Spatio-temporal patterns of tree-growth response to climatic change

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Abbreviations

ALM = Average Linkage Method
AWL = Available Water Capacity
Elev. = Elevation
Exp. = Exposition
HCA = Hierarchical Cluster Analysis
IPCC = Intergovernmental Panel on Climate Change
PCA = Principal Component Analysis
PDSI = Palmer Drought Severity Index
Sl. = Slope

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Preface and structure

This thesis addresses tree growth in temperate forests with its complex responses to climatic change. It aims at contributing to a profound assessment of the suitability of temperate tree growth for climate reconstructions, as well as a better understanding of the impact of recent climatic change on temperate forest growth. A new, extensive tree-ring network with high spatial resolution has been established in Central-West Germany, including data from three dominant Central European tree species; oak (*Quercus spp.*), beech (*Fagus sylvatica*), and pine (*Pinus sylvestris*). The combination of this sampling design and the application of multivariate methodological approaches, various standardization techniques, and different climate parameters enabled improved analyses of temperate forests growth/climate relations.

This dissertation is divided in seven chapters, with the main body including four manuscripts (**Chapter 3-6**) of which is one published, one in press, and two in review. **Chapter 1** provides an overview of the rationale for this study, introduces the Central European tree-growth/climate complexity, and presents the aim and approach of this thesis. **Chapter 2** describes the characteristics of the study area, explains tree growth, introduces the climate data, and addresses the central methodological approaches applied in this study. **Chapter 3** specifies oaks temperature and precipitation response along a small-scale west-east-transect from the Eifel to the Sieg valley in temperate forests. This transect is included in the new oak tree-ring network, which is used for classification analysis (**Chapter 4**). Commonly applied classification methods in dendroecology are compared to investigate methodological differences and specific characteristics. **Chapter 5** details climate response of the oak tree-ring network to the commonly applied climate parameters temperature and precipitation, and additionally to vapor pressure, cloud-cover, and drought. It provides an analysis of spatiotemporal differences in growth/climate relations. Species-specific differences in climate sensitivity between oak, beech, and pine are compared in **Chapter 6** to assess climate-change induced changes in forest composition and species shift. Finally, a general discussion and conclusion are provided in **Chapter 7**.

The concepts of the manuscripts (**Chapter 3-6**) have been developed in cooperation with the respective co-authors. Data preparation and all analyses were carried out by me. The results were interpreted and discussed with the co-authors. I wrote the manuscripts with consideration of helpful comments and suggestions of the co-authors.

1. Introduction

1.1 Rationale

The fourth assessment report of the IPCC specifies the linear trend of global mean surface temperatures over the last century – from 1906 to 2005 – with 0.74°C ±0.18°C. Eleven of the twelve warmest years in the instrumental record of global surface temperature (since 1850) are found in the period 1995-2006. Climate warming is by now unequivocal, as it is evident from observations of increases in global average air and ocean temperatures, widespread melting of snow and ice, and rising global average sea level (IPCC 2007). However, these changes do not proceed similarly over the different areas of the world and regional-specific differences in the extent of climate change and its effects exist.

Climate reconstructions of monthly and seasonal surface temperature fields for Central Europe highlight the extraordinary warming in the late 20th and early 21st century compared to the last centuries (Luterbacher et al. 2004, Casty et al. 2007). Climate change is assumed to lead to a future temperature increase of 2.3-5.3°C over the 21st century, accompanied by an overall decrease of summer precipitation (Christensen et al. 2007). Both these climate factors would subsequently result in a long-term shift towards drier conditions with an increased likelihood of extreme droughts (Schär et al. 2004). The increase of extreme events – such as happened in autumn 2006 and winter 2007 – has already proceeded over the last decade (Pauling and Paeth 2007, Luterbacher et al. 2007), and the record-breaking heat wave over Western and Central Europe in 2003 is an example of an exceptional recent extreme (Stott et al. 2004, Beniston and Diaz 2004). This year was characterized by mean June-August temperatures, which have exceeded the 1961-90 mean by ~ 3°C (Schär et al. 2004) and annual precipitation was up to 50% below the average (Luterbacher et al. 2004, Ciais et al. 2005).

Effects of recent climate warming on terrestrial vegetation are multifarious. Increased temperatures contribute to an extension of the vegetation period, a second flowering, and enhanced plant growth (Penuelas and Filella 2001, Luterbacher et al. 2007). However, climate change can simultaneously affect a reduction in primary productivity by severe droughts (Ciais et al. 2005, Jolly et al. 2005), induce species shifts (Thuiller 2004, Penuelas et al. 2007), or even increase species extinction risk (Thomas et al. 2004). Whether rising atmospheric carbon dioxide (CO_2) concentrations cause forests to grow faster and store more carbon in the long-term still remains unclear, because several conditions cause changes in the way of CO_2 impact, e.g. tropical versus boreal forest conditions (Hyöven et al. 2007). Körner et al. (2005) found no overall stimulation in stem growth and leaf litter production after applying free air CO_2 release for four years under temperate forest conditions.

The influence of climate change on tree growth and forest functioning is of particular interest in many respects, as trees have a high economic importance (Geßler et al. 2007), are important CO_2 sinks (Denman et al. 2007), and serve as millennial-long proxy record for climate reconstructions (Jansen et al. 2007). A profound assessment of the influence of climate change on forest growth can only be obtained if species-specific responses to climate variability are well understood (Saxe et al 2001).

The climate conditions at the timberline, where species grow at the edge of their ecological range, have an exceptional strong influence on tree growth since species boundaries are induced by limiting climate conditions (Ellenberg 1996). Wherever timberlines occur, at thermal (high elevations and northern latitudes) or drought (arid zones) induced limitations, they represent an abrupt transition in life form dominance caused by one limiting climate factor (Körner 1998). Changes in climate conditions therefore directly influence tree growth and species vitality, often regarded as early indicators for climate change (Weber et al. 2007; Büntgen et al. 2008). Besides an early assessment of climate change impact, the strong relationship between tree growth and the limiting climate parameter enables a successful use of tree-rings as proxies for climate reconstructions (Esper et al. 2002, Cook et al. 2004, Osborn and Briffa 2006, Treydte et al. 2006, Büntgen et al. 2008).

In Europe, where one third of the land surface is currently forested (Bredemeier and Schüler 2004), tree growth is usually not controlled by one dominant factor since large parts are located in the temperate vegetation belt growing under temperate climate conditions (Ellenberg 1996). Most of the dominant tree species grow in the centre of their natural distribution areas affected by numerous growth influences (Fritts 1976). Biotic and abiotic factors and their interaction lead to complex growth control in temperate forests. A detailed assessment of the effects of climate variability on tree growth is complex, despite the significant influence of climatic conditions on tree growth (Schweingruber 1996).

Several physiological studies over the last years have analyzed the response of tree species to increasing temperatures and have provided important information on the reaction of temperate tree species to stressful influences (Saxe et al. 2001, Bréda et al. 2006). The extraordinary summer drought 2003 has been the focus of attention in numerous analyses (e.g. Ciais et al. 2005; Leuzinger et al. 2005; Granier et al. 2007) that describe region and species-specific reductions in tree physiological processes. A consensus about the strength of impact on trees, however, could not be reached. These studies often suffer from the short-term nature of laboratory and field experiments, which do not enable the interpretation of climate impact in a long-term context.

The analysis of long tree-ring chronologies allows for investigation of past climate sensitivity and helps to assess species' vigor and tree response to climate variability. Growth/climate relationships across Central Europe have been studied extensively (e.g. Hughes et al. 1978, Kelly et al. 1989, Bridges et al. 1996). The occurrence of extremely narrow or wide tree-rings, so-called pointer-years (Schweingruber et al. 1990), could be explained fairly well by temperature and precipitation anomalies (Schweingruber and Nogler 2003, Neuwirth et al. 2007, Kahle et al. 2007), but the impact of temperature or precipitation on time series as a whole was found to be moderate (Pilcher and Gray 1982, Lebourgeois et al. 2004). Besides the description of relevant monthly mean temperatures and precipitation sums for temperate tree growth, the influence of other factors, such as tree aging or disturbance, on growth and their relevance for climate sensitivity has been studied (Lebourgeois et al. 2004, Dittmar and Elling 2007). Comparisons between the climate sensitivities of several tree species show differences in the ability to cope with stressful climate circumstances (Neuwirth 2005). The growth of beech (*Fagus sylvatica*), the most dominant deciduous tree species in temperate forests, is influenced by climate conditions more strongly than oak (*Quercus spp.*) growth (Bonn 1998). In addition to this, tree-ring networks have been established to evaluate climatic influence under different environmental conditions (Dittmar et al. 2003, Lebourgeois et al. 2005, Neuwirth 2005, Ufnalski 2006).

A lot of dendrochronological studies have been carried out in Central European temperate forests, but a comprehensive assessment of tree-ring suitability for climate reconstructions and climate change impact on growth is still lacking, due to several problems:

i) The established dendroclimatological network analyses are based on strong environmental gradients focusing on the differentiation of supra-regional growth responses and comparing temperate with limiting conditions. However, for analyzing complex growth/climate relations in temperate forests themselves, it is necessary to investigate growth variations on a more regional scale (Schweingruber and Nogler 2003). The consideration of slight growth variations within relatively homogeneous growth patterns induced by smaller environmental gradients can likely provide important information about varying influences on tree growth effecting climate sensitivity.

ii) Many studies are based on tree-ring chronologies that end several years ago (in the 1980s and early 1990s), not including the recent climate change. Certain studies, e.g. Neuwirth (2005), consciously studied growth/climate response over a period without recent warming to achieve information about prior growth sensitivity, but extending growth/climate analysis into the 21st century is indispensable.

iii) The temporal variability of climatic influences on tree growth has not been analyzed comprehensively. Dendroclimatological studies in temperate forests are primarily based on fixed timeframes that do not evaluate changes in climate sensitivity over time. However, knowledge about the temporal development of growth/climate relations is essential to assess climate change impact on trees.

iv) The simultaneous consideration of various climatic parameters e. g. vapor pressure, cloud-cover, and drought, in addition to temperature and precipitation, could be particularly helpful to gain a comprehensive understanding of complex growth/climate relations in temperate forests.

1.2 Aim and approach

The main aim of this thesis is to improve the understanding of spatio-temporal patterns of tree-growth responses to climatic change in Central European temperate forests in order to contribute to a profound assessment of i) the suitability of temperate tree growth as proxy for climate reconstructions and ii) the impact of recent climatic change on temperate tree growth. Details about growth/climate relations will be obtained by a combination of i) a new extensive, high-resolution tree-ring network in Central-West Germany, ii) new comprehensive multivariate methodological approaches, and iii) the utilization of various climate factors (Figure 1.1).

Firstly, the establishment of a new high-resolution tree-ring network was necessary to analyze climate sensitivity of tree species on a regional scale, while taking differing site environmental conditions into consideration. Tree-ring samples of three dominant Central

European tree-species, oak (*Quercus spp*.), beech (*Fagus sylvatica)*, and pine (*Pinus sylvestris*), were collected for comparison of climate responses to enable differentiated conclusions of climate influence on temperate forests and assess changes in forest composition and species shifts.

A combination of standard dendroclimatological methods and new approaches allowed for a comprehensive evaluation of climate sensitivity. This is the first study in which classification results of three commonly applied classification methods in dendroclimatology were evaluated and compared for identifying methodologically induced differences in tree-ring analysis. Classifications were performed to identify homogeneous growth subsets within the tree-ring network and to detect responsible environmental factors. Growth responses to temperature and precipitation were evaluated using correlation analysis, redundancy analysis, and moving correlation analysis. Climate parameters that have only seldomly or never been used in previous dendroclimatological studies in temperate forests, such as vapor pressure, cloud-cover, and a drought index, were used to enhance the understanding of complex climatic controls. Finally, the species-specific differences in climate sensitivity were compared between *Quercus* sub-species and between *Quercus spp*., *Fagus sylvatica*, and *Pinus sylvestris*.

Figure 1.1 illustrates a schematic overview of the most relevant working operations for the analysis of the complex growth/climate relations in temperate forests. Further explanations about the various operations are given in chapter 2.

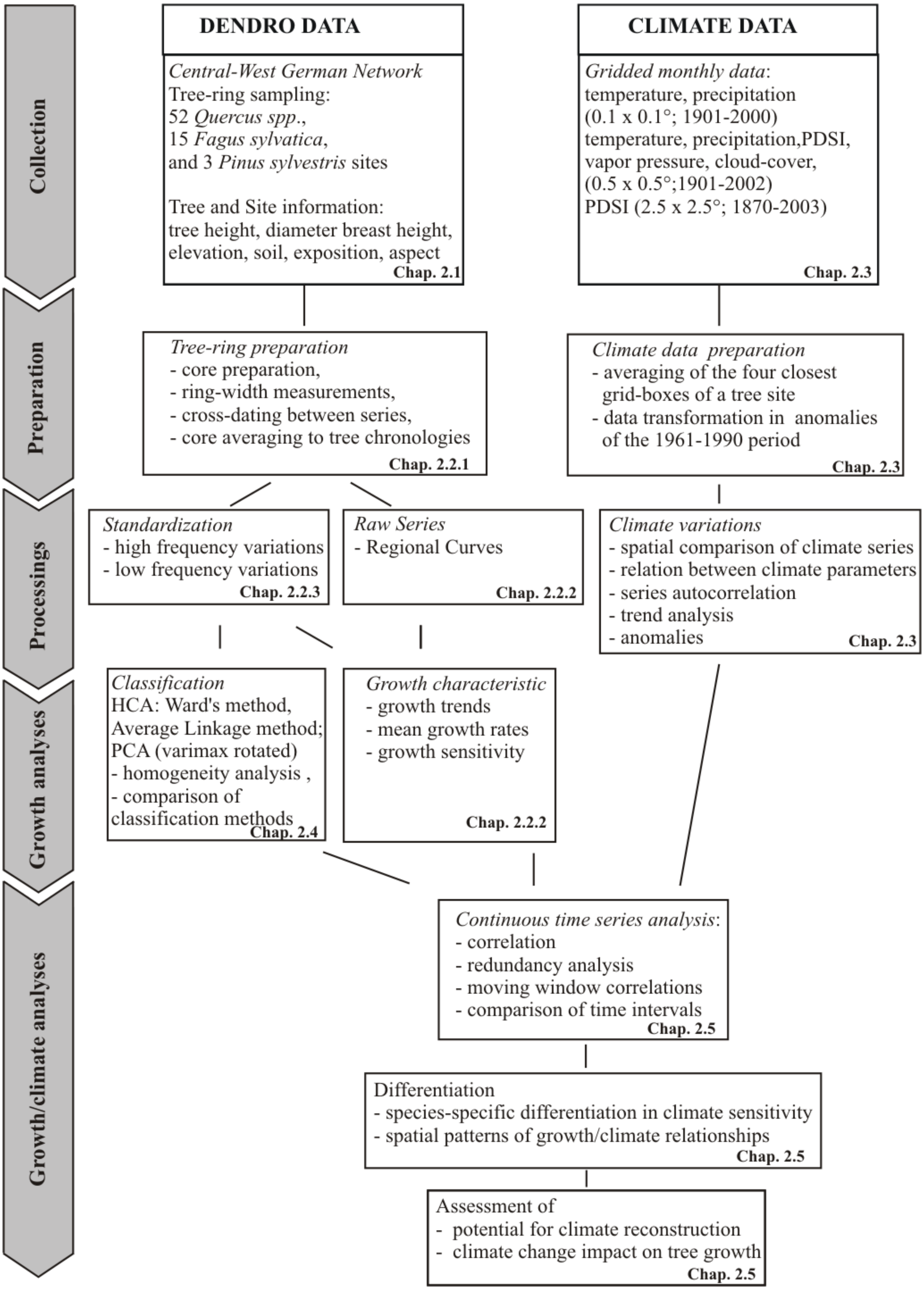

Figure 1.1 Flow diagram of the various methodological operations of the dendroclimatological network analysis. Detailed information about the different operations is given in chapter 2.

2. Material and methods

2.1 Research area and site characterization

A new dendroclimatological tree-ring network was established in Central-West Germany, an area characterized by gradually changing topographic and climatic conditions. The area, herein roughly defined from 6-10° E and 49-53° N (Figure 2.1), alters from temperate lowland in the north to low mountain ranges over the rest of the network.

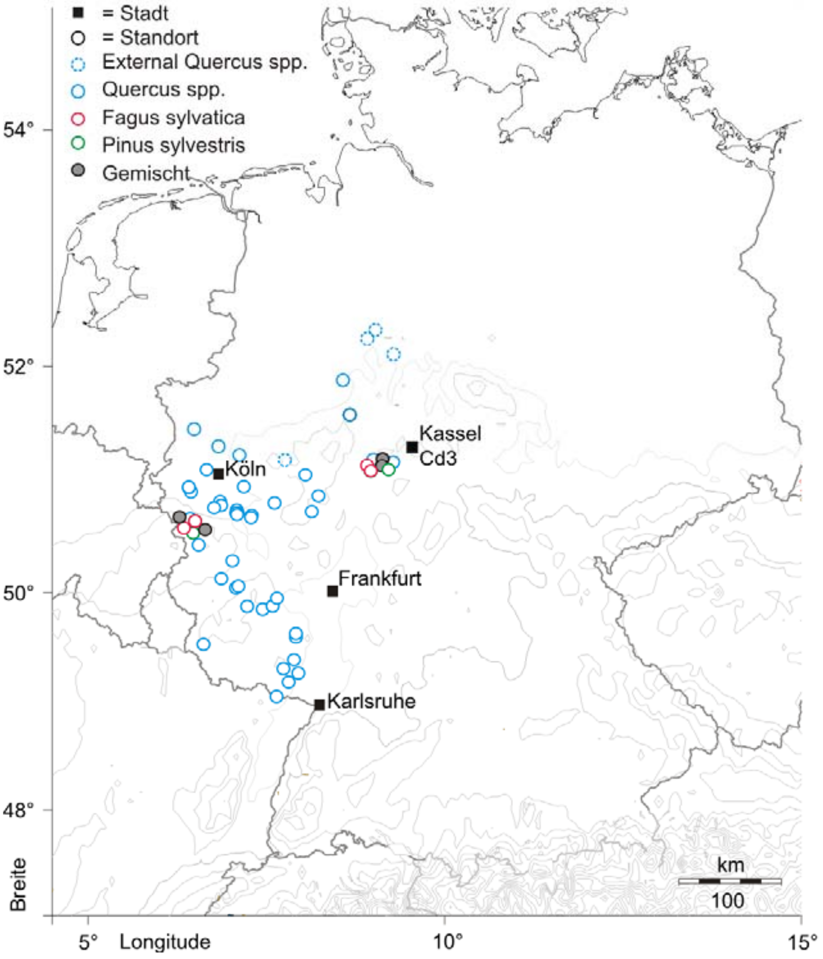

Figure 2.1 Location of the tree-ring sites used in this thesis (based on OMC 2006). Climate diagrams of the four meteorological stations are illustrated in Figure 2.2

The tree-sites range in elevation from 30-560 m a.s.l. The area is subject to a gradient from wetter (more oceanic) conditions in the north-western parts to drier (continental) climate conditions in the eastern and southern parts (see Figure 2.2). The synoptic conditions of the whole area are dominated by the North Atlantic Oscillation (NAO) in winter, whereas more localized pressure cells occur in summer (Hurrell et al. 2003, Raible et al. 2006). The primary atmospheric flow comes from the west-northwest, which, in concert with local topography, results in luff and lee settings with generally more precipitation on the west sides of the mountain ranges and in West than Central Germany.

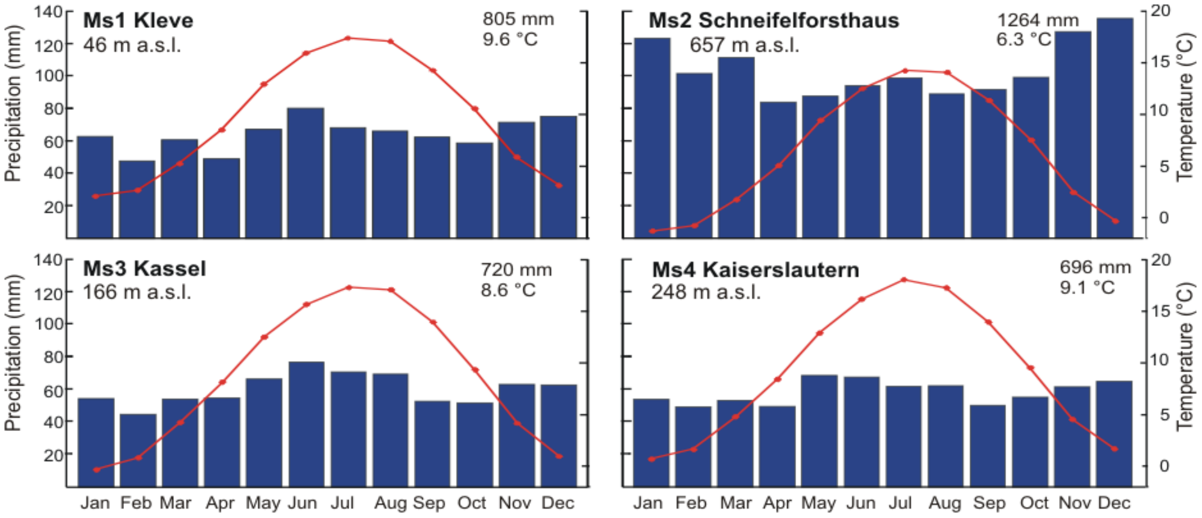

Figure 2.2 Climate diagrams of four meteorological stations in the research area (see locations in Figure 2.1).Ms = meteorological station; Ms1 (51.46° N, 6.06° E), Ms2 (50.18° N, 6.25°E), Ms3 (51.19° N, 9.30° E), Ms4 (49.27° N, 7.47° E). Average monthly temperatures (red) and precipitation sums (blue) are averaged over 1961-1990. Annual values are stated in the upper right corner of the diagrams. Station data were provided by the 'Deutsche Wetterdienst'.

The new network consists of 48 *Quercus spp.* sites, 15 *Fagus sylvatica* sites, and three *Pinus sylvestris* sites. Four external *Quercus spp.* sites were added to the network to help cover sparsely represented regions. The largest part of the network consists of *Quercus spp.* sites (**Chapter 3-5**). *Quercus spp.* was chosen for comprehensive spatiotemporal growth/climate analyses because *Quercus spp.* wood is the predominant historical timber species in Central Europe and a profound suitability assessment for climate reconstructions can only be based on this species. *Fagus sylvatica* and *Pinus sylvestris* were investigated in two regions of the research area to compare climate sensitivity between species (**Chapter 6**). Most of the sites were sampled in nature forest reserves, which were established in old forest stands with low forestry operation disturbance levels, that represent natural forest associations and are intensively monitored (Balcar 1996, Schulte and Scheible 2005). The tree species were sampled in pure as well as mixed forest stands. The sites vary in exposition, aspect, elevation, and soil water capacity – which was documented in a comprehensive meta-database – to present various kinds of growth conditions in the research area (Figure 2.3).

