

Frequency-dependent signals in multi-centennial oak vessel data

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ABSTRACT

This work evaluates whether vessel size data contain a coherent spring precipitation signal over different frequency domains, and how this climatic information varies from the signal encoded in radial growth. The study was conducted at a forest site dominated by old oak trees (*Quercus petraea* (Mattuschka) Liebl.) located in the southern part of the Swiss Alps. Measurements of earlywood vessel size of 27 cores from 12 oak trees were performed in order to build an unprecedented multi-centennial vessel size chronology. Age-independent long-term growth changes and climatic responses in the high-, mid- and low-frequency domains of differently composed chronologies are explored to test the stability of the signals. Results are compared with analyses of tree-ring width measurements from the same material to gain a deeper understanding of physiological processes. We find that mean vessel size data, in contrast to tree-ring width, carry a frequency-dependent signal. Although the signal of both parameters is similar in the low-frequency domain, the climate response in the high-frequency domain differs: vessel size responds negatively to wet spring conditions, whereas ring width mainly responds positively to water availability during the summer. We hypothesize that the processes responsible for signal registration in the specific frequencies are different. The differing high-frequency signals appear to be directly linked to dissimilar responses to weather conditions driving ring and vessel formation. In contrast, the long-term response is related to conditions that affect tree vigour and, due to a positive feedback on growth, is indirectly reflected in the vessels and ring width characteristics. Due to the change in the frequency related response observed in this pioneering study, it appears that the mean earlywood vessel size of oak is not an adequate proxy for long-term reconstruction of spring precipitation.

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1. Introduction

Tree rings are important archives of palaeo-ecological change and have become a well-established proxy to reconstruct changes in past climate (Esper et al., 2002). The most widely used parameters have been tree ring width (RW) and maximum latewood density (MXD), since, in situations where growth is clearly limited by a dominant factor, these measures well integrate the prevailing climatic condition during the growing season. Examples include RW data from trees grown in dry environments that are used to reconstruct the frequency and magnitude of past drought events (e.g., Wilson et al., 2005; Esper et al., 2007), or RW and MXD data from high elevation trees that are used to place ongoing global warming in a long-term context (e.g., Esper et al., 2003b; Büntgen et al., 2005; Frank and Esper, 2005; Büntgen et al., 2006).

Analogous to continuous time-series of annual RW and MXD, series of wood cell anatomical features should also encode valuable ecological information (Schweingruber, 2001). Tree rings do not only integrate the yearly growing conditions, as through the continuous

formation of new cells, intra-seasonal influences are also registered. In fact, climatic conditions that prevail during xylem development can determine the anatomical characteristics of the wooden cells, such as the size of tracheids in conifers and vessels in deciduous trees. Since the characteristic periods of the division, expansion, and maturation of wood cells range from several days to a few weeks (Suzuki et al., 1996; Schmitt et al., 2000; Frankenstein et al., 2005; Rossi et al., 2006), there is good potential that the course of shorter term weather conditions occurring during the growing season are chronologically archived in the anatomical structure of annual rings. Time-series of such cell anatomical characteristics might thus provide more detailed information about seasonal climatic variability.

While growth-climate analysis of the high-frequency variability of the size of water-conductive cells (tracheids or vessels) indicates that cell anatomical characteristics can encode intra-seasonal information, the specific content of this information varies depending on the biology of the species, the seasonality of climate in a particular region and on specific site conditions (e.g., García-González and Eckstein, 2003; Kirilyanov et al., 2003; Panyushkina et al., 2003; Fonti and García-González, 2004; Fonti et al., 2007). Distinct spring precipitation signals have been obtained from the annual variability in the size of the earlywood vessels of relatively young oak (*Quercus petraea* (Matt.) Liebl) growing on mesic sites in Switzerland (Fonti and

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García-González, 2008). These results are, however, based on climate-growth analysis of high-frequency variations (using 32-year spline detrended records) of relatively short chronologies (50 yr). Despite of these novel findings it remains unclear if vessel parameters contain information about long-term environmental changes and could thus be utilized to reconstruct climate-change related processes.

In this paper we evaluate whether the spring precipitation signal observed by Fonti and García-González (2008) can also be applied to reconstruct long-term climate changes. Specifically the objectives were i) to develop an ecologically comparable multi-centennial tree-ring chronology of ring width and earlywood vessel size of sessile oak, ii) to explore the specific climatic signals in different frequency domains (inter-annual to centennial scale), and iii) to evaluate

common variance and climate signals among ring width and vessel size chronologies.

2. Materials and methods

2.1. Wood material and tree-ring data

The wood cores analysed in this study were collected in a mature *Quercus petraea* stand located in a protected forest above the village of Caveragno (latitude 46°21' N, longitude 8°36' E), in the southern Swiss Alps. The sampling site, which likely originated from an ancient landslide, is characterised by dry, poor and shallow soils, located on a steep and south exposed slope at about 900 m asl. The closest

