2006. However, annual P varied slightly among the considered periods (1,112 mm in 1910–1951, 1,202 mm in 1952–1980, and 1,194 mm in 1981–2006).

There was no relationship between the average LW chronology and T of previous December in 1952–1980, while in 1981–2006 this relationship was highly significant, linear, and opposite (Fig. 5B). The relationships between LW growth and winter temperature (Tmax of previous November–December in BAI, Tmax of previous December in BIS, T of previous December in EST, and T of previous December–March in SAM) were also significant and opposite in 1981–2006 at the four study sites (Appendix S2). By contrast, in 1910–1951 and 1952–1980, LW growth was independent of winter temperature; the exception was Bispo, the mildest site, which showed a positive significant correlation with December Tmax in 1952–1980.

SOI-regional climate relationships

The spatial field correlations showed a large-scale association between October SOI and several climatic variables in the Iberian Peninsula, but only for 1952–1980, not for 1910–1951 or 1981–2006 (Fig. 6). The inverse association between October SOI and mean annual temperature was widespread throughout the Iberian Peninsula in 1952–1980 (Fig. 6A), with a significant correlation in the study area ($r = -0.468$, $p = 0.010$). By contrast, the influence of SOI on precipitation and PDSI data was more local, as the negative effect

of October SOI was mainly restricted to the western Iberian Peninsula in 1952–1980 (Fig. 6B-D). In the study area, both annual PDSI ($r = -0.497$, $p = 0.006$) and PDSI in September-December of the previous year ($r = -0.560$, $p = 0.001$) showed significant correlations with October SOI, but not annual precipitation ($r = -0.347$, $p = 0.065$). Similarly, a large-scale inverse association of previous October SOI and vapor pressure in current September was found significant ($r = -0.467$, $p = 0.011$) in the study area for 1952–1980 (Fig. 6E).

Discussion

We found significant effects of ENSO dynamics on *Q. robur* growth in the NW Iberian Peninsula, with almost identical patterns of seasonal, non-stationary, and non-linear sensitivity to ENSO for the four populations studied, which covered most of the complete altitudinal range of the species in this region. Although some connection between tree-ring growth and NAO have been previously observed in southern Europe (Piovesan and Schirone 2000; Rozas et al. 2009), this work demonstrates that the connection of oak growth with ENSO was more important than that with NAO in NW Spain, which was mediated by a robust ENSO modulation of regional climate. The relationships of Iberian climate with NAO were studied in a previous work (Zorita et al. 1992), which showed that winter precipitation and NAO are negatively related in southwestern Iberia, but correlations are low in the northwest.

Effects of ENSO on tree growth have been described at tropical latitudes in America, Africa and Asia, usually for water-limited climates or in seasonally-inundated forests, owing to the strong link of hydrological regimes to ENSO dynamics (Fichtler et al. 2004; Schöngart et al. 2004; Stahle et al. 1998). Evidences of extratropical tree-growth sensitivity

to ENSO have also been established in North America and New Zealand (Cleaveland and Duvick 1992; Fowler et al. 2000, 2008). In accordance to our results, which are to our knowledge the first confirmations of ENSO impacts on tree growth in Europe, the negative relationships between SOI and the subsequent tree growth are general in all extratropical cases (Fowler et al. 2008; Stahle et al. 1998).

The previously reported tropical and extratropical relationships between tree growth and ENSO were stationary, i.e., consistent through time (Cleaveland and Duvick 1992; Fowler et al. 2000; Schöngart et al. 2004). In fact, stationarity and robustness of the ENSO-growth relationships have allowed the reconstruction of past ENSO dynamics based on long tree-ring proxy records (Fowler et al. 2008; Stahle et al. 1998). However, there is also evidence that ENSO teleconnection on both regional climate and tree growth can vary through time (Swetnam and Betancourt 1998). The observed relationships between ENSO, LW growth, and regional climate in NW Spain were non-stationary, with significant correlation only during 1952–1980. In general, support for non-stationary effects of regional climate on tree growth has been recently shown for different species, mainly related to variations in local conditions, deposition of contaminants, or climate change (Oberhuber et al. 2008). In our case, the influence of ENSO on diverse regional climatic descriptors in our study area was significant only for 1952–1980, supporting the non-stationarity of the ENSO-growth relationships. The impact of interannual ENSO dynamics is most consistent in the tropical Pacific Ocean and bordering areas where the atmosphere responds directly to ENSO, whereas the geographical variation of their teleconnections can result from extratropical processes and random atmospheric disturbances (McPhaden et al. 2006; Timmermann and Jin 2002). Both observational and modelling studies revealed that the strength of ENSO teleconnections can vary in time and space owing to interactions

with other large-scale atmospheric patterns, heat flux anomalies, stochastic forcing, and the recent warming trend (Sterl et al. 2007; Ye and Hsieh 2006).

