

1 **Frequency-dependent signals in multi-centennial oak**  
2 **vessel data**

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4 **Patrick Fonti<sup>1\*</sup>, Kerstin Treydte<sup>1</sup>, Sebastian Osenstetter<sup>1</sup>, David Frank<sup>1</sup>, Jan Esper<sup>1</sup>**

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8 <sup>1</sup> Swiss Federal Research Institute WSL, Dendro Sciences Unit,  
9 Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland

10  
11  
12  
13  
14  
15 **\* Corresponding author**

16 Fax: +41 44 739 22 15  
17 e-mail: [patrick.fonti@wsl.ch](mailto:patrick.fonti@wsl.ch)  
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## 20 **Abstract**

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

43 **Keywords:** Dendrochronology, climate proxy, earlywood vessels, *Quercus petraea*, spring  
44 precipitation, cell size, frequency components, Swiss Alps

45

## 46 **Introduction**

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

57 Analogous to continuous time-series of annual RW and MXD, series of wood cell anatomical  
58 features should also encode valuable ecological information (Schweingruber, 2001). Tree  
59 rings do not only integrate the yearly growing conditions, as through the continuous formation  
60 of new cells, intra-seasonal influences are also registered. In fact, climatic conditions that  
61 prevail during xylem development can determine the anatomical characteristics of the wooden  
62 cells, such as the size of tracheids in conifers and vessels in deciduous trees. Since the  
63 characteristic periods of the division, expansion, and maturation of wood cells range from  
64 several days to a few weeks (Suzuki et al., 1996; Schmitt et al., 2000; Frankenstein et al.,  
65 2005; Rossi et al., 2006), there is good potential that the course of shorter term weather  
66 conditions occurring during the growing season are chronologically archived in the  
67 anatomical structure of annual rings. Time-series of such cell anatomical characteristics might  
68 thus provide more detailed information about seasonal climatic variability.

69 While growth-climate analysis of the high-frequency variability of the size of water-  
70 conductive cells (tracheids or vessels) indicates that cell anatomical characteristics can encode

71 intra-seasonal information, the specific content of this information varies depending on the  
72 biology of the species, the seasonality of climate in a particular region and on specific site  
73 conditions (e.g., García-González and Eckstein, 2003; Kirilyanov et al., 2003; Panyushkina et  
74 al., 2003; Fonti and García-González, 2004; Fonti et al., 2007). Distinct spring precipitation  
75 signals have been obtained from the annual variability in the size of the earlywood vessels of  
76 relatively young oak (*Quercus petraea* (Matt.) Liebl) growing on mesic sites in Switzerland  
77 (Fonti and García-González, 2008). These results are, however, based on climate-growth  
78 analysis of high-frequency variations (using 32-year spline detrended records) of relatively  
79 short chronologies (50 years). Despite of these novel findings it remains unclear if vessel  
80 parameters contain information about long-term environmental changes and could thus be  
81 utilized to reconstruct climate-change related processes.

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

89

## 90 **Material and methods**

### 91 **Wood material and tree-ring data**

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

96 exposed slope at about 900 m asl. The closest meteorological station in Cevio (416 m asl),  
97 located <10 km from study site, recorded a mean annual temperature of 9.5 °C and a total  
98 annual precipitation of 481 mm with >60% falling between April and September (data from  
99 1950 to 2005; MeteoSwiss).

100 A total of 27 cores (5 mm diameter) were collected from 12 trees at stem breast height and  
101 perpendicular to the slope direction to reduce influences due to reaction wood. Measurements  
102 of RW and average earlywood vessel area of the first row of vessels in each ring (**P1**) were  
103 performed on the transversal section of the core samples. Before measurement, each core was  
104 progressively sanded (up to 400 grit paper), cleaned with high-pressure water jet to remove  
105 tyloses and wood dust from inside the vessel lumina, and lumina refilled with white wax to  
106 improve vessel recognition (Fonti et al., 2009). RW was measured using the LINTAB and  
107 TSAP system (Rinn, 1996), and crossdating of RW-series assessed using COFECHA  
108 (Holmes, 1983). P1 was measured ring-by-ring using Image Pro Plus (v4.5, Media  
109 Cybernetics, USA) applied to whole core images captured with a high-resolution and  
110 distortion-free digital scanner (256 grey scale level with a resolution of 2,400 dpi; Epson  
111 Expression 10000 XL, Seiko Epson Corporation, Japan). Due to occasional anomalies in  
112 wood structure caused by reaction to damages, measurements of P1 do not cover all juvenile  
113 tree-rings in some cases.