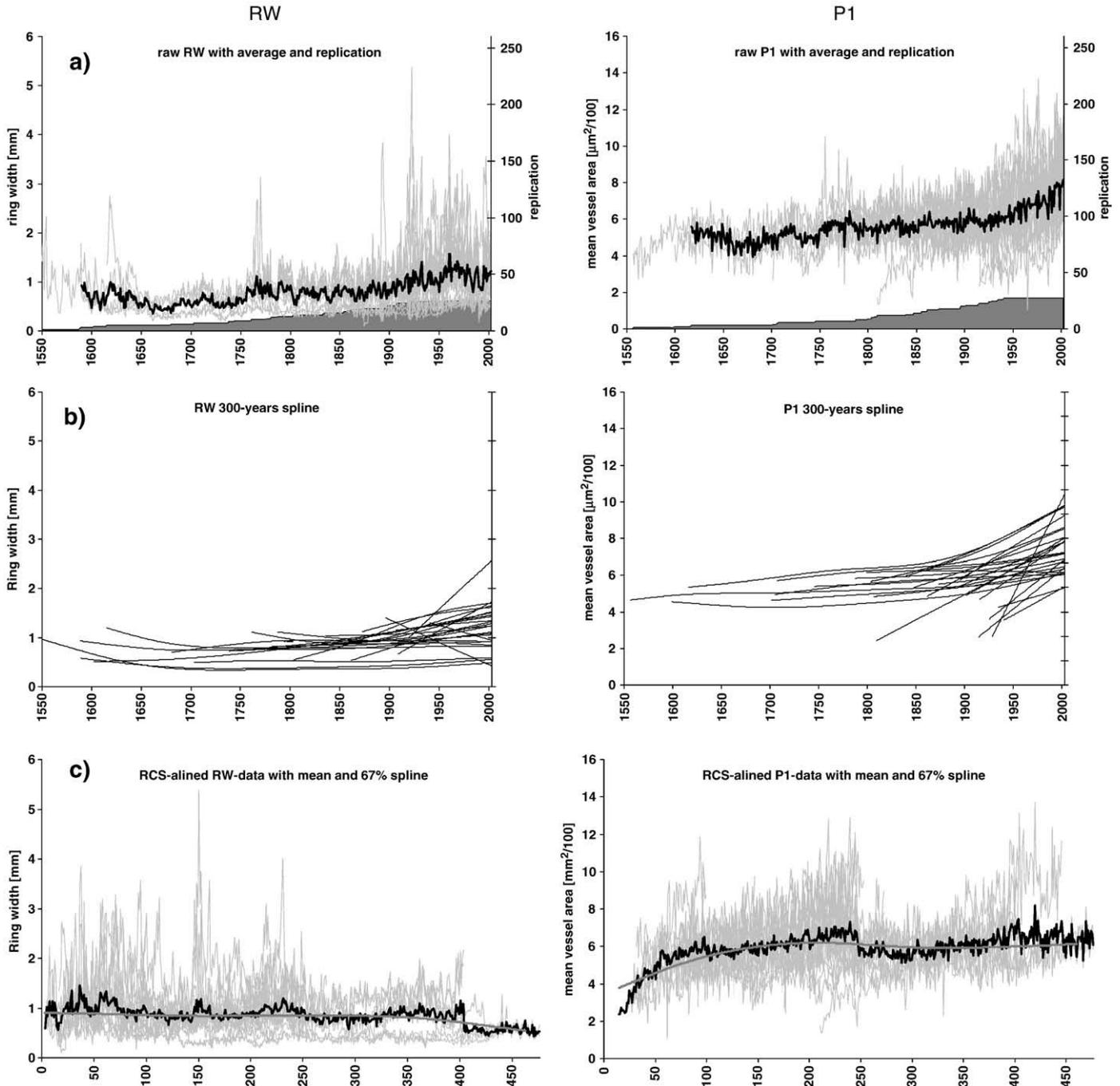


Fig. 1. a) Raw measurement series (grey) with average (bold, truncated at <3 series) and sample replication (grey surface) of ring width (RW) and mean size of first vessel row (P1); b) 300-year splines fitted to these time-series; and c) age aligned average chronology.

meteorological station in Cevio (416 m asl), located <10 km from study site, recorded a mean annual temperature of 9.5 °C and a total annual precipitation of 481 mm with >60% falling between April and September (data from 1950 to 2005; MeteoSwiss).

A total of 27 cores (5 mm diameter) were collected from 12 trees at stem breast height and perpendicular to the slope direction to reduce influences due to reaction wood. Measurements of RW and average earlywood vessel area of the first row of vessels in each ring (P1) were performed on the transversal section of the core samples. Before measurement, each core was progressively sanded (up to 400 grit paper), cleaned with high-pressure water jet to remove tyloses and wood dust from inside the vessel lumina, and lumina refilled with white wax to improve vessel recognition (Fonti et al., 2009). RW was measured using the LINTAB and TSAP system (Rinn, 1996), and crossdating of RW-series assessed using COFECHA (Holmes, 1983). P1 was measured ring-by-ring using Image Pro Plus (v4.5, Media Cybernetics, USA) applied to whole core images captured with a high-resolution and distortion-free digital scanner (256 grey scale level with a resolution of 2400 dpi; Epson Expression 10000 XL, Seiko Epson Corporation, Japan). Due to occasional anomalies in wood structure caused by reaction to damages, measurements of P1 do not cover all juvenile tree-rings in some cases.

