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Species-specific climate sensitivity of tree growth in Central-West Germany

Dagmar A. Friedrichs · Valerie Trouet · Ulf Büntgen · David C. Frank · Jan Esper · Burkhard Neuwirth · Jörg Löffler

Abstract Growth responses to twentieth century climate variability of the three main European tree species *Fagus sylvatica*, *Quercus petraea*, and *Pinus sylvestris* within two temperate low mountain forest sites were analyzed, with particular emphasis on their dependence upon ecological factors and temporal stability in the obtained relationships. While site conditions in Central ($\sim$51°N, 9°E, KEL) and West (50.5°N, 6.5°E, EIF) Germany are similar, annual precipitation totals of $\cong$700 mm and $\cong$1,000 mm describe a maritime-continental gradient. Ring-width samples from 228 trees were collected and PCA used to identify common growth patterns. Chronologies were developed and redundancy analysis and simple correlation coefficients calculated to detect twentieth century temperature, precipitation, and drought fingerprints in the tree-ring data. Summer drought is the dominant driver of forest productivity, but regional and species-specific differences indicate more complex influences upon tree growth. *F. sylvatica* reveals the highest climate sensitivity, whereas *Q. petraea* is most drought tolerant. Drier growth conditions in KEL result in climate sensitivity of all species, and *Q. petraea* shifted from non-significant to significant drought sensitivity during recent decades at EIF. Drought sensitivity dynamics of all species vary over time. An increase of drought sensitivity in tree growth was found in the wetter forest area EIF, whereas a decrease occurred in the middle of the last century for all species in the drier KEL region. Species-specific and regional differences in long-term climate sensitivities, as evidenced by temporal variability in drought sensitivity, are potential indicators for a changing climate that effects Central-West German forest growth, but meanwhile hampers a general assessment of these effects.

Keywords Climate change · Dendroclimatology · Tree rings · Water supply · Drought

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Introduction

Tree growth in temperate forests is influenced by a complex interplay of various climatic parameters as well as by biotic and abiotic disturbances, and competition for water, light, nutrients, and other ecological resources (Schweingruber 1996; Kozlowski and Pallardy 1997). A warmer and drier climate could thus impact tree growth behavior directly, but also indirectly through influences on forest composition and vitality (Saxe et al. 2001; Thuiller 2004). Given that physiological adaptations and different growth strategies of various species have resulted in considerable differences in response to past climatic variability (e.g., Cook et al. 2001), it stands to reason that the influence of future climatic changes on forest growth can only be assessed if species-specific responses are well understood with respect to changes in ecological site conditions.

Drought responses of the main Central European tree species in the framework of climate warming have been extensively studied in the recent past. Particular attention has been given to extraordinary events, such as the severe European summer heat of 2003 (e.g., Ciais et al. 2005;

Granier et al. 2007). Ciais et al. (2005) reported a Europe-wide reduction in primary productivity and assumed large effects of climate warming on common beech (*Fagus sylvatica* L.). More regional studies under varying temperate ecological conditions (e.g., Leuzinger et al. 2005; Jolly et al. 2005), however, did not reveal such radical influences of climatic change on tree growth of the main Central European tree species. There seems to be a lack of consensus on the position of many species within their theoretical ecological distribution, particularly with respect to future climate change. For example, Rennenberger et al. (2004) concluded that future growth conditions most likely will be unfavorable for *F. sylvatica* in southern Germany. They recommend a replacement by more drought-tolerant species such as sessile oak (*Quercus petraea*). However, Ammer et al. (2005) disputed that climate change effects will be unfavorable for *F. sylvatica* in most Central European temperate forests. They stressed the importance of ecological studies that consider a range of tree species and ecological settings. In this context, the importance of ecological studies that consider a range of tree species and ecological settings has been stressed.

Fagus sylvatica and *Q. petraea.* in Central Europe are growing near the center of their current natural distribution areas. *F. sylvatica* tends to out-compete all other species in its potential natural habitat (Ellenberg 1996). In contrast, the recent distribution of *Q. petraea* differs strongly from its potential ecological distribution due to weaker competitiveness. Scots pine (*Pinus sylvestris* L.), another key Central European tree species, is also characterized by low competitive ability. *Q. petraea* and *P. sylvestris* are known to be more drought resistant than *F. sylvatica* (Epron and Dreyer 1993; Bréda et al. 2006) and a dominant occurrence of *Q. petraea* and *P. sylvestris* is restricted to areas of extreme ecological settings, where growth of *F. sylvatica* is generally less vigorous (Härdtle et al. 2004).

The temporal assessment of growth/climate response patterns via the comparison of tree-ring chronologies and meteorological time-series provides unique long-term understanding of the interplay between terrestrial ecosystems and external forcing agents (Büntgen et al. 2008; Esper et al. 2007). To date, climatic responses of each of the main tree species *F. sylvatica*, *Q. petraea*, and *P. sylvestris* have been analyzed separately (Dittmar et al. 2003; Lebourgeois et al. 2005; Di Filippo et al. 2007; Neuwirth et al. 2007; Friedrichs et al. 2008b). Most of the studies do not show strong climate controls of temperate forest trees (Dittmar et al. 2003; Lebourgeois et al. 2005; Neuwirth et al. 2007). Friedrichs et al. (2008b), however, found strong climate sensitivity of *Q. petraea* and *Q. robur* to June precipitation, annual vapor pressure, and spring to summer drought. In-depth comparison of the tree species under comparable ecological conditions are rare (e.g.,

Bonn 1998) but urgently needed in the discussion of species-specific responses to climate change and in the anticipation of trends in regional forest dynamics (Ammer et al. 2005; Geßler et al. 2007). Furthermore, the temporal stability of climatic influences on tree growth in Central European temperate forests has not been studied sufficiently, despite the fact that such knowledge is essential to assess the effects of climate change upon forest productivity.