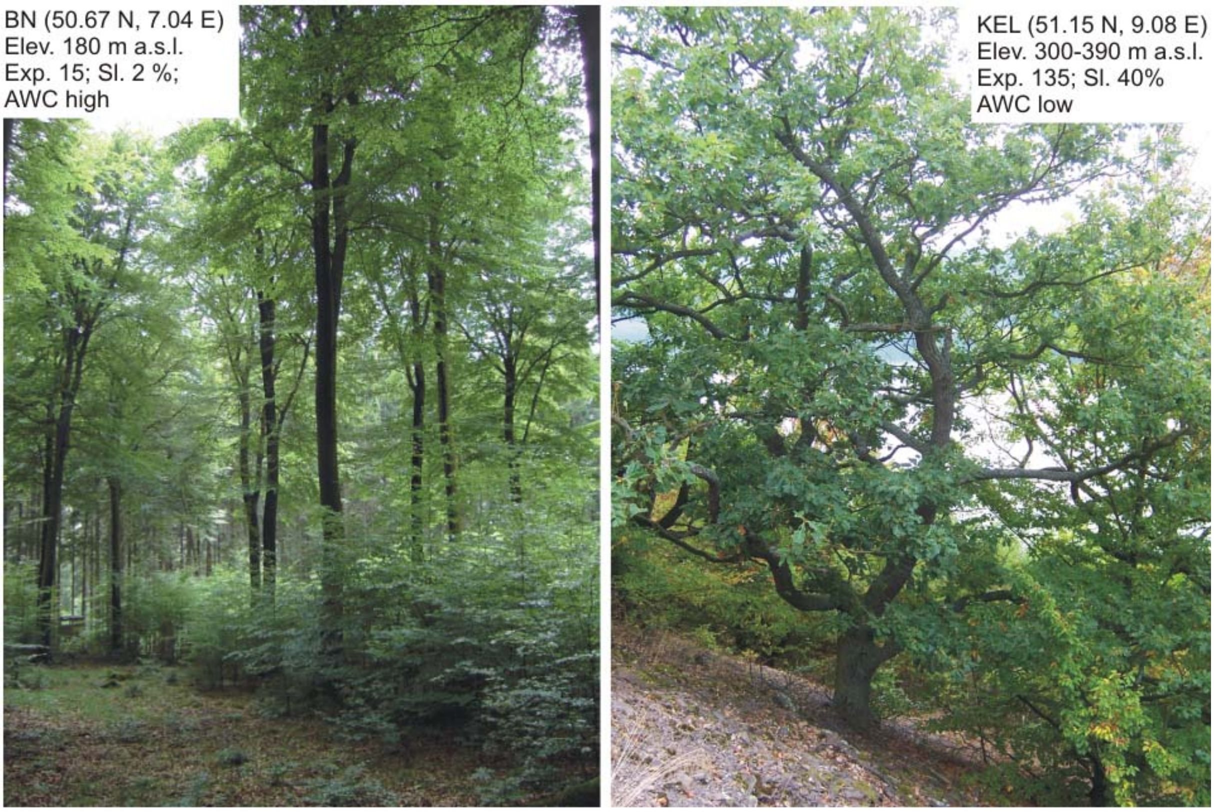

Figure 2.3 Photographs of sampling sites (BN = Bonn; KEL = Kellerwald), characterized by different ecological settings.

2.2 Tree rings

Tree rings are formed in most perennial woody plants, from very small herbs and dwarf-shrubs to large trees (Schweingruber 1996). Growth in areas without periodic plant dormancy, e.g. in the tropics, is not necessarily limited to traceable time periods, but annually defined tree rings can be found in most areas of the world characterized by seasonal climates.

2.2.1 Ring formation

The seasonal cycle of climate conditions leads to a vegetation period, where cells are developed, differentiate, and grow, and a dormancy period, which occurs during winter in temperate regions. The differentiation process of wood cells varies over the vegetation periods and earlywood and latewood zones are formed. Earlywood cell production occurs from April to July approximately, while latewood is generated from August until September. Characteristic anatomical features of these two wood zones allow annual rings to be defined.

Earlywood is characterized by wide cells with thin walls and light in color, while latewood cells appear dark, are narrow and have thick walls. Furthermore, genetic factors determine the basic structure of tree rings, while environmental factors modify the size and cell-wall thickness of cells (Kozlowski and Pallardy 1997). Each species reveals its specific wood structure (see Figure 2.4). Tracheids are the predominant cells in coniferous wood (e.g. *Pinus sylvestris*). Angiosperms additionally form vessels. Several species are characterized by ring-porous wood (e.g. *Quercus spp.*), where large vessels are found in the earlywood. Other species belong to the diffuse-porous group (e.g. *Fagus sylvatica*), characterized by similar-sized vessels over the whole tree-ring.

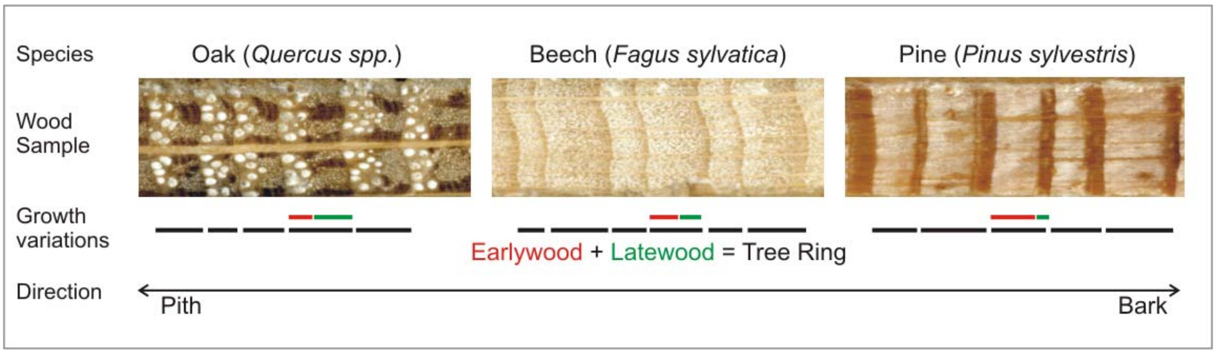

Figure 2.4 Overview of the anatomical wood structure of Quercus spp., Fagus sylvatica and Pinus sylvestris analyzed in this thesis. The photos and the schematically illustrated ring widths portray the growth variations in the measured tree-ring sequences.

For this study, cores were collected from at least twelve trees at each site. These cores were prepared in the laboratory following standard procedures outlined in Stokes and Smiley (1968) to visualize the tree-ring structure. Treatment with a sharp knife and chalk enabled exact counting and measuring of the individual rings. Tree-ring widths were measured for each core to the nearest 0.01 mm using the program TSAPWin (Rinn 2005) and two cores were averaged to tree series before site chronologies were developed. Dating errors were corrected on a site-by-site basis using the program COFECHA (Holmes 1983).

2.2.2 Growth response

The degree to which trees respond to external factors is named their sensitivity (Fritts 1976). Tree sensitivity can be derived from tree-ring sequences when a change or increase of particularly narrow or wide tree rings is visible (Figure 2.4). Growth response to external factors varies between the different tree species and depends on the environmental site conditions for tree growth. As mentioned before, complex growth controls are found under temperate climate conditions where dominance of a single growth factor is lacking. Several climate parameters influence tree growth and the interaction between influencing climate factors and tree-physiological reactions affect the formation of tree-rings (Figure 2.5A, Fritts 1976). Besides climatic influences, local factors such as aspect, slope, elevation, avalanches, soil nutrients, animals, and human interference can have impact on annual ring formation (Schweingruber 1996, Figure 2.5B).

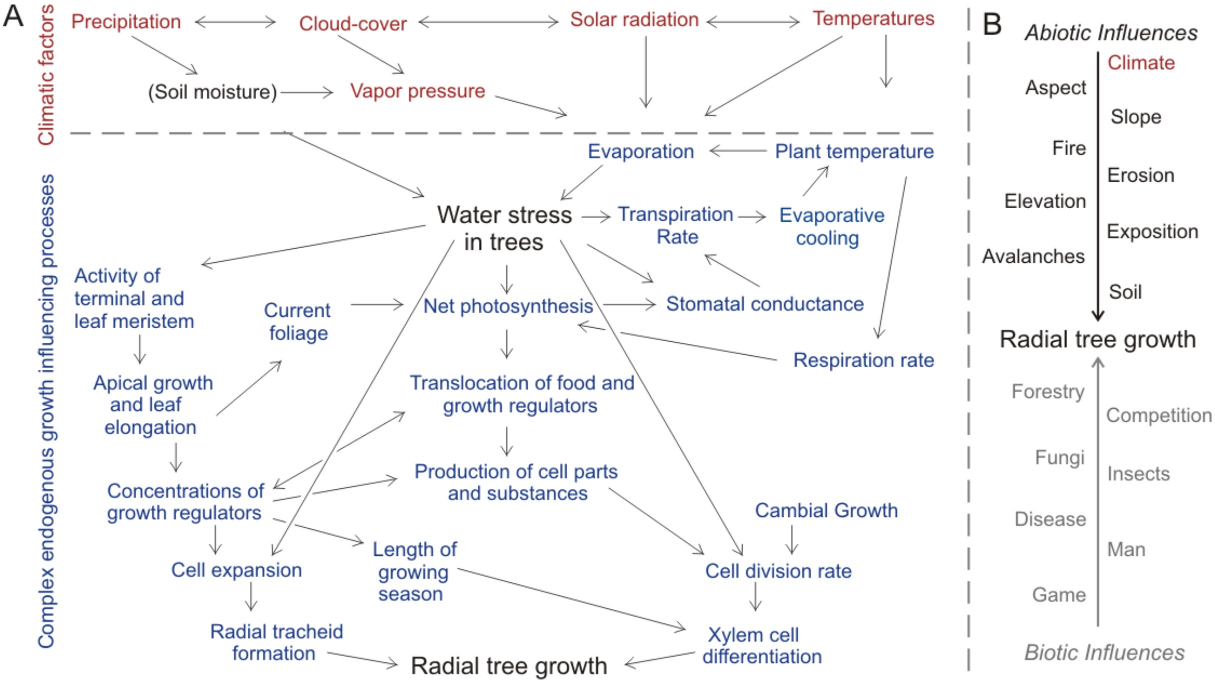

Figure 2.5 Schematic diagram of the complex influences on tree-ring growth. A) Influence and interaction of climate parameters and tree physiological reactions affecting the formation of tree-rings (based on Fritts 1976); B) Listing of important abiotic and biotic growth influencing factors.

The influence of factors affecting only individual tree growth, e.g. competition, was reduced within the following analyses by analyzing mean site chronologies. In addition to this, the impact of human influences is reduced by selecting nature forest reserves as research sites. The comparison of several sites with different ecological settings within the network helped to estimate the influence of local factors on the strength of growth/climate relations and hence, their own control on tree-ring growth. Growth response to external factors is not constant during the lifetime of a tree, age-specific sensitivities have been detected (Schweingruber 1996).

Several growth analyses within this thesis investigated the growth characteristics of temperate forest trees. The age trends of two oak species were compared by regional-curve (RC) analysis (**Chapter 5**), and average growth rates (AGR) of all species under varying environmental influences were investigated and discussed (**Chapter 3, 5-6**). Several chronology statistics, which estimate the growth homogeneity, the chronology signal strength, and the potential climate signal in the series, were determined (see **Chapter 3-6** for respective use). Signal strength is a measure for the amount of climate information in a tree ring and therefore for the value of a chronology for reconstructing climatic variation patterns (Fritts 1976).

2.2.3 Standardization

Growth trends are a function of tree age and diameter and are found in most raw measurements. They need to be removed for growth/climate analysis. The trend of declining growth with increasing age is caused by the more or less constant amount of annual stem biomass production, which is distributed around an increasing stem circumference (Figure 2.6). Consequently, averaging differently aged sequences of trees leads to a mean chronology biased by age-trend (Bräker 1981). Furthermore, heteroscedastic raw series need to be variance stabilized for a comparison of tree-ring sequences between slow and fast growing trees. Standardization (also detrending) is a transformation of the raw series with internal changes of growth level and spread into homoscedastic index series, free from age-trend disturbances (Cook and Kairiukstis 1990). Different standardization techniques have been developed in dendroclimatology. They can be divided into at least two types of procedures: either i) stochastic; different smoothing functions are fitted to each tree, or ii) deterministic; only one function is used for all trees (Esper and Gärtner 2001).

The standardization method applied in this study was based on the stochastic individual series standardization (Cook et al. 1995). According to the individual series – e.g. differing in the extent of age-trend – different functions (e.g. splines, Cook and Peters 1981) describing the series-specific noise were chosen within the same data set to obtain a rise of common signals and to achieve a mean chronology reflecting climatic variation.

Climate varies on different time scales and tree-ring sequences thus reflect a composite of different frequencies (Esper and Gärtner 2001). Different filters can be used to study variance at particular frequencies and to remove undesirable variance (Figure 2.6). Depending on the length of the filter, the maximum length of tree-ring width variation in the resulting index series is defined. For example, high frequency variation (inter-annual) is emphasized choosing a filter that eliminates all information beyond the inter-annual scale. The preservation of century- or multi-century- scale variation is required in climate reconstructions to illustrate long-term climatic trends (e.g. Esper et al. 2002, Cook et al. 2004, Büntgen et al. 2008).

Different smoothing splines were used to preserve high frequency (inter-annual scale; **Chapter 3-4, 6**), mid frequency (till decadal scale, **Chapter 4**), and low frequency (till multi-decadal scale, **Chapter 5**) variations. Cubic smoothing splines with 50% frequency cut-off at 32 years were individually fitted to each tree-ring series to retain high frequency variations, while 150-year and 300-year cubic smoothing splines with 50% frequency-response cutoff were calculated to preserve the mid and low frequency variations (Cook and Peters 1981). Indices of both standardization procedures were then calculated as ratios from the estimated growth curves. Finally, the series were averaged using a bi-weight robust mean (Cook 1985) in order to obtain variance stabilized site chronologies (Frank et al. 2007).

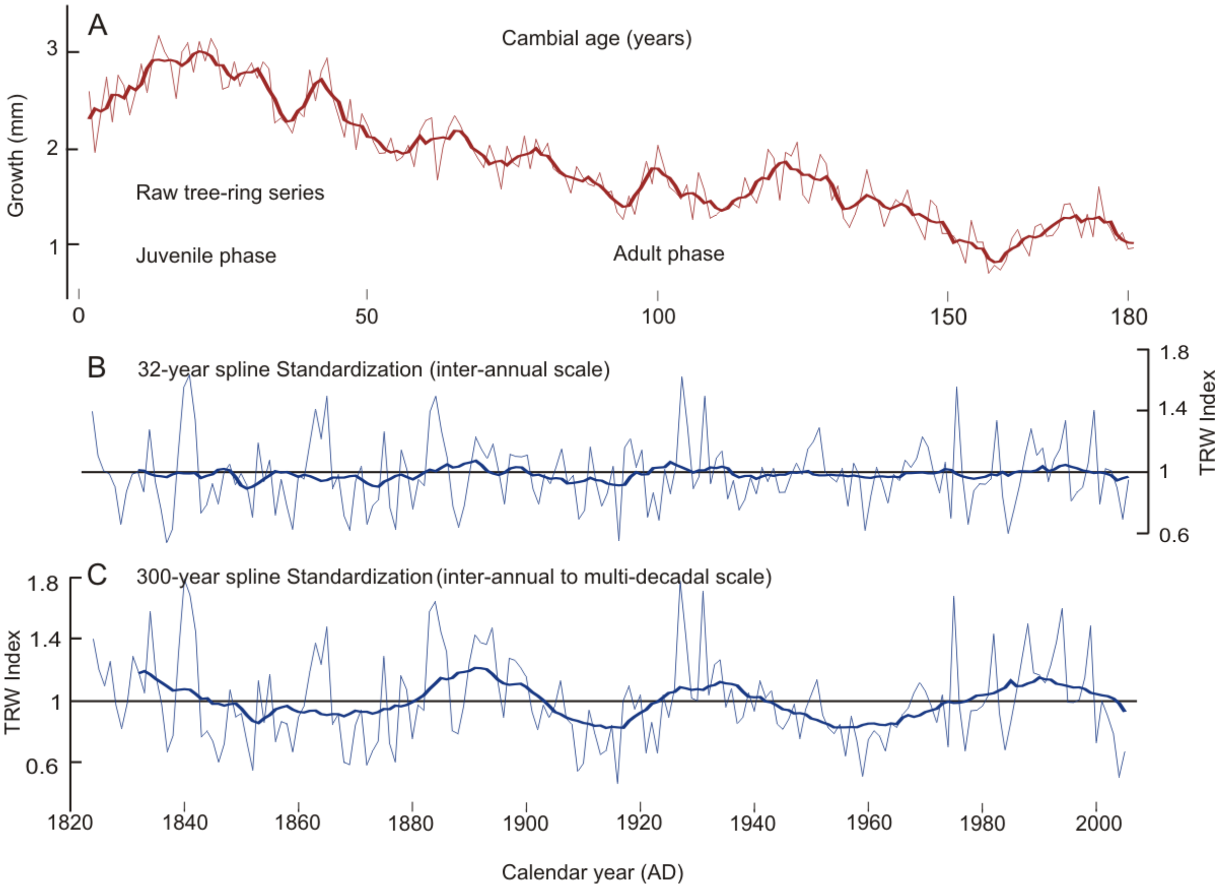

Figure 2.6 Raw curve of a Quercus petraea site in the north-western lowlands of the research area and its index series after two standardization methods. A) Age-trend characterized by decreasing ring diameter with increasing tree age; B) standardized chronology illustrating inter-annual growth variations; C) standardized chronology preserving multi-decadal variability. Ten-year moving averages (bold lines) highlight the different chronology trends.

2.3 Climate data

Monthly, seasonal, and annual temperature, precipitation, vapor pressure, cloud-cover, and drought index data were used for growth/climate response analyses. Drought conditions were represented by the Palmer Drought Severity Index (PDSI), a measure of regional soil moisture availability. The index is calculated using a rather complex water budget system based on records of precipitation, temperature, and soil characteristics (van der Schrier et al. 2006).

High resolution climate information about the tree sites was necessary for a detailed growth/climate analysis (**Chapter 3, 5-6**). Gridded temperature averages and precipitation sums with a 0.1° x 0.1° spatial resolution covered the time period 1901-2000 (CRUTS1.2, Mitchell et al. 2004; **Chapter 3, 5**). In comparison, cloud-cover percentage, vapor pressure (CRUTS2.1, Mitchell and Jones 2005; **Chapter 5**), and PDSI (van der Schrier et al. 2006; **Chapter 5-6**), were characterized by lower spatial resolution (0.5° x 0.5°), but longer time periods (1901-2002). The first years of cloud-cover data were characterized by missing data and therefore, we only used cloud cover data for 1950-2002. Temperature averages and precipitation sums of a lower resolution dataset (CRUTS2.1, Mitchell and Jones 2005) were used for representing climate conditions of the Eifel and the Kellerwald regions (**Chapter 6**). Furthermore, 2.5° x 2.5° gridded PDSI data (Dai et al. 2004) were used to extend growth/climate analyses for the period 1885-2004 (**Chapter 6**).

Generally, gridded datasets were used because of the absence of nearby climate stations recording all climate parameters with complete and homogenized long-term series. Climate parameters from the four grid-boxes closest to a site were averaged for growth/climate analyses. All parameters were expressed as anomalies with respect to the 1961-1990 reference period.

2.4 Site classification

Classification methods are applied in dendroecology for the identification of homogeneous subsets and the detection of growth patterns inherent in tree-ring transects or networks (Fritts 1974, Peters et al. 1981). Classifications are determined based on growth variations (e.g. Neuwirth 2005, Di Filippo et al. 2007, **Chapter 4-6**), and growth/climate relations (Lebourgeois et al. 2005). Several variants of principal component analysis, PCA (e.g. Büntgen et al. 2007) and hierarchical cluster analysis, HCA (e.g. Koprowski and Zielski, 2006) are used as classification methods in dendroecological studies. These methods differ strongly in their statistical approach: PCA is a data reduction technique, whereas HCA groups all objects of a dataset in stepwise calculations (Leyer and Wesche 2007). Both methods, however, reveal patterns of growth variations in tree-ring networks. Detailed information about the characteristics and statistics of the methods are found in **Chapter 4**.

A detailed comparison of frequently applied classification methods is carried out to clarify methodology-induced differences between differently obtained datasets (**Chapter 4**). According to the results of the comparison, homogeneity analyses based on PCAs and HCAs were carried out in **Chapters 5-6**. Ward's method, a HCA method, was applied to analyze the influence of environmental conditions on growth similarities on regional scale (**Chapter 5**). PCA was used to quantify the amount of common variance between the single trees of a dataset and to detect similarities and differences among them (**Chapter 6**).

2.5 Growth/climate analysis

In dendroclimatology, the relationships between tree growth and climate are usually calculated by means of correlation functions (Cook and Kairiukstis 1990). The influence of various climate factors on tree growth in this study was analyzed by calculating Pearson's correlation between ring width and climate data (**Chapter 3-6**). The relevance of monthly climate conditions – of the year prior to tree growth and of the growth year – was investigated. In addition to this, seasonal climate averages, for spring (March-May), summer (June-August), fall (September-October), vegetation period (April-September), and annual means were averaged to estimate climatic influence across temporal scales.

Another effective, but not frequently used, method to quantify climate influence on tree growth is redundancy analysis (RDA; Trouet et al. 2001, Tardif et al. 2006). This method is a direct extension of multiple regression applied to multivariate data (Legendre and Legendre 1998) and enables the analysis of the combined effects of climate factors on tree growth. The percentage of growth variability explained by climate variables can be determined (**Chapter 5 and 6**).

The temporal stability of the relationship between climate and tree growth is important information for comprehensive growth/climate analysis, particularly with respect to the assessment of climate change impact and tree-rings as proxies. Different temporal stability analyses are applied in dendroclimatology (Fritts 1976). In this thesis, moving correlation analysis (**Chapter 3, 5**) and a comparison of different temporal intervals of growth/climate analysis (**Chapter 6**) were carried out.

3. Dendroclimatology in the Low Mountain Ranges, Germany

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3.1 Introduction

The world-wide precipitation amount increased at about 2% within the 20th century due to a changing atmospheric circulation (IPCC 2001). The spatial and temporal variability of this increase is not completely understood. Hence, for a profound assessment of the impact of global change on the regional scale further spatial high resolution analyses are indispensable. Although earlier studies indicate that precipitation is a dominant growth-limiting factor at specific sites (Spurk 1997, Schweingruber & Nogler 2003, Neuwirth 2005), only few attempts have been made in low mountain ranges of Central Europe to reconstruct precipitation from tree rings (Wilson et al. 2005).

In this study initial dendroecological investigations in the Rheinische Schiefergebirge confirm the strong influence of precipitation on growing-patterns of oak at several sites. They demonstrate that tree-ring/climate-relationships are not constant over the last century, which complicates a precipitation reconstruction.

3.2 Material and methods

The research area consists of three parts, from west to east: the northern Eifel, the area close to Bonn, and the Sieg valley (Fig. 1). The sites embrace different ecological conditions, for example the elevation varies from 120 m a.s.l. in Bonn up to 570 m a.s.l. in sites of the Eifel. Further parameters are the exposition, the inclination as well as the composition of species.

For the climate/growth analysis oak cores from 13 sites were taken. Six sites are located in the northern Eifel, five in and close to Bonn and two 40 kilometers east from Bonn in the Sieg valley. The meteorological data is provided from the Tyndall Research Centre, UK (Mitchell et al. 2004). These data are high resolution grids (10 minutes resolution) for the time period 1901-2000. Monthly temperature and precipitation values are used for this study.

Prior to growth/climate analysis the internal site homogeneity of the different tree-ring series was calculated to describe the common signal of trees in the low mountain areas. The chosen statistical parameters were: mean growth, standard deviation, variation coefficient, Gleichläufigkeit (Schweingruber 1983), interseries correlation $r_{xy,}$ autocorrelation (Bahrenberg et al. 1992), and NET (Esper et al. 2001). The parameter NET represents the coefficient of variation and Gegenläufigkeit, the defined threshold is 0.8. The chosen time interval for the investigation comprises the period 1920-2000, in consequence of the correlation coefficient.

By the processing of the climate data, the four closest grid points to a tree site have been selected to get representative climate information for each site. For the monthly values of precipitation and temperature the mean of the four grids was computed.

The raw series of climate and tree growth were both standardized by a 5-year moving average and ratios were calculated to emphasize the inter-annual signal.

Correlation coefficients between tree-ring width and climate data were calculated for each year with different temporal resolutions (monthly, periods and annual values). Due to the restriction of climate data over time, the research period covers the interval 1903 to 1998. In order to assess the behaviour and stability of the relationship in time, 31-year moving correlations were computed.