## 114 **Chronology building**

115 RW and P1 measurement series were detrended to remove possible biological age trends  
116 (Fritts, 2001; Fonti et al., 2002). This process includes fitting growth curves to the raw  
117 measurement series, and dividing the original data by the fitted curves (Cook and Kairiukstis,  
118 1990). Two conceptually different age-trend fittings were performed: (i) a 300-year cubic  
119 smoothing spline applied to each individual measurement series (**300 SPLINE**; Cook and  
120 Peters, 1981), and (ii) the regional curve standardization (**RCS**; details in Esper et al., 2003)

121 that involves fitting a spline function to the arithmetic mean of all cambial age-aligned time-  
122 series and removing the age-trend via this so-called regional curve. Inter-series correlations  
123 ( $\bar{R}$ ) were calculated between all 27 individual 300-spline and RCS detrended series of RW  
124 and P1 to assess the strength of common underlying signals. Data were then averaged to  
125 chronologies using the biweight robust mean (Cook, 1985).

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

### 132 **Frequency differentiation and climate-growth analysis**

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

136 Frequency components were defined in order to separately account for signals in the annual to  
137 centennial scale domains. We applied splines as high and low-pass filters: high-pass filtering  
138 was done with a 20-year spline (HIGH) and low-pass filtering with a 50-year spline (LOW).  
139 Wavelengths between the high- and low-frequency domains were assessed with a 20-50 year  
140 band-pass filter (MID). Before frequency differentiation, RW and P1 chronologies were  
141 adjusted using the 50-year running standard deviation, to remove changes in variance related  
142 to unequal sample depth, cross-correlation, or other biasing sources (Frank et al., 2007b).

143 Long meteorological time-series including monthly data of the Palmer Drought Severity Index  
144 (**PDSI**, a standardized index of surface moisture conditions; Palmer, 1965), mean temperature  
145 (**T**) and total precipitation (**P**) have been considered to allow for correlation analyses over all

146 frequency domains. PDSI data from 1901 to 2002 were obtained from 4 grid-boxes (0.5° x  
147 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  
148 from 1864 to 2002 from the MeteoSwiss station of Lugano located in 273 m asl about 50 km  
149 apart from the tree site. Monthly calibration against meteorological data (i.e., Pearson's  
150 correlation) was performed for previous June to current October.

151

## 152 **Results**

### 153 **Raw data**

154 The period covered by the measured series span from 1542 to 2002 for RW and from 1556 to  
155 2002 for P1, however minimum sample replication of 3 cores is reached only after 1589 and  
156 1616, respectively (Fig. 1a). The mean segment length, i.e., the average number of years per  
157 sample, is 218 (range 63 to 461) for RW and 188 (63 to 447) for P1. The average annual  
158 increment (RW) over the whole period is 0.81 mm ( $\pm$  0.26 standard deviation) and the  
159 average vessel area of the first row of earlywood vessels (P1) is 54,930  $\mu\text{m}^2$  ( $\pm$ 8,090). The  
160 apparent increase in scatter towards present of both RW and P1 (Fig. 1a) is mainly due to the  
161 inclusion of younger individuals into the data sets. The low pass filters fitted to the raw time-  
162 series reveal a long-term increase in RW and P1 after 1650. This increase seems accelerated  
163 in P1 after about 1930. Positive trends are generally stronger for young than for old trees (Fig.  
164 1b). Age alignment (Fig. 1c) reveals that RW data have almost no age trend whereas P1  
165 clearly show an increasing trend on vessel size in the juvenile wood, i.e., up to an age of about  
166 50 years.

