Complex climate controls on 20th century oak growth in Central-West Germany

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Summary We analyze interannual to multi-decadal growth variations of 555 oak trees from Central-West Germany. A network of 13 pedunculate oak (*Quercus robur* L.) and 33 sessile oak (*Quercus petraea* (Matt.) Liebl.) site chronologies is compared with gridded temperature, precipitation, cloud-cover, vapor pressure and drought (i.e., Palmer Drought Severity Index, PDSI) fluctuations. A hierarchic cluster analysis identifies three groups for each oak species differentiated by ecologic settings. When high precipitation is primarily a characteristic for one *Q. robur* and one *Q. petraea* cluster, the other clusters are more differentiated by prevailing temperature conditions. Correlation analysis with precipitation and vapor pressure reveals statistically significant ($P \leq 0.05$) correlations for June ($r = 0.51$) and annual ($r = 0.43$) means. Growth of both species at dry sites correlates strongly with PDSI ($r = 0.39$, $P \leq 0.05$), and weakly with temperature and cloud-cover. In natural stands, *Q. robur* responds more strongly to water depletion than *Q. petraea*. Twenty-one-year moving correlations show positive significant growth response to both PDSI and precipitation throughout the 20th century, except for the 1940s – an anomalously warm decade during which all oak sites are characterized by an increased growth and an enhanced association with vapor pressure and temperature. We suggest that the wider oak rings that are exhibited during this period may be indicative of a nonlinear or threshold-induced growth response to drought and vapor pressure, and run counter to the general response of oak to drought and precipitation that normally would result in suppressed growth in a warmer and drier environment. As the wide rings are formed during the severe drought period of the 20th century, a complex model seems to be required to fully explain the widespread oak growth. Our results indicate uncertainty in estimates of future growth trends of Central European oak forests in a warming and drying world.

Introduction

Global climate change is projected to lead to a temperature increase in Central Europe between 2.3 and 5.3 °C in the 21st century, accompanied by an overall decrease of summer precipitation (Christensen et al. 2007). Both these factors would subsequently result in a long-term shift towards drier conditions with an increased likelihood of extreme droughts (Schär et al. 2004). Such changes will likely cause a decline in forest growth productivity and increased tree mortality (Thomas et al. 2002), with subsequent implications on terrestrial carbon sequestration (Kurz et al. 2007).

Beside the uncertainties related to the wide range of future climate estimates, a variety of biotic and abiotic factors influencing tree growth in temperate climates (Kozlowski and Pallardy 1997) complicate our understanding of the interactions between biotic ecosystems and their abiotic environments. In contrast to the higher elevations, where tree growth is mainly limited by a single climatic factor (Körner 1998), radial growth of trees in low-elevation temperate forests reflects the interplay of temperature, precipitation and radiation both before and during the growth season. Additional disturbances derive from biotic and other exogenous factors. It is therefore necessary to explore a variety of climatic parameters in more integrated approaches to understand the complex relationships between climate variability and tree physiologic responses in temperate forests.

To date, relationships between temperature, precipitation and annual growth of *Quercus robur* L. and *Quercus petraea* (Matt.) Liebl., which in terms of surface area and economic value are important Central European forest

species (Ellenberg 1996), have been intensively studied (e.g., Kelly et al. 1989, Becker et al. 1994, Bridge et al. 1996). The occurrence of the so-called pointer years (Schweingruber et al. 1990) across Europe has been explained by temperature and precipitation anomalies (Neuwirth et al. 2007) associated with changing atmospheric circulation patterns (Kelly et al. 2002). However, several 'time-series' studies in temperate Central European forests show only moderate coherency between oak growth and temperature and precipitation (Pilcher and Gray 1982, Bonn 1998, Lebourgeois et al. 2004), indicating that these parameters alone do not place strict limits on radial growth. In this regard, the simultaneous consideration of various climatic parameters that, for example, appear to be relevant in model simulations (Nemani et al. 2003), may be particularly helpful to provide a comprehensive interpretation of climate change impacts on larger scale plant growth (Esper et al. 2002).

Ecophysiologic studies focusing on stomatal conductance, photosynthetic activity and hydraulic conductivity (Epron and Dreyer 1993, Gieger and Thomas 2005, Bréda et al. 2006) and dendroclimatologic analyses (Lévy et al. 1992, Becker et al. 1994) have demonstrated differences in the drought response of *Q. robur* and *Q. petraea* (Thomas et al. 2002). *Quercus petraea* is known to be more drought tolerant.

The overall objective of this study was to assess the influence of various climatic parameters on growth of *Q. robur* and *Q. petraea*. A network of 13 *Q. robur* sites (149 trees)

and 33 *Q. petraea* sites (406 trees) has been established in temperate Central-West German forests to compare oak growth and climate under different site ecologic conditions. We compare species growth trends and cluster sites of similar growth behavior, separated for each species. Our second objective was to identify the dominant climatic factors influencing oak growth. Beside temperature and precipitation, we analyzed the influence of cloud-cover, vapor pressure and drought conditions, as expressed in the Palmer Drought Severity index (PDSI), on radial growth. We hypothesized that these climate parameters would explain growth variations beyond the influences of temperature and precipitation and therefore help to assess climate controls on oak growth in widespread temperate forests. Our third objective was to assess temporal stability of growth responses to 20th century climate variability.

Materials and methods

Study area

The study area is located in Central-West Germany and covers the region 49–53° N and 6–10° E (Figure 1). This area includes parts of the German temperate lowlands and some low mountain ranges. The synoptic conditions influencing this area are dominated by the North Atlantic
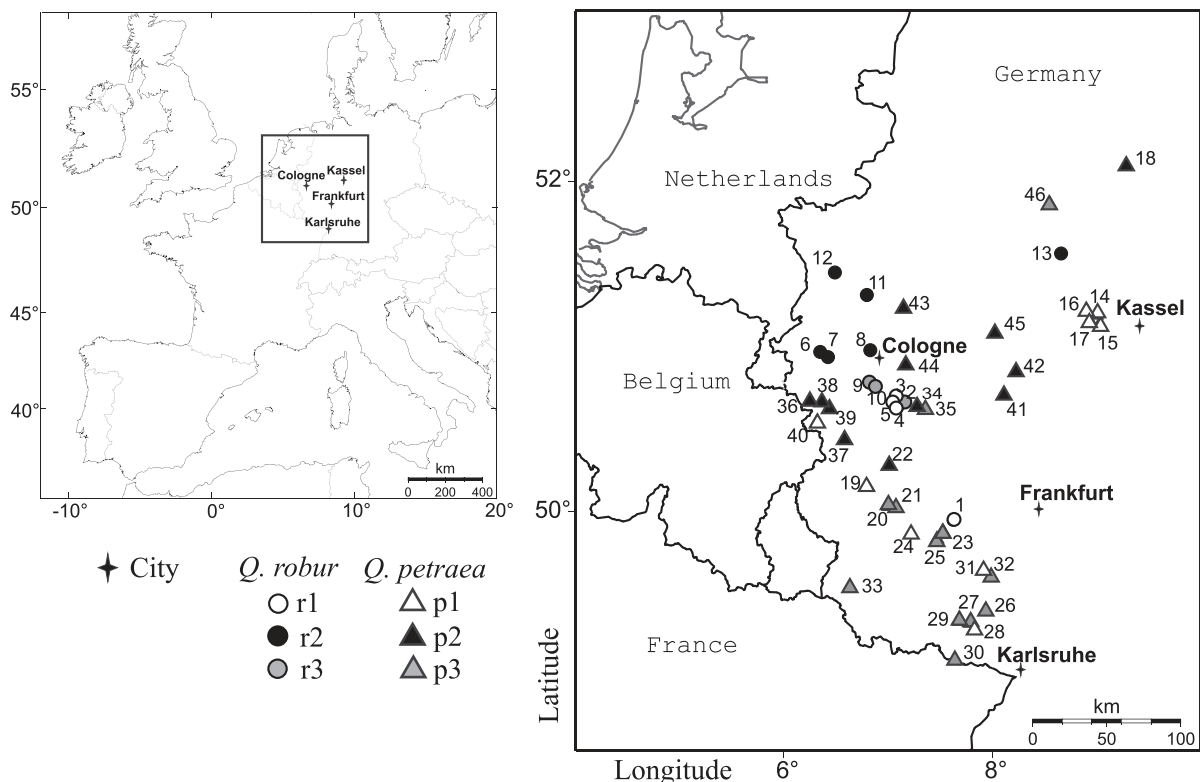