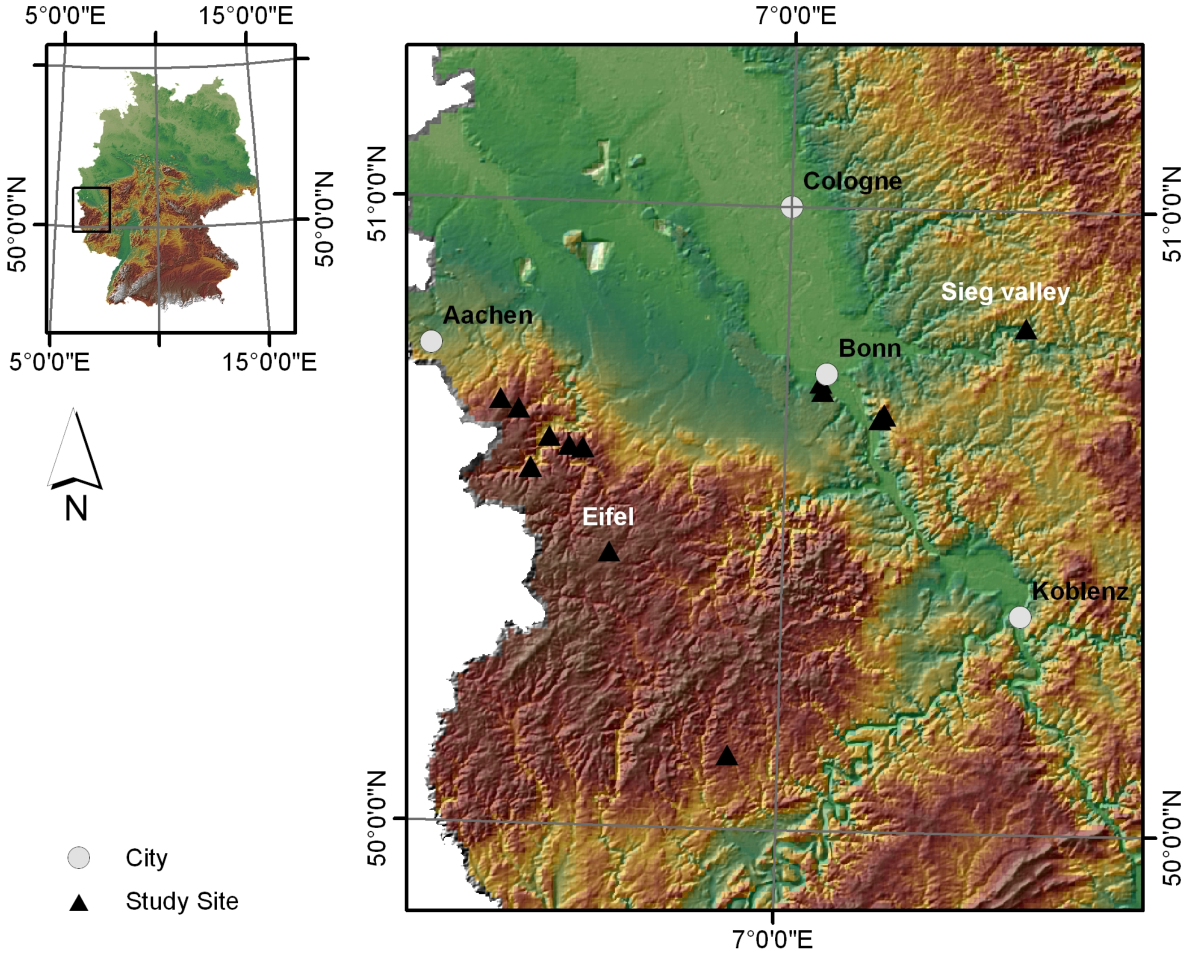

Figure 1: Location map illustrating the study sites (map based on SRTM data).

3.3 Results and interpretation

The analysis of growth variability, carried out by the internal site comparison, leads to a high level of similarity in tree-ring growth in the research area. The values of all statistical parameters are under/above the defined thresholds and accordingly confirm site homogeneity. The minimum and maximum values are shown in table 1. The significance of the correlation coefficient in each site lies above the 95% level. The mean growth varies from 1.09 mm/y to 2.19 mm/y, which can be explained by the different site conditions. NET, which characterises the signal strength, is adequately below the threshold even in the site of the maximum value. Thus, high signal strength is given in the whole research area.

Table 1: Internal Site Analysis; minimum and maximum values based on all 13 sites; x = mean growth, s = standard deviation, v = variance, GLK = Gleichläufigkeit, corr = correlation, autocorr = autocorrelation; time period is from 1920 to 2000.

Value	**x (mm)**	**s (mm)**	**v**	**GLK (%)**	**NET**	**Corr**	**Autocorr**
Min.	1.09	0.29	0.27	75	0.49	0.49	-0.24
Max.	2.19	0.82	0.48	84	0.71	0.69	-0.38

All sites show significant relations to the climate parameters. The trees of some sites respond in different ways to precipitation and temperature. One group of sites including the one in the Sieg valley, shown in figure 2, reacts highly significant in several months and time resolutions; others react significantly only in a few months.

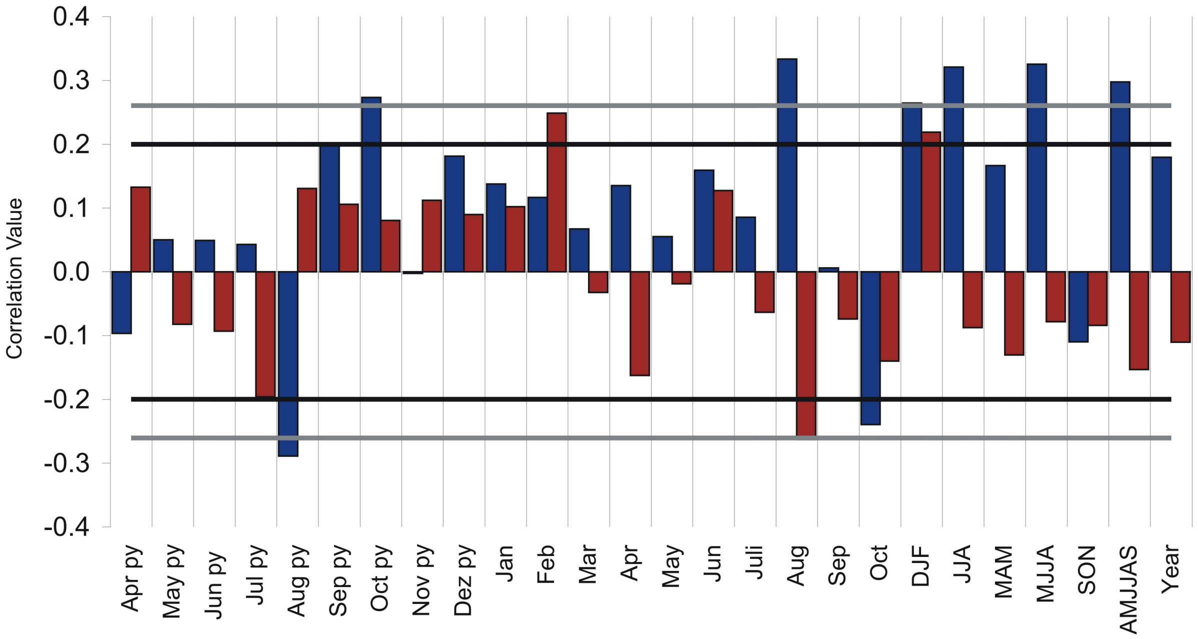

Figure 2: Correlation coefficients between growth and precipitation (blue bars), growth and temperature (red bars). The 95% (black) and 99% (grey) significant levels are indicated by the horizontal lines. py = previous year; DJF = mean December-February; JJA=mean June-August; MAM=mean March-May; SON=mean September-November; AMJJAS= mean April-September.

A spatial distribution is given, separating the sites of the northern Eifel from the rest. The Eifel sites react generally weaker on climate parameters than sites in Bonn and the Sieg valley. Temperature and precipitation differ in the sort of influence, especially in the months

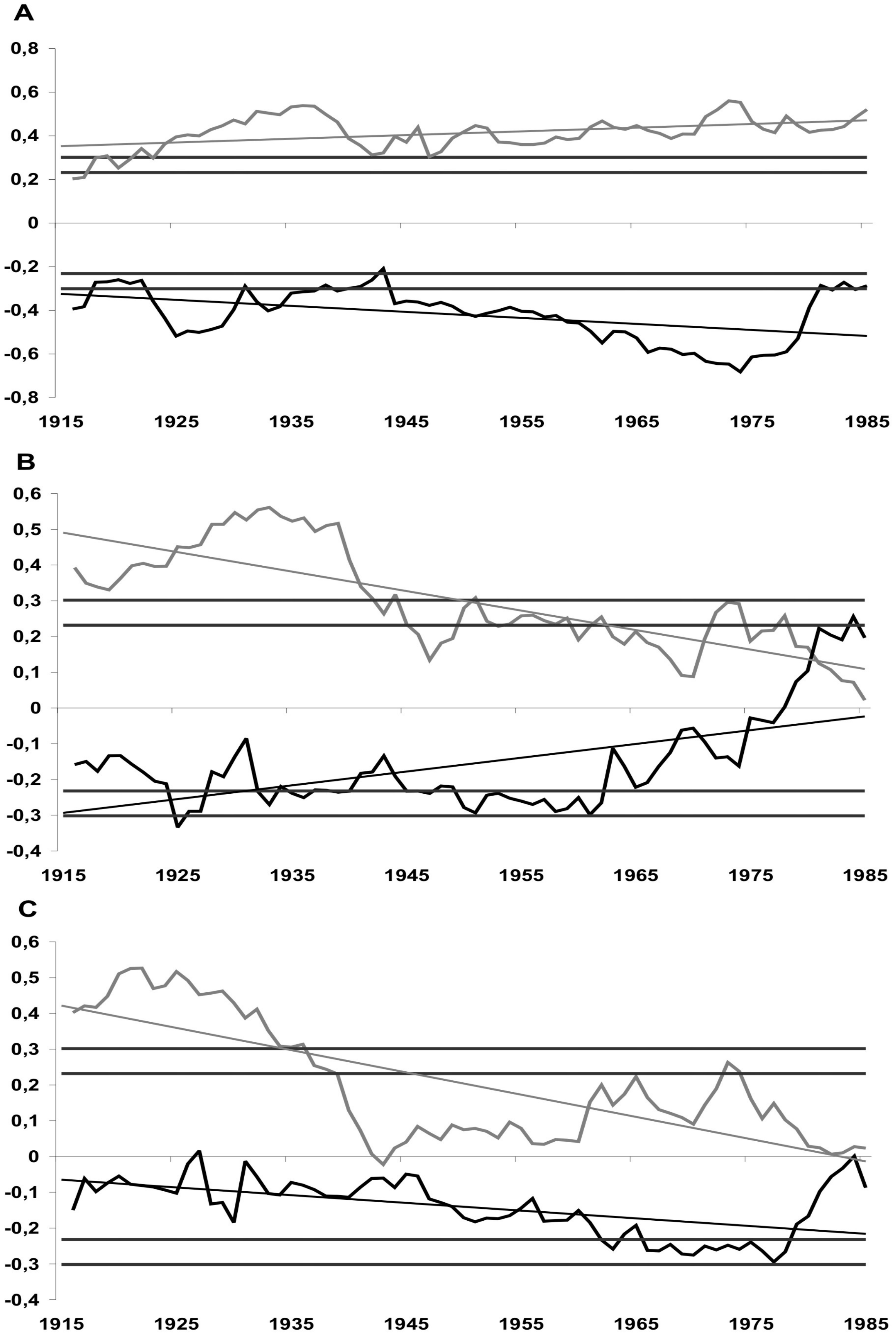

Figure 3: 31-year moving correlation with trend curve between growth and precipitation (grey curve) and temperature (black curve). The 95% (value +/- 0, 2319) and 99% (value +/- 0, 3017) significant levels are indicated by the horizontal lines. A: Sieg valley site, B: Bonn site, C: Eifel site

of the actual growth year. Correlations between precipitation and growth are most extensively positive, while temperature and tree-ring growth show mainly negative relations. Seven sites show positive significant correlations to precipitation for the time period of April to September, whereas only four of these sites react significantly with temperature. In order to get detailed information about the relationship of growth and the climate parameters in these sites the moving correlations were calculated. Three sites are illustrated in figure 3.

The relation between growth and both climate parameters varies over time. Time periods without a significant correlation are found in several sites. Regarding the trend lines, the Sieg valley site (A) represents significant values over the whole time period for both temperature and precipitation. However, going back in time the correlation coefficients decrease and the first precipitation values reveal no longer significance. The two other sites illustrate a contrary trend in the relationship of precipitation and growth. In both cases no significance in the present can be found and the values increase going back in time. Thus, the influence of precipitation on ring growth was in the beginning of the century very strong, whereas precipitation in the present loses its importance as influencing factor.

Temperature in the Eifel site is not only insignificant; it also has a contrary relation to ring growth than precipitation. Temperature influence decreases while the importance of precipitation rises. Hence, the precipitation represents a self-contained signal.

3.4 Conclusion

Our first investigations confirm a strong relationship between climate parameters and ring growth in the low mountain ranges in Germany. The subdivision of the research area in regions of diverse growth/climate relations can be explained by the cooler and wetter conditions in the Eifel opposite to the warmer and drier conditions in the rest of the research area. These circumstances can be caused by the regional climate situation and the ecological influencing factors, particularly elevation. Especially precipitation from the period of April to September is an influencing factor on tree-ring growth in several sites. The influence of temperature is in most of the sites less important than precipitation. Both climate parameters have no constant influence on growth over time and their trends vary between the different sites. A stabilisation of the relationship is necessary for reconstructing climate. One approach could be the classification of several sites to achieve a stronger homogenous growth/climate relationship over time.

4. Methodological-induced differences in oak site classifications in a homogeneous tree-ring network

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4.1 Abstract

Spatiotemporal variations in tree growth are induced by varying environmental conditions. Different methods like variants of the principal component analysis and the hierarchical cluster analysis are commonly applied in dendroecology to separate subsets of growth patterns within large tree-ring datasets. To seek for methodological differences in classification techniques and their specific characteristics, we compared three standard methods using a homogeneous oak (*Quercus spp.*) network from temperate forests in Central-West Germany. Classifications of the original dataset consisting of 46 oak ring-width sites, carried out with the varimax rotated principle component analysis, Ward's method and the Average Linkage method, reveal differences in the classification of approximately 20% of the sites. Analyses with modified datasets are calculated to evaluate effects of dataset extension, different time periods and different tree-ring detrendings. The application of the principal component analysis generally leads to the most stable site classifications, whereas the most sensitive response to changes in the dataset is obtained by Ward's method. The Average Linkage method separates single sites in the classification and thus emphasises outliers within the tree-ring network.

4.2 Introduction

Spatiotemporal variations in tree growth caused by varying natural or anthropogenic influencing factors are of particular interest in dendroecological studies (Schweingruber 1996). On a large scale, strong gradients of influencing factors are the main reason for growth variations between tree sites (LaMarche 1974, Kienast et al. 1987). It has been shown that different elevations and local biotic and/or abiotic factors can particularly explain the growth heterogeneity between different sites (Meko et al. 1993, Hughes and Funkhouser 2003, Neuwirth et al. 2004, Zhang and Hebda 2004). Growth heterogeneity is usually more pronounced on a large scale than on a regional scale. However, even slight growth variations within overall homogeneous growth patterns on regional scale provide information about varying influences on tree growth (Tardif et al. 2003, Andreu et al. 2007). The consideration of these slight growth variations is necessary for the analyses of the complex relationship between temperate forest growth and environmental factors. Particularly with respect to climate warming an enhanced comprehension of spatiotemporal growth variations on regional scale and the identification of the responsible environmental factors are required (Briffa et al.

2002, Neuwirth et al. 2007). For this purpose, it is necessary to identify homogeneous subsets within regional tree-ring datasets.

For the identification of homogeneous subsets within tree-ring transects or networks, different classification methods are applied (Fritts 1974, Peters et al. 1981). Dendroecological classifications are performed using several variants of the principal component analysis, PCA (Frank and Esper 2005, Tardif et al. 2006, Büntgen et al. 2007) or the hierarchical cluster analysis, HCA (Zhang et al. 2004, Bunn et al. 2005, Neuwirth 2005, Koprowski and Zielski 2006). Since these methods differ in statistical procedure of classification, they do not necessarily lead to identical results (Orlóci 1978). However, comparisons between them looking for specific properties or suitability of each method do not exist. Nothing is supposed about differences in the classification results and their relevance for growth homogeneity analyses. Peters et al. (1981) addressed similarities of the classification results and assumed similar results between the methods utilising the same similarity measures. Wilson and Hopfmueller (2001) and Campell et al. (2007) used different classification methods in their studies and obtained similar classification results. However, a detailed comparison of the methods is missing.

Here, we compare three classification methods to seek for methodological-induced differences in the obtained datasets. Classifications are performed using a relatively homogeneous tree-ring network, because differences between the methods rather occur in homogeneous datasets than in datasets characterised by a strong internal structure. Therefore, growth variations within a network of 52 ring-width chronologies of temperate forest oaks (*Quercus spp.*) in Central-West Germany are analysed. The analysis is calculated with frequently applied methods in dendroecology, a varimax rotated PCA, Ward’s method (WAM) and the Average Linkage method (ALM; two HCAs). Our first objective was the comparison of the classifications of the three methods over the common time period of the original dataset consisting of 46 sites. The second objective was to identify the stability of classification with respect to a dataset extension. The third objective was to test the temporal stability by classifications of the original dataset using three different time periods. The fourth and final objective was to detect changes in classification of the methods affected by slight differences of frequency growth variations by the application of two different tree-ring detrendings.

4.3 Materials and methods

Tree-ring data and detrending

An oak network of 48 sites has been developed between 2004 and 2006 (Fig. 1). Four sites from the ITRDB (International Tree-Ring Data Bank) were added to the existing data, to help cover sparsely represented regions. Plots were selected to obtain characteristic site conditions of the temperate Central-West German forests (here defined from 6° to 10° E and 49° to 53° N, Fig. 1). Site variations concern the exposition and topography, the moisture conditions, and the elevation, ranging from 30 m a.s.l. to 560 m a.s.l (Table 1).

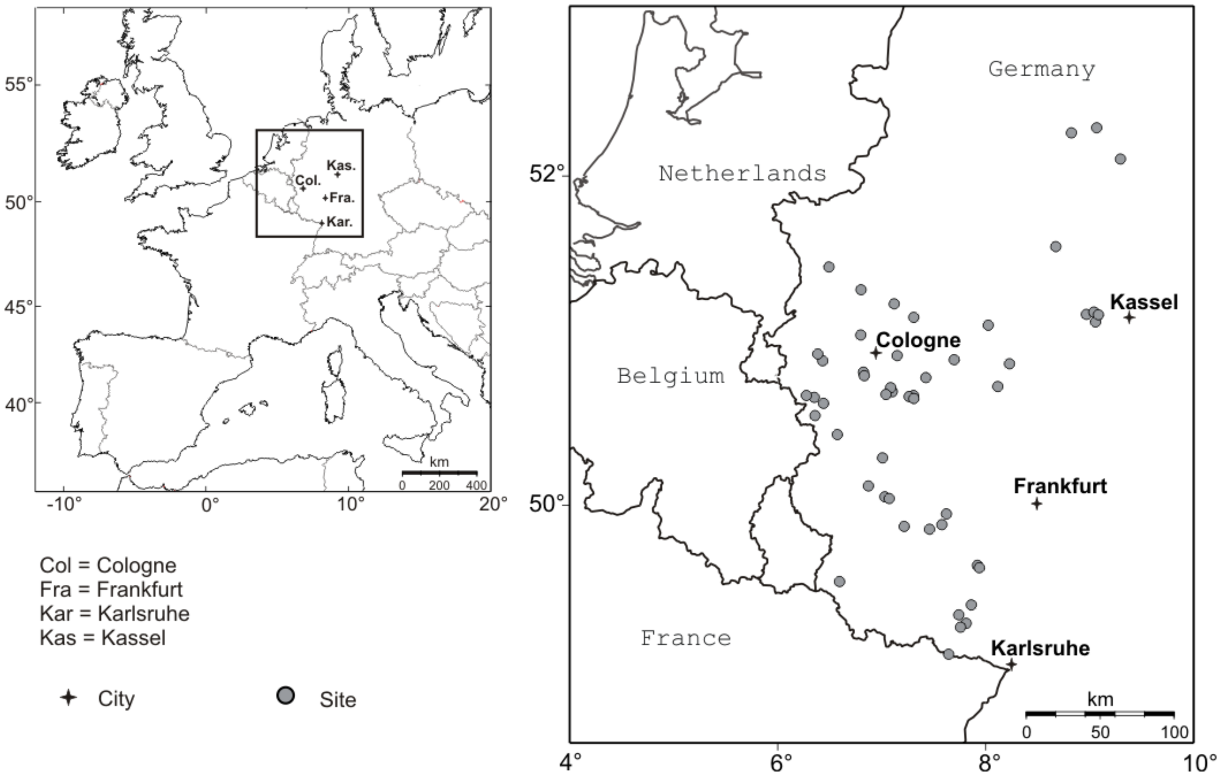

Figure 1. Location map showing 52 study sites in Central-West Germany (based on OMC 2006).

Tree-ring series were prepared following standard procedures (Stokes and Smiley 1968). Synchronisation and cross-dating were carried out with TSAP (Rinn 2003) and COFECHA (Holmes 1983) and age-related trends (Bräker 1981) and/or stand dynamics (Fritts 1976) were reduced by detrending with the programme ARSTAN (Cook 1985). To emphasise inter-annual variability, series were individually detrended using 32-year cubic smoothing splines with 50% frequency-response cutoff equal 32 years (Cook and Peters 1981) and indices calculated as ratios from the estimated growth curves. In addition, the same detrending procedure was calculated utilising 150-year cubic smoothing splines for preserving inter-annual to decadal frequencies. After detrending, series were averaged to site chronologies using a biweight robust mean (Cook et al. 1992). The chronologies were variance adjusted by utilising the sample size information and the average correlation between series (Osborn et al. 1997). Chronologies were truncated at a minimum sample size of three trees, resulting in the common 1900-1970 period.

The mean values of the statistical parameters *Rbar* (0.25) and *EPS* (0.98) confirm the overall homogeneous growth within the network. *Rbar* is a measure of common variance between single series and *EPS* quantifies the degree to which a particular sample chronology represents the theoretically perfect chronology (Briffa and Jones 1992). *EPS* values should remain above the applied threshold of 0.85 (Wigley et al. 1984).

Classification

The varimax rotated PCA and the two hierarchical cluster methods, WAM and the AL method, are based on different statistical procedures. The PCA transforms *n* original correlated variables (tree sites) into a number of uncorrelated principal components (PC), which are linear combinations of the *n* original variables and explain their whole variance (Peters et al. 1981). The correlation coefficient between the PC and the variables is the component loading (Mather 1976). The sum of the squared loadings of a principal component is its eigenvalue, used as criterion for extracting the number of PCs.

Each PC should represent an eigenvalue > 1, indicating that the explained variance of the PC is higher than the variance explained by a single variable (Kaiser Criterion). A second criterion is an explained variance portion above 5% of a PC (Mather 1976). Herein, the PCA was based on the correlation matrix of the sites and the PCs with eigenvalues > 1 were chosen for varimax rotation, improving the interpretation of PCA. The rotation leads to high loadings of few variables on a PC, whereas the other PCs reveal low values (Richman 1986).

The hierarchical clustering proceeds in stepwise calculations, leading from *n* clusters of one object (tree site) to one cluster containing all objects (Jongman et al. 1987). Regarding the ALM, all sites of a cluster are considered to calculate the similarity between two clusters. The similarity is assessed by the average distance of all possible pairs of sites between two clusters, measured in squared Euclidian distance. The Euclidian distance is suitable for dendroecological studies, as it sensitively reveals quantitative aspects like percentages of trees showing growth reduction in a given year (Oberhuber et al. 1998). Using WAM, the cluster variance, presented as mean squared Euclidian distance, is evaluated for each cluster and the sum of all clusters describes the overall variance within the clusters. This variance approach maximises variance between clusters, while the variance within the clusters is minimised.