### 167 **Characteristics of the chronologies**

168 Spline and RCS detrended RW and P1 chronologies show common multi-decadal variations  
169 (Figure 2). Rbar values over the full chronology lengths are 0.36 and 0.17 for the RW and P1

170 after RCS detrending. RCS-detrending, which removes the biological growth trend common  
171 to all measurement series, preserved substantially more low-frequency information -  
172 characterized by a centennial scale increasing trend - than spline detrending, which in turn  
173 emphasized inter-annual to multi-decadal scale variations.

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

### 178 **Frequency domains and climate response**

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

188 Frequency-dependent climate/growth analyses using monthly PDSI (period 1901-2002), P,  
189 and T data (1864-2002) indicate that the RW and P1 contain in part a different response to  
190 climate (Figure 5). In the low-frequency domain, both the RW and P1 tend to be larger in  
191 warmer and dryer climatic conditions, although due to the substantially reduced degrees of  
192 freedom of the smoothed data, none of these values are significant ( $p<0.05$ ). Differences in  
193 climatic responses are revealed for the mid-frequency component. While RW responds to  
194 drought (positive to PDSI, although not significant ( $p>0.05$ )), P1 appears insensitive to PDSI.



195 Differing responses to climate are further emphasized for the high-frequency component, and  
196 due to sufficient observations these results also are characterized by greater statistical  
197 confidence. RW increases in wet and cold summers, which results in generally positive and  
198 significant relationships to PDSI, whereas P1 is larger in association with winter PDSI, dry  
199 springs and warm Aprils and cold Mays ( $p < 0.05$ ).

200

## 201 **Discussion**

### 202 **Characteristics of the chronologies**

203 While preservation of high- and mid-frequency variance is fairly independent of the choice of  
204 the detrending method, application of RCS clearly increases the low-frequency loading RW  
205 and P1 timeseries. Both the traditional RW and novel P1 parameters contain a positive long-  
206 term trend over the past 250-300 years. Variability in the high- and mid-frequencies is,  
207 however, different between the two parameters. The common variance between single  
208 measurement series (as measured by  $R_{bar}$ ) is additionally much lower for P1 than for RW.  
209 This latter finding is also reported in the recent literature using shorter P1 timeseries (García-  
210 González and Eckstein, 2003; Fonti and García-González, 2004; García-González and Fonti,  
211 2006; Fonti et al., 2007; García-González and Fonti, 2008; Fonti and García-González, 2008).

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

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

### 222 **Frequency-dependent responses and climatic signals**

223 Separation of the data in the frequency domain indicated that both variables, RW and P1,  
224 show coherent low, partly coherent mid, and clearly different high-frequency variations. The  
225 climatic responses suggested by the low-frequency analysis (i.e., positive responses to warmer  
226 and dryer climatic conditions) are unexpected for such a site, which, being characterized by  
227 steep slopes, shallow soils and near-south exposure, predestine the trees to water stress. The  
228 results from the climate/growth analyses instead indicate that generally "unfavorable"  
229 growing conditions, as reduced precipitation and increased temperature, favor larger RW.  
230 Since the magnitude of these long-term trends in PDSI, P and T are relatively small compared  
231 to year-to-year variability (data not shown) and due to the largely reduced number of degrees  
232 of freedom of the low-frequency component, it seems premature to attribute drought stress  
233 with increased growth and vessel area. Other possible explanations for the long-term increase  
234 include responses to increasing CO<sub>2</sub> concentrations (Huang et al., 2007) or modifications in  
235 site conditions due to an improved water storage capacity favored by increasing soil depths  
236 (Kalbitz et al., 2000; Sayer, 2006). In fact, reports on site development, which was likely  
237 influenced by rock fall, suggest that the initial soil conditions and shallow root systems may  
238 have led to relatively severe water limitations, with subsequent soil and root development  
239 mitigating water deficits.

240 In contrast to the low-frequency component, high-frequency RW variability well reflects the  
241 dry condition of the site, whereby radial growth positively responds to summer water  
242 availability (e.g., positive to precipitation and PDSI, and negative to temperature).  
243 Observations of growth in comparable ecological situations have yielded similar findings  
244 (e.g., Bréda et al., 2006; Weber et al., 2007). Earlywood vessels instead respond to conditions

245 at the beginning of the growing season (negative to precipitation) and to early summer  
246 precipitation and winter PDSI. The observed spring precipitation signal is consistent with  
247 results from previous work in the same region with the same species (García-González and  
248 Fonti, 2008; Fonti and García-González, 2008) and contemporaneously corroborate the ability  
249 of cell size chronologies to encode climatic information which is different and with a finer  
250 time scale than that of RW (García-González and Eckstein, 2003; Fonti and García-González,  
251 2004; Fonti et al., 2007).