Here, we used a dendroecological approach to understand growth responses of *F. sylvatica*, *Q. petraea*, and *P. sylvestris* to twentieth century climate variability. Analyses were carried out in two forest regions in Central-(Kellerwald; KEL) and West-Germany (Eifel; EIF) to identify the importance of minor differences in water availability on growth/climate relationships under temperate forest conditions. Our main research questions were: (1) "What are the most important climate factors influencing temperate forest growth?" (2) "To what extent do various tree species react to climate variability?", and (3) "Are the observed growth/climate relationships stable over time?"

Materials and methods

Setting

Three tree species *F. sylvatica*, *Q. petraea*, and *P. sylvestris* were sampled in mixed and pure even-aged forest stands in two German temperate forest national park areas (Table 1). Both parks were established in old forest stands with relatively low-management regimes. *F. sylvatica* was collected at five different locations in the Eifel in Western Germany and three locations in the Kellerwald in Central Germany (Fig. 1). *P. sylvestris* was sampled at two EIF sites and one KEL site, respectively, and *Q. petraea* at four locations in each area. The two different regions EIF and KEL were chosen to best represent tree-growth/climate relationships under slightly different moisture conditions, even though, both areas are synoptically influenced by atmospheric flows that predominantly come from the Atlantic (Hurrell et al. 2003). This leads to high annual precipitation totals on the upwind side of the western low mountain ranges (EIF), and slight rain shadow effects in the more eastward-located low mountain ranges (KEL). Mean annual precipitation totals over 1961–1990 in EIF and KEL are approximately 996 and 719 mm, respectively. Summer precipitation amounts are similar in both regions, but precipitation sums in fall, winter, and spring are higher in EIF (Fig. 2). As a result, EIF is characterized by moist temperate forest conditions, while conditions in KEL are generally drier. The annual temperature profiles of both regions (Fig. 2) and their variability over the past century

Table 1 Site description and characteristics of selected stands

Site	Species/region	Chronology time span (≥3 trees)	Number of trees (1880–2004)	MSL (year)	Elev. m a.s.l.	Asp. (°)	AWC	Slope (%)	Stand Struct.
1	Q.petraea/KEL	1839	15	159	290	135	2	30	Mixed
2	Q.petraea/KEL	1844	11	159	350	180	1	30	Pure
3	Q.petraea/KEL	1856	7	148	380	180	2	25	Pure
4	Q.petraea KEL	1851	10	148	390	150	2	20	Pure
5	F. sylvatica/KEL	1838	11	150	310	150	3	30	Mixed
6	F. sylvatica/KEL	1792	11	175	280	180	1	35	Mixed
7	F. sylvatica/KEL	1798	16	188	420	345	n/a	3	Pure
8	P. sylvestris/KEL	1864	12	137	360	180	2	20	Pure
9	Q.petraea/EIF	1868	10	135	560	90	3	5	Pure
10	Q.petraea/EIF	1809	15	170	460	–	1	0	Mixed
11	Q.petraea/EIF	1812	14	181	400	300	2	40	Pure
12	Q.petraea/EIF	1847	14	153	500	150	2	15	Mixed
13	F. sylvatica/EIF	1838	16	158	530	315	1	15	Pure
14	F. sylvatica/EIF	1866	11	133	470	60	1	10	Pure
15	F. sylvatica/EIF	1862	9	136	440	–	1	0	Mixed
16	F. sylvatica/EIF	1820	14	179	490	150	2	15	Mixed
17	F. sylvatica/EIF	1828	13	160	480	150	2	15	Mixed
18	P.sylvestris/EIF	1860	9	143	470	280	n/a	25	Pure
19	P.sylvestris/EIF	1856	10	141	450	220	n/a	25	Pure

MSL mean segment length, *Elev.* elevation, *Asp.* aspect, *AWC* available water capacity: 1 = low (60–110 mm), 2 = mean (110–170 mm), 3 = high (170–240 mm), *n/a* not applicable, *Stand Struct.* stand structure
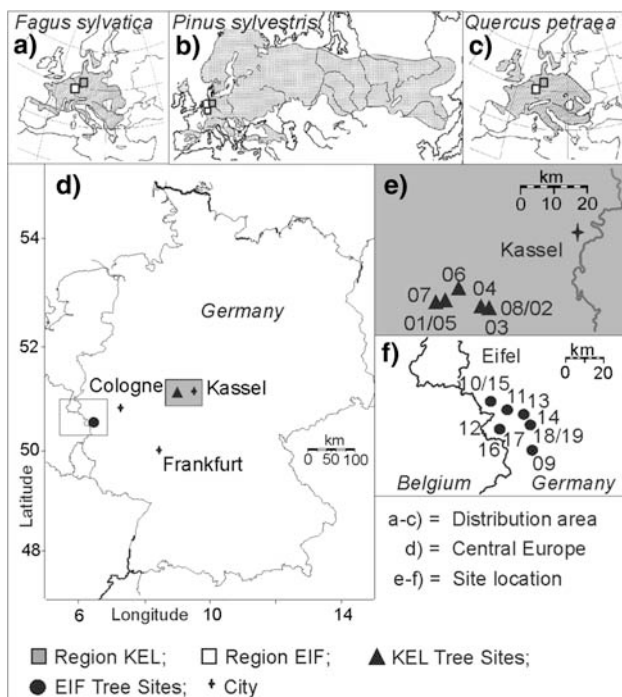

Fig. 1 Distribution of three common Central European tree species *F. sylvatica*, *P. sylvestris*, and *Q. petraea* (**a–c**) and geographical location of the study areas (**d**). Site distribution within the study areas (*gray* KEL, *white* EIF) is illustrated in **e–f**. Site numbers in **e–f** are in accordance with Table 1. Maps of **a–c** are based on Schweingruber (1993) and Härdtle et al. (2004)

(Fig. 3) are very similar. Both regions are characterized by a temperature increase towards the present. There is a pronounced offset of total annual precipitation between both sites over the twentieth century, but both regions show increased precipitation amounts in the most recent years (Fig. 3). The 1940s are characterized by differing precipitation and drought conditions for both regions. Extremely low precipitation sums for 1944–1947 accompanied by extreme warm temperatures in 1947–1949 led to drought conditions in EIF. In contrast, average precipitation sums in KEL resulted in moisture conditions in the 1940s close to average, despite warmer temperatures (Fig. 3).