Table 1. Chronology information and site location

Site	Region	Latitude/ longitude	Elevation	Period (?3 trees)	No.of trees	MSL[1] (years)	AGR[2]
1	Kellerwald	51,17N/8,97E	290	1839-2005	15	159	1.516
2	Kellerwald	51,16N/9,08E	350	1844-2005	12	159	1.349
3	Kellerwald	51,16N/9,08E	380	1856-2005	7	148	1.380
4	Kellerwald	51,16N/9,08E	390	1851-2005	10	148	1.648
5*	Teutoburg Forest	52,25N/8,90E	45	1851-1972	11	118	2.416
6*	Teutoburg Forest	52,32N/9,03E	50	1831-1972	12	127	2.039
7	Teutoburg Forest	52,10N/9,30E	205	1809-2004	8	193	1.778
8	South Eifel	50,12N/6,88E	430	1825-2004	11	174	1.497
9	South Eifel	50,05N/7,07E	370	1849-2005	12	150	1.719
10	South Eifel	50,04N/7,07E	370	1831-2005	12	170	1.198
11	South Eifel	50,30N/7,00E	480	1832-2005	10	166	1.649
12	Hunsrück	49,94N/7,63E	510	1778-2005	11	182	2.017
13	Hunsrück	49,88N/7,58E	500	1813-2005	13	182	1.604
14	Hunsrück	49,87N/7,23E	510	1661-2005	12	342	0.926
15	Hunsrück	49,85N/7,47E	420	1824-2005	10	176	1.398
16	Pfalz	49,38N/7,87E	500	1819-2005	14	177	1.454
17	Pfalz	49,30N/7,75E	400	1708-2005	11	288	1.185
18	Pfalz	49,26N/7,81E	480	1717-2005	13	282	0.889
19	Pfalz	49,24N/7,79E	490	1715-2005	11	257	1.128
20	Pfalz	49,05N/7,64E	390	1713-2005	12	246	1.321
21	Donnersberg	49,61N/7,92E	500	1805-2005	10	192	0.969
22	Donnersberg	49,62N/7,92E	500	1840-2005	10	164	1.029
23	Saar	49,52N/6,60E	290	1649-2005	12	276	1.145
24	Kölner Bucht	50,72N/7,09E	150	1847-2002	14	138	1.586
25	Kölner Bucht	50,70N/7,09E	120	1833-2002	10	148	1.875
26	Siebengebirge	50,66N/7,24E	230	1863-2004	11	119	1.924
27	Siebengebirge	50,67N/7,25E	355	1863-2004	17	126	1.441
28*	Siebengebirge	50,67N/7,25E	375	1883-2004	13	118	1.494
29	Ville	50,67N/7,05E	170	1832-2005	12	153	1.739
30	Ville	50,67N/7,05E	170	1850-2005	11	150	1.975
31	North Eifel	50,67N/6,33E	320	1846-2004	10	152	1.404
32	North Eifel	50,44N/6,57E	560	1868-2004	12	135	1.525
33	North Eifel	50,68N/6,28E	440	1809-2004	15	170	1.465
34	North Eifel	50,62N/6,40E	400	1812-2004	14	181	1.496
35	North Eifel	50,57N/6,36E	490	1847-2004	14	153	1.263
36	Siegen area	50,73N/8,11E	480	1750-2005	16	188	1.301
37	Siegen area	50,87N/8,23E	480	1857-2005	13	144	1.143
38*	Siegen area	51,10N/7,77E	80	1819-1973	24	142	1.925
39	north-western lowlands	50,93N/6,42E	105	1835-2005	15	147	2.176
40	north-western lowlands	50,92N/6,42E	100	1766-2005	15	195	1.575
41	north-western lowlands	51,04N/6,80E	45	1865-2005	12	128	2.343
42	Ville	50,79N/6,84E	160	1861-2005	12	142	1.459
43	Ville	50,79N/6,85E	160	1855-2005	6	162	1.431
44*	Kölner Bucht	50,75N/6,77E	130	1786-1971	15	157	1.492
45	Oberbergisches Land	51,23N/7,11E	260	1863-2005	11	137	1.545
46	Kölner Bucht	50,93N/7,14E	120	1820-2005	12	168	1.689
47	north-western lowlands	51,31N/6,80E	40	1850-2005	13	141	2.233
48	north-western lowlands	51,46N/6,49E	30	1812-2005	8	173	2.009
49	Siegen area	51,10N/8,02E	470	1842-2005	14	147	1.255
50	Paderborn area	51,58N/8,67E	260	1799-2005	10	176	1.780
51*	Siegen area	50,81N/7,60E	200	1871-2002	14	121	1.329
52	East Münsterland	51,89N/8,58E	110	1837-2005	9	164	1.559

[1] MSL= mean segment length; [2] AGR= average growth rate per year;*= added sites in the dataset extension;

A formal criterion for identifying the number of clusters in both methods is a jump in the squared Euclidean distance between two steps, indicating a connection of dissimilar clusters (Jongman et al. 1987).

The original dataset utilised for the comparison of the three classification methods consists of 46 oaks sites, all inter-annually detrended (32-year spline) and calculated over the common time period (1900-1970). The further calculations analysing the site classifications with respect to i) dataset extension, ii) temporal stability and iii) different detrendings represent modifications of the original dataset. For the i) extension of the dataset six further sites (marked in Table 1) were added to the original dataset and classifications were calculated over the time period 1900-1970. The temporal stability analysis (ii) was carried out with an extended time-frame, divided into three 45-year periods (1870-1914, 1915-1959, 1960-2004).

The analysis of different detrendings (iii) was reached by the comparison between the 32-year spline detrended chronologies and the 150-year spline detrended chronologies of the original dataset over the common time period (1900-1970).

4.4 Results

The original dataset (46 sites, 1900-1970, 32-year spline)

The three classification methods distinguish the 46 sites into different numbers of main groups. Using the PCA five main groups can be separated, instead of nine groups in the ALM and six groups in WAM (Fig. 2). The first five PCs of the PCA represent the 46 sites and explain 72% of their overall variance. These five PCs have higher eigenvalues than 1 and each of them explains more than 5% of the overall variance. Comparing all methods, differences in the classification of sites are found. While the distribution of 37 (80.4%) sites into the main groups is similar, nine sites (19.6%) are found in various site constellations. The constellations of five sites are distributed differently between the PCA and the HCAs. These five sites represent one group (C3) in both cluster analyses, while they are found in different constellations in the PCA (see filled squares in Fig. 2). Four sites differ between the two HCAs (see filled circles in Fig. 2). Slight differences between the HCAs exist in the site classifications within the main groups and in the linkage distances.

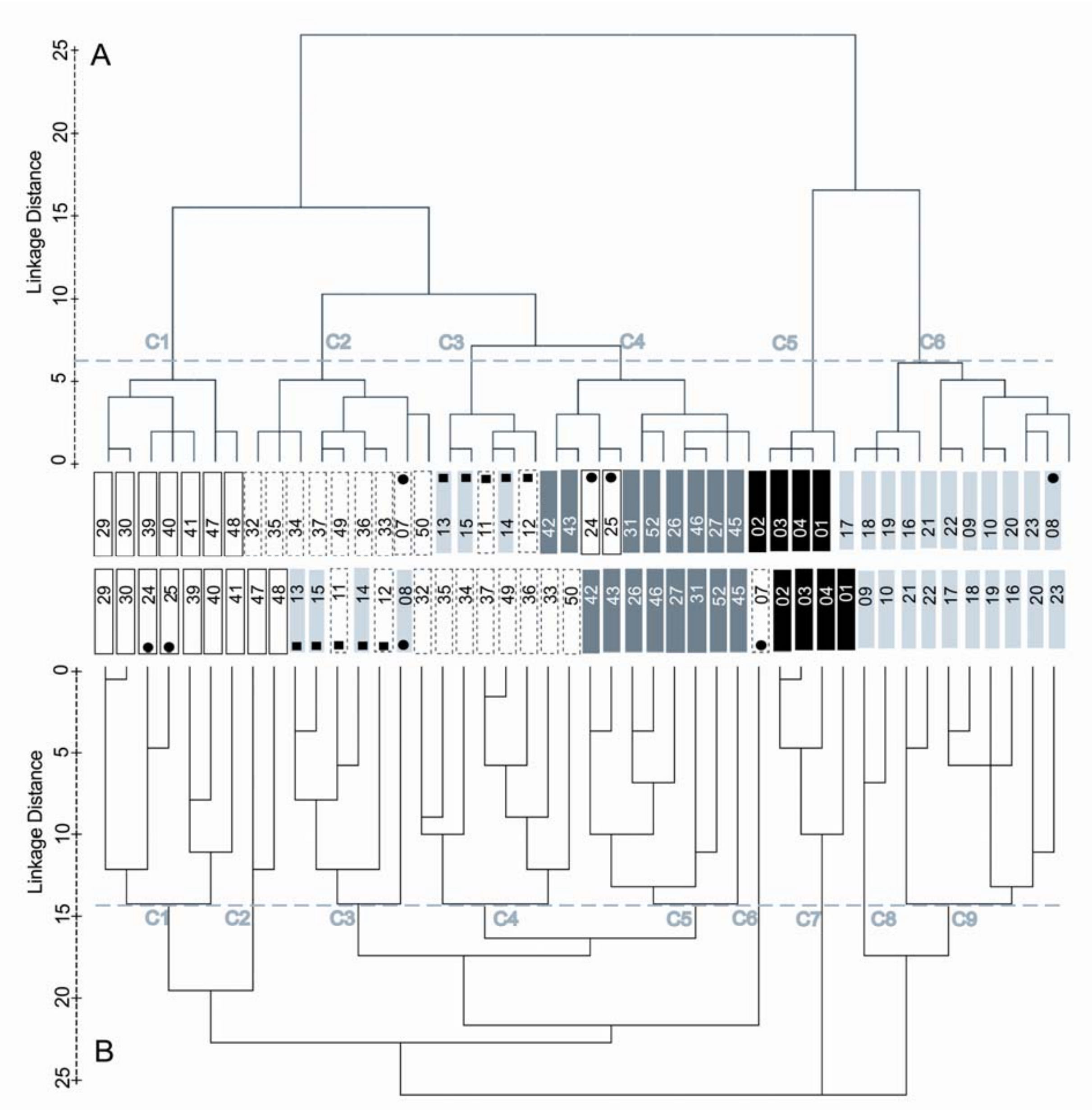

Figure 2. Results of the three different classification methods over the time period 1900-1970; (A) dendrogram of Ward's classification, (B) dendrogram of the AL classification. The groups of the PCA are illustrated by squares around the site numbers; the squares of: group 1 are filled with light grey; group 2 have grey dashed lines; group 3 are lined grey; group 4 are filled with dark grey; group 5 are filled with black colour. The dashed grey lines reveal the level of similarity within the HCAs the number of clusters (C1, C2, C3 …) are chosen. Filled circles mark sites classified differently between Ward's and AL method and filled squares illustrate sites classified differently between PCA and both HCAs.

The classification of WAM generates groups containing several sites on a low linkage distance and single sites are only found at the beginning of the procedure (Fig. 2a). At a linkage distance of six, all sites are subdivided into the six groups, whereas the classification of the ALM still separates 32 groups (Fig. 2b). At this linkage distance a jump in the squared Euclidian distance to the next level of classification is observed in WAM. The ALM does not reach a comparable classification and jump in the squared Euclidian distance before a linkage distance of approximately 14. However, three groups still contain a low number of sites and nine groups are necessary for integrating all sites.

Extension of the dataset (52 sites, 1900-1970, 32-year spline)

Comparison between the classifications of the original dataset and the classifications of the extended dataset reveals different classification stabilities between the methods (Fig. 3a-c). The PCA leads to the most constant classifications. The ALM reveals also constant site constellations, while the classifications of WAM react more sensitive on changes in the dataset. In the PCA, the site constellations of the original dataset remain similar after extension to 52 sites (Fig.3a). The six new sites are integrated into the five main groups already existent in the 46 site classification. In contrast, the six new sites in the WAM classification are found in main clusters leading to new site constellations in comparison to the 46 site classification (Fig. 3b). Regarding the ALM constant site constellations are found; however three of the added six sites are not fully integrated into the main groups (Fig.3c). One site represents a group of its own and is most different from all other oak sites, whereas the other two sites are more similar to six of the main groups. One of these sites represents a group together with a site of the original dataset.

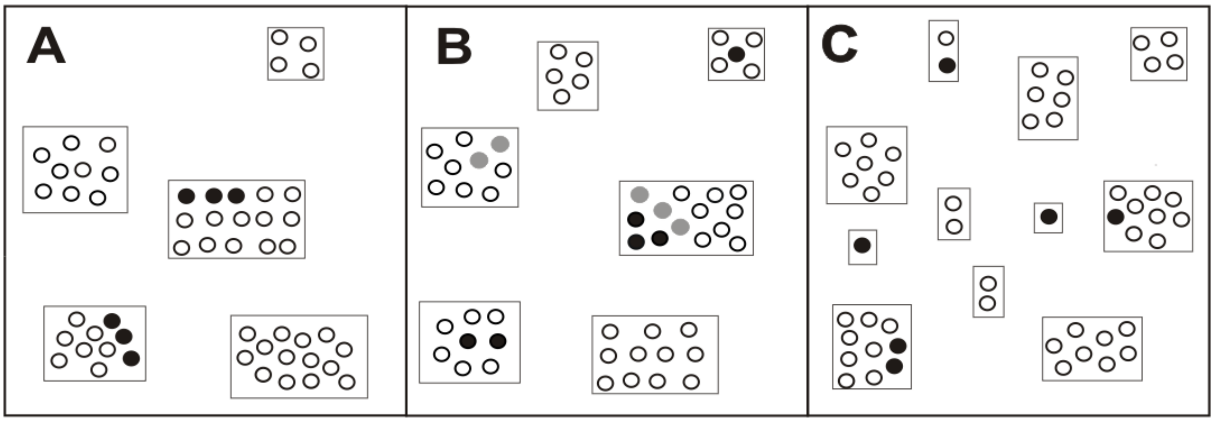

Figure 3. Schematic diagram of the effects of dataset extension on the classification of (A) the PCA, (B) WAM, and (C) the ALM. The white circles represent sites of the original dataset; black circles stand for the added sites and grey circles highlight sites of the original dataset, which changed into a different main group due to the dataset extension. The squares including the circles illustrate the different main groups.

Temporal stability of the classifications (46 sites, 32-year spline)

In all three methods, the site constellations vary over the three time periods (1870-1914, 1915-1959, 1960-2004). There are three different possibilities how a site can behave over the three time periods: a site can be either (i) associated with the same sites in all three time periods (stable), or (ii) can be found in a different site constellation in one of the time periods (flexible), or (iii) can be associated differently in each of the three time periods (most flexible). Depending on the applied classification method, several sites behave differently and therefore, fall in different categories. Only 19 sites are equally categorised by all three methods, of which eleven are categorised as stable, four as flexible and four as most flexible (Fig. 4a-c). Only eight of the eleven stable sites are associated with the same sites in all methods, whereas three stable sites are associated with different sites. Most of the stable sites are located at the edge of the research area, e.g. in the south, in the east and in the north-east, whereas the four most flexible sites are rather located in the middle of the tree-ring network (Fig. 4a-c). The number of sites belonging to one of the categories is different between the methods (Fig. 4a-c). PCA reveals 22 stable, 19 flexible and 5 most flexible sites (Fig. 4a), whereas WAM yields 24 stable, 13 flexible and 9 most flexible sites (Fig. 4b), and ALM shows 19 stable, 14 flexible and 13 most flexible sites (Fig. 4c).

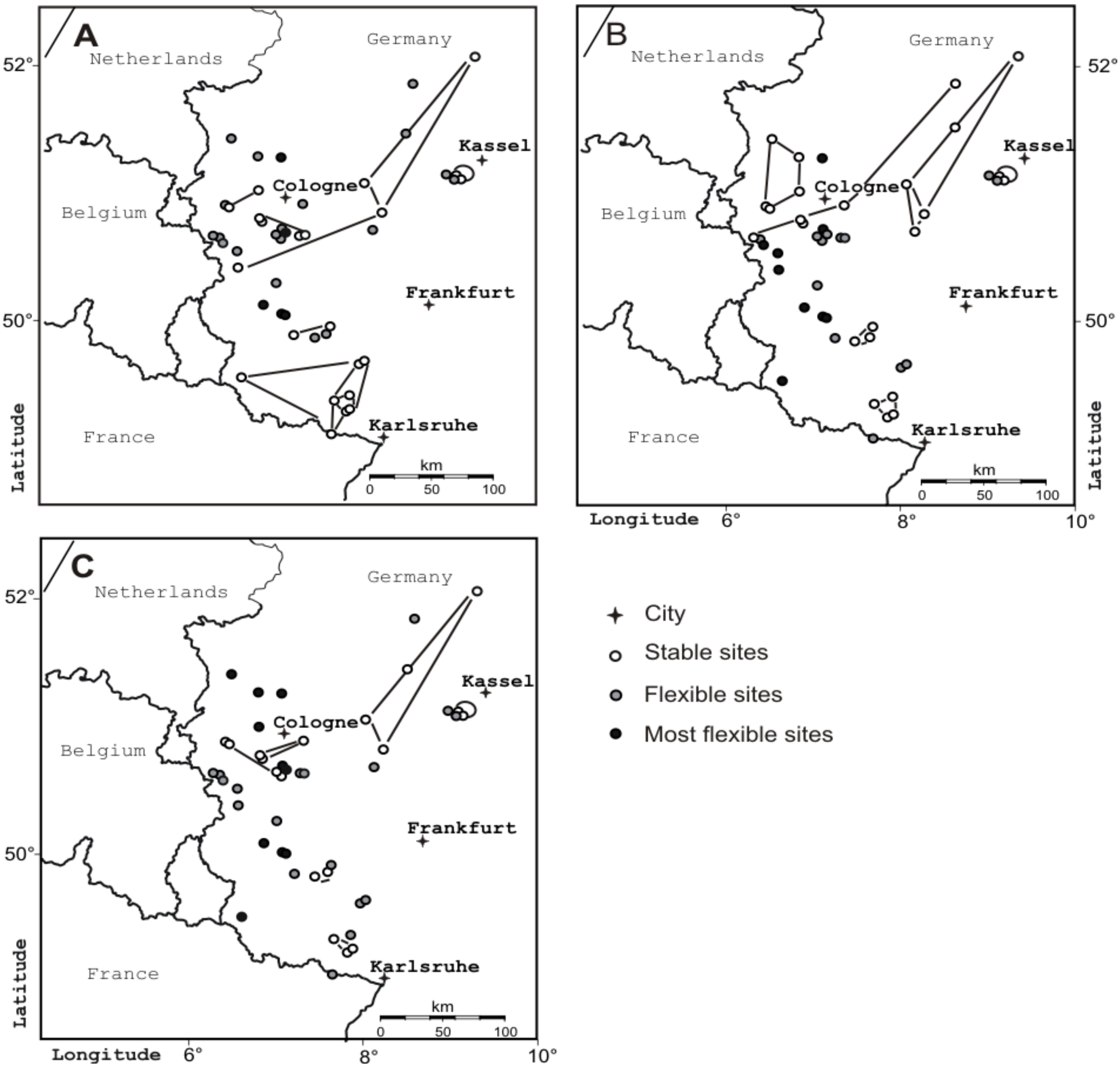

Figure 4. Spatial distribution of the stable and flexible sites of the temporal stability analysis based on the comparison of the classification results of the different time periods (1870-1914, 1915-1959, 1960-2004). Sites are either associated with the same sites in all periods (stable), classified differently in one period (flexible), or classified differently in each period (most flexible); (A) PCA; (B) WAM; (C) ALM.

Two different detrendings (46 sites, 1900-1970)

The 46 site classifications of the inter-annual dataset and the decadal dataset lead to several changing site constellations. Only two of the changing sites are identical in all methods. WAM reveals most changes; eight sites are grouped differently between the two detrendings, whereas seven and five sites change the site constellation in the PCA and the ALM, respectively. One of the changing sites in WAM and ALM belongs to the stable category of the temporal stability analysis, while four changing sites belong to the stable category in the PCA. The loadings of five changing sites reveal similar high values on two PCs and the affiliation changes between the inter-annual and the decadal classification.

While the two detrendings result in the same number of main groups in WAM, they lead to changes in the number of main groups in the ALM and the PCA. Nine and five inter-annual groups of the ALM and the PCA increase to ten and six decadal groups, respectively (Fig. 5). Overall, the intra-group correlations of the inter-annual frequency data are slightly higher (Fig. 5a) than the correlations of the decadal data (Fig. 5b). However, a direct comparison is only possible for group 4, consisting of similar sites in both detrended datasets. The correlations decrease from 0.792 of the inter-annual to 0.763 of the decadal data.

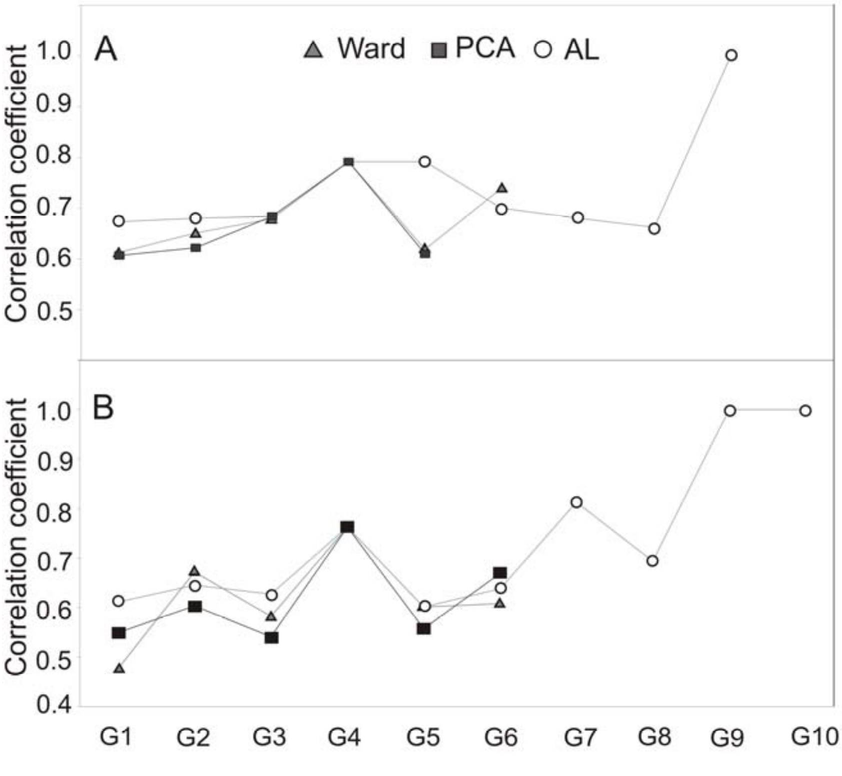

Figure 5. Comparison of the intra-group correlation of the different groups (G1, G2, G3 ...) based on the (A) intra-annual dataset and the (B) decadal dataset for the time period 1900-1970. The groups of the different methods are reordered for comparison (e.g. G1 of all methods includes similar sites, except slight differences indicated by various classification results). Note that the groups nine and ten of the ALM consist of only one site leading to the correlation value one.

4.5 Discussion

For a better understanding of climate impact on Central-European temperate forest growth it is necessary to investigate growth variations on the regional scale (Schweingruber and Nogler 2003). In contrast to Wilson and Hopfmuller (2001) and Campell et al. (2007), who investigated more heterogeneous datasets, in our homogeneous network the application of the different classification methods did not yield overall similar results. In the original dataset approximately 20% of all sites are found in different site constellations and the resulting classifications of the three methods are differently affected by i) extension of the dataset, ii) temporal subdivision and iii) different detrendings.

The extension of the dataset clearly reveals specific characteristics of each method. The specific algorithm of the PCA (Peters et al. 1981) leads to a robust site classification, the dataset extension results in similar site constellations to the original dataset. However, the classification procedure of WAM (Jongman et al. 1987) reveals a sensitive response to the addition of sites resulting in restructured site constellations of the original dataset. Such restructuring can be problematically in studies dealing with dataset extensions. Further WAM leads to an inclusion of all sites into approximately similar sized clusters and a clear separation between them. These characteristics are also found in the classification of Koprowski and Zielski (2006). In contrast, the classification of the ALM (Orlóci 1978) tends to highlight outliers within the network. The ALM might be useful to detect extraordinary growth variations in dendroclimatic network analysis, where a careful assessment of growth variations and different relationships between radial growth and site conditions improves dendroclimatic reconstructions (Tardif et al. 2003, Büntgen et al. 2007).

Our temporal stability analysis confirms the tendency to more robust classifications of the PCA by the lowest number of most flexible sites. However, the number of stable sites is similar to WAM’s categorisation. The temporal variability of the ALM is likely the highest, due to its accentuation of outliers. The number of flexible sites is increased by the overall separation of twelve sites over the three time periods. Our results demonstrate that the site classifications are only representative for the time period of their calculation. Therefore, the reference period for classification – depending on the common overlap of all tree chronologies – should be identical with the time period of a study’s key analysis, e.g. growth/climate analysis. The temporal match between the period of classification and the period of climate analysis in dendroclimatic reconstructions is almost impossible (e.g. Frank and Esper 2005, Büntgen et al. 2007). Our findings stress the importance of choosing classification periods being as long as possible in dendroclimatic reconstructions.

Due to the different site categorisations of the methods, a general estimation of the stable and flexible sites is not reasonable. We only comment on the sites being identified as “most flexible” or “stable” in all methods. The most flexible sites which are primarily located in the middle of the tree-ring network easily change their affiliation to a group due to changes in the highest growth homogeneity to different sites between the three time periods. Their different affiliations likely affect a connecting function between the groups. Such connecting function is supported by the geographical location of the flexible sites between the groups. In contrast, stable sites are particularly found at the edge of the network. Generally, the consideration of temporal changes in growth variations between sites might be helpful to explain the relation between tree growth and influencing factors (Fritts 1976, Schweingruber 1996). Thus, we recommend the analysis of temporal stability of classification to detect flexible sites. To guaranty growth homogeneity within a group over the whole period of analysis, flexible sites should be treated separately in e.g. growth/climate analysis.