Figure 1. Location of the 13 pedunculate (*Q. robur*, circle) and 33 sessile oak (*Q. petraea*, triangle) sites in Central-West Germany, classified into three ecophysiologic clusters of each species. Site numbers are identical with site numbers in Table 1.

Table 1. Description and characteristics of the 46 site chronologies. Species: QURO = *Quercus robur*, QUPE = *Quercus petraea*; Period (> 3 trees); MSL = mean site segment length (years); AGR = average growth rate (mm year^{-1}); Rbar and EPS (Expressed Population Signal) are calculated over 30 years lagged by 15 years; Elev. = Elevation (m a.s.l.); AWC = available water capacity: 1 = low (60–110 mm), 2 = mean (110–170 mm), 3 = high (170–240 mm) and 4 = very high (> 240 mm); n/a = not applicable; Asp. = Aspect: N north, NE northeast, NW northwest, E east, W west, S south, SE southeast and SW southwest; a.Temp. = annual temperature means; a.Prec. = annual precipitation sums; the last column indicates the cluster to which a site is grouped, Clu. = cluster.

Site	Latitude/longitude	Species	Period	MSL	AGR	Rbar	EPS	Elev.	AWC	Asp.	a.Temp.	a.Prec.	Clu.
1	49.94N/7.63E	QURO	1778–2005	182	2.01	0.45	0.92	510	3	–	8.9	716	r1
2	50.72N/7.09E	QURO	1847–2002	138	1.58	0.58	0.94	150	1	–	9.9	780	r3
3	50.71N/7.09E	QURO	1833–2002	148	1.87	0.58	0.90	120	3	–	9.9	780	r1
4	50.67N/7.05E	QURO	1832–2005	153	1.73	0.60	0.94	170	3	–	9.9	780	r1
5	50.67N/7.05E	QURO	1850–2005	150	1.97	0.43	0.83	170	3	–	9.9	780	r1
6	50.93N/6.42E	QURO	1835–2005	147	2.17	0.40	0.87	105	3	–	9.7	897	r2
7	50.92N/6.42E	QURO	1766–2005	195	1.57	0.58	0.93	100	4	–	9.7	897	r2
8	51.05N/6.80E	QURO	1865–2005	128	2.34	0.61	0.94	45	3	–	10.3	830	r2
9	50.79N/6.84E	QURO	1861–2005	142	1.45	0.53	0.91	160	2	–	9.7	835	r3
10	50.79N/6.85E	QURO	1855–2005	162	1.43	0.46	0.85	160	4	–	9.7	835	r3
11	51.32N/6.79E	QURO	1850–2005	141	2.23	0.57	0.94	40	2	–	10.4	819	r2
12	51.46N/6.49E	QURO	1812–2005	173	2.00	0.56	0.93	30	3	–	10.2	761	r2
13	51.58N/8.67E	QURO	1799–2005	176	1.78	0.53	0.91	260	1	–	8.3	825	r2
14	51.17N/8.97E	QUPE	1839–2005	159	1.51	0.48	0.93	290	2	SE	8.1	748	p1
15	51.16N/9.08E	QUPE	1844–2005	159	1.34	0.57	0.93	350	1	S	8.4	748	p1
16	51.16N/9.08E	QUPE	1856–2005	148	1.38	0.53	0.93	380	2	S	8.4	748	p1
17	51.16N/9.08E	QUPE	1851–2005	148	1.64	0.47	0.87	390	2	S	8.4	748	p1
18	52.10N/9.30E	QUPE	1809–2004	193	1.77	0.57	0.93	205	n/a	–	8.8	783	p2
19	50.12N/6.88E	QUPE	1825–2004	174	1.49	0.54	0.92	430	n/a	SW	9.2	748	p1
20	50.05N/7.07E	QUPE	1849–2005	150	1.71	0.58	0.93	370	n/a	SW	9.4	734	p3
21	50.04N/7.07E	QUPE	1831–2005	170	1.19	0.41	0.84	370	n/a	S	9.4	734	p3
22	50.30N/7.01E	QUPE	1832–2005	166	1.64	0.54	0.95	480	n/a	E	8.8	778	p2
23	49.88N/7.58E	QUPE	1813–2005	182	1.60	0.37	0.85	500	n/a	S	8.9	716	p3
24	49.87N/7.23E	QUPE	1661–2005	342	0.92	0.50	0.90	510	n/a	E	8.6	770	p1
25	49.85N/7.47E	QUPE	1824–2005	176	1.39	0.47	0.91	420	n/a	SE	8.7	747	p3
26	49.38N/7.87E	QUPE	1819–2005	177	1.45	0.56	0.93	500	1	SW	9.2	721	p3
27	49.30N/7.75E	QUPE	1708–2005	288	1.18	0.60	0.94	400	n/a	NW	9.3	727	p3
28	49.26N/7.81E	QUPE	1717–2005	282	0.88	0.59	0.93	480	2	SW	9.3	727	p1
29	49.24N/7.79E	QUPE	1715–2005	257	1.12	0.35	0.85	490	2	S	9.3	727	p3
30	49.06N/7.64E	QUPE	1713–2005	246	1.32	0.60	0.95	390	2	–	9.5	721	p3
31	49.61N/7.92E	QUPE	1805–2005	192	0.96	0.55	0.94	500	1	NE	9.3	696	p1
32	49.62N/9.72E	QUPE	1840–2005	164	1.02	0.49	0.93	500	1	SW	9.3	696	p3
33	49.52N/6.61E	QUPE	1649–2005	276	1.14	0.48	0.89	290	n/a	E	9.5	806	p3
34	50.66N/7.24E	QUSP	1863–2004	119	1.92	0.66	0.96	230	2	W	9.3	769	p2
35	50.67N/7.25E	QUSP	1863–2004	126	1.44	0.57	0.94	355	2	N	9.3	769	p3
36	50.67N/6.33E	QUSP	1846–2004	152	1.40	0.55	0.93	320	2	N	8.0	1146	p2
37	50.44N/6.57E	QUPE	1868–2004	135	1.52	0.49	0.91	560	3	E	8.0	958	p2
38	50.68N/6.28E	QUPE	1809–2004	170	1.46	0.55	0.93	440	1	NE	8.7	1058	p2
39	50.62N/6.41E	QUSP	1812–2004	181	1.49	0.51	0.84	400	2	NW	8.0	1057	p2
40	50.57N/6.36E	QUPE	1847–2004	153	1.26	0.64	0.95	490	2	SE	8.0	1057	p1
41	50.73N/8.12E	QUPE	1750–2005	188	1.30	0.58	0.94	480	2	S	8.3	773	p2
42	50.87N/8.23E	QUPE	1857–2005	144	1.14	0.42	0.90	480	2	S	8.2	793	p2
43	51.23N/7.11E	QUPE	1863–2005	137	1.54	0.51	0.83	260	1	SW	10.1	860	p2
44	50.93N/7.14E	QUPE	1820–2005	168	1.68	0.58	0.92	120	1	W	10.4	800	p2
45	51.10N/8.02E	QUPE	1842–2005	147	1.25	0.43	0.84	470	1	SE	8.4	807	p2
46	51.89N/8.58E	QUPE	1837–2005	164	1.55	0.52	0.90	110	2	N	9.5	751	p3