Cambisol is the predominant soil type in both regions and the available water capacity (AWC) ranges from low (60–110 mm) to high (170–240 mm) at the different sites, but with AWC at most being classified as either "low" or "mean". Sites in both regions vary slightly in aspect and slope. These and other ecological site conditions are summarized in Table 1.

Tree-ring data

A minimum of two cores was collected at breast height from at least 12 dominant trees at each site. Samples were prepared following standard procedures outlined in Stokes and Smiley (1968). Individual tree-ring measurement cores were averaged and dating errors corrected using the program

Fig. 2 Climate diagrams for KEL and EIF. Mean monthly precipitation sums (mm) and temperatures (°C) are anomalies with respect to the 1961–1990 period
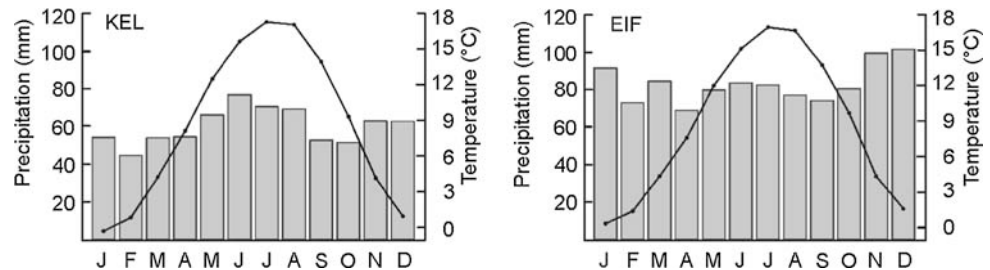
COFECHA, which computes cross correlations between individual series and a reference chronology (Holmes 1983). Finally, a total of 228 tree-ring series were considered for growth/climate response analysis.

Tree-ring standardization, the removal of biologically induced age-trends (Fritts 1976), was performed using the program ARSTAN (Cook 1985). Cubic smoothing splines with 50% frequency cut-off at 32 years were individually fitted to each tree-ring series to retain high frequency (inter-annual) variations (Cook and Peters 1981). Indices were then computed as ratios from the estimated growth curves. Variance in the resulting chronologies was stabilized following methods described in Frank et al. (2007b). Principal component analysis (PCA) was performed to investigate differences and similarities in growth variations of the individual tree-ring series and to detect spatial and species-specific patterns in growth homogeneity (Friedrichs et al. 2008a).

Various statistical parameters were calculated to compare the standardized tree-ring chronologies. Inter-series correlation (Rbar) and the Expressed Population Signal (EPS) were calculated using a moving window approach (Wigley et al. 1984). Mean sensitivity (MS) and autocorrelation (AC) were calculated for each series. MS is a measure of the relative difference in ring width between consecutive years and AC is a measure of the influence of previous year conditions upon ring formation (Fritts 1976).

Climate data

Gridded (0.5° × 0.5°) datasets of monthly temperature and precipitation series (CRUTS2.1, Mitchell and Jones 2005), and the self-calibrated Palmer Drought Severity Index (PDSI; van der Schrier et al. 2006) were used as predictor variables for growth/climate analyses over the 1901–2002 period. PDSI is a measure of regional soil moisture availability based on water supply and demand, calculated by a rather complex water budget system based on historic records of precipitation, temperature, and soil texture. The self-calibrated PDSI improves the geographical comparison of climates of diverse regions (van der Schrier et al. 2006). Climate data from the four closest grid points to

each study area were averaged and expressed as anomalies with respect to the 1961–1990 mean.

Lower resolution (2.5° × 2.5°) PDSI data were used (Dai et al. 2004) for an extended analysis of the growth response to drought conditions (1885–2004). These data are highly correlated with the monthly high-resolution PDSI grid-data from EIF (minimum $r = 0.80$, maximum $r = 0.88$) and KEL (minimum $r = 0.67$, maximum $r = 0.87$) over their common 1901–2002 period.

Statistical analysis

Relationships between the species-specific regional chronologies and climate parameters were analyzed for both regions using redundancy analysis (RDA) over the 1901–2002 period. RDA is a direct extension of multiple regression and principal component analysis (Legendre and Legendre 1998) and RDA ordination axes are constrained to be linear combinations of supplied environmental variables (Legendre and Legendre 1998). RDA was conducted using the program CANOCO (Version 4.5, ter Braak and Smilauer 2002). Climate data sets included monthly data over an 18-month window, from May of the year prior to ring formation to current year October, and annual means. Significant ($P < 0.05$) climate variables were obtained using a Monte Carlo permutation based forward selection.

Pearson's correlation coefficients were calculated over the same period to detail species-specific growth responses, and seasonal temperature means and precipitation sums of March–May, April–September, and June–August were additionally considered. Temporal stability of the obtained relationships was analyzed using five 40-year time intervals lagged by 20 years and covering the past 120 years (1885–2004).