In addition to its non-stationarity, the observed ENSO-LW growth relationships were non-linear in 30% of the analyzed period in the four studied populations, i.e. the effects of ENSO on LW growth were asymmetrical, with markedly positive effects of negative SOI values. The nature of ENSO dynamics is non-linear, showing asymmetries between the warm and cold phases with characteristically stronger El Niño than La Niña events (McPhaden et al. 2006). The reasons for this non-linearity are not completely understood, being both the vertical mixing of the upper ocean layers and the heat flux to the equatorial eastern Pacific Ocean, asymmetrical processes that can contribute to the non-linearity of ENSO (An and Jin 2004).

The absence of a significant correlation between SOI and precipitation in our study area, even for 1952–1980, supports previous studies that did not find significant effects of ENSO on precipitation in the NW Iberian Peninsula (Knippertz et al. 2003; Rodó et al. 1997). In fact, Rodó et al. (1997) established a close link between ENSO events and spring precipitation in Spain; in some areas ENSO can explain up to 50% of the observed rainfall during the period 1953–1994, but the effect is strongest in south-eastern areas of Spain, away from our study area. During 1952–1980, LW growth was probably enhanced by negative SOI extremes through the combination of a greater annual–winter soil moisture, and a higher atmospheric vapor pressure at the end of the active growing season. When sufficient soil and air moisture exist, as expressed respectively by PDSI and VP, the stomata can dilate, allowing for higher transpiration and photosynthetic rates (Friedrichs et al. 2009).

For the most recent period, the results of this study are consistent with previous findings showing that radial increment variation of *Q. robur* in northwest Spain is

inversely related to prior winter temperatures (Rozas 2005; Rozas et al. 2009), probably owing to a threshold-induced growth response to increasing temperatures (Wilmking et al. 2004; D'Arrigo et al. 2004), but also due to the independence of local climate and ENSO since 1980 (Fig. 6). The negative relationship between winter temperature and growth was evident since 1980, when mean temperatures in the study area significantly increased by 1°C in comparison to previous periods. In accordance to a previous study at a nearby site, this negative dependence was evident in the LW but not in the EW (Rozas et al. 2009). Warmer winters increase respiration rates and the consequent use of stored carbohydrates, when losses cannot be replaced by photosynthesis (Hamerlynck and Knapp 1996). Such conditions negatively affected LW growth of *Q. robur*, whereas it could be *a priori* expected that EW and LW formation were supported by previous- and current-year photosynthates, respectively (Robertson et al. 1996).

Large EW vessels of ring-porous trees are essential for survival, because they are responsible for more than 90% of water conductivity, but remain functional only during a single growing season (Cochard and Tyree 1990). Since they are usually formed before bud break (Suzuki et al. 1996), at least part of the EW and current year's leaves and fine roots, which are strong carbon sinks, need to be supported by the previously stored reserves (Gallé et al. 2007; Yang and Midmore 2005). As a consequence, carbohydrate storage is maximum before leaf fall in autumn and minimum just after leaf expansion (Barbaroux and Bréda 2002). Climate must therefore be affecting the consumption of reserves during the dormant period. In a previous work we hypothesized that mild winters in northwest Spain were causing a significant consumption of stored reserves in *Q. robur* by increasing respiration rates (Rozas et al. 2009). Thus, winter temperatures would mediate LW production by affecting the amount of reserves available for leaf flushing and fine root growth, and according to our present results, this increase of respiration rates

should have mostly occurred since 1980, as compared with colder conditions in previous periods. A trade-off between carbohydrate investments for LW growth and storage to be used in the following year is also expected during the active growing season. The recent extension of the active growing season, observed in many tree species throughout Europe (Chmielewski and Rötzer 2001; Lebourgeois et al. 2010; Linderholm 2006) probably also modulate this trade-off by reducing the amount of stored carbohydrates and exacerbating the negative effects of winter temperatures on subsequent growth (Rötzer et al. 2004).