Oscillation during winter, whereas more localized pressure cells occur during summer (Hurrell et al. 2003, Raible et al. 2006). For a comprehensive analysis of complex climate–growth interactions across Central-West Germany, oak sites were selected to represent the full climatologic range from temperate, moist oceanic conditions to colder and drier continental settings. The mean annual temperature of the study region over the period 1961–1990 is 9.1 °C ranging from 6.7 to 11.7 °C. The mean annual precipitation sum is 808 mm and ranges from 450 to 1452 mm (for detailed information about the climate parameters see Table 2).

Table 2. Correlations between the five climate parameters using unfiltered (upper right) and 20-year low-pass filtered data (bold numbers illustrate significant – $P \leq 0.05$ – relationships), and mean, minimum and maximum values of each climate parameter (precipitation (Prec.) in mm; temperature (Temp.) in °C; PDSI from 4.0 to −4.0 = extreme wetness to extreme drought; cloud-cover in %; vapor pressure in Pa) for the annual period; the vegetation period (April–September, A–S); and summer period (June–August, J–A). Values are calculated over the period 1961–1990. Minimum and maximum values are absolute.

	Prec.	Temp.	PDSI	CC	VP
Prec.		−0.08	**0.68**	**0.61**	0.17
Temp.	0.19		−0.17	**−0.36**	**0.79**
PDSI	**0.55**	**−0.33**		**0.53**	0.09
CC	0.07	−0.09	**0.72**		−0.06
VP	**0.39**	**0.94**	−0.03	0.06	
Annual mean	808	9.1	0.25	75	9.4
minimum	450	6.7	−3.66	64	8.4
maximum	1452	11.7	4.45	83	10.7
A–S mean	423	14.1	0.11	68	11.8
minimum	177	11.6	−4.00	51	10.6
maximum	736	16.6	4.13	78	13.4
J–A mean	282	16.7	0.12	66	13.5
minimum	94	13.8	−4.00	43	11.8
maximum	464	20.3	4.35	80	15.6

Tree data

During 2005 and 2006, we collected 13 *Q. robur* (149 trees) and 33 *Q. petraea* sites (406 trees). In each site, two cores were extracted from at least 12 dominant trees at breast height (~ 1.3 m above ground). All trees were sampled in the so-called nature forest reserves that have been established in old stands with less silvicultural influence (Balcar 1995, Schulte and Scheible 2005). The oaks are primarily located in closed and mature stands often associated with beech (*Fagus sylvatica* L.). While all *Q. robur* sites are found on plateaus ($< 5\%$ slope), slopes of the *Q. petraea* sites range between 5% and 40%, including a variety of aspects. Soil analyses revealed predominant cambisols and luvisols typical for temperate forests in Central-West Germany (Schulte and Scheible 2005). The sites of the network exhibit low (60–110 mm) to very high (> 240 mm) available water capacity (AWC) (Table 1), determined using data from various soil parameters. The network ranges from 30 to 560 m a.s.l. The sites located in the north-western part (Nos. 6–8, 11 and 12 in Figure 1) represent the lowlands with the warmest temperatures and the highest precipitation. In contrast, coldest temperatures occur at the higher elevation sites in the western and central parts of the research area, accompanied by increased precipitations (for ecologic site information see Table 1). Southern and eastern sites generally receive less precipitation.

Meteorologic data

For growth/climate response analyses (Frank and Esper 2005a), gridded ($0.1 \times 0.1°$) monthly temperature means and precipitation sums (CRUTS1.2, Mitchell et al. 2004),

monthly cloud-cover percentage, vapor pressure ($0.5 \times 0.5°$; CRUTS2.1, Mitchell and Jones 2005) and the self-calibrated PDSI ($0.5 \times 0.5°$; van der Schrier et al. 2006) were used. All parameters were expressed as anomalies during the 1961–1990 period and significance levels conservatively corrected for lag-1 autocorrelation (Trenberth 1984). Values from the four closest grid-boxes were averaged for Pearson's correlation analyses with the tree-ring chronologies, whereas the mean climate series of all grids were used for redundancy analysis (RDA). Cloud-cover data were only used from 1950 to 2002, as earlier data represent little more than the average seasonal cycle.

Tree-ring analysis

Tree-rings of each core were measured to the nearest 0.01 mm using the program TSAPWin (Rinn 2003). Two radii were averaged to one tree series and dating errors were corrected on a site-by-site basis using the program COFECHA (Holmes 1983). The raw measurement series were aligned by cambial age to best describe age-related growth trends (Fritts 1976), using the program ARSTAN (Cook 1985). The resulting Regional Curves (RCs) were analyzed for species- and site-specific differences (Esper et al. 2003). Standardization was applied to remove non-climatic, tree-age-related growth trends from the raw data. For the preservation of interannual to centennial-scale variability, series were individually detrended using 300-year cubic smoothing splines with 50% frequency-response cutoff equal to 300 years (Cook and Peters 1981). Indices were then calculated as ratios from the estimated growth curves and series averaged using a bi-weight robust mean (Cook 1985) to form variance adjusted site chronologies (Frank et al. 2007b), truncated at < 3 trees.

Signal strength of the site chronologies was assessed using a moving window approach of the interseries correlation (Rbar) and the expressed population signal (EPS). The Rbar is a measure of common variance between single series, which does not specifically consider changes in sample replication, whereas EPS, considering both Rbar and sample replication, is a measure that determines how well a chronology, based on a finite number of trees, represents the theoretical population chronology from which it has been drawn (Wigley et al. 1984).

Cluster analysis was performed to identify homogeneous subsets within the tree-ring network (for details on this particular dataset, see Friedrichs et al. 2008). The hierarchic clustering proceeded in stepwise calculations leading from n clusters of one object (tree site) to one cluster containing all objects (Jongman et al. 1987). Using Ward's method, the cluster variance, calculated as mean squared Euclidian distance, was evaluated for each cluster and the sum of all clusters represented the overall variance within the clusters. This procedure maximizes the variance among clusters, whereas the variance within clusters is minimized (Bahrenberg et al. 2003).

Growth/climate response analysis

The classified sites of the cluster analysis were averaged and the 'mean cluster chronologies' were considered for growth/climate analysis. For a detailed growth/climate response assessment, Pearson's correlations were computed over the maximum period of each climate parameter over a 17-month window from May of the year before tree growth until September of the current year. The five climate parameters, temperature, precipitation, vapor pressure, cloud-cover and PDSI, were additionally averaged to various seasonal means: March–May, April–September, June–August, September–October and June (year before growth)–July (year of growth), and annual means. The RDA was applied to detect the most important growth influencing climate variables that were extracted from monthly and annual data of all climate parameters over the common time interval of 1951–2000, using the program CANOCO (Version 4.5, ter Braak and Smilauer 2002). The RDA is a multivariate 'direct' gradient analysis and its ordination axes are constrained to represent linear combinations of supplied environmental variables (Legendre and Legendre 1998). Significant ($P < 0.05$) climate variables were obtained using a Monte Carlo permutation-based forward selection. The temporal stability of growth/climate relationships was analyzed using 21-year moving correlation windows. This window-length is a compromise between isolating signal changes with the highest possible temporal resolution and having enough data-points to estimate the signal.