Results

High intra-chronology Rbar values (0.43–0.62), with higher Rbar values for KEL than for EIF, confirmed common variance and suggest a strong common climatic forcing. Intra-series EPS values (0.93–0.97) were high for
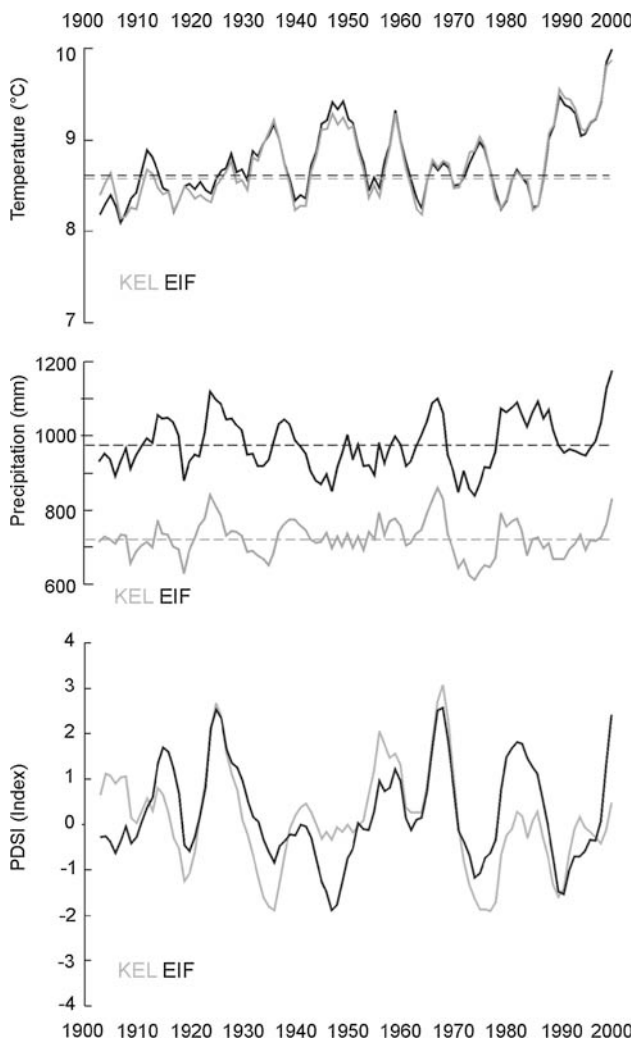
Fig. 3 Annual temperature, precipitation, and PDSI variability over the time period 1901–2002 for KEL (*gray curves*) and for EIF (*black curves*); dashed temperature and precipitation lines denote the average values over the 1961–1990 period

Fig. 4 Standardized species-specific tree-ring chronologies and running Rbar and EPS for KEL (*gray curves*) and EIF (*black curves*). Tree-ring chronologies are smoothed by a 5-year moving average

all species indicating that the theoretical population for each species and region is well represented. Running Rbar and EPS values confirm the common variance over time (Fig. 4). Mean sensitivity was highest for *F. sylvatica* and lowest for *Q. petraea* at both sites. Intra-chronology statistics are given in Table 2. Inter-chronology correlations between the regions reveal highest similarity between *F. sylvatica* chronologies ($r = 0.60$). The lowest similarity between the species is found for *Q. petraea* and *P. sylvestris* in EIF ($r = 0.24$). Generally, all correlations, EPS, and MS values are higher for KEL tree growth than for EIF (Tables 2, 3).

Differences in growth patterns between the three species and two regions were evident from the PCA analysis (Fig. 5). The first axis explained 29.7% variance indicating common variance of all trees (not shown). The second axis
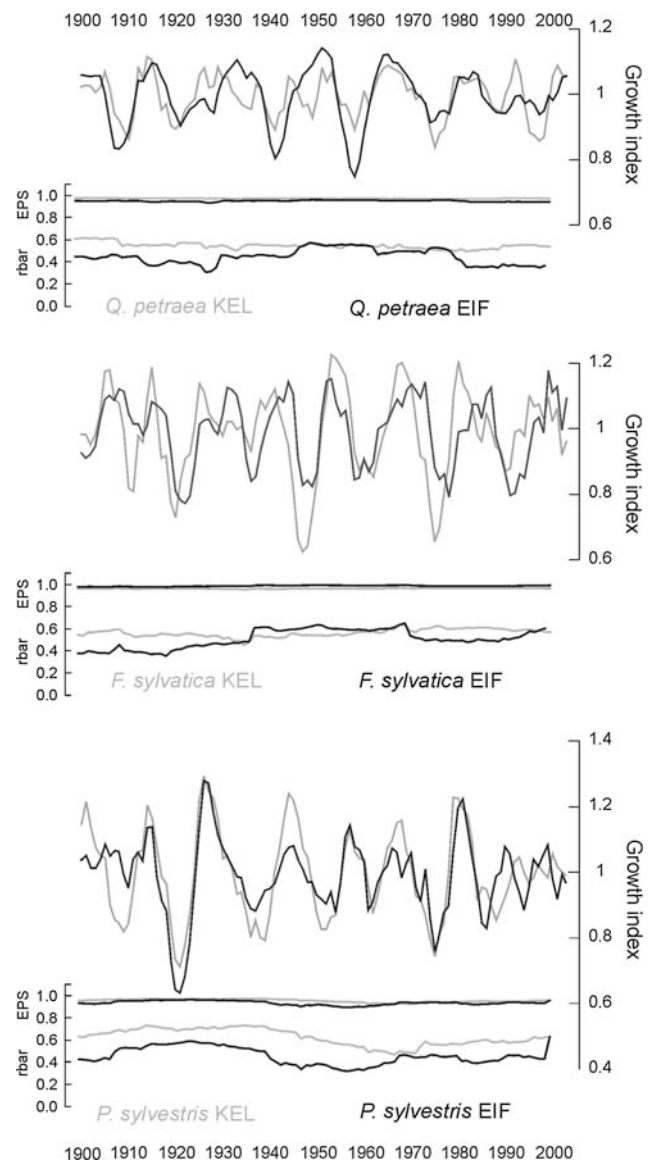
explained 10.1% variance and the third axis 8.2%. The eigenvalues for the first four axes exceeded a value of 1. The second PCA axis divided trees of each species by region (Fig. 5): higher loadings were found for *Q. petraea*, *F. sylvatica*, *and P. sylvestris* at KEL compared to the respective species at EIF. *F. sylvatica* trees from EIF in particular scored significantly lower on the second axis than the rest of the network. Species-specific separations are represented by position on the third axis, with *Q. petraea* (negative loadings) indicating the most pronounced cluster.