Conclusions

We found evidences of a seasonal (only in the latewood growth), non-stationary (significant for the period 1952–1980), and non-linear (markedly positive effects of negative SOI values) dependency of *Q. robur* growth on the interactions between ENSO dynamics and regional climate. Whereas the physical and physiological processes for the observed responses of *Q. robur* growth in NW Iberian Peninsula were not conclusively identified in this work, our findings suggest that growth dynamics have been largely driven by ENSO in 1952–1980. The dynamics of ENSO have changed since the late 1970s with increased frequency, persistence and intensity of El Niño events, and changes in ENSO connectivity to extratropical regions (Wang and An 2001; Ye and Hsieh 2006). In our study area, changes in ENSO teleconnection have been found as a large-scale association between October SOI and several climatic variables in the Iberian Peninsula in the period 1952–1980 only. However, elevated winter temperatures became the main factor limiting growth in 1981–2006, probably as a consequence of phenological changes in the duration of the active period, and the loss of larger amounts of stored carbohydrates by enhanced winter respiration. The non-stationary nature of the tree growth-climate relationships in

NW Spain precludes climate reconstructions based on ring widths without miscalibration of past climate time series. However, the connection between ENSO and regional climate proved to be of great importance on the growth and productivity of deciduous broadleaved trees, even at lower altitudes and under a mild Atlantic climate, on the NW Iberian Peninsula.

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Table 1 Site characteristics and statistics for the tree-ring chronologies of *Quercus robur* earlywood and latewood widths. Tree age was estimated as the number of rings in the longest tree-ring series per tree.

Site name (code)		Baio (BAI)	Ribeiro do Bispo (BIS)	Estornín (EST)	San Mamede (SAM)
West longitude (°)		8.96	7.72	7.22	7.53
North latitude (°)		43.14	43.58	43.05	42.19
Elevation (m)		170	300	850	970
Number of trees / cores		20 / 36	31 / 63	24 / 56	18 / 39
Mean age $\pm$ SD (yr)		129 $\pm$ 14	92 $\pm$ 35	82 $\pm$ 18	48 $\pm$ 8
Chronology period (*)		1867–2006	1872–2006	1909–2007	1952–2008
Optimum common period		1901–2005	1939–2006	1945–2007	1976–2008
EW chronology	SNR	2.53	4.05	2.26	2.56
	EPS	0.72	0.80	0.69	0.72
	Rbar	0.13	0.14	0.08	0.14
	PC1 (%)	17.48	19.30	12.92	20.97
LW chronology	SNR	9.65	10.70	20.58	8.63
	EPS	0.91	0.91	0.95	0.89
	Rbar	0.34	0.31	0.48	0.37
	PC1 (%)	37.47	34.33	50.28	39.78

(*) The chronology period includes at least five trees. EW, earlywood; LW, latewood; SNR, signal-to-noise ratio; EPS, expressed population signal; Rbar, mean interseries correlation; PC1, percentage of variance accounted for the first principal component.

Table 2 Statistics of the multiple regressions of tree-ring latewood chronologies for each of the four study sites (BAI, BIS, EST, and SAM) with the climatic variables for the periods 1910–1951 (n = 42), 1952–1980 (n = 29), and 1981–2006 (n = 26).

Site	Period	Model r^2_{adj}	Predictor variable ^(*)	Var (%)	t -value	p -value
BAI	1910–1951	0.271	P Mar (t)	18.7	3.31	0.002
			VP Jul (t)	8.4	2.37	0.023
	1952–1980	0.484	(SOI Sep-Nov (t-1) + 2) ^{1/2}	25.9	−3.84	0.001
			T Jan (t)	12.9	2.99	0.006
			Tmax Sep (t-1)	9.6	2.42	0.023
	1981–2006	0.731	Tmax Nov-Dec (t-1)	46.8	−4.97	<0.001
			VP Aug (t)	13.3	3.23	0.005
			P Feb (t)	13.0	4.03	0.001
BIS	1910–1951	0.310	Tmax Jul (t)	17.7	−4.27	<0.001
			P Sep (t-1)	13.3	2.95	0.005
	1952–1980	0.457	(SOI Sep-Nov (t-1) + 2) ^{1/2}	34.0	−4.69	<0.001
			VP Jul (t)	11.7	2.73	0.011
	1981–2006	0.645	Tmax Dec (t-1)	38.5	−5.47	<0.001
			P Feb (t)	13.2	4.96	<0.001
			Tmax Apr (t)	12.8	3.85	0.001
EST	1910–1951	0.340	P Jul (t)	25.9	3.89	<0.001
			Tmax May (t)	8.1	2.43	0.020
	1952–1980	0.453	(SOI Sep-Nov (t-1) + 2) ^{1/2}	35.5	−4.11	<0.001
			T Apr (t)	9.8	2.42	0.023
	1981–2006	0.655	T Dec (t-1)	33.6	−4.22	<0.001
			P May (t)	21.4	−3.55	0.002
			Tmax Jun (t)	10.5	−2.60	0.018
SAM	1952–1980	0.461	(SOI Sep-Nov (t-1) + 2) ^{1/2}	23.6	−4.24	<0.001
			PDSI Mar (t)	14.5	3.26	0.003
			P Jun (t-1)	8.0	−2.20	0.037
	1981–2006	0.581	T Dec (t-1)-Mar (t)	21.2	−3.64	0.002
			P Mar-Jul (t)	18.8	−3.17	0.005
			Tmax Apr (t)	18.1	3.48	0.002