2.2. Chronology building

RW and P1 measurement series were detrended to remove possible biological age trends (Fritts, 2001; Fonti et al., 2002). This process includes fitting growth curves to the raw measurement series, and dividing the original data by the fitted curves (Cook and Kairiukstis, 1990). Two conceptually different age-trend fittings

were performed: (i) a 300-year cubic smoothing spline applied to each individual measurement series (300 SPLINE; Cook and Peters, 1981), and (ii) the regional curve standardization (RCS; details in Esper et al., 2003a) that involves fitting a spline function to the arithmetic mean of all cambial age-aligned time-series and removing the age-trend via this so-called regional curve. Inter-series correlations (R_{bar}) were calculated between all 27 individual 300-spline and RCS detrended series of RW and P1 to assess the strength of common underlying signals. Data were then averaged to chronologies using the biweight robust mean (Cook, 1985).

Age-dependent long-term growth changes of the RCS-detrended RW and P1 data were explored using the novel tree-ring analysis program SPOTTY (Esper et al., 2009), which permits analyses of changing growth trends for defined age-classes. The program allows selecting data corresponding to defined age classes (years or ranges) and fitting spline functions to the respective age class data clouds. We fitted 100-year (low-pass filter) splines to age-class ranges of 50 yr, and analyzed the common variance of these low-pass filters.

2.3. Frequency differentiation and climate-growth analysis

Climate-growth relationships were explored by computing Pearson's correlation coefficients between specific frequency components of the RCS-detrended tree-ring chronologies and meteorological time-series.

Frequency components were defined in order to separately account for signals in the annual to centennial scale domains. We applied splines as high and low-pass filters: high-pass filtering was done with a 20-year spline (HIGH) and low-pass filtering with a 50-year spline (LOW). Wavelengths between the high- and low-

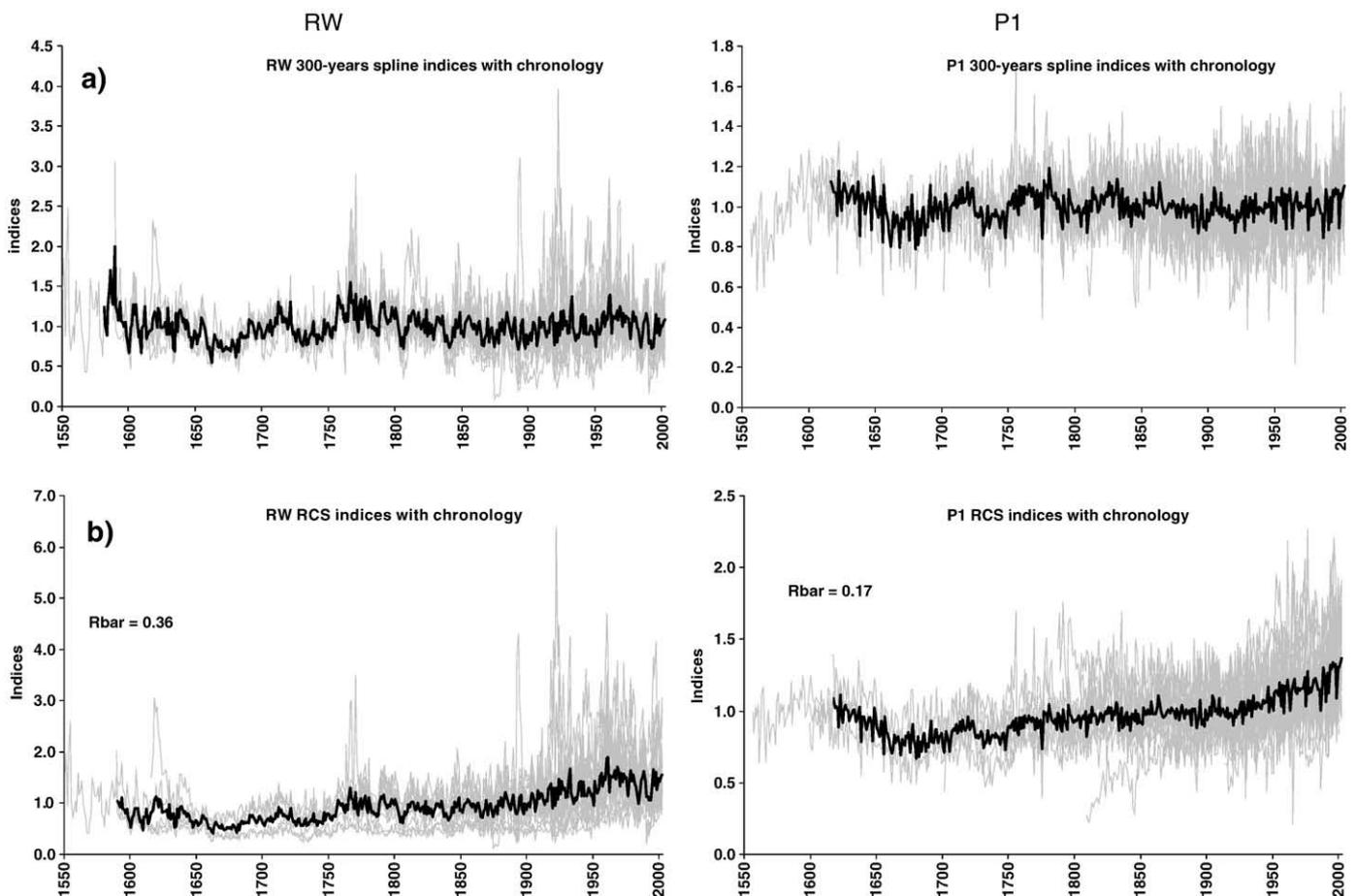


Fig. 2. a) 300-year spline and b) RCS detrended time-series (grey) with mean chronology (bold, truncated at <3 series) for ring width (RW) and mean size of first row vessels (P1).

frequency domains were assessed with a 20–50 year band-pass filter (MID). Before frequency differentiation, RW and P1 chronologies were adjusted using the 50-year running standard deviation, to remove changes in variance related to unequal sample depth, cross-correlation, or other biasing sources (Frank et al., 2007b).