Differences between species- and site-specific chronologies confirmed the PCA patterns (Fig. 4). Growth
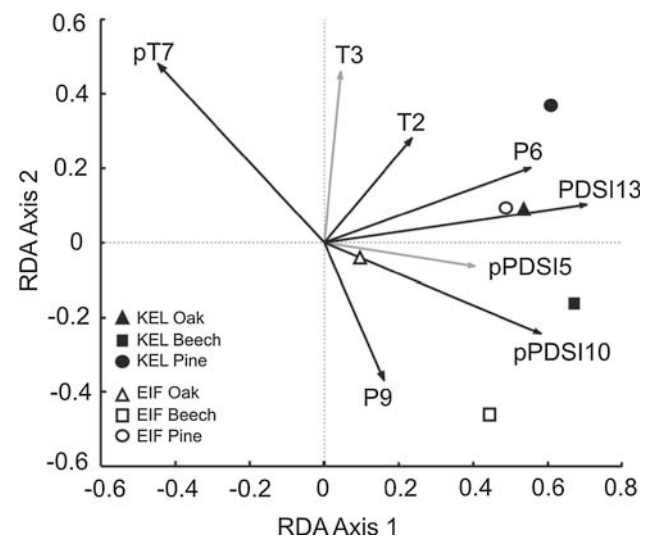
Table 2 Mean values of chronology statistics of species' regional chronologies

	F. sylvatica		*Q. petraea*		*P. sylvestris*	
	KEL	EIF	KEL	EIF	KEL	EIF
AGR	1.58	1.49	1.48	1.45	1.10	1.13
AC	0.32	0.24	0.21	0.35	0.24	0.35
Rbar	0.50	0.47	0.49	0.43	0.62	0.44
EPS	0.97	0.96	0.97	0.93	0.95	0.93
MS	0.33	0.30	0.24	0.22	0.95	0.93

AGR average growth rate (mm/year), *AC* first year autocorrelation, *EPS* expressed population signal, *MS* mean sensitivity; Rbar, AC, and MS are calculated on the basis of the detrended chronologies

Table 3 Correlation statistics between (a) the different species chronologies of the regions and (b) the chronologies of one species between the regions

	F. sylvatica	*Q. petraea*
(a) KEL		
Q. petraea	0.41	
P. sylvestris	0.43	0.61
EIF		
Q. petraea	0.35	
P. sylvestris	0.38	0.24
(b) KEL/EIF		
F. sylvatica 0.60	*Q. petraea* 0.40	*P. sylvestris* 0.56
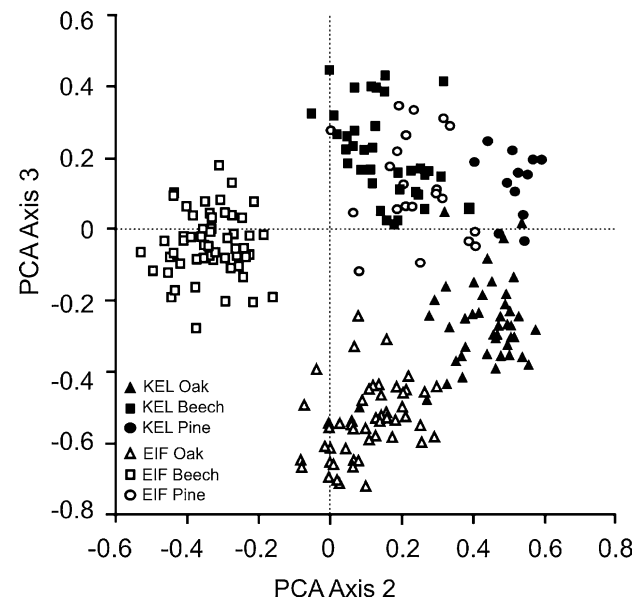
Fig. 6 Biplot of the redundancy analysis (RDA) of six species-specific regional chronologies for KEL and EIF and monthly, and annual climate parameters of both regions for the period 1901–2002. Vectors (*arrows*) represent significant climate factors; the strength of the influence of the climatic parameter is reflected by vector length. Vectors pointing in the direction of a tree-ring chronology indicate a positive correlation, whereas vectors pointing in opposite direction mean a negative correlation. *Black arrows* KEL climate data, *gray arrows* EIF climate data, *PDSI* Palmer Drought Severity Index, *P* precipitation, *T* temperature, *p* previous year; number suffixes represent months (e.g., 9 = September, 13 = annual value)

variations in the chronologies differ slightly between sites as well as between species. *Q. petraea* and *P. sylvestris* tend to increase growth during the climatologically interesting 1940s, whereas a strong growth depression is characteristic for *F. sylvatica* during this period.

