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Growth reactions of temperate forest trees to summer drought —a multispecies tree-ring network approach

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The Tree

I stood still and was a tree amid the wood,
Knowing the truth of things unseen before;
Of Daphne and the laurel bow
And that god-feasting couple old
that grew elm-oak amid the wold.
'Twas not until the gods had been
Kindly entreated, and been brought within
Unto the hearth of their heart's home
That they might do this wonder thing;
Nathless I have been a tree amid the wood
And many a new thing understood
That was rank folly to my head before.

Ezra Pound

Preface

This study was funded by the Bavarian State Ministry of Agriculture and Forestry via the board of trustees of the Bavarian State Institute of Forestry LWF, grant E 45 “Baumarteneignung bei verstärkter Trockenheit in Folge des Klimawandels”. The dissertation has been supervised by Prof. Dr. Dr. Hans Pretzsch (Technische Universität München, Chair of Forest Growth and Yield Science) and Prof. Dr. Andreas Rothe (University of Applied Sciences Weihenstephan, Faculty of Forestry). The main research was conducted at the University of Applied Sciences Weihenstephan, Freising, under the leadership of Prof. Dr. Andreas Rothe from September 2006 to December 2009. The research on allocation patterns between root and shoot was part of an independent project conducted at the Technische Universität München at the same time, in cooperation with Dr. Petia Nikolova and under the leadership of Prof. Dr. Dr. Hans Pretzsch, with partial funding by the Technische Universität München, Life Science Centre, Gender Issue Incentive Fund and the German Research Foundation DFG as part of the Collaborative Research Centre SFB 607 “Growth and Parasite Defence”.

The present dissertation focuses on tree growth subject to climatic limitations with an emphasis on summer drought, and comprises six main parts and four appendices. Parts one to five form the canonical part of the dissertation from introduction to conclusions. An additional short outlook and perspectives for future research are given in part six. The first appendix details on an unpublished study on calibration performance of several regression approaches, which is referenced in the dissertation’s methods section. The second appendix contains the abstracts of six original research papers written during the dissertation project. The third appendix contains a selection of seven peer-reviewed abstracts for national and international conferences, and an overview of eighteen (co)supervised student theses is given in the fourth appendix.

Thesis Abstract

The predicted increase in frequency and intensity of climatic extremes, like drought episodes, imposes a challenge on the choice of commercial forest trees under climate change conditions. The present dissertation aims at quantifying the impact of summer drought on growth of spruce, pine, silver fir, beech and oak as the main forest tree species in Southern Germany, and includes Douglas fir as a possible alternative for spruce.

Series of tree-ring widths from more than 1400 trees from 48 sites all over Bavaria and adjacent states are employed for growth/climate modeling and pointer year analysis to derive predications about the climatic limitation of tree growth subject to species, regional climate and site quality. The dendroclimatic tool-set is further enhanced by a newly developed approach of dendroclimatic benchmarking, using multivariate extremes of tree-ring growth patterns. Soil water balance modeling was applied to refine the connections between regional climate and growth reactions to drought in terms of site quality.

To study size-related effects of drought impact on tree physiology for a subset of oak, pine and spruce trees, stable carbon isotope analysis has been carried out. Furthermore, allometric analysis was applied on a subset of the study sites representing a precipitation gradient to investigate the allocation patterns between root and shoot subject to increasing water scarceness.

For all species under investigation, critical areas for tree growth could be identified. Generally, the warmer and drier northern part of the investigation area is more unfavorable, with spruce generally being more affected than other species. As a main result, oak is superior to all other species under investigation regarding drought tolerance throughout the investigation area. But also silver fir could replace the most critical spruce on a wide range of sites. These results drawn from dendroclimatic analysis and pointer year analysis are confirmed by dendroclimatic benchmarking: archetypal growth patterns of drought-intolerance could be associated mainly with spruce growth, and hardly with oak growth.

A generally more effective scaling of hydraulic properties related to drought resistance in oak as compared to spruce is suggested by the comparison of growth reaction of small versus tall trees. These findings contribute to the explanation of species-specific differences in drought tolerance versus intolerance.