Long meteorological time-series including monthly data of the Palmer Drought Severity Index (PDSI, a standardized index of surface moisture conditions; Palmer, 1965), mean temperature (T) and total precipitation (P) have been considered to allow for correlation analyses over all frequency domains. PDSI data from 1901 to 2002 were obtained from 4 grid-boxes (0.5° × 0.5°) that cover 45.75°–46.25° N and 8.25°–8.75° E (Van der Schrier et al., 2006), T and P data from 1864 to 2002 from the MeteoSwiss station of Lugano located in 273 m asl about 50 km apart from the tree site. Monthly calibration against meteorological data (i.e., Pearson's correlation) was performed for previous June to current October.

3. Results

3.1. Raw data

The period covered by the measured series span from 1542 to 2002 for RW and from 1556 to 2002 for P1, however minimum sample replication of 3 cores is reached only after 1589 and 1616, respectively (Fig. 1a). The mean segment length, i.e., the average number of years per sample, is 218 (range 63 to 461) for RW and 188 (63 to 447) for P1. The average annual increment (RW) over the whole period is 0.81 mm (±0.26 standard deviation) and the average vessel area of the first row of earlywood vessels (P1) is 54 930 μm² (±8090). The apparent increase in scatter towards present of both RW and P1 (Fig. 1a) is mainly due to the inclusion of younger individuals into the data sets. The low pass filters fitted to the raw time-series reveal a long-term increase in RW and P1 after 1650. This increase seems accelerated in P1 after about 1930. Positive trends are generally stronger for young than for old trees (Fig. 1b). Age alignment (Fig. 1c) reveals that RW data have almost no age trend whereas P1 clearly show an increasing trend on vessel size in the juvenile wood, i.e., up to an age of about 50 yr.

3.2. Characteristics of the chronologies

Spline and RCS detrended RW and P1 chronologies show common multi-decadal variations (Fig. 2). Rbar values over the full chronology lengths are 0.36 and 0.17 for the RW and P1 after RCS detrending. RCS-detrending, which removes the biological growth trend common to all measurement series, preserved substantially more low-frequency information – characterized by a centennial scale increasing trend –

than spline detrending, which in turn emphasized inter-annual to multi-decadal scale variations.

The 100-year low-pass filters fitted to differently old tree-rings (here for 50-year age-class filters ranges, Fig. 3) show that the long-term trend seen in the RCS chronologies is preserved in almost all age classes. Only few exceptions do not show the same increasing pattern, including the youngest (<50 yr) P1 class, and some older, less replicated age classes.

3.3. Frequency domains and climate response

Due to the similar long-term trend in the RCS detrended chronologies, correlations for both RW and P1 over the common period (1616–2002) are higher for the RCS ($r=0.66$) than for the spline detrended chronologies ($r=0.35$). Separation of the frequency components in the RCS data (Fig. 4) clearly shows that these similarities are mainly related to the multi-decadal and centennial oscillations. As expected, (lag-1) autocorrelation values increase with increasing time scales of variability. These values are 0.179, 0.961, 0.994 and –0.202, 0.969, 0.987 for high-, mid- and low-frequency of RW and P1, respectively. Correlations between RW and P1 over the common 1616–2002 period are 0.87 ($p<0.05$), 0.39 (ns), and 0.13 ($p<0.01$) for the low-, mid- and high-frequency components, respectively.

Frequency-dependent climate/growth analyses using monthly PDSI (period 1901–2002), P, and T data (1864–2002) indicate that the RW and P1 contain in part a different response to climate (Fig. 5). In the low-frequency domain, both the RW and P1 tend to be larger in warmer and dryer climatic conditions, although due to the substantially reduced degrees of freedom of the smoothed data, none of these values are significant ($p<0.05$). Differences in climatic responses are revealed for the mid-frequency component. While RW responds to drought (positive to PDSI, although not significant ($p>0.05$)), P1 appears insensitive to PDSI. Differing responses to climate are further emphasized for the high-frequency component, and due to sufficient observations these results also are characterized by greater statistical confidence. RW increases in wet and cold summers, which results in generally positive and significant relationships to PDSI, whereas P1 is larger in association with winter PDSI, dry springs and warm Aprils and cold Mays ($p<0.05$).