### 252 **Physiological explanations**

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

256 On one hand, the fact that radial growth of these trees tends to show nearly constant and  
257 increasing values, suggests that long-term increases in vigour accelerate biological  
258 autocorrelation (Frank et al., 2007a). It is not clear to what extent these increases in  
259 productivity are related to regional climatic influences, site-specific effects, or long-term  
260 growth processes which result in increased capacity of the tree to uptake water and nutrients.  
261 In any case, increases in radial growth suggest increases in photosynthesis and net primary  
262 productivity (as foliage, root, stem, storage and defence compounds), which eventually results  
263 in a positive feedback on tree vigour and on tree growth (Larcher, 2001). The low-frequency  
264 signal of P1, which analogously to RW is characterized by a long-term increase, might have  
265 similar origins as those of RW, i.e. it appears linked to the vigour of the tree. Specifically, we  
266 suggest that the P1 low-frequency trend reflects processes linked to allocation, storage and  
267 mobilization of carbon. In sessile oak, a ring-porous species, all of the previous year's  
268 earlywood vessels are embolized by frost events each winter (Hacke and Sauter, 1996; Hacke  
269 and Sperry, 2001). Since not embolized small latewood vessels of previous year sapwood

270 rings contribute only marginally to the overall water conductivity (Tyree and Zimmermann  
271 2002), new large earlywood vessels need to be produced before bud burst and leaf expansion  
272 (Suzuki et al., 1996; Bréda and Granier 1996; Schmitt et al., 2000) to guarantee adequate  
273 hydraulic conductivity. If the foliage biomass increases so does the size of the new forming  
274 vessels increase accordingly. These processes that set the resumption of photosynthetic  
275 activities in spring, in particular earlywood vessel and foliage production, rely entirely on the  
276 mobilization of reserves stored during previous year growing season (Barbaroux and Bréda,  
277 2002; Kagawa et al., 2006) and strongly depend on tree vigour. Thus, from a long-term  
278 perspective, overall favourable growing conditions eventually promote better performing trees  
279 that allocate more reserves to be invested into the photosynthetic apparatus and that fulfill the  
280 increased needs of hydraulic conductivity by increasing the size of the newly formed  
281 earlywood vessels.