Furthermore, the surprisingly high variability in reaction to drought observed on regional and stand level implies a high adaptive potential of the populations within the possibilities of their inherent genetic diversity. A potential mechanism for adaption to increasing drought stress is found in terms of increased allocation of biomass towards root growth with decreasing mean precipitation sums, as revealed by allometric analysis.

Kurzfassung

Im Rahmen des Klimawandels wird die Zunahme von Frequenz und Intensität extremer Witterungsereignisse, wie etwa Trockensommer, prognostiziert. Vor diesem Hintergrund ist die Anbaueignung der heimischen Baumarten mit großen Unsicherheiten verbunden. Diese Dissertation versucht auf der Basis eines großen und nach einheitlicher Methode erhobenen Datensatzes die Reaktion von Fichte, Kiefer, Tanne, Buche und Eiche abzuschätzen, und bezieht weiterhin die Douglasie als mögliche Ersatzbaumart für die Fichte mit in die Untersuchungen ein.

Als Datengrundlage dienen Jahrringserien von über 1400 Bäumen von 48 Waldstandorten in ganz Bayern und angrenzenden Gebieten, die mittels Klima-Wachstums-Beziehungen und Weiserjahr-Analysen zur Beurteilung der klimatischen Limitierung des Baumwachstums in Abhängigkeit von Baumart, Großklima und Standort herangezogen werden. Diese dendroklimatischen Werkzeuge werden durch den neuentwickelten Ansatz des dendroklimatischen Benchmarkings ergänzt, der auf der Ausscheidung artübergreifender archetypaler Zuwachsmuster auf der Basis multivariater Extrema beruht. Mit Hilfe des modellierten Bodenwasserhaushaltes wurde weiterhin versucht, die Beziehungen zwischen Zuwachsreaktion auf Trockenstress und regionalem Klima weiter zu verfeinern.

Größenabhängige Effekte der physiologischen Reaktion auf Trockenheit wurden für einen Teildatensatz mit Eiche, Kiefer und Fichte anhand stabiler Kohlenstoffisotope untersucht. Weiterhin wurde die Allokation von Biomasse in das unterirdische vs. oberirdische Kompartiment mittels allometrischer Analysen entlang eines Niederschlagsgradienten quantifiziert.

Für alle untersuchten Arten ließen sich innerhalb des Untersuchungsgebietes kritische Bereiche in Bezug auf die Reaktion auf Sommertrockenheit ausweisen. Im wärmeren und trockeneren nördlichen Teil des Untersuchungsgebietes zeigten alle Arten die deutlichsten Zuwachsreaktionen, wobei sich jedoch die Fichte als besonders gefährdet herausstellte. Die Eiche zeigte eine standortsübergreifende Überlegenheit gegenüber allen anderen untersuchten Baumarten in Bezug auf Trockenresistenz, aber auch die Tanne stellte sich gegenüber der als am kritischsten einzustufenden Fichte als deutlich trockenresistenter heraus, und könnte diese auf vielen Standorten ersetzen. Diese Ergebnisse aus der Klima-Zuwachs-Modellierung sowie der Weiserjahranalyse wurden durch das dendroklimatische Benchmarking bestätigt: archetypische Wachstumsmuster mit einem starken Bezug zu Trockenheitsanfälligkeit sind bei Fichten am deutlichsten ausgeprägt, und am wenigsten bei Eichen.

Eine generell effektivere hydraulische Architektur im Hinblick auf Trockenheitsresistenz bei Eichen im Vergleich zu Fichten wird durch den Vergleich der Reaktionen von kleineren im Gegensatz zu größeren Bäumen nahegelegt. Diese Ergebnisse tragen zu einem verbesserten Verständnis der artspezifischen Unterschiede in Bezug auf Toleranz oder Intoleranz gegenüber Trockenstress bei.

Überraschend ist die hohe Variabilität der Reaktion auf regionaler Ebene und auf Bestandesebene, die ein hohes evolutives Anpassungspotential der Populationen im Rahmen ihrer genetischen Diversität nahe legt. Durch allometrische Analysen wurde eine mögliche Anpassungsstrategie im Rahmen der phänotypischen Plastizität in Form einer verstärkten Allokation von Biomasse Richtung Baumwurzeln bei geringeren mittleren Niederschlagsmengen nachgewiesen.