4. Discussion

4.1. Characteristics of the chronologies

While preservation of high- and mid-frequency variance is fairly independent of the choice of the detrending method, application of

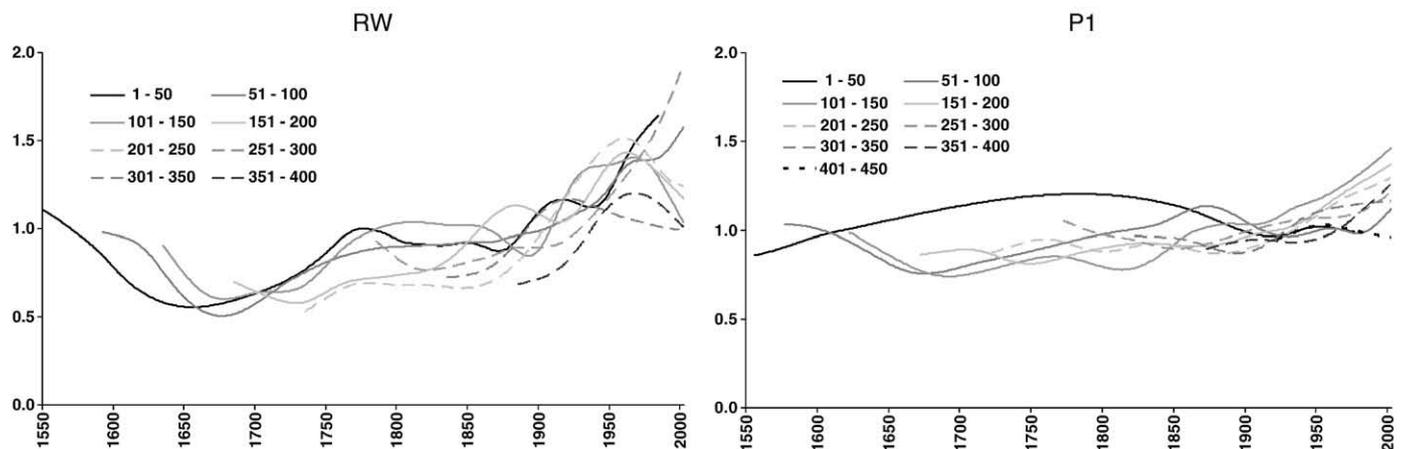


Fig. 3. 100-year splines fit to 50-year age-class segments of RCS-detrended RW and P1 data.