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

293

294 **Conclusions**

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

314

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319

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424



425 **Figures**

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

429

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

432

433 Figure 3: 100-year splines fit to 50-year age-class segments of RCS-detrended RW and P1  
434 data.

435

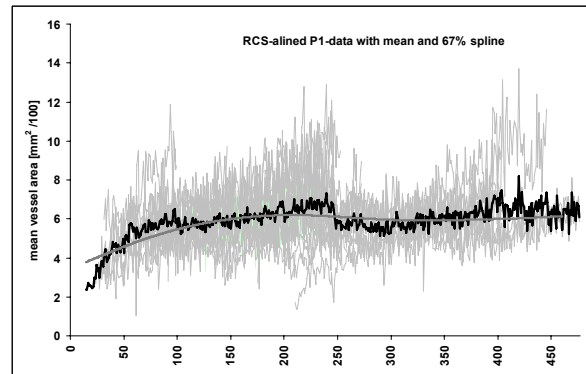
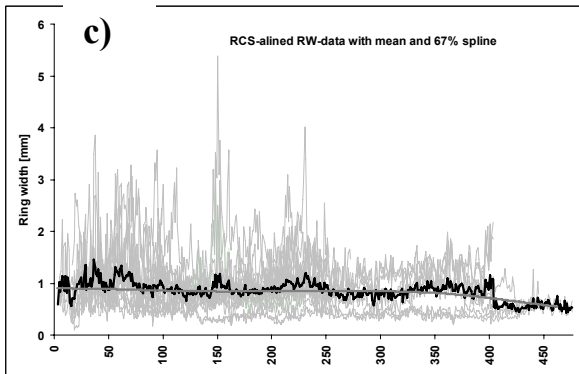
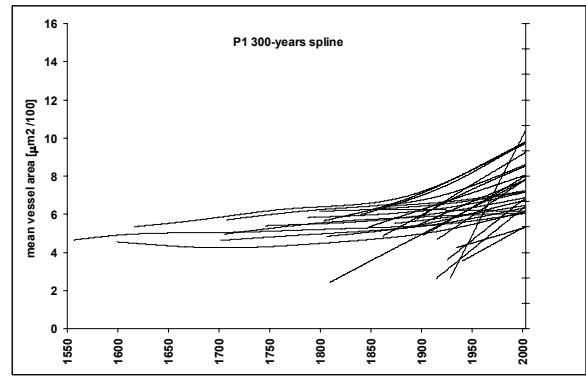
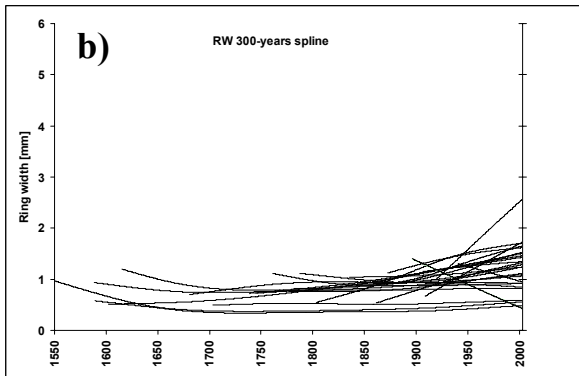
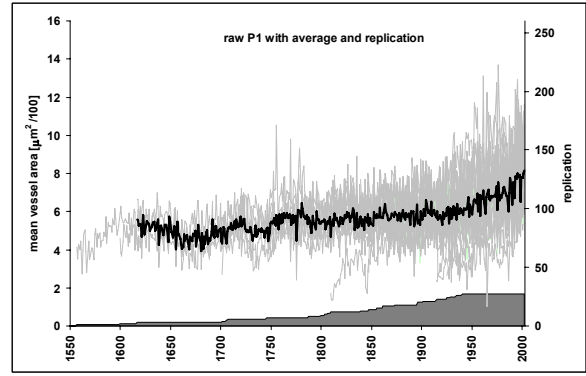
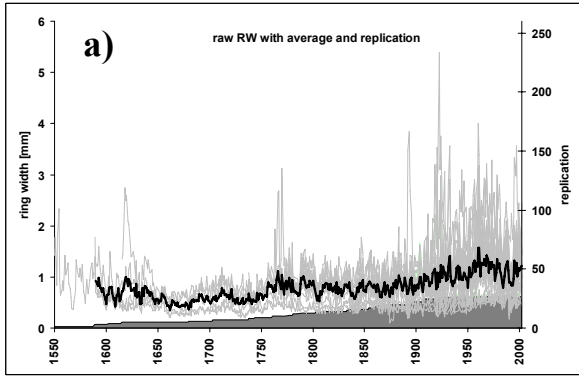
436 Figure 4: Variance stabilized RCS chronology of RW (black) and P1 (grey), and their high-  
437 (wavelength <20 yr), mid- (wavelength 20-50 yr) and low- frequency (wavelength >50 yr)  
438 components for the period 1616-2002. r-values = correlation between RW and P1  
439 chronologies. \*, \*\*,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

441

442 Figure 5: Climate-growth relationship between original, high (wavelength <20 years), mid  
443 (20-50 years) and low (>50 years) frequency-components of both average monthly climate  
444 time-series of previous June to current October (PDSI, 1901-2002; P and T, 1864-2002) and  
445 RCS chronologies of RW and P1. \* = significance levels for  $p < 0.05$ , after correction for  
446 reduced number of degrees of freedom.