Results

Growth trends and clusters

The average growth rates per tree (AGR) of *Q. robur* and *Q. petraea* were 1.88 mm (range 0.93–3.08) and 1.36 mm (range 0.69–2.64), respectively. During the first 100 years, differences in AGR of *Q. robur* and *Q. petraea* (2.00 and 1.38 mm year^{-1}) are even more distinct. The RCs of both species (Figure 2A) confirm these differences that are typical of species with varying life spans. Initially, *Q. robur* reveals enhanced growth (2.56 mm year^{-1}) in comparison to *Q. petraea* (< 2 mm year^{-1}; Figure 2A), while in the following years growth rates become more similar (Figure 2A). Both species show age-related growth trends, a widely known association between decreasing ring diameter and increasing tree age. Trees of *Q. robur* are younger (mean age: 156 years) than trees of *Q. petraea* (mean age: 183 years). The mean site segment length (MSL, number
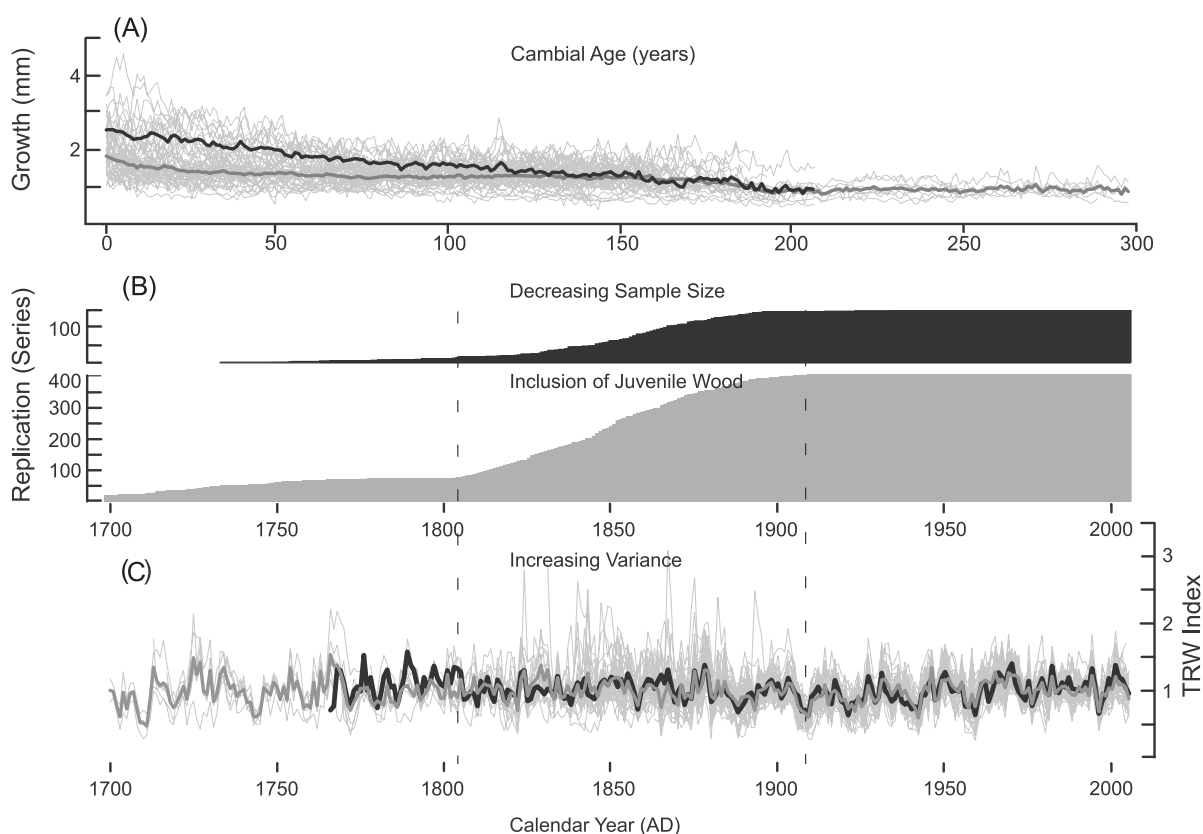

Figure 2. (A) Mean growth trends (the RCs) of the 46 sites after aligning all measurement series by cambial age (light gray). Mean RCs were calculated from *Q. robur* (black) and *Q. petraea* (gray). (B) Temporal distribution of the 149 *Q. robur* series (black) and 406 *Q. petraea* series (gray), with each bar representing one tree. (C) The 46 site chronologies (light gray) after 300-year spline detrending, the mean of *Q. robur* (black) and the mean of *Q. petraea* (gray).

of rings per core) ranges from 71 to 272 and from 99 to 363 years, respectively (Figure 2B).

The oak network is characterized by a continuous reduction in sample replication over the 19th century, with 18 trees reaching back to 1700. After the 300-year spline detrending, fairly common growth variations between the *Quercus* chronologies are obtained (Figure 2C). *Quercus robur* and *Q. petraea* have mean Rbar and EPS values of all site chronologies of 0.30 and 0.37, and 0.95 and 0.98, respectively. Although EPS values slightly decrease toward the record's earlier portions, they generally remain above the frequently applied threshold of 0.85 (Wigley et al. 1984), and suggest robust mean chronologies.

To identify sites with similar and different variations in growth, to achieve a higher signal coherency within the data, and to reach a better understanding of tree responses to environmental conditions, three clusters of common growth patterns are compiled for each species. The clusters vary in the numbers of site chronologies included ($r = Q.$ *robur*, $p = Q.$ *petraea*, r1 = 4, r2 = 6, r3 = 3, p1 = 9, p2 = 12 and p3 = 12) and in their ecologic settings. Most of the *Q. robur* sites are located in the north-western part of the research area, characterized by higher temperatures (Figure 1). Sites of r2 represent north-western lowlands with high precipitation, whereas sites of r1 and r3 are located between the western and central low mountain ranges. The p1 includes sites of the eastern and southern parts, characterized by less precipitation and slightly cooler temperatures compared to the other parts of the research area. Sites growing under more rain-laden conditions in the western and central low mountains primarily occur in p2. In contrast, warmer and drier growth conditions of southern sites dominate p3 (details in Table 1).

Spatial patterns of growth/climate responses

The five climate parameters that are used for comparison with tree growth are cross-correlated and thus are not fully independent. The highest correlation is observed between temperature and vapor pressure (0.79), and it increases to 0.94 when low-pass filtering the data (Table 2). This strong positive relation is induced by the physical dependency of vapor pressure values on temperature variation. The direct influence of the amount of precipitation on the strength and frequency of droughts leads to a strong positive coupling between precipitation and PDSI (0.68). A consistent increase or decrease in the climate correlation values between the unfiltered and low-pass filtered data is not observed (Table 2).