The comparison of the different detrendings confirms the already received impression that WAM reacts most sensitive to changes. Only in the ALM, some sites being integrated in a main group in one of the detrendings are separated in the other detrending. Therefore, similar to the findings of the dataset extensions, this method’s emphasis on outliers influences the results depending on the applied detrending. As expected, the PCA reveals not as many changes as WAM, however, in this case the ALM shows even less changes. In general, the detrending with the higher-frequency variance (inter-annual dataset) generates higher overall similarities within the chronologies, as also described by Hughes and Funkhouser (2003), and Osborn and Briffa (2000).

4.6 Conclusion

Our comparison between different statistical methods points out significant differences in the classification results and therefore reveals that the application of a classification method considerably influences the results in a homogeneous tree-ring network. Overall, the application of the PCA leads to the most stable classifications, especially with respect to dataset extensions. The classification of WAM tends to the most sensitive response to changes in the dataset and the calculation of the ALM highlights outliers. The differences in the influence of the methods probably decrease with increasing growth heterogeneity. However, the characteristics of a chosen method likely influence tendencies within the results of all tree-ring networks. Classifications of datasets located in different regions and arranged on different spatial scales will prove the transferability of the characteristics of the methods of our regional scaled temperate forest network. Furthermore, these analyses might lead to an advanced assessment of the detection and special treatment of flexible sites within tree-ring networks and their value for dendroclimatological analyses.

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

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5.1 Summary

We analyze inter-annual 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 hierarchical cluster analysis identifies three groups for each oak species differentiated by ecological settings. While high precipitation is primarily 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 most strongly with PDSI ($r = 0.39$, $p \leq 0.05$), and only weakly with temperature and cloud cover. In natural stands, *Q. robur* responds more strongly to water depletion than *Q. petraea*. 21-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 increased growth and enhanced association with vapor pressure and temperature. We suggest that the wider oak rings exhibited during this period may be indicative of a non-linear 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. Due to the wide rings formed under the most severe drought period of the 20th century, a complex model seems to be required to fully explain widespread oak growth. Our results indicate uncertainty in estimates of future growth trends of Central European oak forests in a warming and drying world.

5.2 Introduction

Global climate change is projected to lead to a temperature increase in Central Europe between 2.3-5.3°C over 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).

Besides 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 prior to 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 physiological 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 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 both 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).

Ecophysiological studies focusing on stomatal conductance, photosynthetic activity, and hydraulic conductivity (Epron and Dreyer 1993, Gieger and Thomas 2005, Bréda et al. 2006) and dendroclimatological 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). *Q. 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 ecological 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.

5.3 Material 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 Oscillation during winter, whereas more localized pressure cells occur during summer (Hurrell et al. 2003, Raible et al. 2006).

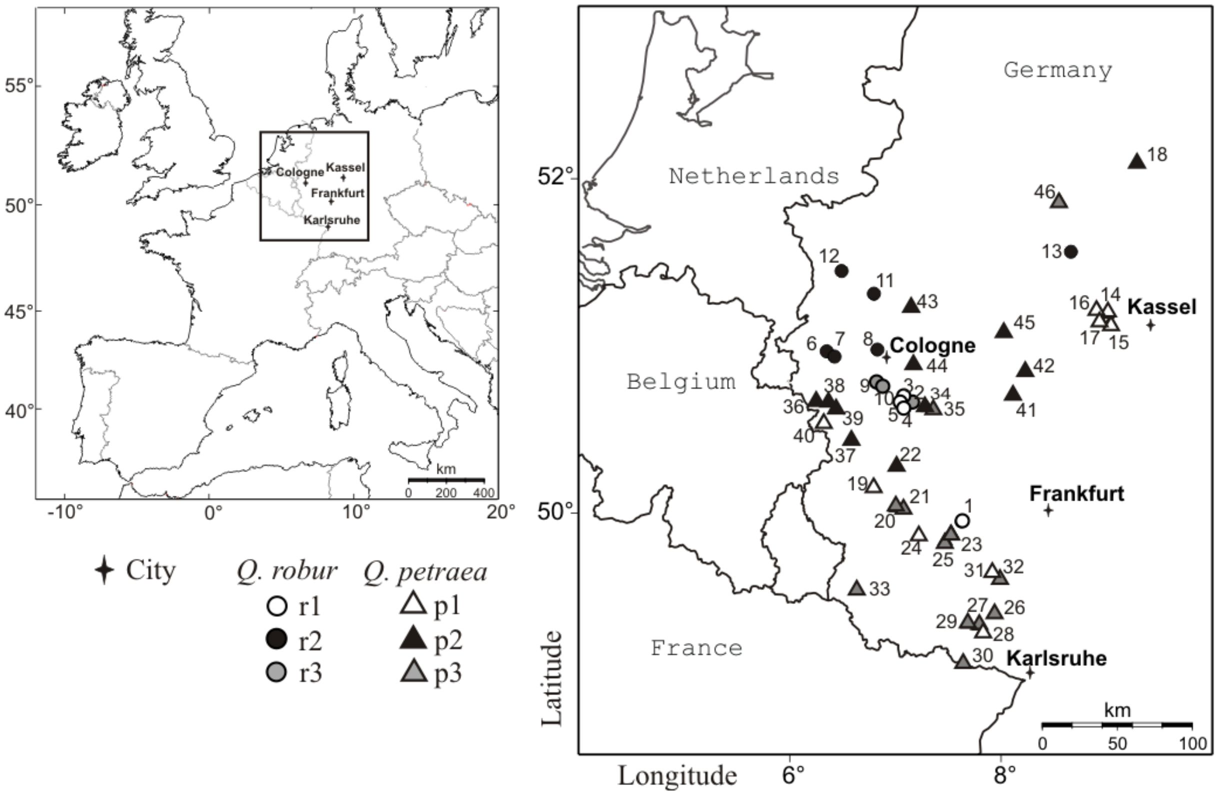

Figure 1. Location of the 13 pedunculate (Quercus robur, circle) and 33 sessile oak (Quercus petraea, triangle) sites in Central-West Germany, classified into three ecophysiological clusters of each species. Site numbers are identical with site numbers in Table 1.

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 6.7-11.7° C. The average annual precipitation sum is 808 mm and ranges from 450-1452 mm (for detailed information about the climate parameters see Table 2).

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 twelve dominant trees at breast height (~1.3m above ground). All trees were sampled in so-called nature forest reserves, which have been established in old stands with little silvicultural influence (Balcar 1995, Schulte and Scheible 2005). The oaks are primarily located in closed and mature stands often associated with beech (*Fagus sylvatica*). While all *Q. robur* sites are found on plateaus (< 5% slope), slopes of the *Q. petraea* sites range between 5-40%, including a variety of aspects. Soil analyses revealed predominant cambisols und 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 30-560 m a.s.l.. The northwestern located sites (No. 6-8, 11-12, Figure 1) represent the lowlands with the warmest temperatures and 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 ecological site information see Table 1). Southern and eastern sites generally receive less precipitation.

Meteorological data

For growth/climate response analyses (Frank and Esper 2005a), gridded (0.1 x 0.1°) monthly temperature means and precipitation sums (CRUTS1.2, Mitchell et al. 2004), monthly cloud-cover percentage, vapor pressure (0.5 x 0.5°; CRUTS2.1, Mitchell and Jones 2005), and the self calibrated PDSI (0.5 x 0.5°; van der Schrier et al. 2006) were used. All parameters were expressed as anomalies with respect to the 1961-90 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, while the mean climate series of all grids were used for redundancy analysis. Cloud-cover data were only used from 1950-2002, as earlier data represent little more than the average seasonal cycle.

Table 1. Description and characteristics of the 46 site chronologies. Species: QURO = Quercus robur, QUPE = Quercus petraea; Period (>3 trees); MSL= mean segment length (years); AGR= average growth rate (mm/year); 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); 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, 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	Lat/Long	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

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 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 with respect to 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 inter-annual to centennial-scale variability, series were individually detrended using 300-year cubic smoothing splines with 50% frequency-response cutoff equal at 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.

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 in mm; temperature in °C; PDSIndex from 4.0 to -4.0 = extremely wet to extreme drought; cloud-cover in %; vapor pressure in Pa) for the annual period; the vegetation period (April-September); and summer period (June-August). 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	-0.19	0.72		-0.16
VP	0.39	0.94	-0.03	0.06	
Ann. mean	808	9.1	0.25	75	9.4
min.	450	6.7	-3.66	64	8.4
max.	1452	11.7	4.45	83	10.7
A-S mean	423	14.1	0.11	68	11.8
min.	177	11.6	-4.00	51	10.6
max.	736	16.6	4.13	78	13.4
J-A mean	282	16.7	0.12	66	13.5
min.	94	13.8	-4.00	43	11.8
max.	464	20.3	4.35	80	15.6

Signal strength of the site chronologies was assessed using a moving window approach of the interseries correlation (*Rbar*), and the expressed population signal (*EPS*). *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 (details on this particular dataset, see Friedrichs et al. 2008). The hierarchical 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, while the variance within clusters is minimized (Bahrenberg et al. 2003).

Growth/climate response analysis

The classified sites of the cluster analysis were averaged and "mean cluster chronologies" considered for growth/climate analysis. For 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 prior to tree growth until current-year September. 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 prior to growth) -July (year of growth) and the annual means. Redundancy analysis (RDA) was applied to detect the most important growth influencing climate variables extracted from monthly and annual data of all climate parameters over the common time interval 1951-2000, using the program CANOCO (Version 4.5, ter Braak and Smilauer 2002). 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.

5.4 Results

Growth trends and clusters

The average growth rate 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). During the first 100 years, differences in AGR of

Q. robur and *Q. petraea* (2.00 and 1.38mm/year) are even more distinct. The regional curves (RCs) of both species (Figure 2a) confirm these differences, which are typical of species with varying life spans. Initially, *Q. robur* reveals enhanced growth (2.56 mm/year) in comparison to *Q. petraea* (<2 mm/year; 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 of rings per core) ranges from 71-272 and 99-363 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 300-year spline detrending, fairly common growth variations between the *Quercus* chronologies are obtained (Figure 2c). *Q. 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 towards 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, achieve even higher signal coherency within the data, and 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, p3 = 12) and their ecological settings. Most of the *Q. robur* sites are located in the north-western part of the research area, characterized by higher temperatures (Figure 1). While sites of r2 represent north-western lowlands with high precipitation, sites of r1 and r3 are located between the western and central low mountain ranges. 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).

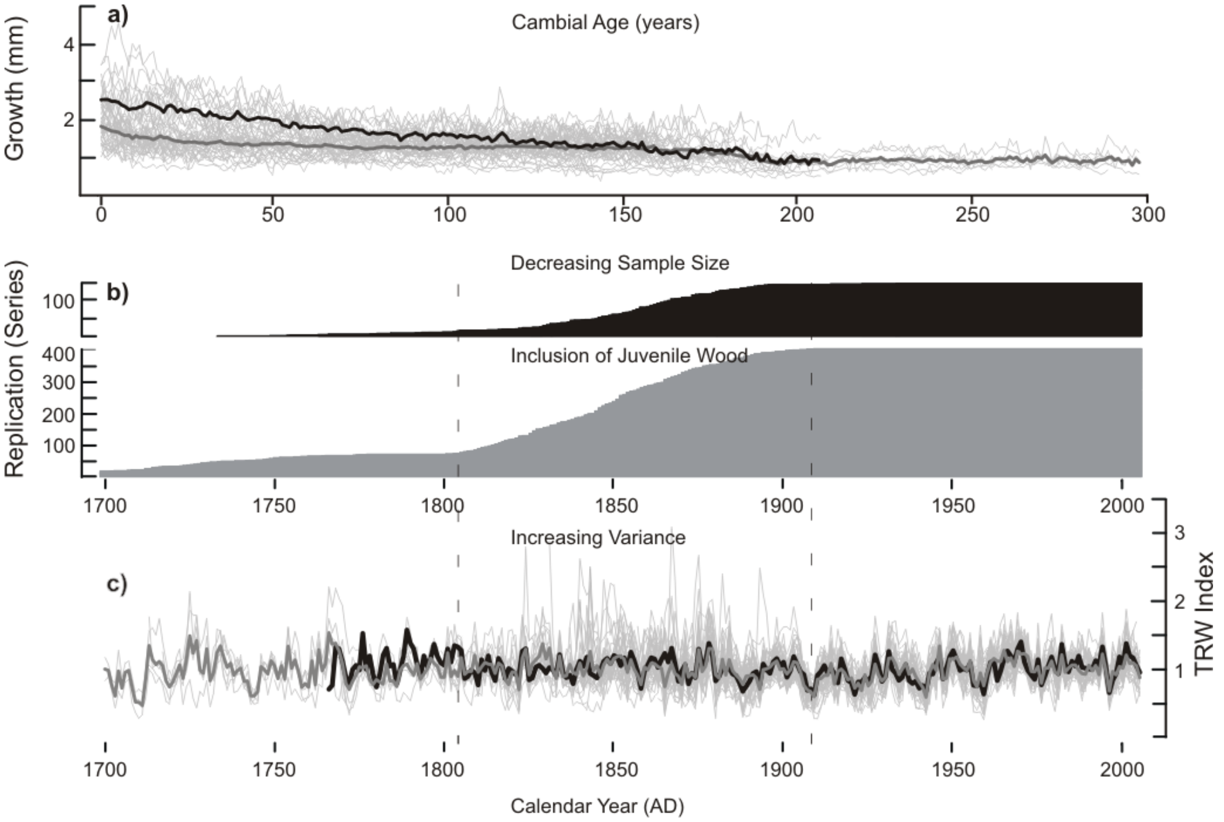

Figure 2. a) Mean growth trends (Regional Curves, RCs) of the 46 sites after aligning all measurement series by cambial age (light grey). Mean RCs were calculated from Q. robur (black) and Q. petraea (grey). b) Temporal distribution of the 149 Q. robur series (black) and 406 Q. petraea series (grey),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

Spatial patterns of growth/climate responses

The five climate parameters used for comparison with tree growth are cross-correlated and thus not fully independent. The highest correlation is observed between temperature and vapor pressure (0.79), and 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 of 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 fairly weak temperature influences on tree growth, as results are mostly non-significant (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.

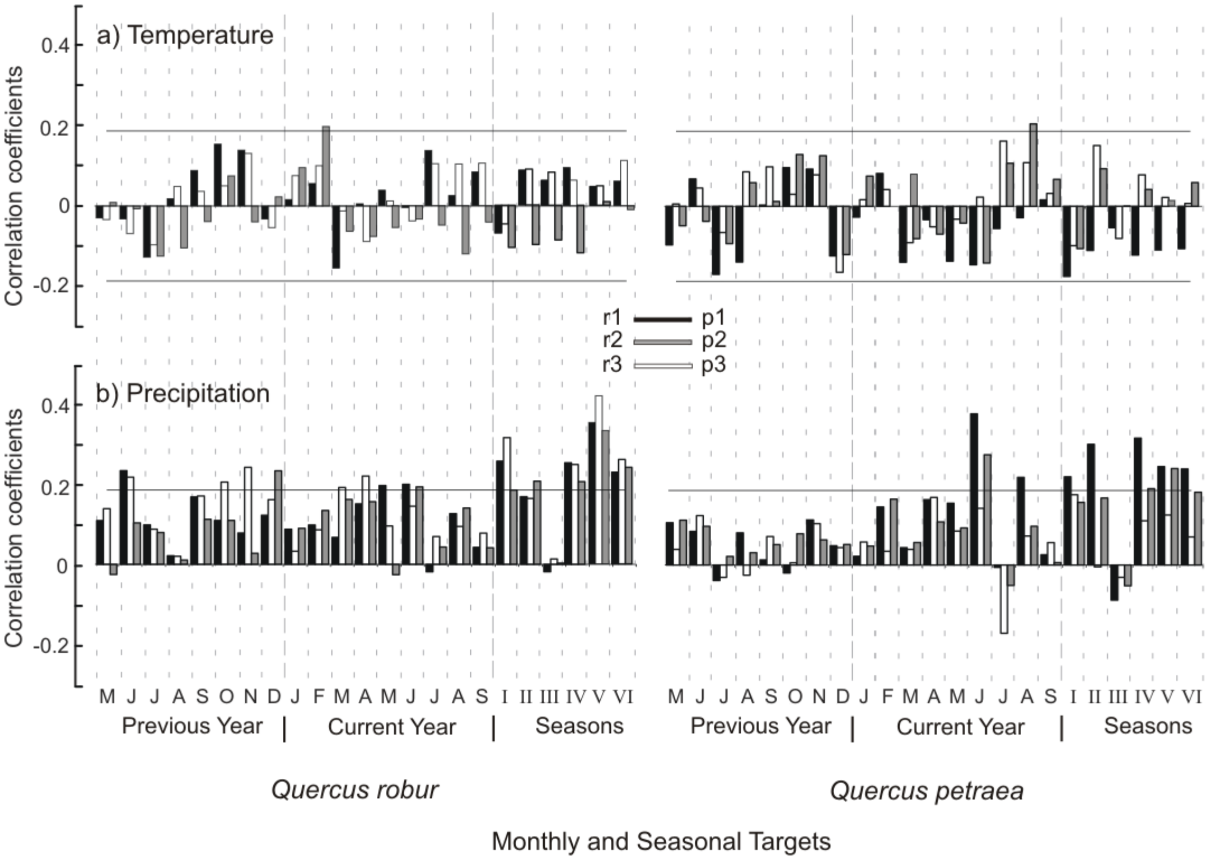

Figure 3. Monthly and seasonal correlations between the three cluster chronologies of each species and a) temperature means and b) precipitation sums over the period 1901-2000. Seasonal means are averaged over I = March - May, II = June-August, III = September-October, IV = April-September, V = previous year June-current year July, VI = calendar year. Horizontal lines denote 95% significance levels. Vertical dashed lines separate the single months' and seasons' growth/climate sensitivities.

Comparison among growth rates and 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. Correlations between p2, p3, r2 and cloud-cover data are all 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). P2 and p3 reveal non-significant 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 pressure 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, where other climate parameters don't show any effects.

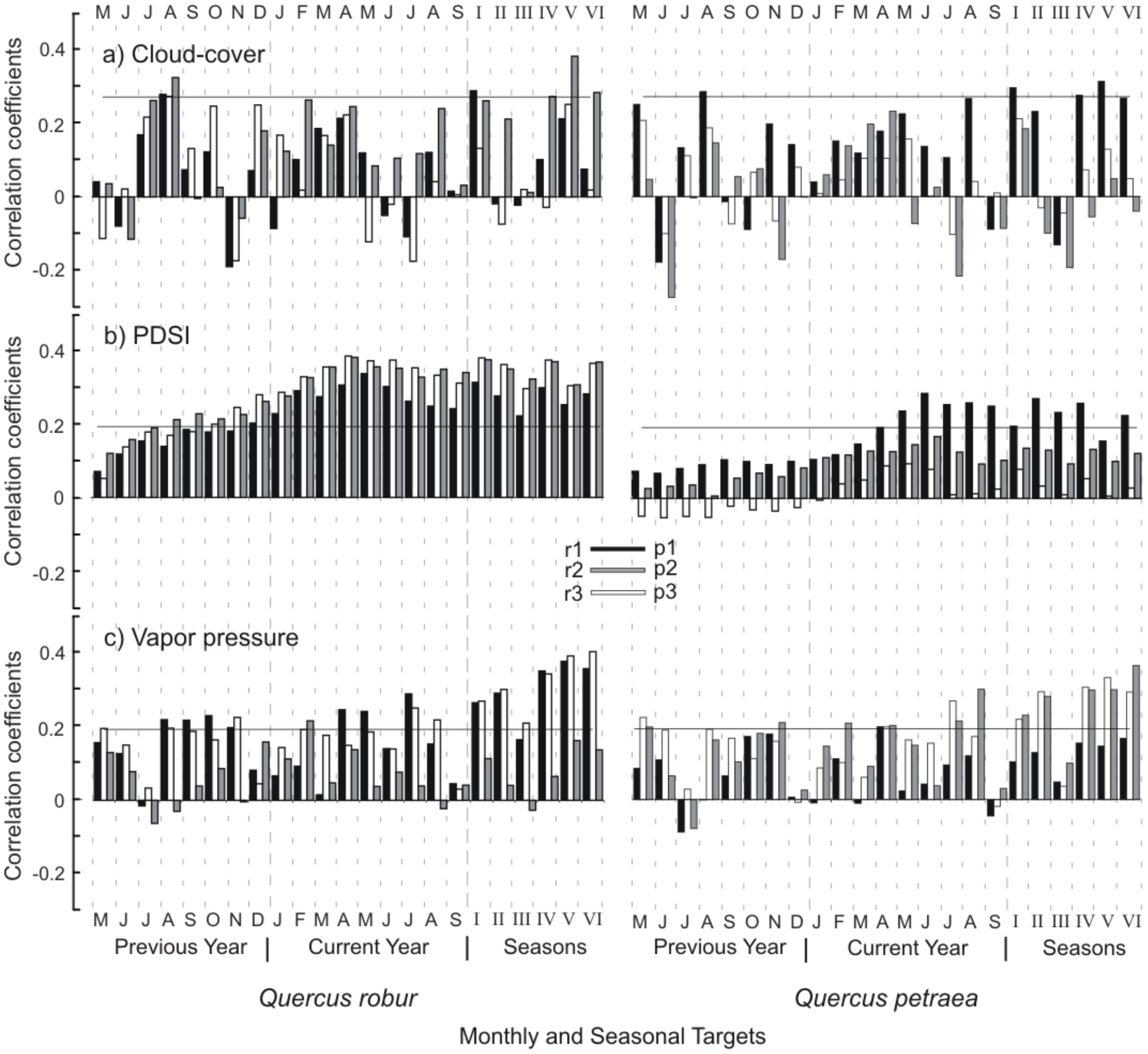

Figure 4. Monthly and seasonal correlations between the three cluster chronologies of each species and a) cloud-cover, b) PDSI and c) vapor pressure over the period 1901-2002. Cloud-cover correlations refer to the 1950-2002 period. Seasonal means are averaged over I = March - May, II = June-August, III = September-October, IV = April-September, V = previous year June-current year July, VI = calendar year. Horizontal lines denote 95% significance levels. Vertical dashed lines separate the single months' and seasons' growth/climate sensitivities.

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 data set 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, while species-specific differences cannot be detected. However, the stronger response of *Q. petraea* (p1) to summer than *Q. robur* (r1, r2, r3) to spring drought, shown in the correlation analysis, is also found.

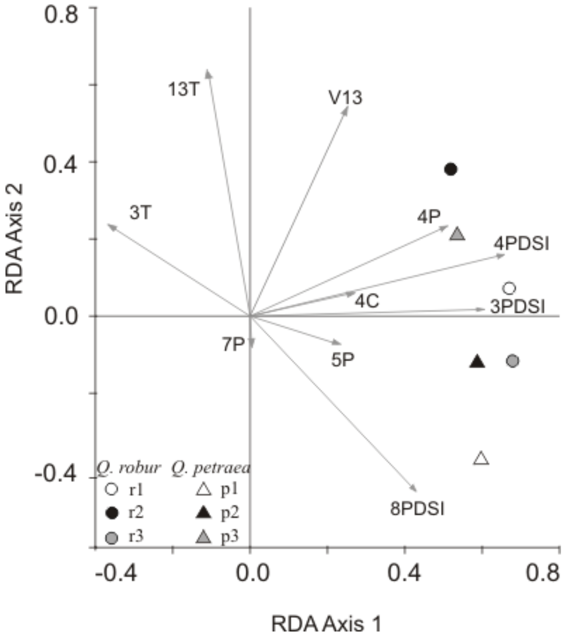

Figure 5. Redundancy analysis (RDA) calculated from the species cluster chronologies and the monthly and annual climate parameters for the period 1951-2000. The vectors (arrows) represent the significant climate factors; the longer the vector the more important the climate parameter. PDSI = Palmer Drought Severity Index, P = Precipitation, T = Temperature, C = cloud-cover, 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).

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 *Q. robur* clusters indicating strongest responses. Correlations of the respective three 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, non-significant site correlations appear during several periods in the 20th century. All clusters reveal a loss of sensitivity to PDSI, with a maximum from 1947-1950, 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 non-significant 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 during this period primarily increases. Decadal-scale variations of oak growth are very 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.