^(*)Code interpretation: T, mean temperature; Tmax, maximum temperature; P, total precipitation; SOI, Southern Oscillation Index; PDSI, Palmer drought severity index. Owing to the non-linear relationship between LW growth and SOI, SOI values were transformed according to (SOI + 2)^{1/2}. (t-1) and (t): year before tree growth and current growth year, respectively.

Fig. 1 (A) Location of the sampling sites in the NW Iberian Peninsula near the southwestern range boundary of *Quercus robur* (according to Ducousso and Bordacs 2004). Site codes are described in Table 1. Mean annual temperature (B) and total annual precipitation (C) for the period 1910–2006, averaged annually from the gridded CRU TS 3 datasets of T and P series in those $0.5^\circ \times 0.5^\circ$ squares corresponding to the four study sites. The considered annual period extends from October 1st of the prior year to September 30th of the current year. Dashed lines represent the adjusted trends, and statistics of regressions from these trends are shown.

Fig. 2 Comparison between earlywood (EW) and latewood (LW) indexed tree-ring chronologies at the four study sites. Site abbreviations are given in Table 1. Only periods with at least five trees are shown.

Fig. 3 Correlations between earlywood (A) and latewood (B) tree-ring chronologies, and monthly series of SOI for the common period 1952–2006. Horizontal lines indicate the significance boundaries ($p = 0.05$ and $p = 0.01$) for correlation coefficients. (t-1) and (t): year before tree growth and current growth year, respectively.

Fig. 4 Moving 25-year bootstrapped correlations, lagged by two years, between seasonal SOI values previous to tree growth and latewood growth indices at the four study sites. Each correlation represents the central year of the 25-year interval. Symbols represent significant correlations ($p < 0.05$). Vertical lines indicate the years 1952 and 1980.

Fig. 5 (A) Relationships between latewood (LW) growth indices, averaged from the four study sites, and mean SOI in September–October–November of the year before growth (SOI Sep–Nov (t-1)), for the periods 1952–1980, and 1981–2006. (B) Relationships between latewood (LW) growth indices, averaged out of the four study sites, and mean temperature in December of the year before growth (T Dec (t-1)). The best adjustments relating LW growth indices and the climatic variables, for the periods 1952–1980 and

1981–2006, along with the corresponding statistics, are shown. Note the inverted scale of the growth index axes. n.s.: non-significant relationship.

Fig. 6 Spatial correlations between SOI in October of the previous year, and the gridded $0.5^\circ \times 0.5^\circ$ CRU TS 3 and CRU self-calibrating PDSI datasets of mean annual surface temperature (A), total annual precipitation (B), mean annual PDSI (C), mean PDSI from September to December of the previous year (D), and mean vapour pressure in September

of the actual year (E), for the periods 1910–1951, 1952–1980, and 1981–2006. Only correlations significant at the $p < 0.1$ level are shown.

Supplementary material

Appendix S1 Relationships between latewood growth indices and mean SOI in September–October–November of the year before growth (SOI Sep–Nov (t-1)) at the four study sites (BAI, BIS, EST, and SAM) for the periods 1910–1951, 1952–1980, and 1981–2006. n.s.: non-significant relationship.

Appendix S2 Relationships of winter mean (T) and maximum (Tmax) temperatures with the latewood growth indices at the four study sites (BAI, BIS, EST, and SAM). The statistics of the linear adjustments in the periods 1910–1951, 1952–1980, and 1981–2006 are shown. Note the inverted scale of the growth index axes. n.s.: non-significant relationship.