Correlation analyses with the six clusters (Figure 3A) indicate weak temperature influences on tree growth, as the results are mostly nonsignificant (significance is defined with $P \leq 0.05$). Coherence between growth and precipitation is generally positive and stronger in comparison to temperature (Figure 3B). While June is the month with the most relevant rainfall for growth of *Q. petraea*, months of the previous year, winter and spring also influence

growth of *Q. robur*. The cumulative effect of single month precipitation sums, such as March, April and May, leads to notably higher correlations with the seasonal means. Precipitation sums of previous year June–July most frequently influence tree growth (r1, r2, r3, p1 and p3), including the overall highest correlation ($r = 0.44$) with the north-western lowland cluster r2. Only p2, including the high-elevation sites in the western and central low mountains, shows no significant response to precipitation.

Comparison among the growth rates and the cloud-cover data reveals small influences. Previous year August cloudiness and conditions of spring and of the previous year June–July period partly influence growth of r1, r3 and p1. All correlations between p2, p3, r2 and cloud-cover data are insignificant (Figure 4A).

In contrast, PDSI conditions strongly influence growth of all *Q. robur* sites (Figure 4B). Drought conditions in spring and summer are most relevant with the highest correlation between April PDSI and r2 ($r = 0.39$). In comparison, significant response of *Q. petraea* is only found in p1 with highest correlation in June ($r = 0.29$). The p2 and p3 reveal nonsignificant correlations with PDSI suggesting that drought sensitivity separates the oak species more strictly than the other climate parameters.

In addition, significant correlations are found for monthly and seasonal vapor pressures in both species, including generally positive growth responses to increasing pressure (r1, r2, p2 and p3). Annual and previous June–July pressure values have strong influence on growth (Figure 4C). Vapor pressure even influences growth of p2, whereas other climate parameters show no effect.

The RDA confirms water supply as the most important growth influence and explains 48% of growth variability by the selected climate parameters, with April PDSI (17%) being most influential (Figure 5). Spring conditions of PDSI, precipitation and cloud-cover are positively correlated with the first axis, and all cluster chronologies have a positive loading on the first axis, which explains 38% of the total dataset variance, indicating that both species are affected in a similar way by regional climate. Annual temperature and vapor pressure have high scores on the second (orthogonal) RDA axis, which accounts for 6% of the total variance. Overall, growth variations between the clusters are verified by the clusters' position on the second axis, but species-specific differences cannot be detected. However, the stronger response of *Q. petraea* (p1) to summer than of *Q. robur* (r1, r2 and r3) to spring drought, shown in the correlation analysis, is also found.

Temporal response changes

To explore temporal changes in the relationships between the various climatic parameters and tree growth, moving window correlations were applied between the oak clusters and gridded instrumental data. Results for PDSI and the six clusters are generally positive, with the *Q. robur* clusters
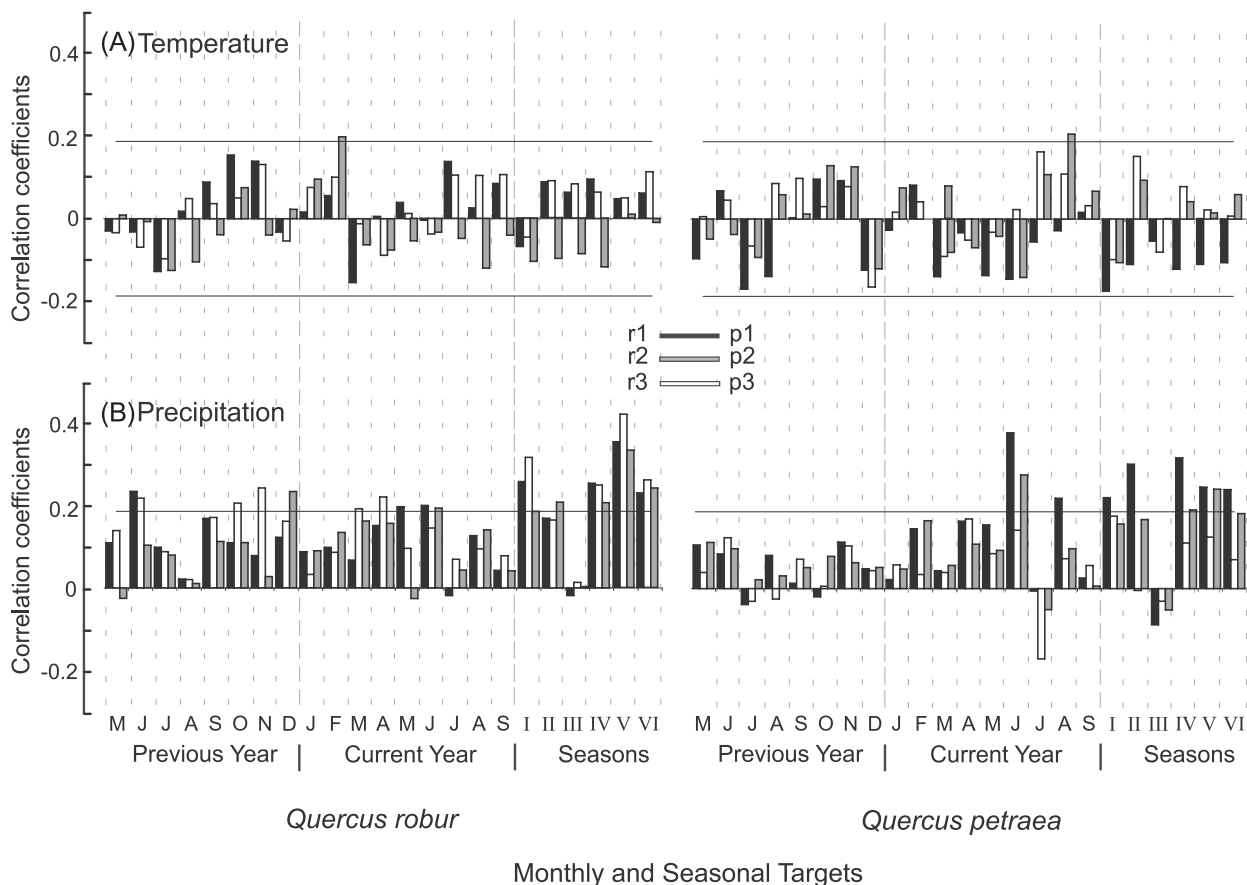
Figure 3. Monthly and seasonal correlations between the three cluster chronologies of each species and (A) temperature means and (B) precipitation sums over the period 1901–2000. Seasonal means are averaged over I = March–May, II = June–August, III = September–October, IV = April–September, V = previous year June–current year July and VI = calendar year. Horizontal lines denote 95% significance levels. Vertical dashed lines separate the single months' and seasons' growth/climate sensitivities.

indicating the strongest responses. Correlations of the three respective clusters are significant ($P < 0.05$), except for the 1940s during which a sizeable growth depression is recorded (Figure 6A). For comparison, *Q. petraea* shows similar responses; however, nonsignificant site correlations appear during several periods in the 20th century. All clusters reveal a loss of sensitivity to PDSI, with a maximum from 1947 to 1950, including 1947 as the driest European summer of the 20th century (van der Schrier et al. 2006). Similar correlation patterns are observed for precipitation (not shown).

Vapor pressure generally displays nonsignificant effects on growth, apart from a positive influence during the exceptionally dry 1940s and increasing effects during the most recent decade (Figure 6B).

Except for the most recent years, the 1940s are characterized by the highest temperatures of the century (Figure 7). Tree growth primarily increases during this period. Decadal-scale variations of oak growth are similar to those of the PDSI and precipitation data, with only the period from ∼ 1940 to ∼ 1960 deviating substantially, but being in line with temperature and vapor pressure during this time.