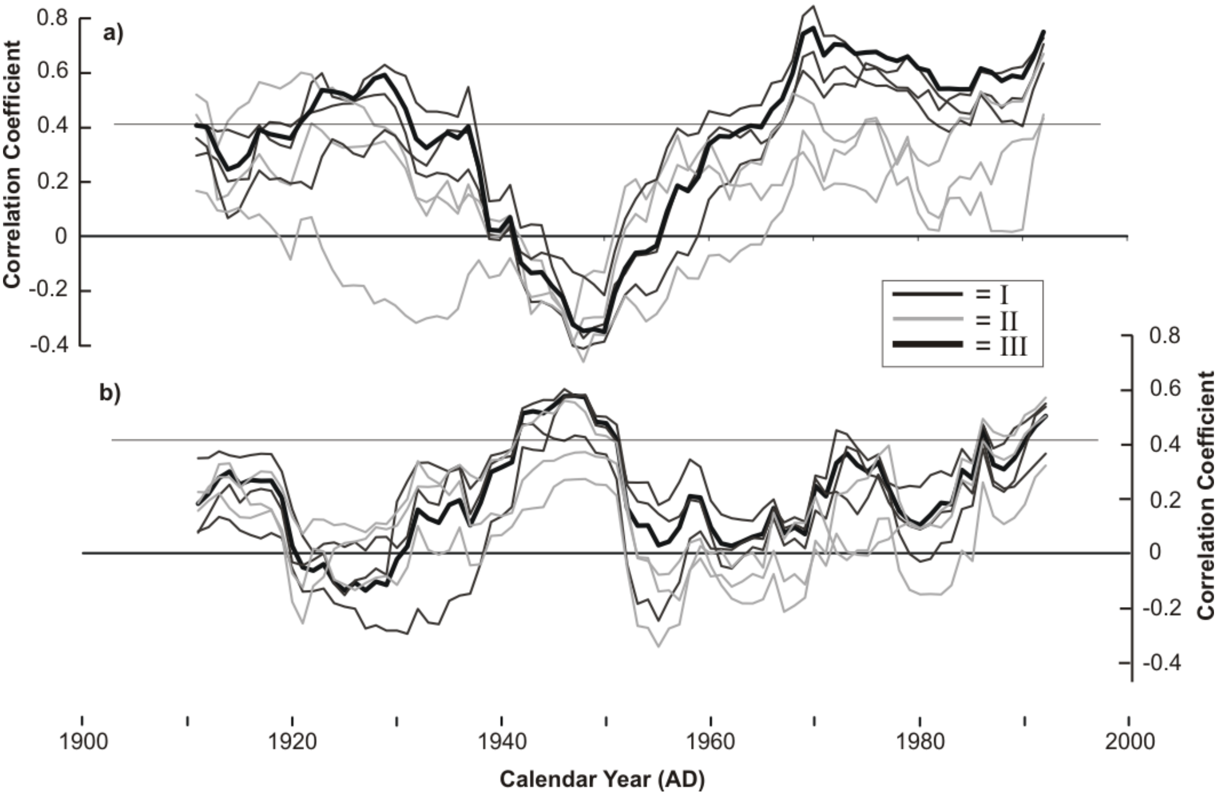

Figure 6. 21-year moving correlation analysis between (A) annual PDSI and (B) annual vapor pressure and the three species-specific cluster chronologies (Q. robur = dark grey = I; Q. petraea = light grey = II) plus the mean chronology of Q. robur (CM = bold black line III). Horizontal lines denote 95% significance levels.

5.5 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) 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 e.g. by varying life spans. Shorter-lived species tend to grow more quickly than their faster growing congeners (Kozlowszki and Pallardy 1997). Growth rate differences can also be caused by different physiological 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. While *Q. robur* is mainly located in valley bottoms, *Q. petraea* are commonly found on slopes and ridges. *Q. 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 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

Growth dominating climate parameters, such as summer temperatures at higher elevations (Esper et al. 2005a,b, Frank and Esper 2005a,b, Büntgen et al. 2005, 2008) do not 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, while 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. While drought can have significant impacts on all *Q. robur* clusters, only p1 of the *Q. petraea* clusters responds significantly. Besides the higher drought sensitivity of *Q. robur*, which is well-known (Cochard et al. 1992, Lévy et al. 1992), different response patterns between both species under temperate forest conditions are noteworthy. *Q. robur* responds to 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* is primarily controlled by summer droughts (Figures 4b, 5, also found for precipitation in Figure 3b). Therefore, climate in the year prior to ring formation is primarily relevant for *Q. robur* (Figure 3 and 4). These lag-responses indicate the importance of carbohydrate storage (Kozlowski and Pallardy 1997), which is mainly modulated via tree physiological 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 prior to 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-Gonzaléz and Fonti 2006).

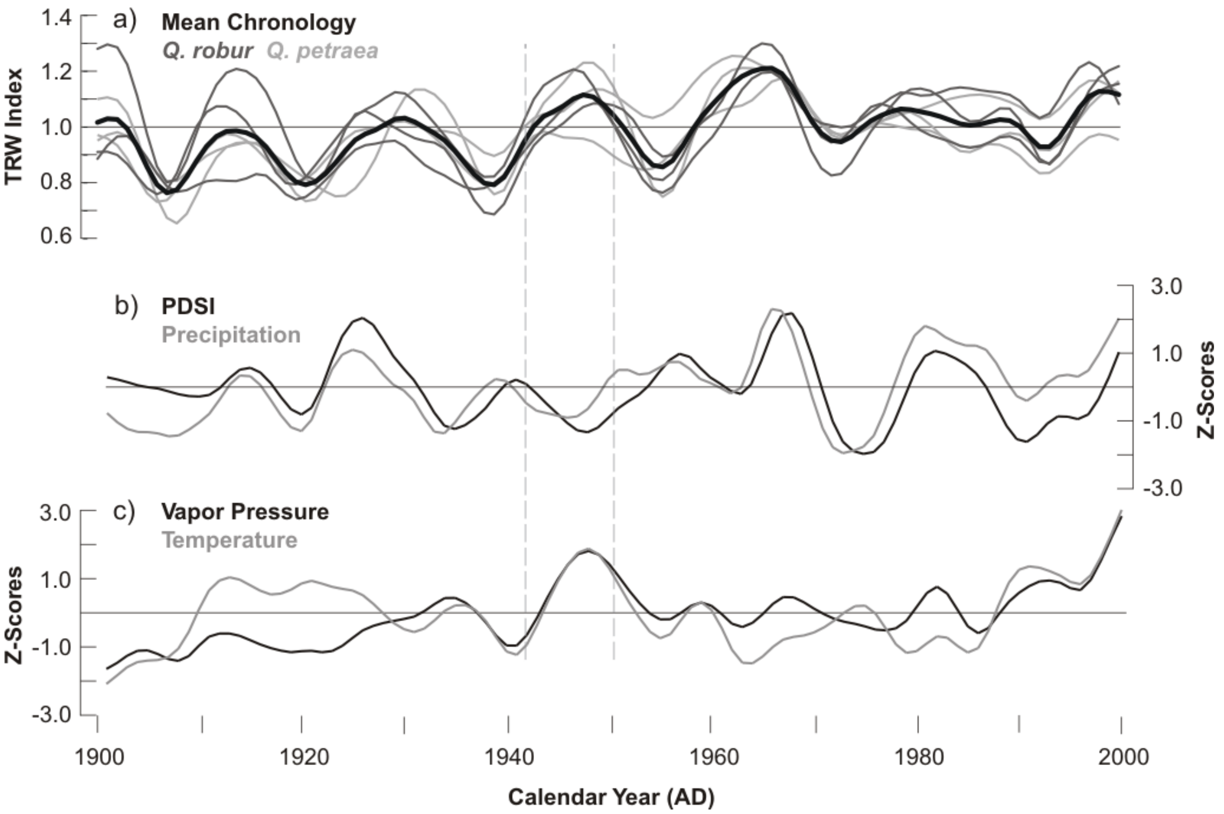

Figure 7. a) Ring-width chronologies of the three species-specific clusters (Q. robur, dark grey; Q. petraea, light grey) plus the mean chronology CM of all clusters (black). 20th century climate variations of the parameters b) PDSI (black) and precipitation (grey), and c) vapor pressure (black) and temperature (grey) after 10-year low-pass filtering. Vertical dashed lines define the period with extraordinary climate/growth relationships.

Not only the previous year PDSI and precipitation, but also hydroclimatic spring – mainly March and April – conditions effect all *Q. robur* sites and clusters (Figures 3b, 4b, 5). Positive growth responses demonstrate the importance of water supply at the beginning of the growing season (García-Gonzaléz and Eckstein 2003). For *Q. petraea*, significant coherence with rainfall variations is primarily found in summer (Figures 3b, 4b, 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 earlywood (previous autumn – winter and current spring) and latewood growth (late spring and summer), while significant correlations of *Q. petraea* are found with summer months.

Besides 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 available water capacity (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 p1does Explanation of differences between the cluster responses by means of the available ecological 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.

Q. robur clusters only show 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 amongst 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). PDSI broadly represents water availability: when sufficient moisture exists, the stomata can dilate, allowing for greater photosynthetic activity (Kozlowszki and Pallardy 1997). While, precipitation reveals no persistence between years – lag-1 autocorrelation is 0.09 calculated over the 1902-2000 period (mean of all station data) – inter-annual persistence is quite high in PDSI (0.57) and in the same order is found in tree-ring data (0.50, 1902-2000, mean of all values).

The strong growth controls of vapor pressure are likely not only induced by the vapor pressures' dependence on temperature, because several significant vapor pressure influences are found (Figure 4c) where 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 stomata 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 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, while the drier sites integrated in p1 mainly reveal soil moisture signals but no reaction to vapor pressure changes. The *Q. robur* clusters r1 and r2 respond to atmospheric and soil water conditions, while growth of r3 depends solely on PDSI fluctuations, with no vapor pressure signal being found.

Temporal response shifts

21-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 physiological threshold effects (Rozas 2005, Geßler et al. 2007). Most importantly, significant positive correlations between PDSI and oak growth are interrupted during the exceptionally warm 1940s. While 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 utilization 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. While such data uncertainty obscures the relationship between tree-ring and instrumental data, quantification of such error remains challenging (Frank et al. 2007a). 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 promotes 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 ~1920) that are characterized by low precipitation rather than high temperatures (Figure 7).

In summary, the growth increase under warm and dry climate conditions in the 1940s emphasizes the complex 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. 2007b). Repeated defoliation by lepidopteron larvae, for example, which occurs in certain time intervals, can additionally affect 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.

5.6 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 utilized 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 likely gain importance in a warmer and drier climate as predicted by climate models. *Q. robur* will likely 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.

6. Twentieth century climate sensitivity of Central European tree species

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Abbrevations: AC = Autocorrelation; AGR = Average growth rate; AWC = Available water capacity; EIF = Eifel; EPS = expressed population signal; *F. sylvatica* = *Fagus sylvatica*; KEL = Kellerwald; MS = mean sensitivity; PCA = principal component analysis; *P. sylvestris* = *Pinus sylvestris*; *Q. petraea* = *Quercus petraea*; RDA = redundancy analysis

6.1 Abstract

Question: What are the dominant climatic controls of Central European temperate forest growth with particular emphasize on differences in climate sensitivity of the most common tree species *F. sylvatica*, *Q. petraea,* and *P. sylvestris*?

Location: Two temperate low mountain forest ecosystems in Central and West Germany.

Methods: Species-specific radial growth and climate response patterns were assessed using redundancy analysis and Pearson correlation coefficients. 20th century temperature, precipitation, and PDSI data were related to tree-ring width measurements revealing spatiotemporal variations in growth/climate relationships.

Results: Drought stress is the dominant influence on forest growth and it affects the three tree species with varying intensity *F. sylvatica* and *P. sylvestris* reveal an overall strong sensitivity to previous and current year moisture conditions, but moisture influence on *Q. petraea* is much lower. Higher water availability in the western forests most likely protects *Q. petraea* from drought-induced growth depressions. Drought sensitivity of the three tree species increases over the 20th century.

Conclusions: Tree growth in temperate forests reacts sensitively to water depletion. Projected future increases in drought frequency and severity are assumed to negatively affect the vigor of Central European forests. If drought tolerance becomes more important under changing climatic conditions, species shifts and changes in temperate forest composition are likely to occur due to the strong species-specific differences in drought adaptation.

6.2 Introduction

The influence of global warming on forest growth can only be assessed if species-specific responses to climate variability are well understood (Saxe et al. 2001; Geßler et al. 2007). Tree species in temperate forests are greatly influenced by non-climatic parameters such as disturbance and competition for light, nutrients, and other resources, but their growth is also to a large extent affected by climatic conditions (Schweingruber 1996; Kozlowski & Pallardy 1997). A changing climate can thus directly impact forest composition, vitality, and productivity (Thomas et al. 2004; Thuiller 2004).

Common beech (*Fagus sylvatica* L.) and sessile oak (*Quercus petraea* Matt *Liebl.*) within Central Europe are located in the center of their natural distribution areas. *F. sylvatica* is the most abundant tree species dominant to all competing 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. A dominant occurrence of both species is restricted to areas with extreme ecological settings, where *F. sylvatica* growth is generally hampered (Härdtle et al. 2004).

Q. petraea and *P. sylvestris* are more drought resistant than *F. sylvatica* (Epron & Dreyer 1993; Bréda et al. 2006). The competitive dominance of *F. sylvatica* thus rather results from attributes like canopy architecture and shade tolerance than from the ability to cope with drought stress (Ellenberg 1996). Many recent studies have focused on species drought responses, photosynthetic activity, hydraulic conductivity, and growth reactions as a result of climate warming (see references herein). Extraordinary events, such as the severe European summer heat of 2003, have been the focus of much attention (e.g. Ciais et al. 2005; Leuzinger et al. 2005; Granier et al. 2007). However, a clear implication of extreme events on temperate forests and the relevance of drought tolerance for species' competitive abilities can not be concluded. While Ciais et al. (2005) reported a European-wide reduction in species' primary productivity and assumed large effects of climate warming on *F. sylvatica*, Leuzinger et al. (2006) did not find radical influences on sap flow and photosynthetic activity of the main Central European tree species.

The analysis of long-term tree-ring chronologies allows for investigation of past climate sensitivity and helps to assess species' vigor and tree response to recent climate warming. Each of the three tree species has been analyzed dendroclimatologically under differing climatic and environmental conditions (Oberhuber & Kofler 2000; Lebourgeois et al. 2005; Friedrichs et al., submitted). The species often show only moderate growth/climate relations in temperate Central European forests (Dittmar et al. 2003; Lebourgeois et al. 2004). Strong growth sensitivity to one dominant climate parameter is found at species distribution limits (Di Filippo et al. 2007; Neuwirth et al. 2007). Therefore, dendroclimatological studies are mostly carried out at species' distribution limits. Slight changes in species climate sensitivity likely influence species vitality and subsequently effect competitive ability, often being regarded as early indicators for climate change (Weber et al. 2007; Büntgen et al., in press). In-depth comparisons of the climate sensitivity of temperate forest tree species based on dendroclimatological analyses are rare but would be helpful in the discussion of species-specific responses to climate change and in the anticipation of regional forest dynamics.

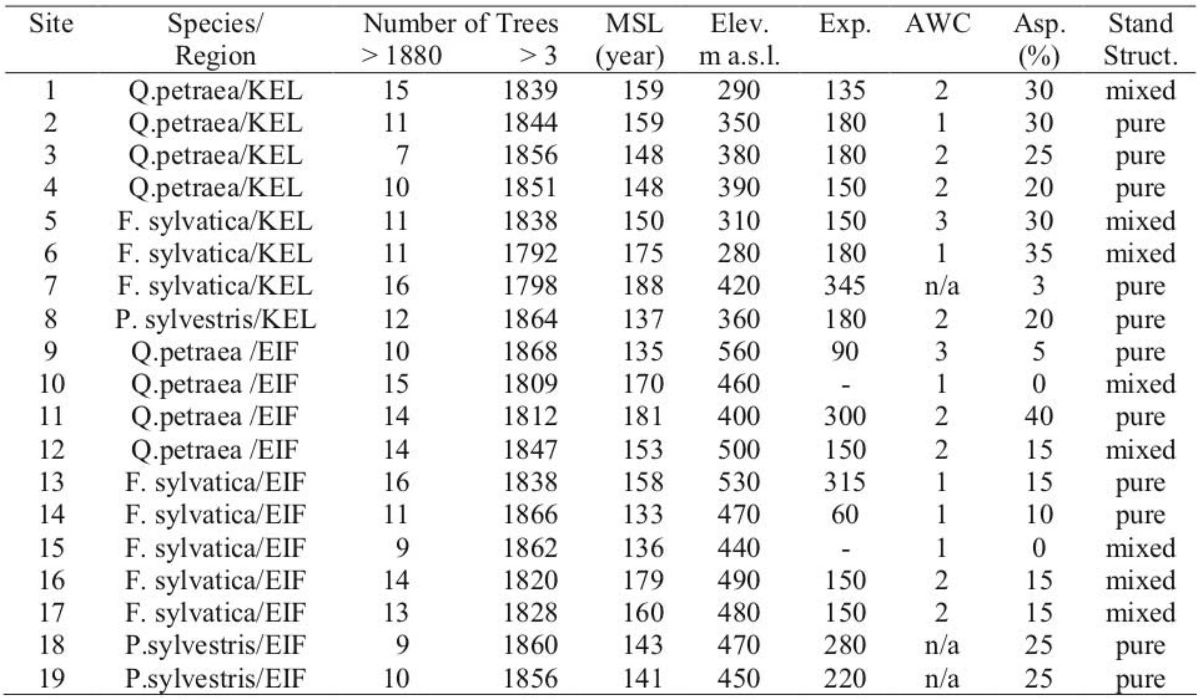
Therefore, we assess species-specific growth trends, growth rates, and climate responses of the main temperate forest tree species *F. sylvatica*, *Q. petraea,* and *P. sylvestris* over the 20th century. Research questions are: i) What are the most important influencing climate factors and to what extend do they affect temperate forest growth? ii) What species-specific differences in adaptation skills can be distinguished? iii) How stable are the obtained climate response patterns over the last 120 years?

6.3 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 areas (Table 1). Three *F. sylvatica* sites, four *Q. petraea* sites and one *P. sylvestris* site are located in the Kellerwald (KEL) in Central Germany. Five *F. sylvatica* sites, four *Q. petraea* sites, and two *P. sylvestris* sites are located in the Eifel (EIF) in Western Germany (Fig.1).

Table 1. Site description and characteristics of selected stands. MSL = mean segment length; Elev. = elevation; AWC = available water capacity: 1 = low (60-110 mm); 2 = mean (110-170 mm); 3 = high (170-204 mm); n/a = not applicable; Asp. = aspect, Stand Struct. = stand structure



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

Synoptically, both areas are predominantly influenced by atmospheric flows coming from the Northwest (Hurrell et al. 2003). This leads to high amounts of precipitation on the wind side of the western low mountain ranges (EIF), and slight rain shadow effects in low mountain ranges that are located more eastwards (KEL; Marcinek et al. 2002). Annual precipitation differs between EIF (~1000 mm) and KEL (~700 mm) by approximately 300 mm (computed over the 1961-1990 period). Therefore, the main difference between both regions is the amount of water supply: EIF is characterized by moist temperate forest conditions, while conditions in KEL are generally drier. The annual temperature profiles of both regions are, however, very similar (Figure 2). 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; Table 1).

Tree-ring data

A minimum of two cores was collected at breast height from 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 COFECHA, which computes cross correlations between individual series and a reference chronology (Holmes 1983). Finally, 228 tree series were created for growth/climate analysis.

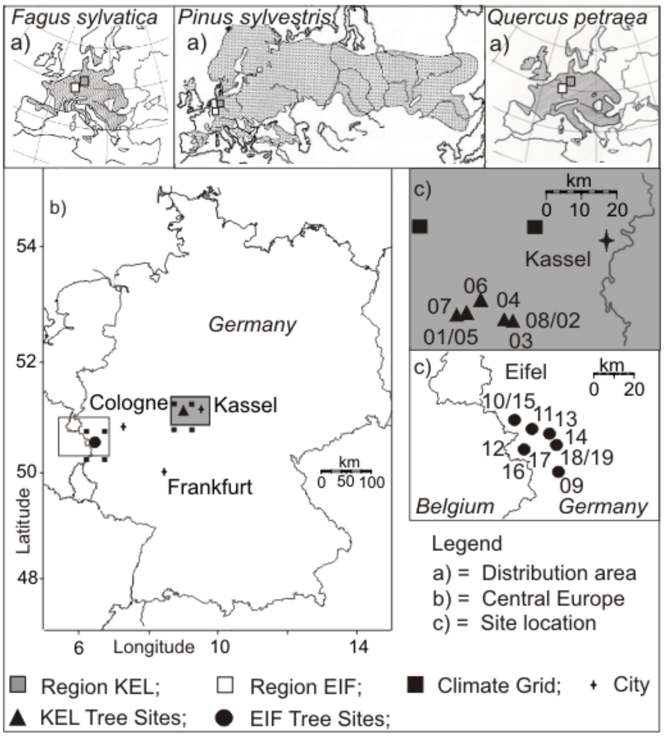


Figure 1. Distribution of three common Central European tree species F. sylvatica, Q. petraea, and P. sylvestris (1-3; based on Schweingruber1990) and geographical location of the study areas; (4) Site distribution within the study areas (grey=KEL, white=EIF) is illustrated in (5-6). Site numbers in (5-6) are in accordance with Table 1.

Tree-ring standardization, the correction for biological-induced age-trends was performed (Fritts 1976), 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 (Friedrichs et al., in press).

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

Climate data

Gridded (0.5° x 0.5°) datasets of monthly temperature and precipitation series (CRU TS 2.1, Mitchell and Jones 2005), and the (self calibrated) Palmer Drought Severity Index (PDSI; van der Schrier et al. 2006) were used for growth/climate analyses over the 1901-2002 period. Climate data from the four closest grid points were averaged for each study area (Fig. 1b), and expressed as anomalies with respect to the 1961-1990 mean.

For an extended analysis of the growth response to drought (1885-2004), lower resolution (2.5° x 2.5°) PDSI data were employed (Dai et al. 2004). These data are strongly correlated with the high-resolution PDSI data from KEL (minimum r = 0.67, maximum r = 0.87) and EIF (minimum r = 0.80, maximum r = 0.88) over their common 1901-2002 period.

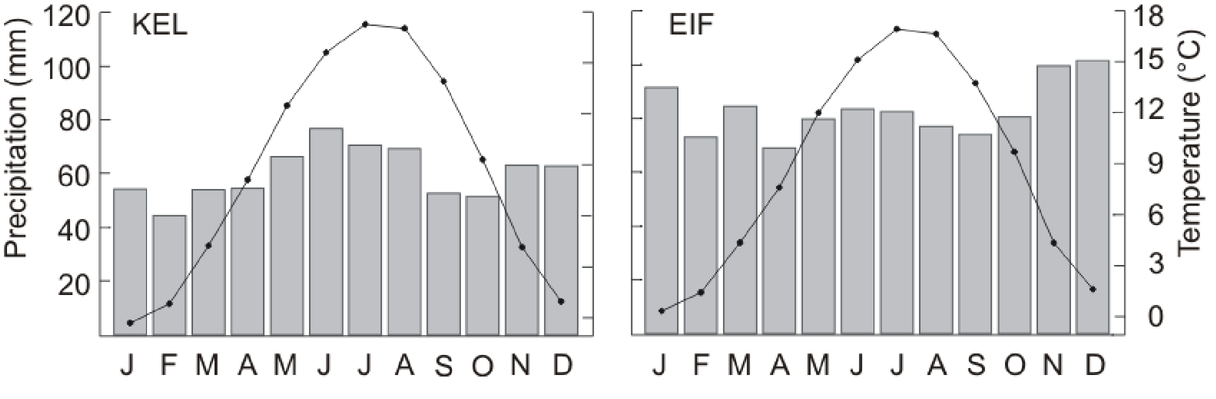


Figure 2. Climate diagrams for KEL and EIF. Mean monthly precipitation sums (mm) and temperatures (°C) were calculated for the period 1961-1990.