Short Contents

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List of Symbols

A_s	Available soil energy
$\boldsymbol{A}$	Matrix of archetypes
$\boldsymbol{a}$	Regression coefficients
$\mathcal{A}, \mathcal{L}, \mathcal{M}, \mathcal{N}$	Parameters for Mualem–van Genuchten parametrization
α, β	Parameters for convex combinations
$\boldsymbol{b}$	Linear transformed regression coefficients
$\boldsymbol{b}^*$	Coefficients of response function
D_0	Vapor pressure deficit in the canopy
D_R	Vapor pressure deficit at reference height
d	Number of reduced dimension in ordination space
δ_r, δ_s	Root (r) and stem (s) radii for a given year
ϵ	Random error
$f(t)$	Smoothing function
$\ddot{f}(t)$	Second derivative of smoothing function
g	Allometric factor
γ	Allometric exponent
γ'	Period wise allometric exponent
$I(t)$	Series of tree-ring indices
$\hat{I}(t)$	Autocorrelation structure in tree-ring series
$\bar{I}(t)$	Site chronology
$\boldsymbol{I}$	Matrix of tree-ring chronologies
K	Hydraulic conductance
K_s	Hydraulic conductivity at saturation
l	Number of archetypes
l_b	Bark thickness
l_s	Sapwood length
λ	Spline parameter
νE	Total potential evapotranspiration
νE_S	Evaporation from soil
νE_C	Transpiration from canopy

p	Number of total dimensions in ordination space
ϕ	Effective frequency response
π	Constant
ψ	Water potential
r	Power parameter for distance weighting
R	Isotopic ratio of δ^{13}C/δ^{12}C
$\boldsymbol{R}$	Matrix of response function coefficients
r_{sa}	Aerodynamic resistance between substrate and canopy
r_{ca}	Boundary layer resistance of the vegetation
r_{ss}	Soil resistance
r_{aa}	Aerodynamic resistance above the canopy
r_{sa}	Aerodynamic resistance between substrate and canopy source height
ρ	Air density
S_r	Sink term for water consumption by roots
S^*	Median absolute deviation
Θ	Saturation
θ	Volumetric soil water content
θ_r	Residual water content
θ_s	Water content at saturation
t	Time
τ	Parameters for AR(n)-model
$\boldsymbol{V}$	Matrix of normalized eigenvectors
w	Weights
$X(t)$	Raw tree-ring width series
$\hat{X}(t)$	Long-term growth trend
$\boldsymbol{X}$	Matrix of climatic predictor variables
Ξ	Optimization criterion for spline smoothing
$\boldsymbol{y}$	Vector of univariate response variable
z	Soil depth
$\boldsymbol{Z}$	Matrix of principal components
ζ	Cut-off frequency
$\zeta_{0.5}$	50% cut-off frequency

List of Abbreviations

EPS	Expressed population signal
GAM	Generalized additive model
GCV	Generalized cross validation
GLK	Gleichläufigkeit
IS	Short-term impact on tree-growth
IL	Long-term impact on tree-growth
JJAP	June-July-August precipitation sum
JJAT	June-July-August temperature mean
MS	Mean sensitivity
OLS	Ordinary least squares
PCA	Principle component analysis
Rbar	Mean interseries correlation
RSS	Residual sum of squares
RWI	Ring-width index
S	Sensitivity

I. Introduction

Trees are fascinating lifeforms. For many a decade they stand fixed in the landscape and have no other choice as to efficiently interact with atmosphere, soil and neighbors. And to the researcher's delight, they keep a record of their activities, strains and successes: year after year, layers of wood are built, that—in seasonal climates—result in distinguishable tree-rings. One of the stories these tree-rings tell is about the climate of the past. Tree growth is a process obeying the principle of uniformitarianism—i.e., that the physical and biological processes that link current environmental processes with current patterns of tree growth have been in operation in the past (Fritts, 1976). Thus, the climate's manifestation in tree-rings allows for either reconstructing past climatic conditions from tree-ring series calibrated with recent climate, or for predicting tree growth subject to climatic conditions known from the past. The former approach is termed dendroclimatology and is a subdiscipline of paleoclimatology. The latter one is termed dendroecology, and could most aptly be assigned to the field of forest ecology. This dissertation contributes to the growing field of dendroecological research, as it aims at the employment of tree-rings as proxies for a tree's past reaction to climatic constraints, to derive predications about current and future tree growth in the context of climatic change, focusing on temperate forest tree species.