Discussion

Growth trends

The average growth rates of the first 100 years of *Q. robur* and *Q. petraea* (2.00 and 1.38 mm year^{-1}) are similar to growth rates reported from other Central European oak stands (Bonn 1998, Neuwirth 2005). Differences in growth rate between *Q. robur* and *Q. petraea* could be caused, for example, by varying life spans. Shorter-lived species tend to grow more quickly than their faster growing congeners (Kozlowski and Pallardy 1997). Growth rate differences can also be caused by different physiologic reactions to climate, such as species-specific adaptations to drought-stress (Gieger and Thomas 2005). Species-specific drought tolerance is caused by water transport strategies, differently developed due to differences in local soil water regimes. When *Q. robur* is mainly located in valley bottoms, *Q. petraea* is commonly found on slopes and ridges. *Quercus petraea* is better adapted to low water availability by mechanisms that largely prevent drought-induced embolism; this results in high drought tolerance. In contrast, at adequate water
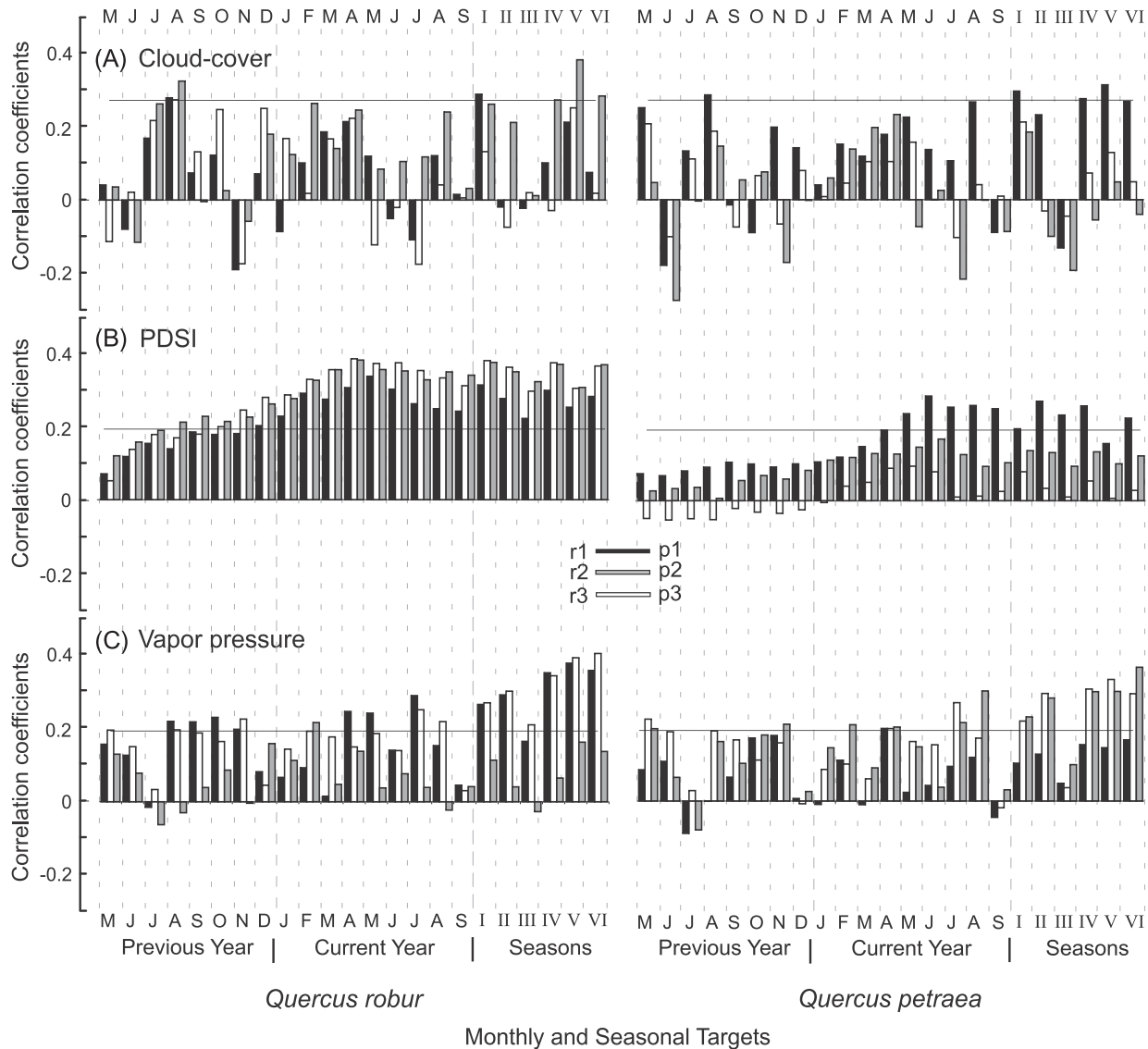
Figure 4. Monthly and seasonal correlations between the three cluster chronologies of each species and (A) cloud-cover, (B) PDSI and (C) vapor pressure over the period 1901–2002. Cloud-cover correlations refer to the 1950–2002 period. Seasonal means are averaged over I = March–May, II = June–August, III = September–October, IV = April–September, V = previous year June–current year July and VI = calendar year. Horizontal lines denote 95% significance levels. Vertical dashed lines separate the single months' and seasons' growth/climate sensitivities.

availability, *Q. robur* uses the available water to a great extent; this results in higher growth rates and lowered water use efficiency (Ponton et al. 2001).

Spatial patterns of growth responses

No growth dominating climate parameters, such as summer temperatures at higher elevations (Büntgen et al. 2005, 2007, 2008, Esper et al. 2005*a*, 2005*b*, Frank and Esper 2005*a*, 2005*b*) appear in this study. Growth of *Q. robur* and *Q. petraea* depends on both soil and atmospheric moisture. Drought conditions, precipitation and vapor pressure values are found to be most important for growth, whereas

cloud-cover and temperature have only little impact on tree-ring growth.

We found a range of cluster-specific responses to PDSI and precipitation that provided a more detailed picture of drought stress. When drought can have significant impacts on all *Q. robur* clusters, only p1 of the *Q. petraea* clusters responds significantly. Beside the well-known higher drought sensitivity of *Q. robur* (Cochard et al. 1992, Lévy et al. 1992), different response patterns between both species under temperate forest conditions are noteworthy. *Quercus robur* responds to the conditions from previous year autumn until the end of the growth period with highest sensitivity in spring (March–May). The responding cluster of *Q. petraea*
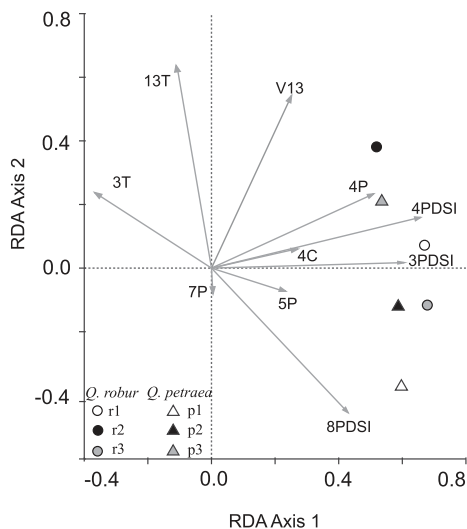
Figure 5. The RDA calculated from the species cluster chronologies and the monthly and annual climate parameters for the period 1951–2000. The vectors (arrows) represent the significant climate factors; the longer the vector the more important the climate parameter. PDSI = Palmer Drought Severity Index, P = precipitation, T = temperature, C = cloud-cover and V = vapor pressure; the numbers represent the months (e.g., 4 = April and 13 = annual value). The correlation between the variables is illustrated by the cosine of the angle between two vectors. Vectors pointing in nearly the same direction indicate a high positive correlation, vectors pointing in opposite directions have a high negative correlation, and vectors crossing at right angles relate to a near zero correlation (Legendre and Legendre 1998).

is primarily controlled by summer droughts (Figures 4B and 5, also found for precipitation in Figure 3B). Therefore, climate in the year before ring formation is primarily relevant for *Q. robur* (Figures 3 and 4). These lag-responses indicate the importance of carbohydrate storage (Kozlowski and Pallardy 1997) that is mainly modulated via tree physiologic processes during previous year summer and autumn (Barbaroux and Bréda 2002). Mobilization of the stored carbohydrates during current year spring is essential for ring formation, as oak earlywood vessels are already determined before or at the time of bud burst (Barbaroux and Bréda 2002), a typical feature of ring-porous deciduous trees (Dougherty et al. 1979, Hacke and Sauter 1996, García-González and Fonti 2006).