RW

P1



RW

P1

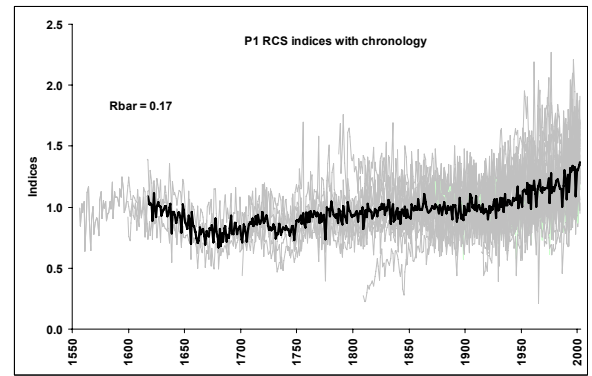
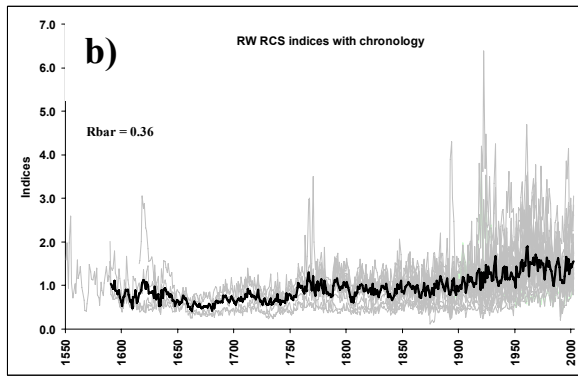
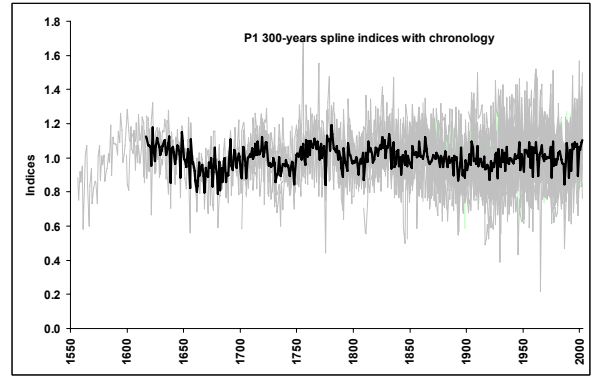
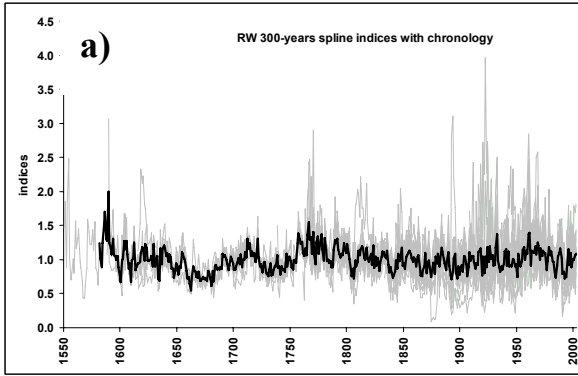
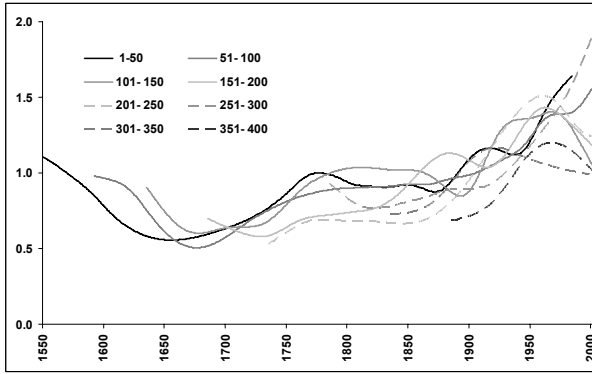