Climate sensitivity

Long PDSI vectors in the RDA analysis (Fig. 6) indicate that drought is the most important and extensive climate factor influencing radial growth for all species at all sites. This was confirmed by the strong correlations we found between monthly and seasonal PDSI data and tree-ring chronologies (Fig. 7). Annual and previous-year May and October drought conditions had high, positive scores on the first RDA axis, which explained 31% of the network's total variance and had positive loadings for all species. According to their location on this axis, all tree-ring chronologies were drought sensitive, except for *Q. petraea* in EIF. Its low loading on both axes illustrated that EIF *Q. petraea* is not strongly related to any climate variable represented in this analysis. Correlations with drought (maximum $r = 0.18$) confirmed this result. Overall, a decreasing intensity in the growth/climate relationship was detected from KEL to EIF. Strong positive correlations between PDSI and *P. sylvestris* (maximal $r = 0.52$) and
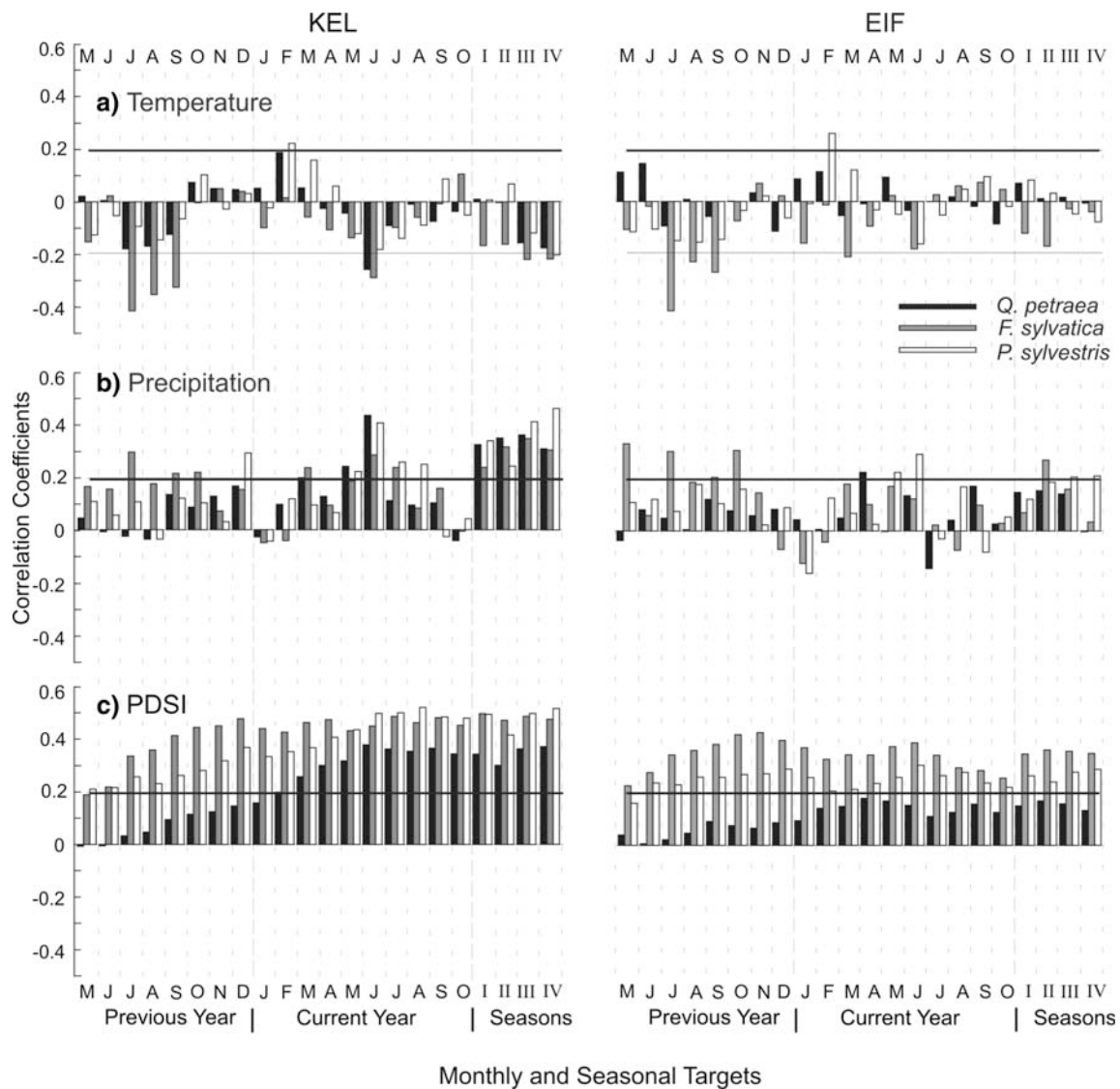

Fig. 5 Biplot of the principal component analysis (PCA) of 228 detrended tree series of three species in two study areas over the period 1901–2002. The second PCA axis explains 10.1% of the variance in the data set, the third axis 8.2%

Fig. 7 Pearson's correlation coefficients between species-specific regional chronologies (black = *Quercus petraea*, gray = *Fagus sylvatica*, white = *Pinus sylvestris*) of the KEL (*left column*) and the EIF (*right column*) and monthly and seasonal (**a**) average temperatures, (**b**) precipitation sums, and (**c**) average PDSI values over the period 1901–2002. Seasonal means are averaged over I = calendar year, II = March–May, III = April–September, IV = June–August. *Horizontal lines* denote 95% significance levels

F. sylvatica (maximal *r* = 0.49) are found at the drier KEL sites, whereas lower values (maximal *r* = 0.32 and *r* = 0.41, respectively) are found at the wetter EIF sites (Fig. 7c). Previous year drought conditions particularly influence growth of *F. sylvatica* (Figs. 6, 7). High correlations between growth and PDSI were observed over several consecutive months because of the high autocorrelation in PDSI.

Growth response to temperature showed species-specific differences (Fig. 6, 7a). Previous-year July and spring (February, March) temperatures had high scores on the second RDA axis, which accounted for 8% of the total variance (Fig. 6). Previous-year July temperatures had the strongest negative effect on growth of *F. sylvatica* in both KEL and EIF (Fig. 7). *F. sylvatica* growth in both regions was negatively correlated with previous-year summer and fall temperatures (minimum *r* = −0.42). Growth of *P. sylvestris* reacted positively to above-average February temperatures (Fig. 7). *Q. petraea* was weakly sensitive to temperature variations and only showed a significant, but relatively weak negative response to June temperatures in KEL.

Previous-year summer and fall precipitation amounts influenced *F. sylvatica* at both sites (Fig. 7b). All species in KEL responded significantly positively to annual and seasonal precipitation sums, but this was not the case for EIF.

Q. petraea growth in KEL showed high sensitivity to June precipitation, which also affected *P. sylvestris* at this site. June precipitation had high scores on the first RDA axis, whereas September precipitation was negatively associated with the second axis (Fig. 6).

In total, 37% of growth variability was explained by the selected climate variables of RDA, of which annual PDSI was the most influential (16%), followed by previous-year July temperature accounting for 6% of variance.