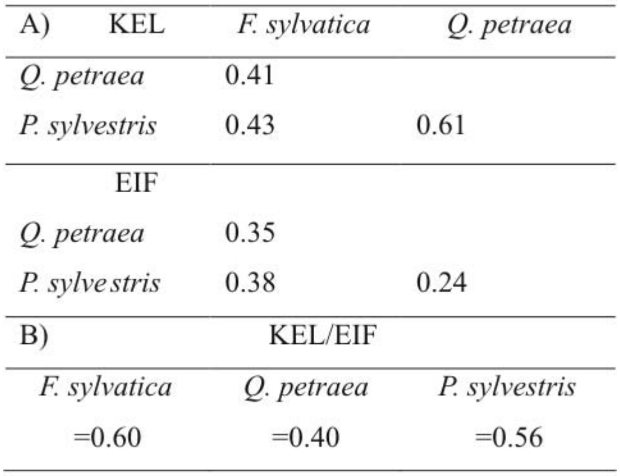
Statistical analysis

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 was conducted using the program CANOCO (Version 4.5, ter Braak & 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. Ordination axes in the RDA are constrained to be linear combinations of supplied environmental variables (Legendre & Legendre 1998). 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 for detailed growth response assessment for each species. Seasonal means and sums for the periods March-May, April-September, and June-August were added to the climate data set for this analysis. Temporal stability of the growth/climate relationships was analyzed using five 40-year intervals starting in 1885. The intervals were lagged by 20 years, with the last interval covering the 1965-2004 period.

Table 2. Rbar statistics between A) the different species chronologies of the regions and B) the chronologies of one species between the regions.



A) KEL	*F. sylvatica*	*Q. petraea*
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	*Q. petraea*	*P. sylvestris*
=0.60	=0.40	=0.56

6.4 Results

Growth trends

Differences in growth patterns between the three species and two regions are evident from the PCA analysis (Fig. 3). The first axis explains 29.7 % variance indicating the common variance of all trees due to the negative loading of all 228 trees (not shown). The second axis still explains 10.1 % variance and the third axis 8.2 %. The second PCA axis clearly divides the species by region (Fig. 3): higher loadings were found for KEL compared to EIF. Especially *F. sylvatica* trees from EIF differ from the rest of the network. However, higher similarity between trees belonging to one site in comparison to other sites is not consistent.

Significant site-specific differences have not been detected. The tree positions on the third axis illustrate a species-specific separation. This axis clearly separates *Q. petraea* (negative loadings) from all other trees.

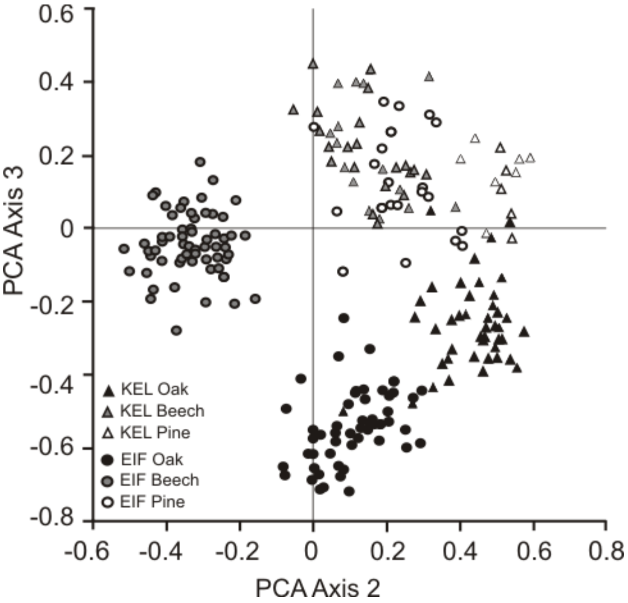


Figure 3. Biplot of the principal component analysis (PCA) of 228 standardized tree chronologies of three species in two study areas over the period 1901-2002. The second PCA axis explains 10.1 % of the variance in the data set, the third axis 8.2 %.

Average species-specific regional chronologies show strong overall similarity (Fig. 4). Hence, slight differences in growth variations must be responsible for the species-specific and regional-specific variability between trees. Growth variations of the regional chronologies differ more between species than between regions (Fig. 4). High Rbar-values between all regional chronologies, with higher Rbar-values for KEL than for EIF, confirm the overall growth variation similarity (Table 2).

The youngest tree of the data set is 125 years old, average tree age is 160 years, and the oldest tree is 226 years (Table 1). Average regional, species-specific growth rates (AGR) range between 1.10 mm/year and 1.58 mm/year (Table 3), being highest for *F. sylvatica* and lowest for *P.* sylvestris. AGRs are similar between sites for the same species. The first-order AC of all regional chronologies is low and comparable between species (0.21-0.35). Low AC indicates a reduced influence of previous year growth conditions on current year ring formation. The regional mean Rbar values (0.44-0.62) of all trees of a species are higher than Rbar values between species and regions (Table 2, 3). EPS values (0.93-0.97) are also high for all species and indicate a strong common forcing. Mean sensitivity is highest for *F. sylvatica* and lowest for *Q. petraea* at both sites. Values of Rbar, EPS, and MS are generally higher for KEL than for EIF.

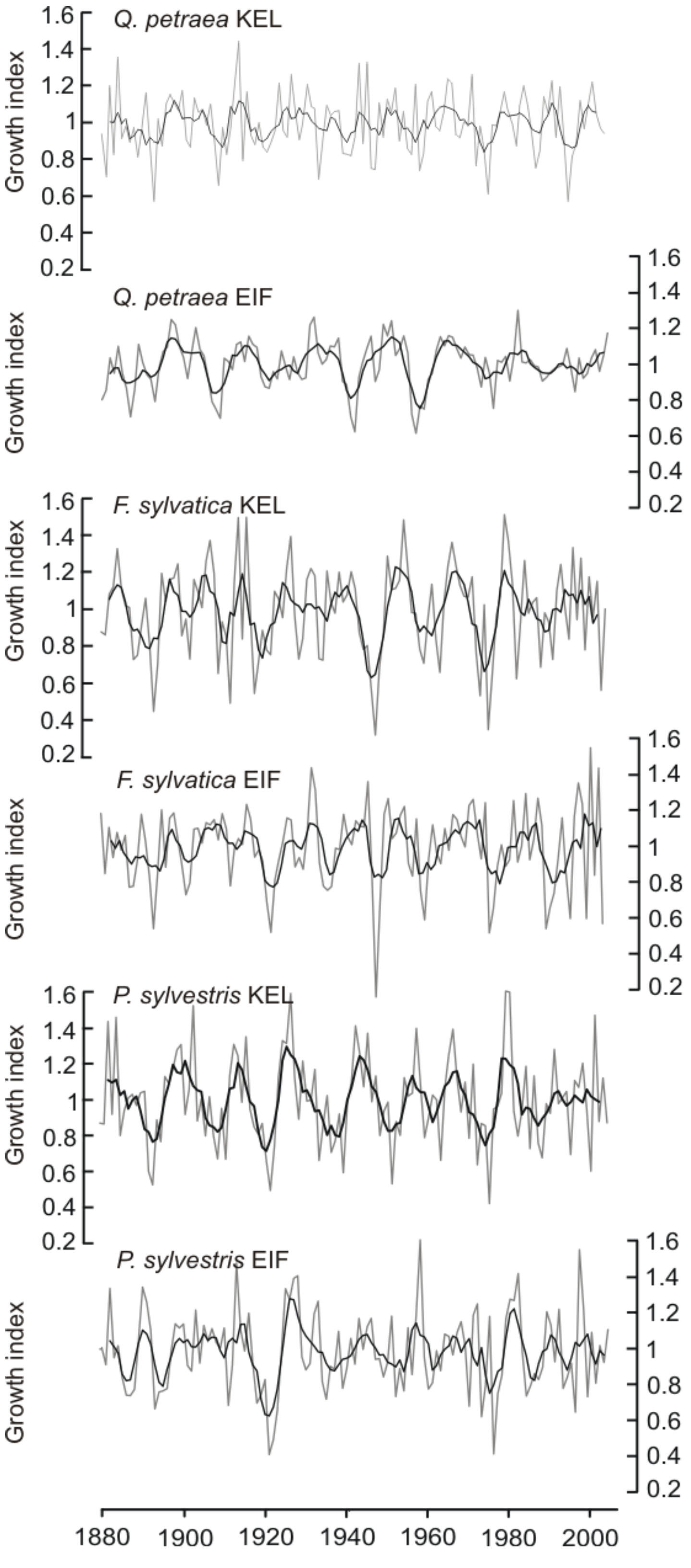


Figure 4. Standardized tree-ring chronologies (1880-2004) per species for KEL and EIF (grey curves) and their 5-year moving averages (bold black curves).

Table 3. Mean values of chronology statistics of species' regional chronologies. AGR = average growth rate (mm/year), EPS = expressed population signal, AC = first year autocorrelation, MS = mean sensitivity, Rbar, AC and MS are calculated on the basis of the detrended 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	0.30	0.28

Climate sensitivity

Drought is the most important and extensive factor on radial growth for all species, indicated by long PDSI vectors in the RDA analysis (Fig. 5), as well as strong correlations between monthly and seasonal PDSI data and tree-ring chronologies (Fig. 6). Annual PDSI, and previous year May and October drought conditions have high, positive scores on the first RDA axis, which explains 31% of the network's total variance and has positive loadings for all species. According to their location on this axis, all tree-ring chronologies are drought sensitive, except for *Q. petraea* in EIF. Its low loading on both axes illustrates that EIF *Q. petraea* is not related to any climate variable. Its correlation values to drought (maximum r = 0.18) confirm the low climate sensitivity. Overall, strong positive Pearson's correlations between PDSI and *P. sylvestris* (r = 0.52) and *F. sylvatica* (r = 0.49) are found at the drier KEL sites, whereas lower values are found at the wetter EIF sites (Fig. 6c). Previous year drought conditions particularly influence growth of *F. sylvatica* (Fig. 5, 6).

Growth response to temperature variability shows strong species-specific differences (Fig. 5, 6a). Previous year July and spring (February, March) temperatures have high scores on the second RDA axis, which accounts for 8% of the total variance (Fig. 5). Previous year July temperatures have the strongest negative effects on growth of *F. sylvatica* in EIF. *F. sylvatica* growth in both regions is negatively correlated with previous year summer and fall temperatures (minimum r = -0.42). Growth of *P. sylvestris* reacts positively to above average February temperatures, with a stronger reaction in EIF than in KEL (Fig. 6). *Q. petraea* is less sensitive to temperature variations and only shows negative response to June temperatures in KEL.

Previous year (summer and fall) precipitation amounts influence *F. sylvatica* at both sites (Fig. 6b). All species in KEL respond significantly positive to annual and seasonal precipitation sums, but this is not the case for EIF. *Q. petraea* growth in KEL shows high sensitivity to June precipitation, which also affects *P. sylvestris* in KEL. June precipitation has high scores on the first RDA axis, whereas September precipitation is negatively associated with the second axis (Fig. 5).

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

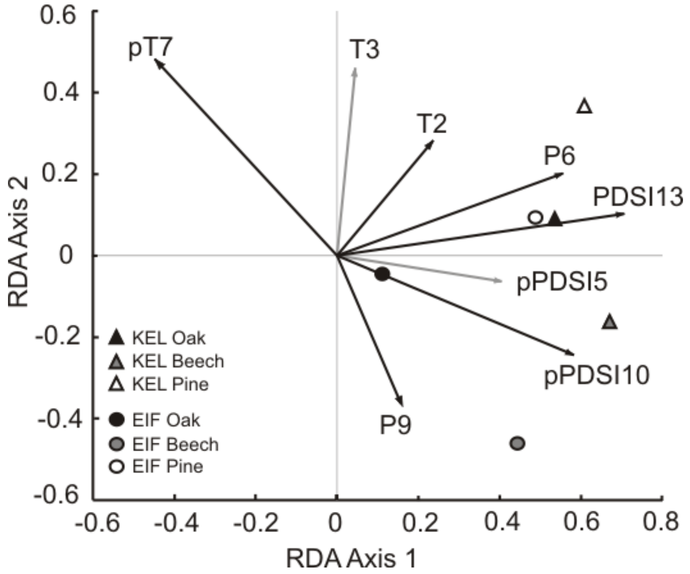


Figure 5. Biplot of the redundancy analysis (RDA) of six species-specific regional chronologies for KEL and EIF and monthly and annual climate parameters of both regions for the period 1901-2002. Vectors (arrows) represent significant climate factors; the strength of the influence of the climatic parameter is reflected by vector length. Black arrows = KEL climate data; grey arrows =EIF climate data; PDSI = Palmer Drought Severity Index, P = Precipitation, T = Temperature, p = previous year; number suffixes represent months (e.g. 9 = September and 13 = annual value).

Temporal stability of growth/climate responses

Growth responses of the three species to PDSI vary over time (Fig. 7). A proceeding drying trend in both regions from the early 20th century to the present (not shown) is causing an increase in drought sensitivity for *Q. petraea* in EIF (Fig. 7b), for *F. sylvatica* in both regions (Fig. 7c, d), and for *P. sylvestris* in KEL (Fig. 7e). Growth of *Q. petraea* in EIF, for example, illustrates strong drought sensitivity only during the second half of the 20th century. The positive correlation between previous year drought conditions and *F. sylvatica* in both regions considerably increased since the 1940s (Fig. 7c and d). Although significant growth responses of *P. sylvestris* in KEL occur in the early periods, the importance of summer and winter precipitation increases over the 1945-1984 period (Fig. 7e). In contrast, the number of months with significant growth/drought correlations of *Q. petraea* in KEL (Fig. 7a) and *P. sylvestris* in EIF (Fig 7f) does not increase over time. *Q. petraea* in KEL responds fairly constant to spring and summer drought conditions, except the 1925-1964 period. The monthly drought influences on *P. sylvestris* in EIF change throughout the periods without a clear increasing or decreasing tendency (Fig 7f).

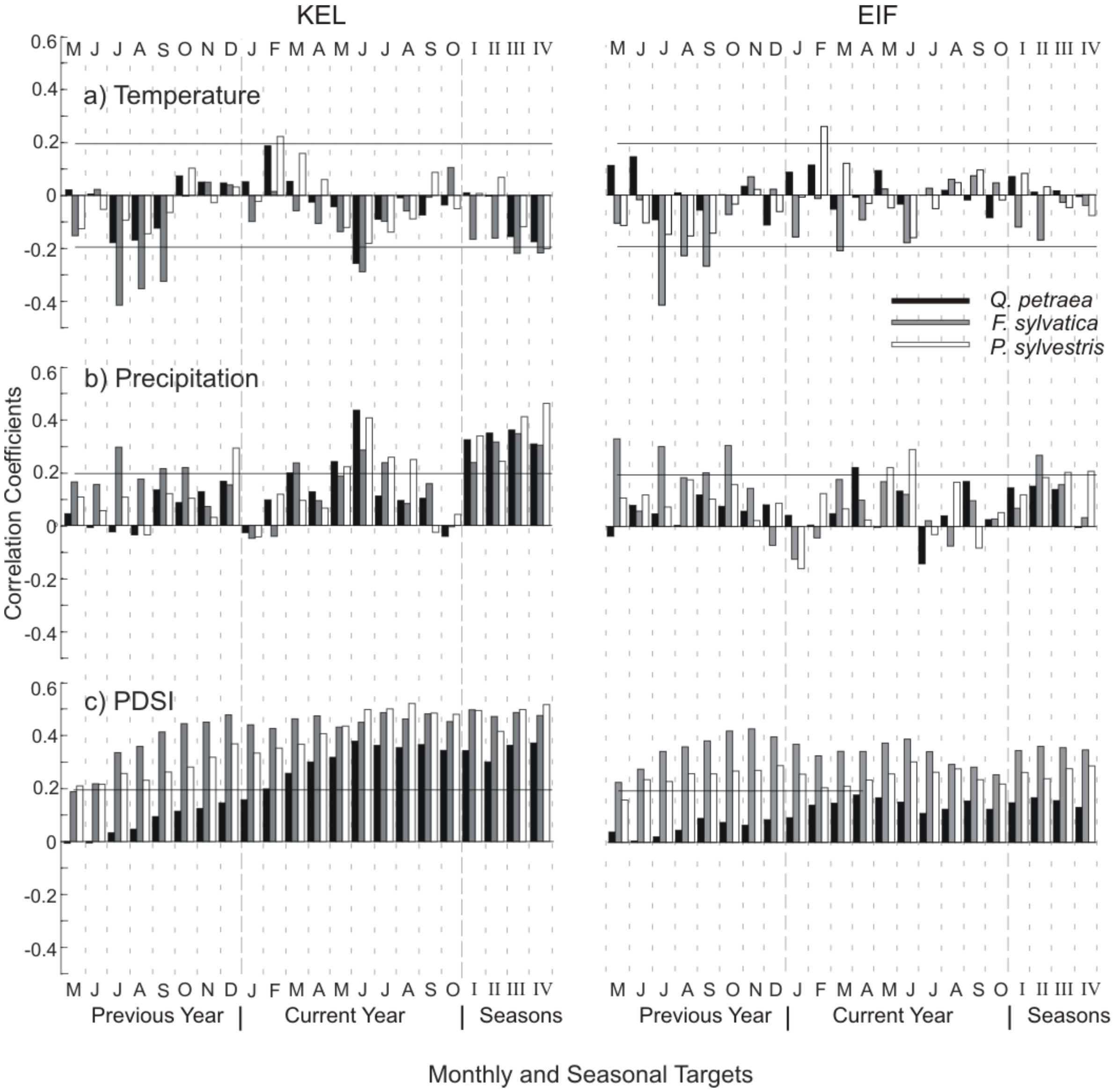


Figure 6. Pearson correlation coefficients between species-specific regional chronologies (black = Quercus petraea, grey = Fagus sylvatica, white = Pinus sylvestris) of the Kellerwald (left column) and the Eifel (right column) and monthly and seasonal (a) average temperatures, (b) precipitation sums, 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.

Species' drought sensitivity between KEL and the wetter EIF differs in the seasonal pattern. Over all time periods EIF growth of *F. sylvatica* and *P. sylvestris* tends to be more sensitive to previous year drought conditions, while trees in KEL respond stronger to water supply of the year of growth. High correlations between growth and PDSI are not only found for single months, they are spun out over several months caused by the lagged character of PDSI. The PDSI values are per definition calculated based on the conditions of several previous months (Palmer 1965).

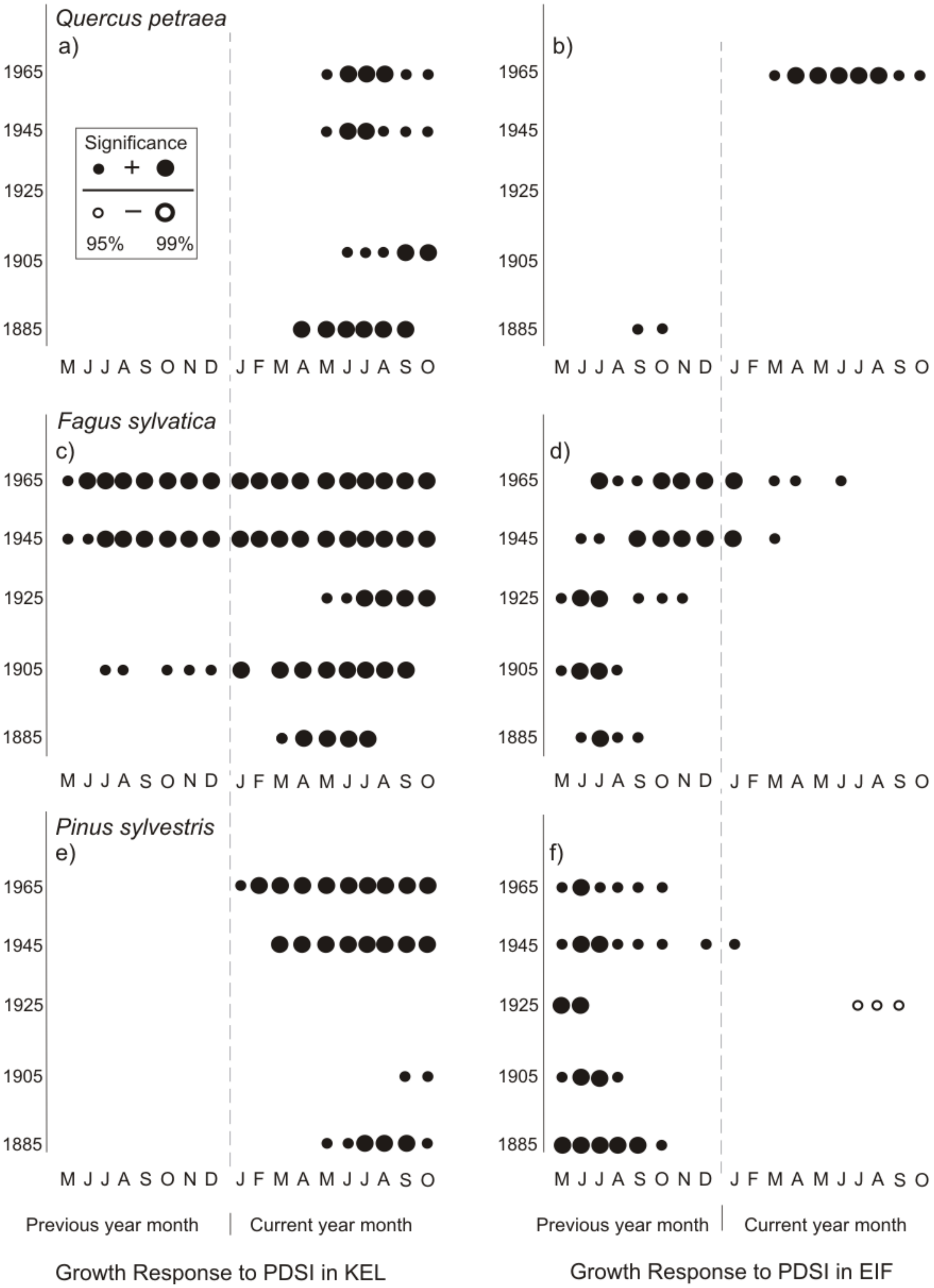


Figure 7. Temporal changes in the correlation between regional (Kellerwald and Eifel) chronologies of Quercus petraea (a,b), Fagus sylvatica (c,d), and Pinus sylvestris (e,f) and monthly PDSI values of the current and previous year. Pearson's correlation coefficients were calculated for five 40-yr periods starting in 1885.

6.5 Discussion

Slight differences in growth variations of the tree species indicate contrasting responses to regional-scale climate variability (Fritts 1976). The separation of *Q. petraea* growth variations (Fig. 3) is likely induced by the weaker climate sensitivity compared to *F. sylvatica* and *P. sylvestris*. Growth variations of *F. sylvatica* on the third axis are likely separated due to the impact of temperature on growth, which is negligible for *Q. petraea* and *P. sylvestris*. The slight differences in climate conditions between KEL and EIF could be responsible for the differences in species-specific growth variations between the regions.

Average growth rates of individual species fall in the range of temperate forest productivity rates reported in other studies (Dittmar et al. 2003; Neuwirth 2005; Friedrichs et al. submitted). Bonn (1998) found distinct differences in growth rates between *Q. petraea* and *F. sylvatica* for Central Europe, but these results are not confirmed by our study. *P. sylvestris* growth rates in our study are considerably lower than growth rates of the deciduous species (Table 3).

Compared to other studies that focused on temperate forest growth (Bonn 1998; Lebourgeois et al. 2005), only weak influences of previous year growth on current year ring formation were found in our study. High Rbar and EPS values indicate a strong signal coherency for all species. Lower signal coherency in EIF indicates higher influences from non-climatic factors leading to more individualistic tree growth patterns. Distinct differences between species' response to environmental factors are indicated by MS (Table 3). The values suggest strong growth sensitivity of *F. sylvatica* and high growth sensitivity of *P. sylvestris* in contrast to weaker exogenous influences on *Q. petraea*. MS values indicate that all species suffer stronger environmental stress in KEL, where the regional climate conditions are drier than in EIF. Nevertheless, MS of *Q. petraea* is lower in KEL than MS of *F. sylvatica* and *P. sylvestris* in EIF. Lower climate sensitivity of tree growth in EIF is in line with less signal coherency, suggesting more effects from other environmental factors.

Our analyses reveal significant growth responses to 20th century climate of *F. sylvatica, Q. petraea,* and *P. sylvestris* in Central European temperate forests. A finding also confirmed for *Picea abies*, another dominant tree-species in Central Europe (Dittmar & Elling 1999; Büntgen et al. 2006). In our study, water availability is the primary growth-limiting factor for all tree species (Fig. 5, 6). Radial growth depends mainly on early summer soil water content (June), emphasized by an inverse growth relation to June temperature (Fig. 6a), and positive growth response to high precipitation sums (Fig. 6b). Comparable influences of June drought conditions are also found in other temperate forest studies (Bonn 1998; Lebourgeois et al.

2005) and at the species distribution limits (Dittmar et al. 2003; Rozas 2001; Weber et al. 2007).