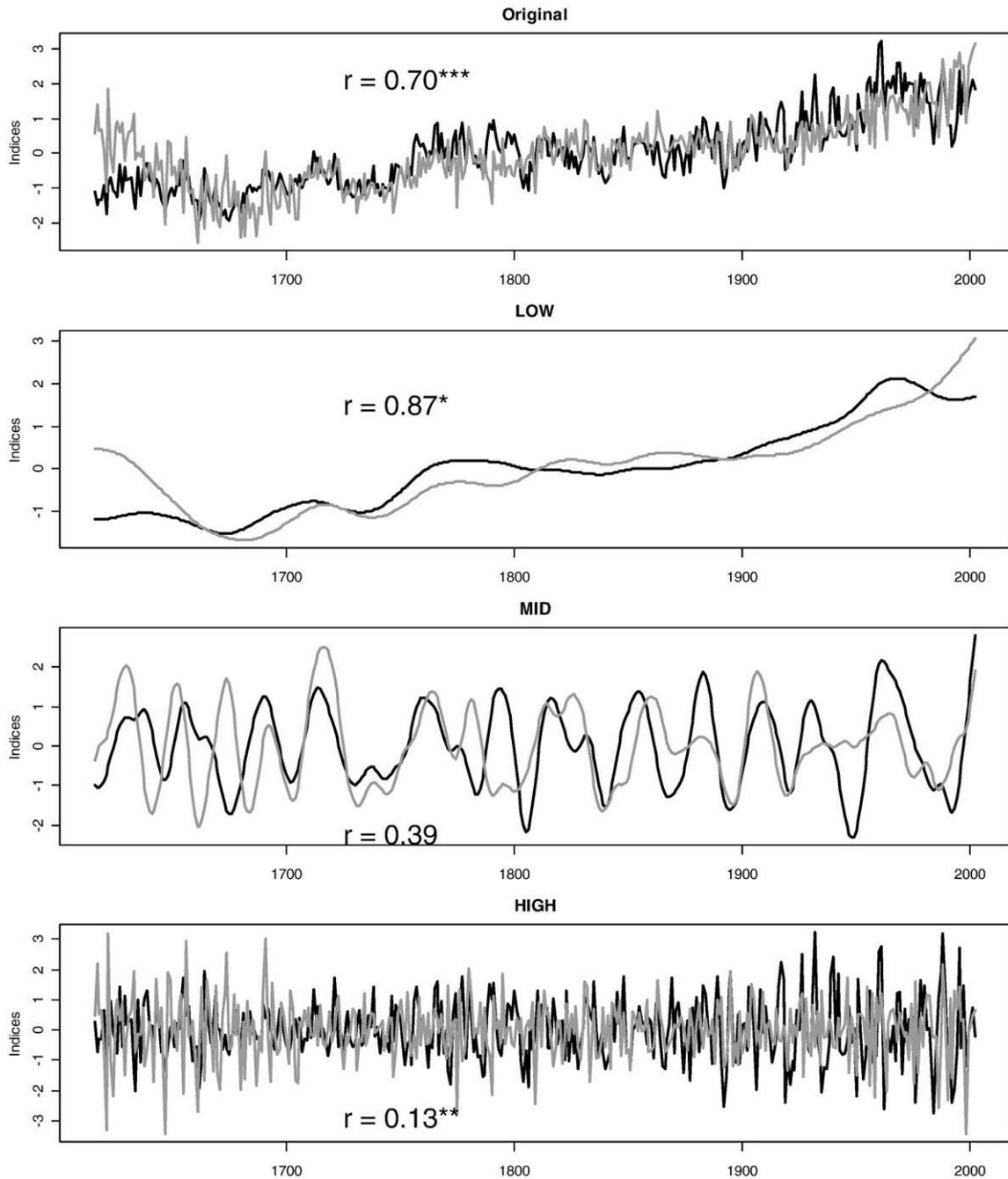


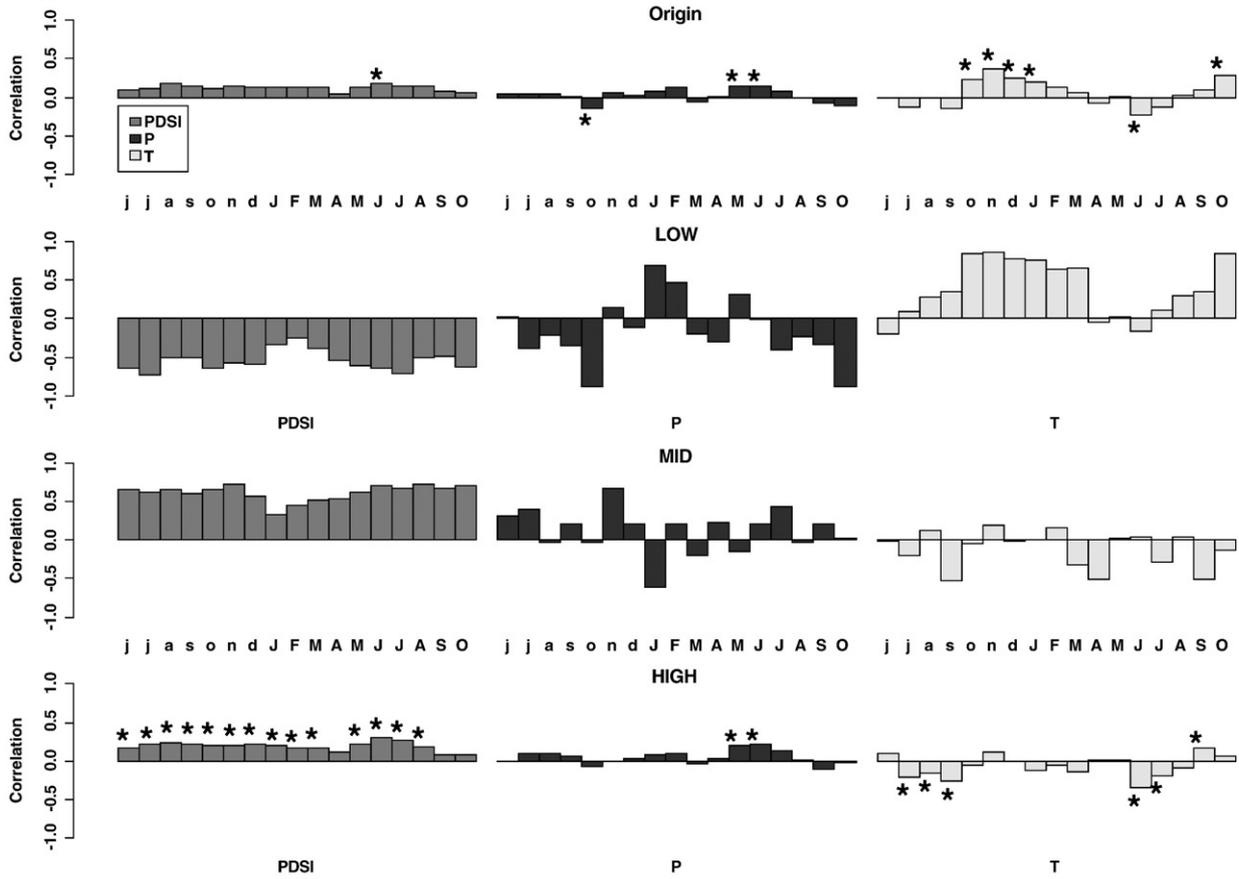
Fig. 4. Variance stabilized RCS chronology of RW (black) and P1 (grey), and their high- (wavelength <20 yr), mid- (wavelength 20–50 yr) and low-frequency (wavelength >50 yr) components for the period 1616–2002. r -values = correlation between RW and P1 chronologies. *, **, *** = significance levels for $p < 0.05$, $p < 0.01$ and $p < 0.001$ after correction for reduced number of degrees of freedom, respectively.

RCS clearly increases the low-frequency loading RW and P1 timeseries. Both the traditional RW and novel P1 parameters contain a positive long-term trend over the past 250–300 yr. Variability in the high- and mid-frequencies is, however, different between the two parameters. The common variance between single measurement series (as measured by R_{bar}) is additionally much lower for P1 than for RW. This latter finding is also reported in the recent literature using shorter P1 timeseries (García-González and Eckstein, 2003; Fonti and García-González, 2004; García-González and Fonti, 2006; Fonti et al., 2007; García-González and Fonti, 2008; Fonti and García-González, 2008).