Temporal stability of growth/climate responses

Analysis of the temporal stability of drought sensitivity (Fig. 8) generally confirmed the results obtained with RDA (Fig. 6) and Pearson's correlations (Fig. 7). The temporal growth/climate correlations over five different time periods demonstrate and emphasize persistent differences between KEL and EIF (Fig. 8). While all species in KEL showed strong seasonal drought sensitivity patterns, drought response in the wetter EIF was weaker. Growth responses of the three species in both regions were not constant (Fig. 8). Drought sensitivity of *Q. petraea* in EIF, of *F. sylvatica* in both regions, and of *P. sylvestris* in KEL appeared to increase towards present (Fig. 8). Growth of *Q. petraea* in EIF illustrated significant drought sensitivity only at the end of the twentieth century. The positive correlation between drought conditions and *F. sylvatica* in KEL considerably increased since the 1940s and drought conditions in EIF started to affect *F. sylvatica* tree growth in the second half of the last century. Although significant growth responses of *P. sylvestris* in KEL occurred in the early periods, the importance of winter and spring conditions increased in the 1945–1984 period (Fig. 8).

The progressive warming in both regions from the early twentieth century to the present (Fig. 8), however, did not lead to a common increase in tree-growth sensitivity to drought. The number of months with significant growth/drought correlations of *Q. petraea* in KEL as well as *P. sylvestris* in EIF did not increase over time. *Q. petraea* in KEL responded fairly constantly to spring and summer drought conditions, except for the 1925–1964 period, when no significant drought response was found. The monthly drought influences on *P. sylvestris* in EIF were weak and a clear increasing or decreasing tendency in the number of responsible months could not be found. *P. sylvestris* in EIF even showed positive correlations to summer drought during the 1925–1964 period. Furthermore, this period was characterized by an abrupt loss or decrease in drought sensitivity for all species in KEL, which interrupted the increasing trends over the twentieth century of *F. sylvatica* and *P. sylvestris*.
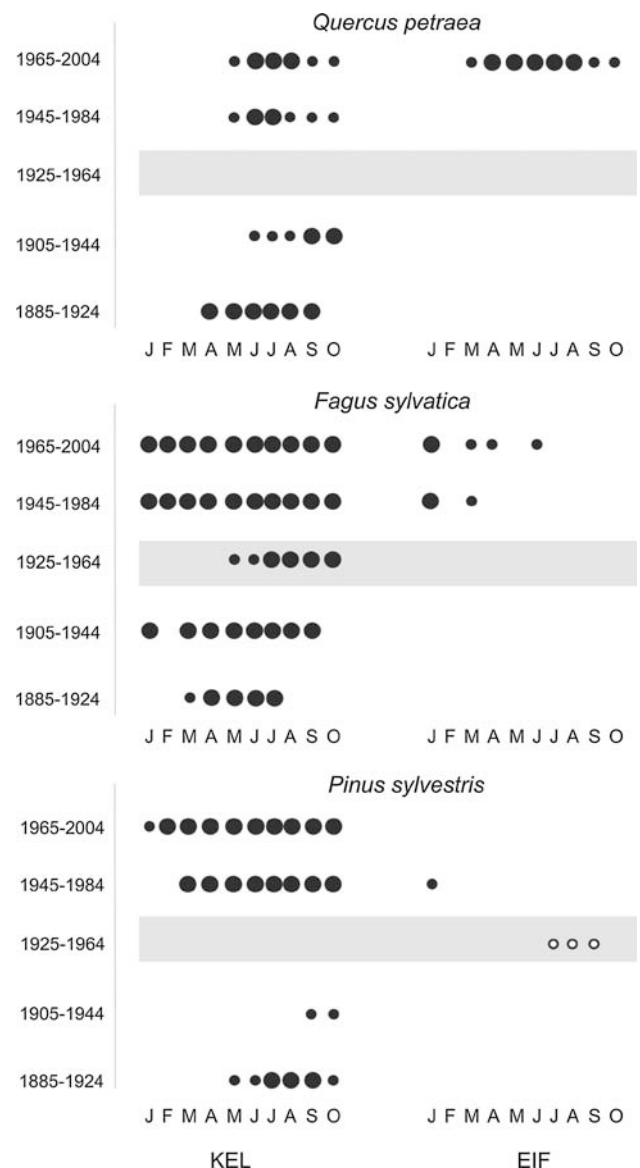

Fig. 8 Temporal changes in the correlation between regional (KEL and EIF) chronologies of *Q. petraea*, *F. sylvatica*, and *P. sylvestris* and monthly PDSI values. Pearson's correlation coefficients were calculated for five 40-year periods starting in 1885. The strength of the correlation is indicated by size of the *circle* (*small circle* $P < 0.05$, *large circle* $P < 0.01$). *Solid* (*open*) circles denote a positive (negative) correlation. *Gray bands* highlight the period of decrease or shift in growth response to drought

Discussion and conclusion

In this study, we provide a detailed analysis of the climatic sensitivity of the three dominant central European tree species at two regions that are characterized by differing moisture conditions. EIF is wetter than KEL and rainfall amounts at EIF are particularly higher in the winter months (Fig. 2). The tree-ring chronologies that we developed for *F. sylvatica*, *Q. petraea*, and *P. sylvestris* showed strong

signal coherency (Table 2) within both regions, but signal coherency was lower at the wetter locations perhaps due to a stronger relative influence of non-climatic factors, leading to more individualistic tree growth patterns.

The climatic parameters at both areas show a remarkably similar inter-annual variability, but differ in the absolute amount of annual precipitation (Fig. 3). According to our PCA analysis, the common inter-annual climatic variability for both KEL and EIF explains close to 30% of variance in tree growth. The second PCA axis divides all species according to region and is likely a representation of the main climatic difference, namely the annual sum of rainfall. The difference in moisture conditions between both locations probably explains an additional fraction of 10% (PCA axis 2). In total, only 48% of common variance is explained by the first three (significant) PCA axes, whereas the rest of variance is linked to ecologic- and genetic-induced growth heterogeneities in the dataset. Interestingly, the clearly differing responses of the *F. sylvatica* and *Q. petraea*—both deciduous broadleaf species—have implications for numerous modeling studies, which parameterize growth according to plant functional types (Betts et al. 2007).