Figure3

RW



P1

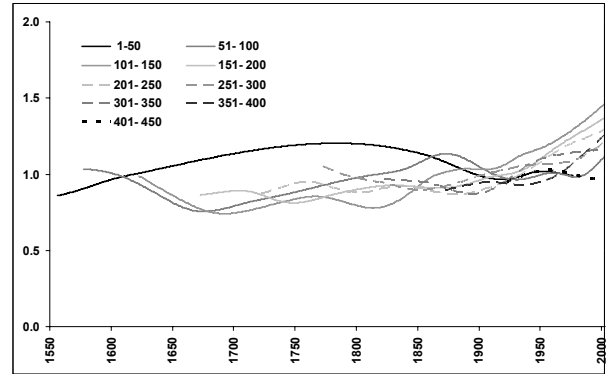


Figure4

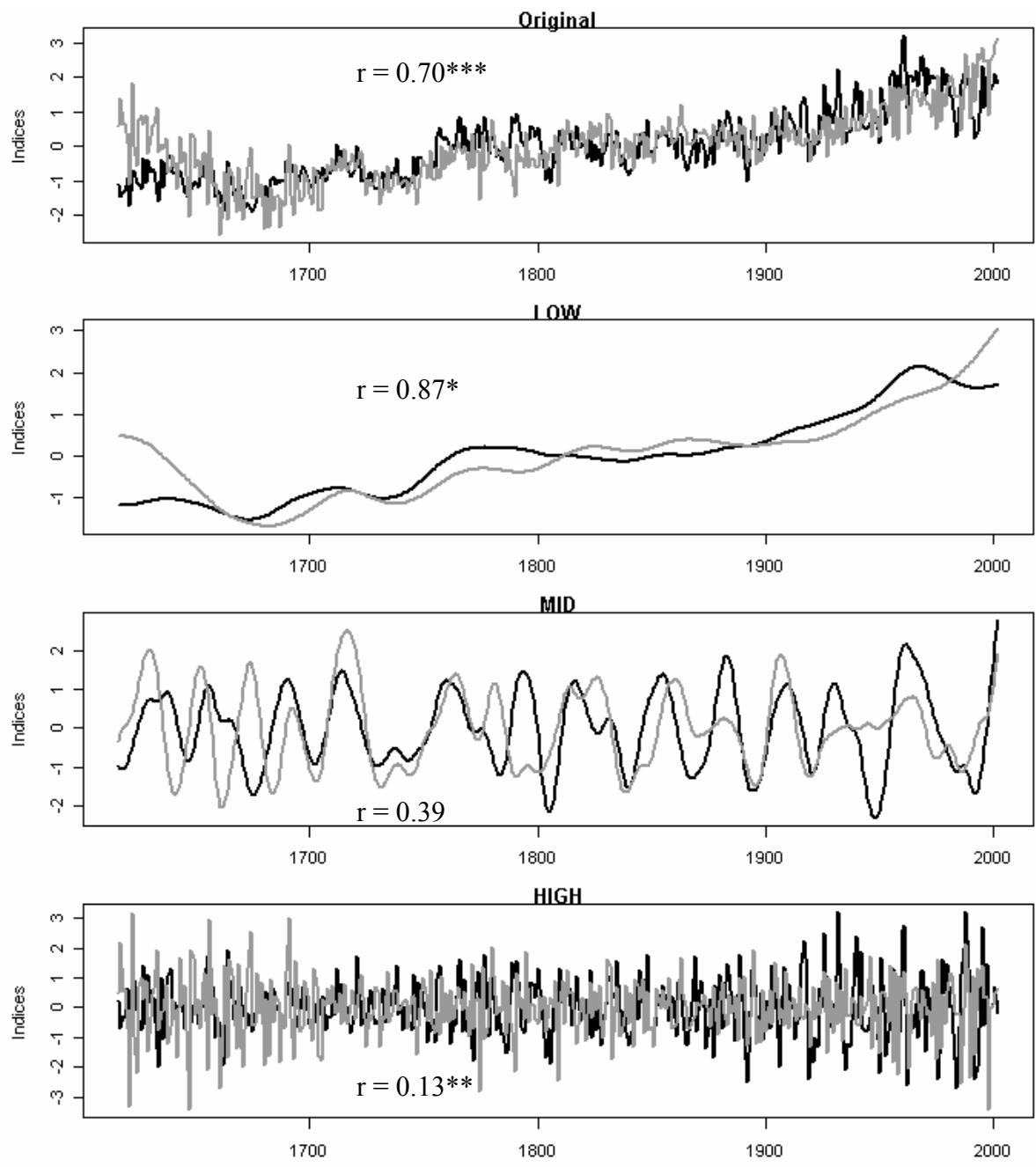


Figure5