We demonstrate clear species-specific differences in the strength of climate sensitivity and a seasonal differentiation of growth responses. *F. sylvatica* and *Q. petraea*, both located in the centre of their climate-induced distribution areas (Fig. 1), differ strongly in climate sensitivity. *F. sylvatica* suffers much more under annual drought events, comparable to climate sensitivity close to its southern distribution limit (Rozas 2001; Di Filippo et al. 2007). Climate circumstances lead to various months with relevant precipitation amounts for growth of *F. sylvatica*, while growth of *Q. petraea* only responds to spring and June conditions (Fig. 5, 6). 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 & 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 eastern Alps (Di Filippo et al. 2007). 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; Griggs et al. 2007; Weber et al. 2007). 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-Gonzaléz & Eckstein 2003).

P. sylvestris reacts less sensitively to 20th century climate conditions than *F. sylvatica* (Fig. 6). Significant responses were found 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 & Pallardy 1997). The strong dependency on summer moisture is also typical for *P. sylvestris* trees under dry climate conditions at their distribution limit (Weber et al. 2007).

The observed differences in regional climate conditions between KEL and EIF (higher precipitation amounts of ~300 mm in EIF) play a role in modulating species-specific climate-growth response patterns, since the species responses to drought are stronger on the drier sites in KEL. Climate sensitivity of *F. sylvatica* and *P. sylvestris* increases slightly at the drier temperate forest sites, but *Q. petraea* shows strong differences in climate sensitivity between both regions, which is in line with the difference in MS values (Table 1). Differences in water availability induce a shift from moderate (EIF) to stressful (KEL) environmental growth conditions for *Q. petraea* (Fig. 6).

Temporal instability of growth/climate relationship in temperate forests hinders a robust reconstruction of meteorological parameters beyond the period of instrumental measurement (Rozas 2001; Friedrichs et al. submitted). Growth sensitivity to drought increased over the 20th century, not only in intensity, but also in the number of months being relevant for water availability (Fig. 7). This increase is likely caused by the recent temperature increase. A projected increase in drought frequency and severity over the next decades (Schär et al. 2004, Christensen et al. 2007) will likely impact temperate forest vigor in a negative way. Consequences might become serious for *F. sylvatica* (Ciais et al. 2005), which shows the strongest increase in drought sensitivity in our study. Our findings indicate that the centre of *F. sylvatica's* distribution area (Fig. 1) is likely to shift towards cooler and wetter site conditions, comparable to shifts found at its southern distribution limit (Penuelas & Boada 2003). Several tree sites of *F. sylvatica* could suffer in Central-West Germany, especially in drier regions like KEL, and such sites could potentially be occupied by *Q. petraea* and *P. sylvestris*. Currently, the competitive strength of *F. sylvatica* in mixed stands is primarily induced by its specific canopy architecture and leaf orientation, suppressing the light-demanding species *Q. petraea* and *P. sylvestris* (Ellenberg 1996; Leuschner et al. 2001a). The future competitive strength of all species will be directly affected by climate change and indirectly by secondary influencing factors, such as CO_2 enrichment and increasing occurrence of defoliating insects. CO_2 enrichment influences species in various ways (Leuzinger & Körner 2007) and the increased occurrence of defoliating insects, e.g., the oak buprestid beetle, negatively affects the vitality of their host-species (Thomas et al. 2002). Changes in forest composition and species shifts induced by climate change are therefore very complex. Potential future changes in species composition in temperate forests will depend on the influence of increasing drought stress on species' vitality and competitive ability (Leuschner et al. 2001b; Breda et al. 2006).

6.6 Conclusion

We show strong dynamics in temperate forest responses to 20th century climate variability. The most influencing parameter on tree growth of *F. sylvatica, Q. petraea*, and *P. sylvestris* is drought stress. This is even more evident at sites characterized by relatively low water availability. *Q. petraea* copes best with water depletion, responding primarily to spring and summer droughts. *F. sylvatica* and *P. sylvestris* additionally depend on previous year moisture conditions. The latter species undergo significant drought stress in both study regions, but the low gradient in water availability between EIF and KEL still induces a shift from moderate to severe environmental conditions for *Q. petraea*. The most recent warming trend causes increasing drought sensitivity in comparison to earlier decades. *F. sylvatica* reacts most sensitively to water depletion and is predicted to be more stressed in a warming world than *Q. petraea* and *P. sylvestris*. Changes in forest composition and shift might occur to the benefit of *P. sylvestris* and especially *Q. petraea* if increasing drought stress weakens *F. sylvatica's* competitive ability. The assessment of climate change effects on species' vitality and composition in temperate forests, however, remains difficult, because the influence of various environmental factors is further modified by different climate change scenarios. Our results emphasize the importance of research continuation towards a more detailed understanding of growth/climate responses in a warming world. Such studies should consider complex growth response in temperate forests to simultaneous changes in multiple environmental parameters.

7. General discussion and conclusion

7.1 Methodological approach

Many methodological aspects applied in this study, i.e. the new regional-scale network analysis, the investigation of spatiotemporal growth variations based on classification analyses, the various standardization techniques, and the variations of temporal stability calculations, were key to improve the understanding of complex spatio-temporal patterns of tree-growth response to climatic change in temperate forests.

The analyses of tree-ring dataset classifications of minimal growth variations (**Chapter 3, 5**), as well as stronger growth differentiations (**Chapter 6**) enabled the detection of the most important environmental factors responsible for growth variations, but also identified the limits of the classification approach in disentangling complex growth influences. Besides the conventional approaches for evaluating tree-ring growth and growth/climate relations in dendroclimatological network analyses (e.g. Oberhuber et al. 1998, Dittmar et al. 2003, Di Filippo et al. 2007), varying influences of classification methods on the results of tree-ring analyses were investigated in this study (**Chapter 4**) to assist the separation of factual growth information from methodologically induced disturbances. This comparison of classification methods, most likely applied for the first time in tree-ring analyses, confirmed differences in classification results according to the classification methods. Therefore, it pointed out that the application of a method considerably influences results in a homogeneous tree-ring network. This thesis yields new information about characteristics of different classification methods and classification properties, which is helpful for the selection of a classification method for growth-variations analysis. The comparison identified PCA as the most stable classification method, described Ward’s method with the most sensitive response to changes in the dataset, and characterized ALM as emphasizing outliers. Furthermore, the study shows that classifications are only representative for the time period of calculation and supports choosing the same reference period for tree-growth classification and other analyses. Classification periods should be as long as possible when classification analyses are used for climate reconstructions (e.g. in Frank and Esper 2005, Büntgen et al. 2007).

Classification periods in this thesis in the regional-scale network (**Chapter 5)** were similar to the studied periods of growth/climate analyses, temporally restricted by the beginning of the climate data series and the end of the shortest tree-ring chronologies. Ward’s method was chosen for site classifications due to its clear separation of clusters caused by its approach of maximizing variance between the clusters, while minimizing the variance within the clusters (Bahrenberg et al. 2002). Its sensitive response to changes in the dataset was dispensable in these analyses because no dataset extensions were applied.

The classification of minimal growth variations in the regional-scale network (**Chapter 5)** resulted in growth clusters primarily based on the spatial distribution of the sites. The sites of a certain cluster are dominated by the same environmental – particularly climatic – conditions, e.g. characterized by warm and dry growth conditions. Differences between the clusters’ environmental conditions explained most of the differences in growth/climate relations and therefore clarified the complex temperate tree-growth influences. However, growth homogeneity of sites within some clusters did not coincide with similar environmental site characteristics. Hence, the complex influence of climatic and non-climatic factors on trees partly hampers the environmental explanation of growth patterns. In contrast to site classifications with stronger environmental gradients (e.g. Lebourgeois et al. 2004, Di Filippo et al. 2007) a particularly careful interpretation of the rationale behind classification is necessary.

Growth/climate relations in two regions representing the strongest differences in environmental conditions in the network were compared to define the maximum magnitude of environmentally induced differences in growth/climate relations (**Chapter 6**). PCA was applied for this approach to quantify the amount of common and individual variance of the investigated trees.

Growth analyses with several chronology statistics confirmed the overall growth homogeneity and suggested robust and climatologically sensitive tree-ring chronologies suitable for growth/climate analyses (**Chapter 3-6**). Mean sensitivity indicated less climatic influence on tree-growth of *Quercus petraea* compared to *Fagus sylvatica* and *Pinus sylvestris* (**Chapter 6**). Generally, statistical parameters are comparable to results of other temperate forest studies (Bonn 1998, Lebourgeois et al. 2005, Dittmar et al. 2003). Average growth rates of individual species vary from 1.10-2.00 mm/year and fall in the range of the large-scale Central European network analyses of Neuwirth (2005).

Another important method assisting the improved understanding of spatio-temporal patterns of tree-growth responses to climatic change is low frequency standardization. Tree-ring series in temperate forest analyses are usually standardized so that they only illustrate high frequency variations, which permits the investigation of inter-annual growth/climate relationships (e.g. Bonn 1998, Lebourgeois et al. 2005, Neuwirth 2005, Dittmar et al. 2007). An exception is a study in the Bavarian Forest region of southeast Germany illustrating low frequency variations of tree-ring series (Wilson et al. 2005). Low frequency standardizations, however, are necessary for assessing longer-term climate change impacts on tree growth and for reconstructing longer-term climate trends. This thesis represents growth/climate analyses based on high- (**Chapter 3, 6**) and low- (**Chapter 5**) frequency standardizations. Low frequency analysis enabled investigation of inter-annual to multi-decadal growth variability over the 20th century by detecting the anomalous period around the 1940s. Growth at oak sites increased over this period despite warm and dry climate conditions, a phenomenon that has not been reported by other temperate forest studies.

Temporal stability analyses, sparsely found in temperate forest studies, provide detailed information about growth/climate responses in this anomalous period. Overall, the moving correlations as well as the comparison of different temporal intervals of growth/climate analysis were suitable herein for illustrating temporal gradients and changes in temperate growth/climate relationships allowing the assessment of dynamics and trends in the relationships (**Chapter 3, 5-6**; for details see section “temporal stability” below).

7.2 Growth/climate analysis

The compilation of growth/climate analyses presented in the previous chapters provides strong relations between temperate forest tree-growth and various climate parameters (**Chapter 3, 5-6**). Even though one growth dominating climate parameter, as described for all differently induced timberlines (for a review see Schweingruber 1996) was not found herein, this thesis evidences that 20th century tree-growth in all temperate forest sites significantly depends on water supply. Three climate parameters, PDSI, precipitation, and vapor pressure amounts, quantified this dependence. Concluding, drought induced by soil and atmospheric moisture conditions is most stressful for Central-West German temperate tree growth.

Spatial differences in growth response to water availability induced by site-specific environmental growth conditions were expressed by different sensitivities to these three climate parameters (**Chapter 3, 5-6**). While high elevation tree-growth in Central Europe is strongly influenced by temperature conditions (e.g. Frank and Esper 2005), this thesis reveals only low temperature controls on temperate tree-growth. Furthermore, cloud-cover was also found to be of secondary importance for tree growth (**Chapter 5-6**).

In contrast to studies only based on precipitation and temperature data and reporting weak growth/climate responses (e.g. Lebourgeois et al. 2004), this thesis considers several climate parameters which allow for an improved assessment of climate-dependent growth variations. Annual ring formation at sites where no response to temperature and precipitation was found could be explained by PDSI and vapor pressure. Particularly PDSI, which is a commonly used parameter in elucidating climate impact on tree growth in arid zones (e.g. Cook et al. 1999, Watson and Luckman 2002, Esper et al. 2007), additionally helped in estimating the growth/climate relations as it broadly represents water availability.

The specific properties of the climate parameters led to differing effects on tree-growth (**Chapter 5-6**) which can improve dendroclimatological analyses in temperate forests. This thesis encourages the introduction of more climate parameters not commonly used in dendroclimatological analyses, such as sunshine duration and air humidity, to detect further properties of tree-growth responses to climatic change in future analysis.

The comparison of growth/climate responses between species increases the low number of analyses of species-specific long-term climate sensitivity in temperate forests. *Quercus petraea* reveals stronger drought tolerance compared to *Quercus robur* (**Chapter 5**), *Pinus sylvestris*, and *Fagus sylvatica*, which shows the strongest general climate sensitivity (**Chapter 6**). Besides the verification of differences in the strength of species-specific drought sensitivities, this thesis provides new information about differences in species-specific seasonal drought response patterns likely influencing the ability of species to cope with climate change. While growth of *Quercus petraea* is characterized by a short period of sensitivity, primarily affected by early-summer (June) moisture conditions, annual ring formation of the other species is also strongly influenced by previous year drought conditions and other periods of the growth year (Figure 7.1). *Quercus robur* responds to water supply conditions from previous year summer until the end of the current vegetation period with highest sensitivity in spring (April). Growth of *Fagus sylvatica* responds sensitively to previous year summer until current year September drought conditions. *Pinus sylvestris* was found to respond significantly to drought conditions of all seasons with highest correlations to current year summer water availability. While *Fagus sylvatica* shows the highest correlation values over all seasons to PDSI, *Pinus sylvestris* illustrates the overall highest correlation value. An increase in summer droughts likely increases the climate impact on tree growth of all species due to sensitivity to summer conditions. The probability of being negatively influenced by other effects of climate change, such as changes in the seasonality of precipitation, extreme events and long-term droughts, however, is likely higher for species that react to more climate periods sensitively. Based on the seasonal pattern of growth/climate relationships, *Quercus petraea* is probably better equipped to cope with a changing climate regime than the other investigated tree species.

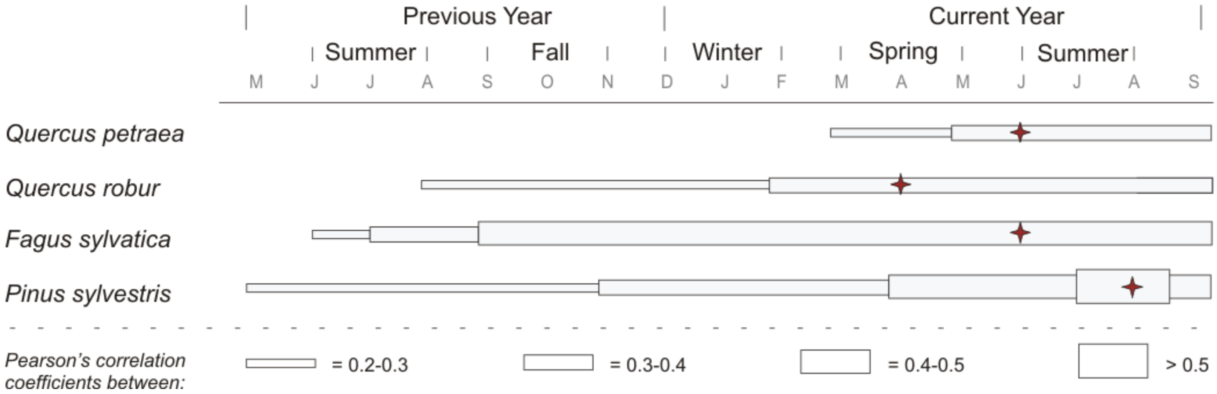


Figure 7.1 Differences in species-specific seasonal drought response patterns. The different sized squares illustrate four categories of Pearson's correlation coefficients between tree growth and PDSI. The lowest correlation coefficient (r=0.2) approximately denotes the 95% significance level (=0.196). Asterisk represents the month with the highest correlation value.

7.3 Temporal variations in growth/climate relations

The temporal stability analyses calculated in this thesis clearly illustrated temporal instabilities in growth/climate relations over the 20th century (**Chapter 3, 5-6**): the strength and significance of growth/climate relations varies over time. The most relevant period characterized by a loss of growth response to PDSI and precipitation is the period around the 1940s (**Chapter 5**). During this exceptionally warm period the otherwise strong correlations between *Quercus spp.* growth and PDSI and precipitation are interrupted, whereas the otherwise insignificant influences of temperature and vapor pressure become relevant. This anomalous period occurred in all investigated *Quercus spp.* sites. Additional investigations of this thesis (Friedrichs unpublished data), carried out to define the spatial extension of this phenomenon, also show insignificant growth/PDSI and precipitation relations during this period in temperate forest sites located eastwards and southwards of the regional-scale network. Although the occurrence of this anomalous period is not yet fully clarified, its detection is of great value for dendroclimatological temperate forest studies.

This extensive lack of significant correlations hampers a statistically robust reconstruction of climate parameters beyond the period of instrumental measurement. While a partial occurrence of the loss of the climate parameter’s impact on ring formation could eventually be stabilized by a combination with sites showing strong signals during that period, the total loss across the network inhibits compensation by such techniques. The factor responsible for this spatially extensive phenomenon can only be one of regional-scale effectiveness, e.g. another climate parameter. Therefore, an expansion of the tree-ring network till sites where significant climate responses are found is likely not meaningful, as the new sites would likely appear in regions climatologically not representative for the herein analyzed Central-West German conditions.

The anomalous period emphasizes that the influence of any single climatic parameter on temperate tree growth is too weak over the entire period to guarantee a consistent relation over time. Even if the calibration period of a study shows an overall significant relation between growth and PDSI or precipitation in temperate forests, this thesis’ analyses strengthen skepticism about the parameters signal strength in earlier centuries characterized by differing centennial-scale climate conditions (e.g. during the Little Ice Age). This consideration also concerns climate reconstructions at timberlines, where temporal instability of growth/climate relations is also found (Fritts 1976, Cook and Kairiukstis 1990). The stronger influence of one dominating climate parameter in comparison to temperate forests, however, likely inhibits the total loss of growth/climate relations.

The alternative use of *Fagus sylvatica* and *Pinus sylvestris* – showing stronger climatic sensitivities – for long reconstructions is problematic because they were sparsely used as construction timber in earlier centuries and recent trees are not older than 300 years at most. Furthermore, most of the historical wood is only available as tree-ring width chronology and reconstructions based on other promising tree-ring parameters, e.g. latewood density, earlywood vessel measurements, and stable isotopes, are not easily available.

The detection of the exceptional 1940s with growth increase despite drought conditions is not only interesting for the assessment of climate reconstructions, but also for recent climate change impact on growth. Generally, an increase in influence of drought conditions on tree growth was found over the 20th century. Moving correlation analysis illustrates only a slight increase in the impact of annual drought conditions (**Chapter 5**), but the influences of monthly drought conditions over various periods on growth (**Chapter 6**) increase not only in intensity, but also in the number of months relevant for water availability. This increased influence of water deficiency on tree-growth of temperate forests is caused by the recent warming trend. The recent and projected increase in drought frequency and severity continuously changes temperate growth conditions to more extreme conditions. This thesis supports evolutions to more unfavorable climate conditions for tree growth (for a review see Bréda et al. 2006) and adds long-term growth/climate information to the existing knowledge from tree physiological analyses.

Furthermore, species-specific abilities to cope with warmer and drier climate conditions indicated a differentiated pattern of recent climatic change impact on temperate forest growth. *Fagus sylvatica* is predicted to be the most stressed in a warming world. If increasing drought stress weakens *Fagus sylvatica's* competitive ability, changes in forest composition and shifts are likely to occur to the benefit of other species, particularly *Quercus petraea*. This species will likely also be negatively influenced by recent climatic change, but the 1940s illustrate that warmer and drier conditions in the range of the expected near future temperature increase will not necessarily lead to suppressed *Quercus spp.* growth. This period indicates non-linear and/or threshold-induced growth responses to climate parameters in temperate forests, which complicates the assessment of climate change impact on temperate forest growth. With the herein obtained gain of knowledge – by elucidating details of the complex spatio-temporal patterns of tree-growth response to climatic change – new questions arise, emphasizing the importance of research continuation towards a more detailed understanding of growth/climate responses in a warming world. The results of this thesis concerning climate influences on temperate tree growth, combined with results about various environmental growth factors, contribute to the completion and understanding of the complex pattern of multiple environmental parameters and their changes and interactions influencing temperate forest growth.

7.4 Conclusion

This thesis analyzes temperate forest growth at a regional scale, where dominance of a single growth factor is lacking and several climatic and non-climatic parameters lead to complex influences on tree growth. By analyzing the magnitude, temporal variability, and spatial characteristics of tree-growth response to climatic change and focusing on inter-annual to multi-decadal variations, this thesis increases our knowledge about climatic controls on temperate forest tree-growth.

Classification is a useful methodological approach to detect differences in the complex growth influences in temperate forest networks, but a careful consideration of the classification method and interpretation of the classifications reasons is a necessity.

Drought conditions quantified by PDSI, precipitation, and vapor pressure amounts have been most important for temperate tree growth over the last century. However, relationships between these climate parameters and tree growth are not stable over time. Particularly due to a period of area-wide loss of trees’ sensitivity to PDSI and precipitation in the 1940s, the accomplishment of suitable climate reconstructions based on temperate tree-ring proxies is assessed as complicated.

The extension of this comprehensive tree-ring network into the 21st century allowed the detection of increased drought stress of temperate forest trees in recent times. Recent climatic change partly leads to a change from temperate to more stressful growth conditions in the center of species distributions, potentially resulting in forest composition changes and species shifts.

8. Summary

Trees growing under temperate climate conditions are affected by numerous growth influences and the assessment of climate controls on temperate forest tree-growth is complicated. Dendroclimatological analyses of tree-ring chronologies in which the long-term growth/climate relations are investigated, help to assess tree-growth response to climatic change. Temperate forest growth in Central Europe has been widely investigated in dendrochronogical studies, but the complex influence of climate on tree growth is still not fully understood. The aim of this study was to improve the understanding of spatio-temporal patterns of tree-growth response to climatic change in Central European temperate forests to contribute to a profound assessment of i) the suitability of temperate tree growth as proxy for climate reconstructions and ii) the impact of recent climatic change on temperate tree growth.

A new regional-scale tree-ring network consisting of 48 oak (*Quercus spp.*), 15 beech (*Fagus sylvatica)*, and three pine (*Pinus sylvestris*) sites was established in Central-West Germany to investigate spatio-temporal growth/climate relation patterns. New insights in complex growth controls were provided by using methodological approaches not commonly used in temperate forest tree-ring analyses.

This study emphasizes the influence of the choice of classification method on the results in a homogeneous tree-ring network and gives a characterization of three classification methods. Classification analyses were performed to identify homogeneous growth subsets within the tree-ring network. Site classifications were primarily characterized by similar environmental and climatic conditions, which can explain differing growth/climate relations for the clusters and therefore elucidate complex growth/climate responses.

Three standardization procedures were applied to enable growth/climate analyses from inter-annual to multi-decadal variations. Climate/growth relations were investigated using correlation analysis, redundancy analysis, moving correlation analysis, and pointer year analysis. Comparing tree growth with temperature, precipitation, vapor pressure, cloud-cover, and drought index, climate influences over the 20th century were determined.

Drought was found to be the most important growth influencing factor, as quantified by three climate parameters PDSI, precipitation, and vapor pressure. In contrast, temperature and cloud-cover were of secondary importance for tree growth. Species-specific investigations illustrate that *Fagus sylvatica* shows the strongest climate sensitivity, whereas *Quercus petraea* is most drought tolerant, followed by *Quercus robur* and *Pinus sylvestris*. Furthermore, this thesis provides new information about differences in seasonal species-specific climate response patterns. While growth of *Quercus petraea* is characterized by a short period of summer sensitivity, annual ring formation of the other species is significantly influenced by climate conditions of previous year and growth year periods.

Temporal stability analyses of this thesis illustrated that the relations between tree growth and climate parameters vary over time. Overall, drought sensitivity increased over the last decades of the 20th century. Furthermore, a period of area-wide loss of sensitivity to PDSI and precipitation in the 1940s was detected.

In conclusion, this thesis considers comprehensive methodological approaches and several climate parameters and improves the understanding of spatio-temporal patterns of growth/climate responses in temperate forests. By analyzing the strength and temporal variability of growth/climate relations, the accomplishment of suitable climate reconstructions based on temperate tree-ring proxies is estimated to be complicated. Furthermore, the impact of recent climatic change will likely continuously change temperate into more extreme growth conditions in the Central-West German research area, thus potentially leading to changes in forest composition and species shifts.

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Publications

Friedrichs, D. A. (in preparation) Growth/climate relationships in temperate forests – assessment of potential for climate reconstruction and future climate change impact. Landscape online.

Neuwirth, B., Büntgen U. and D. A. Friedrichs (in preparation). Drought response of Central European tree-rings. Dendrochronologia

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Talks and Posters

03-06.05.2007 Riga, Lettland, International Conference TRACE: Growth variations of oaks under different climatic and environmental conditions in low mountain ranges (Germany).

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