Water availability is the primary growth-limiting factor for all species at both areas (Figs. 6, 7). Radial growth depends mainly on early summer soil water content (June), evidenced by an inverse growth relation to June temperatures (Fig. 7), and positive growth response to high precipitation sums (Fig. 7). Our study provides results comparable with growth/climate relations found in temperate forests studies located in the east and the south (Bonn 1998; Lebourgeois et al. 2005), and at the species distribution limits (Dittmar et al. 2003; Rozas 2001; Weber et al. 2007). The influence of water availability on tree growth differs strongly between the two regions, despite the fact that precipitation amounts are abundant even in KEL. *F. sylvatica* and *P. sylvestris* show remarkably stronger growth responses to temperature, precipitation, and PDSI at the drier site KEL compared to EIF (Fig. 7). *Q. petraea* is sensitive only to climatic variability at KEL. The differing growth/climate responses according to species and site are in line with the obtained differences in climate sensitivity (Table 2). The weaker climate sensitivity of *Q. petraea* compared to *F. sylvatica* and *P. sylvestris* is also represented by the distinct separation of the oak chronologies at both sites on the third PCA axis (Fig. 5). The difference in precipitation amounts between the areas represents a drought gradient, which leads to a shift from moderate (EIF) to more stressful (KEL) environmental growth conditions (Figs. 6, 8), particularly for *Q. petraea*.

Of the three studied tree species, *F. sylvatica* is most sensitive to annual drought events, and its climate sensitivity is comparable to that close to its southern distribution limit (Rozas 2001; Di Filippo et al. 2007). A key aspect to the reduced drought sensitivity of *Q. petraea* compared to *F. sylvatica* and *P. sylvestris* is the species-specific seasonality and duration of growth responses. *Q. petraea* growth is sensitive only to drought conditions during spring in both regions and summer in KEL of the growth year. Annual ring formation in the other species, on the other hand is strongly influenced by previous-year drought conditions and other periods in the growth year (Fig. 7). This difference in seasonality of growth responses is of particular interest in the two studied regions, which show distinctly differing amounts of winter precipitation, but not summer precipitation.

The strong growth response of *F. sylvatica* to previous-year summer and fall conditions emphasizes the importance of previous-year water availability for physiological processes, such as carbohydrate storage, for growth of the next year (Kozlowski and Pallardy 1997). The importance of previous-year climate conditions has previously been described for forests throughout Europe; e.g., the Pyrenees (Dittmar et al. 2003), throughout France (Lebourgeois et al. 2005), and the Alps (Di Filippo et al. 2007, Frank et al. 2007a). Previous-year climate conditions are not relevant for *Q. petraea's* growth in our analyses. However, other studies of *Quercus spp.*, carried out under more severe climate conditions, revealed a lagged influence (Rozas 2001; Weber et al. 2007; Friedrichs et al. 2008b). In this study, spring precipitation correlates with *Q. petraea* growth, likely indicated by the positive influence of high water supply on earlywood vessel initiation (García-González and Eckstein 2003). *P. sylvestris* reacts less sensitively to climatic variability than *F. sylvatica* (Fig. 7). We found significant responses to winter climate conditions and summer water availability. High amounts of winter rainfall likely improve water availability in spring as suggested by Lingg (1986) and Oberhuber et al. (1998). Furthermore, warm temperatures in February allow an early cambial activity start for conifers, potentially leading to wide growth rings (Kozlowski and Pallardy 1997). *P. sylvestris* growth at the species distribution limit strongly depends on summer soil-moisture availability (Weber et al. 2007).

All tree species within both regions showed an increase in drought sensitivity over the twentieth century (Fig. 8). The features characterizing this increased sensitivity, however, differ between sites. No species at the wetter site shows strong sensitivity to drought in the first half of the twentieth century, but *F. sylvatica* and *Q. petraea* become increasingly sensitive over the second half. At the drier KEL site, the increased drought sensitivity is reflected by more intense growth responses and by an increase in the number of months relevant for water availability.

F. sylvatica, which shows the strongest temporal increase in drought sensitivity in our study, is most likely to be endangered under future drought increases (Ciais et al. 2005). An assessment of the impact of a projected increase in drought frequency and severity over the coming decades (Schär et al. 2004 Christensen et al. 2007) on temperate forest growth remains complicated because of the influence of external factors, such as potential increases in water use efficiency (Leuzinger and Körner 2007) and increasing occurrence of defoliating insects (Thomas et al. 2002).

The 1940s describe a period of particularly complex growth responses to climate (Figs. 3, 8). This period is characterized by higher than normal temperatures and close to average annual precipitation amounts, similar to climatic conditions in the 1990s and leading to drier-than-normal conditions at EIF, but not at KEL (Fig. 3). The drought conditions at EIF appear to be not severe enough to induce a growth response in the studied species (Fig. 8). Growth responses in KEL over this period are characterized by an abrupt loss or decrease in drought sensitivity. The limited drought sensitivity over this period has previously been noted on a regional scale in a temperate forest oak network in Germany (Friedrichs et al. 2008b). Only the temperature-sensitive *F. sylvatica* trees appear to be negatively influenced by the increased temperatures over this period (Fig. 4), whereas *Q. petraea* and *P. sylvestris* profit from reduced drought sensitivity. The identified species-specific growth responses over this period complicate the assessment of climate change impact. High air temperatures are often assumed to generally induce negative growth reactions in low elevation temperate forests (Bonn 1998; Dittmar et al. 2003; Rennenberger et al. 2004) and only induce positive growth reactions at higher elevations (Dittmar et al. 2003; Jolly et al. 2005).

Our findings indicate that even minor differences in precipitation amounts in Central-West German temperate forests can influence the degree of climatic impact on tree growth. *F. sylvatica* could therefore suffer more at drier sites than at wetter sites and dry sites could in the future potentially be occupied by the more drought resistant *Q. petraea* and *P. sylvestris*.

Overall, this study shows that long-term climate sensitivity varies strongly between species and across precipitation gradients and is characterized by abrupt temporal shifts and differing trends in drought. The complex spatio-temporal interaction of climatic parameters hampers a precise assessment of climate change effects on forest growth in Central-West German temperate forests.

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