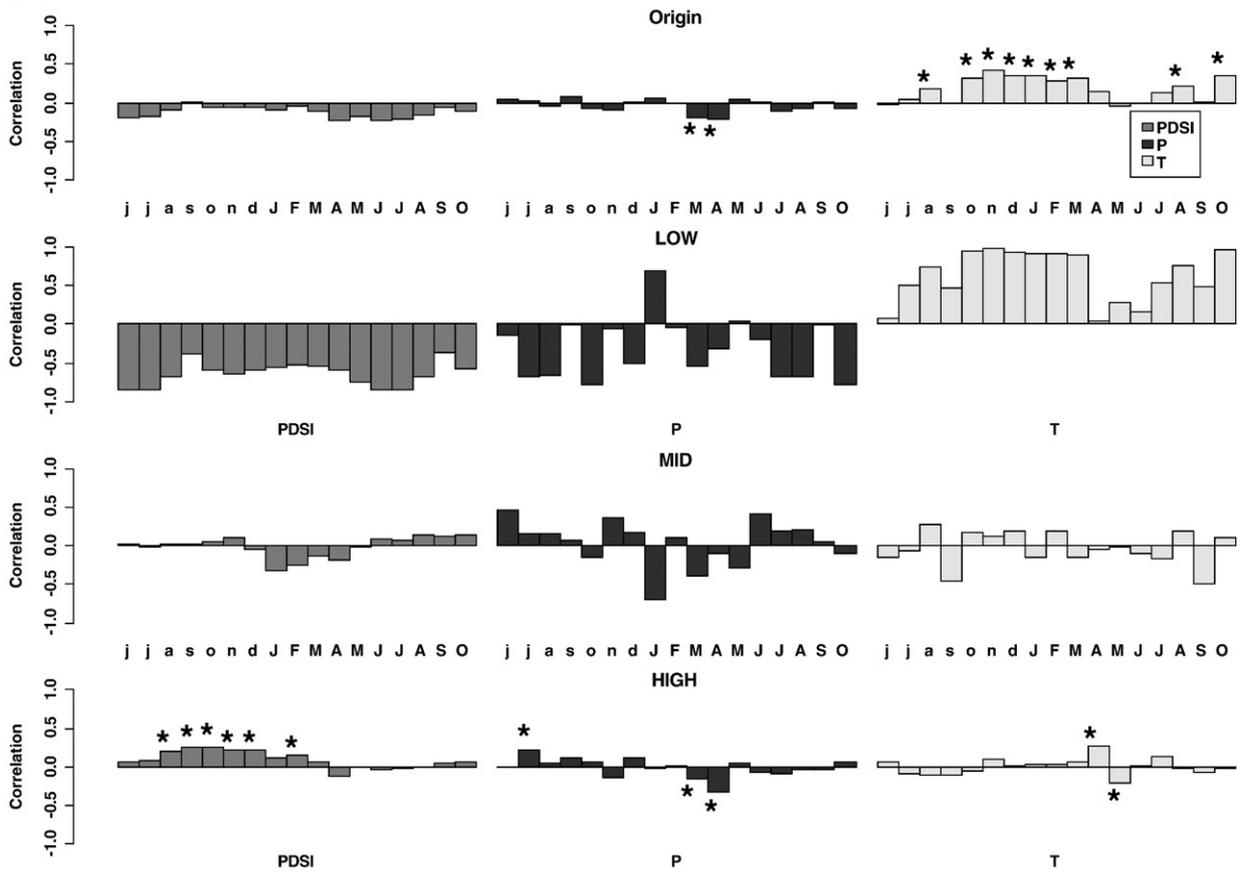
The RCS detrended chronologies, from which the mean age trend common to all data in our study site has been removed, show that both RW and P1 contain an increase of growth starting at around 1750 and accelerated in the 20th century. Further analyses of the low-frequency trends through the separation of data into distinct age classes demonstrated that the long-term increase is consistently observed across independent age classes. With the exception of the juvenile rings [AU1](1–50 yr) of P1, all age classes retain similar centennial scale variability, which seems to make it more likely that some external forcing caused these growth trends. Notably, these increasing trends in

Fig. 5. Climate-growth relationship between original, high (wavelength <20 yr), mid (20–50 yr) and low (>50 yr) frequency-components of both average monthly climate time-series of previous June to current October (PDSI, 1901–2002; P and T, 1864–2002) and RCS chronologies of RW and P1. * = significance levels for $p < 0.05$, after correction for reduced number of degrees of freedom.

RW



P1



RW and particularly P1 are observed in the raw data at the individual series level (Fig. 1b), further emphasizing the prominence of these trends and also suggesting minimal bias in the RCS detrending.

4.2. Frequency-dependent responses and climatic signals

Separation of the data in the frequency domain indicated that both variables, RW and P1, show coherent low, partly coherent mid, and clearly different high-frequency variations. The climatic responses suggested by the low-frequency analysis (i.e., positive responses to warmer and dryer climatic conditions) are unexpected for such a site, which, being characterized by steep slopes, shallow soils and near-south exposure, predestine the trees to water stress. The results from the climate/growth analyses instead indicate that generally “unfavorable” growing conditions, as reduced precipitation and increased temperature, favor larger RW. Since the magnitude of these long-term trends in PDSI, P and T are relatively small compared to year-to-year variability (data not shown) and due to the largely reduced number of degrees of freedom of the low-frequency component, it seems premature to attribute drought stress with increased growth and vessel area. Other possible explanations for the long-term increase include responses to increasing CO₂ concentrations (Huang et al., 2007) or modifications in site conditions due to an improved water storage capacity favored by increasing soil depths (Kalbitz et al., 2000; Sayer, 2006). In fact, reports on site development, which was likely influenced by rock fall, suggest that the initial soil conditions and shallow root systems may have led to relatively severe water limitations, with subsequent soil and root development mitigating water deficits.