Not only the previous year PDSI and precipitation, but also hydroclimatic spring, mainly March and April, conditions affect all *Q. robur* sites and clusters (Figures 3B, 4B and 5). Positive growth responses demonstrate the importance of water supply at the beginning of the growing season (García-González and Eckstein 2003). For *Q. petraea*, significant coherence with rainfall variations is primarily found in summer (Figures 3B, 4B and 5). Sufficient moisture content is essential for increased cambial activity resulting in wide tree-rings, a characteristic feature described for numerous deciduous stands across the European continent (Hughes et al. 1978, Bridge et al. 1996, Rozas 2005, Ufnalski 2006,

Griggs et al. 2007, Neuwirth et al. 2007). Hence, the significant correlation of annual precipitation sums with *Q. robur* represents the combined impact of months influencing early-wood (previous autumn–winter and current spring) and late-wood growth (late spring and summer), whereas the significant correlations of *Q. petraea* are found with summer months.

Beside these differences in species-specific climate sensitivity, variations in response intensity and seasonality are found among the clusters of *Q. petraea*. Overall drier site conditions of p1 located in the eastern and southern part of the research area (Table 1) lead to higher drought sensitivity in comparison to site conditions of p2. Although the AWC is not high, p2 is the only cluster where neither precipitation (Figure 3B) nor PDSI (Figure 4B) significantly influence growth. The combination of cool temperatures and high precipitation likely causes moderate growth conditions in p2, representing sites of the western and central low mountains (Table 1). Oaks of p3, mainly located in the warm southern part of the research area, respond to precipitation and not to PDSI as p1 does. Explanation of differences between the cluster responses by means of the available ecologic site information remains tentative. We suggest that the mean AWC of p3 suffices to endure drought events without any significant growth reductions, however, growth rates are still positively controlled by high precipitation.

Quercus robur clusters show only small differences in the intensity of climate responses; r1 reacts slightly less sensitive to water supply than r2 and r3. However, AWC ranges from medium to high among the clusters r1–r3 (Table 1). Although PDSI and precipitation data are associated, their specific properties obviously lead to different effects on temperate forest growth. As the strength and frequency of drought depends on the amount of precipitation and local temperature, and on the rate of soil–water depletion, PDSI is a better measure for growth conditions than precipitation alone (Esper et al. 2007a). The PDSI broadly represents water availability: when sufficient moisture exists, the stomata can dilate, allowing for greater photosynthetic activity (Kozlowski and Pallardy 1997). When precipitation reveals no persistence between years, lag-1 autocorrelation is 0.09 calculated over the 1902–2000 period (mean of all station data), interannual persistence is high in PDSI (0.57) and is found in the tree-ring data (0.50, 1902–2000, mean of all values) in the same order.

The strong growth controls of vapor pressure are not only induced by the vapor pressures' dependence on temperature, because several significant vapor pressure influences are found (Figure 4C) in which direct temperature impact on growth is negligible (Figure 3A). Effects of vapor pressure on growth of both species are assumed to reflect a change in stomatal conductance related to a vapor pressure deficit. Decreasing vapor pressure means increasing vapor pressure deficit among leaves and air inducing partial stomata closure (Oren et al. 1999), which in turn leads to
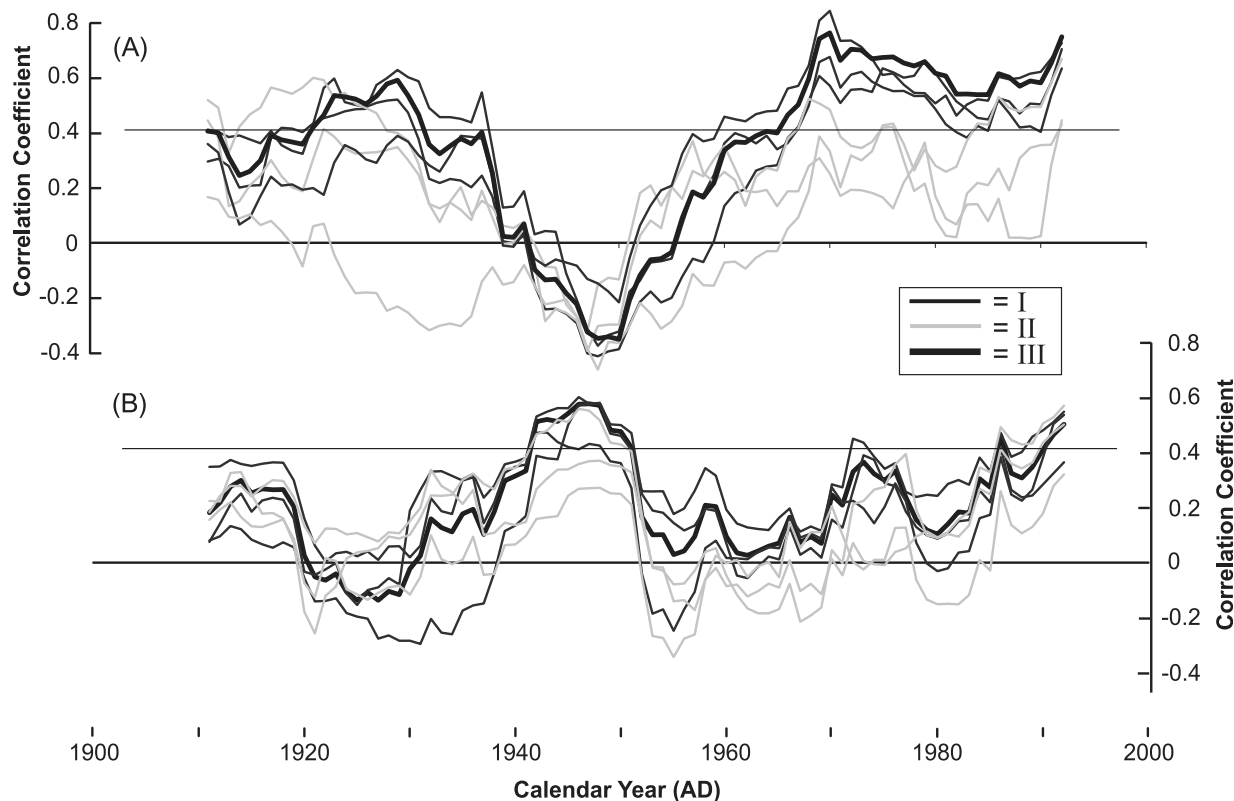
Figure 6. Twenty-one-year moving correlation analysis between (A) annual PDSI and (B) annual vapor pressure and the three species-specific cluster chronologies (*Q. robur*, dark gray line I; *Q. petraea*, light gray line II) plus the mean chronology of *Q. robur* (CM, bold black line III). Horizontal lines denote 95% significance levels.

decreasing photosynthesis and thus growth reductions (Kozlowski and Pallardy 1997). The growth response to vapor pressure, however, varies between the species-specific clusters. The only significant climate response of the wetter and colder sites integrated in p2 is the sensitivity to atmospheric water conditions, whereas the drier sites integrated in p1 mainly reveal soil moisture signals but no reaction to vapor pressure changes. *Quercus robur* clusters r1 and r2 respond to atmospheric and soil water conditions, whereas growth of r3 depends solely on PDSI fluctuations, with no vapor pressure signal being found.