In contrast to the low-frequency component, high-frequency RW variability well reflects the dry condition of the site, whereby radial growth positively responds to summer water availability (e.g., positive to precipitation and PDSI, and negative to temperature). Observations of growth in comparable ecological situations have yielded similar findings (e.g., Breda et al., 2006; Weber et al., 2007). Earlywood vessels instead respond to conditions at the beginning of the growing season (negative to precipitation) and to early summer precipitation and winter PDSI. The observed spring precipitation signal is consistent with results from previous work in the same region with the same species (García-González and Fonti, 2008; Fonti and García-González, 2008) and contemporaneously corroborate the ability of cell size chronologies to encode climatic information which is different and with a finer time scale than that of RW (García-González and Eckstein, 2003; Fonti and García-González, 2004; Fonti et al., 2007).

4.3. Physiological explanations

Frequency-dependent responses of P1 can be explained by the different processes involved in vessel formation. We specifically differentiate between effects related to i) underlying tree vigour and ii) weather variability.

On one hand, the fact that radial growth of these trees tends to show nearly constant and increasing values, suggests that long-term increases in vigour accelerate biological autocorrelation (Frank et al., 2007a). It is not clear to what extent these increases in productivity are related to regional climatic influences, site-specific effects, or long-term growth processes which result in increased capacity of the tree to uptake water and nutrients. In any case, increases in radial growth suggest increases in photosynthesis and net primary productivity (as foliage, root, stem, storage and defence compounds), which eventually results in a positive feedback on tree vigour and on tree growth (Larcher, 2001). The low-frequency signal of P1, which analogously to RW is characterized by a long-term increase, might have similar origins as those of RW, i.e. it appears linked to the vigour of the tree. Specifically, we suggest that the P1 low-frequency trend reflects processes linked to allocation, storage and mobilization of carbon. In

sessile oak, a ring-porous species, all of the previous year's earlywood vessels are embolized by frost events each winter (Hacke and Sauter, 1996; Hacke and Sperry, 2001). Since not embolized small latewood vessels of previous year sapwood rings contribute only marginally to the overall water conductivity (Tyree and Zimmermann, 2002), new large earlywood vessels need to be produced before bud burst and leaf expansion (Suzuki et al., 1996; Breda and Granier, 1996; Schmitt et al., 2000) to guarantee adequate hydraulic conductivity. If the foliage biomass increases so does the size of the new forming vessels increase accordingly. These processes that set the resumption of photosynthetic activities in spring, in particular earlywood vessel and foliage production, rely entirely on the mobilization of reserves stored during previous year growing season (Barbaroux and Bréda, 2002; Kagawa et al., 2006) and strongly depend on tree vigour. Thus, from a long-term perspective, overall favourable growing conditions eventually promote better performing trees that allocate more reserves to be invested into the photosynthetic apparatus and that fulfill the increased needs of hydraulic conductivity by increasing the size of the newly formed earlywood vessels.

On the other hand, high-frequency variations seem instead to be directly influenced by actual weather conditions. Climate-growth analyses clearly indicate that wide rings are developed during wet and cool summers while the size of the earlywood vessels is negatively correlated with spring precipitation. Differences between RW and P1 signals thus result from the differing factors determining their development. While it is obvious that in dry environments water availability controls radial growth, the mechanisms responsible for the direct negative association between vessel size and precipitation, although consistent among several sites (García-González and Fonti, 2008; Fonti and García-González, 2008), remains unclear. More detailed studies monitoring cell formation (e.g., Rossi and Deslauriers, 2007) under differing water regimes might further help understanding the mechanisms driving this inverse relationship.

5. Conclusions

When reconstructing climate from tree-rings, it is assumed that, if adequate detrending procedures are applied, climate response is stable across frequencies (Esper et al., 2005, 2007), and that the signal stored in tree growth reflects a single and primary forcing. This, however, does not seem to be the case for processes of ring and earlywood vessel formation at the studied site, where, depending upon the wavelength analyzed, different ecological and environmental signals appear to be preserved. This notation might not be as relevant for the use of RW as a proxy, since the radial response to climatic forcing and subsequent biological feedbacks – impacting tree vigour – are of the same sign. However, the frequency-dependent signals could have impact on the properties of the signal recorded in the changing size of earlywood vessels. The forcings relevant to this parameter, i.e. a negative response to spring precipitation in the high-frequency and an indirect positive response via the tree vigour in the low-frequency domain, have contrasting effects on vessel size. The weak but consistent precipitation signal recorded in the high-frequency domain is not revealed in the mid- and lower-frequency domains. Therefore – but based on the results from only one study site and species – earlywood vessel size chronologies do not seem to be an adequate proxy to reconstruct long-term changes in spring precipitation. More analyses of multi-centennial earlywood vessel chronologies from different sites with different histories are needed to understand the long-term evolution of the oak hydrologic system and to validate the frequency-dependent signal observed in this study.

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