Temporal response shifts

Twenty-one-year moving correlations between radial oak growth and climate parameters (precipitation, PDSI, vapor pressure and temperature) demonstrate temporal instability in their relationships. The intensity of growth/climate responses varies over time, most likely due to climate change and tree physiologic threshold effects (Rozas 2005, Geßler et al. 2007). Significant positive correlations between PDSI and oak growth are interrupted during the exceptionally warm 1940s. When both PDSI and precipitation values declined during this period, radial growth increased (Figure 7). This reaction seems to be related to a positive response between growth and temperature during an exceptional warm period, which seems physiologically difficult to

explain. There is, however, also a possibility that disturbance signals from changes in human activity, such as increased use of firewood, during World War II could have contributed to changes in site competition and stand dynamics. Furthermore, a reduction in the quality of instrumental station measurements (e.g., number of gaps) is reported for this period (Auer et al. 2007). Between 1945 and 1949 a concentration of missing data exists in 22 out of 26 time-series. When such data uncertainty obscures the relationship between tree-ring and instrumental data, quantification of such error remains challenging (Frank et al. 2007*a*). Overall, the 1940s were somehow exceptional during the 20th century, as this period of rapid oak growth is characterized by extraordinary high vapor pressure and low PDSI values, indicating high atmospheric but low soil water availability. Decreasing vapor pressure deficit between leaf and air results in decreasing transpiration rates (Oren et al. 1999) and high stomatal conductance (Bréda et al. 2006), which promote water savings, photosynthesis and growth. Note that this effect of vapor pressure is associated with high temperatures. These conditions contrast with other periods of severe droughts and growth depressions (e.g., 1970s and ca. 1920) that are characterized by low precipitation rather than by high temperatures (Figure 7).

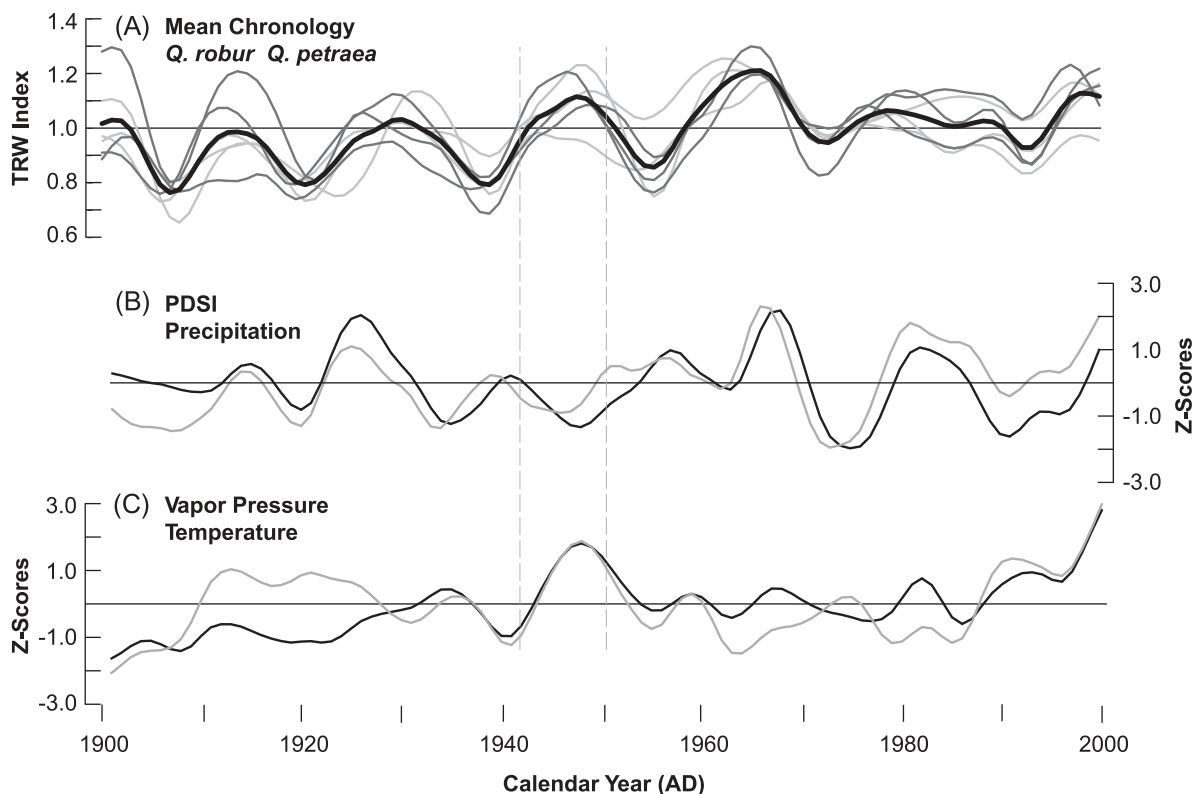In summary, the growth increase under warm and dry climate conditions in the 1940s emphasizes the complex

Figure 7. (A) Ring-width chronologies of the three species-specific clusters (*Q. robur*, dark gray; *Q. petraea*, light gray) plus the mean chronology CM of all clusters (black). Twentieth century climate variations of the parameters; (B) PDSI (black) and precipitation (gray); and (C) vapor pressure (black) and temperature (gray) after 10-year low-pass filtering. Vertical dashed lines define the period with extraordinary climate/growth relationships.

climate factors influencing growth rates of temperate forests. Although obvious influences of biotic factors were not detected in our data, they can obscure the effect of climate conditions (Esper et al. 2007*b*). Repeated defoliation by lepidopteron larvae, for example, which occurs in certain time intervals, can additionally affect the growth of oaks (Thomas et al. 2002). Our analysis of the temporal stability in growth/climate responses illustrates that warmer and drier conditions predicted for the near future will not necessarily lead to suppressed oak growth, as described for beech (Geßler et al. 2007), particularly if vapor pressure increases with increasing temperature.

Conclusions

We detail growth variability separated for *Q. robur* and *Q. petraea* in a new oak network from Central-West Germany. The overall response to climate is modulated by species differences and site ecology. No coherent growth response to a single climate parameter is evident, water supply as quantified by the PDSI, precipitation and vapor pressure is most relevant. Consideration of PDSI and vapor pressure data allows an improved assessment of climate-dependent growth variations. The parameters PDSI and vapor pressure used for comparison between growth and climate,

explained regional-scale growth patterns and allowed annual ring formation to be elucidated for those sites where no response to temperature and precipitation was obvious. Both parameters will gain importance in a warmer and drier climate as predicted by climate models. *Quercus robur* will suffer more in the future, as it is more sensitive to climate, especially drought stress, than *Q. petraea*. However, the estimation of effects of summer warming on oak productivity in temperate forest remains difficult, as we identified an area-wide growth increase despite extraordinary warm conditions during the 1940s.

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