The predicted increase in frequency and duration of drought events associated with climatic change (Beniston, 2004; Luterbacher et al., 2004) sets the backdrop for this study. In temperate forests, drought is a major constraint on plant growth and productivity, as it is for most terrestrial plant communities (e.g. Churkina & Running, 1998; Luyssaert et al., 2010), and the consequences of drought and secondary damages for temperate forests range from losses in productivity and increased mortality rates on stand level to regional forest die-offs covering several million hectares (Allen et al., 2010). Along with the threatening of the integrity of these ecosystems comes the threatening of the economic and social functions they serve: the supply of energy, construction and food resources, the protection of water and soil, and the recreation and conservation they provide. From an integrated ecosystem perspective, among the most important processes affected when forest ecosystems lose their integrity are hydrological cycles, and carbon and energy fluxes between atmosphere and land surface. The understanding of forest response to extreme drought is thus of crucial ecological, economical, and social value.

How growth of temperate forests trees is limited by climate in general, and by severe drought episodes in particular, is the objective of this study. The study sites are located in Bavaria, Southern Germany, and adjacent states, and with latitudes from 47° to 50° N well within the northern temperate zone.

I.1. Climatic change and forest trees

Rising concentrations of greenhouse gases are most probably responsible for the currently observed rising trend in global surface temperatures. Since 1970, this rise amounts to about 0.5 °C absolutely (Intergovernmental Panel on Climatic Change (IPCC), 2007). Even the most moderate climate scenarios imply a further increase of temperatures, coupled with an increase in extreme climatic events like drought episodes (Salinger, 2005; Schär et al., 2004; Sterl et al., 2008). In regional projection this means that Southern Germany will face higher summer temperatures and, at least in some areas, lower precipitation sums during the summer (Jacob et al., 2008). Also, the frequency of severe summer drought episodes is predicted to increase in Southern Germany (KLIWA, 2006).

A foretaste of future drought events was given by the very warm and dry summer of 2003. For Europe, a number of studies report on forest die-off as a consequence of this extreme drought episode (see Allen et al., 2010, for an overview). In the investigation area, the drought of 2003 led to a large-scale depletion of soil water storage, and thus to severe constraints on transpiration of forest trees (Raspe et al., 2004). As a consequence, forest productivity was dramatically reduced (Borchert, 2004), and the vitality of forest trees has been significantly diminished (Bayerisches Staatsministerium für Landwirtschaft und Forsten, 2004). From a historical perspective, this event was a very rare occasion; but according to recent model simulations, it can be well considered a prototype for future—more frequent—extremes under climate change conditions (Beniston, 2004; Schär & Jendritzky, 2004).

I.1.1. Effects of drought episodes on tree vitality

The effects of severe drought events on tree health are rather direct by altering the trees' mortality through physiological predisposition. Under drought stress, a descending water potential along the assimilation pathway from root to leaves results in a restrained transpiration rate. Eventually, the steady state in water flow will be ultimately disrupted by an outage in cohesive flow and xylem cavitations, putting the hydraulic integrity of the tree at risk (Tyree & Sperry, 1988).

The primary mechanism that finally leads to mortality through drought stress is covered by two alternative theories: the hydraulic disruption covered above (Pockman & Sperry, 2000), and a disturbed carbon balance (White, 1989). The latter theory states that a plant cannot survive under enduring drought stress, because no carbon can be assimilated. Both theories are connected via the stomatal control on photosynthesis (Bréda et al., 2006; Martínez-Vilalta et al., 2002).

A secondary pathway to drought induced mortality is through herbivores and pathogens. Both drought-initiated changes in carbohydrate and protein metabolisms and the drought-induced attenuation of active defence mechanisms lead to a predisposition to disease (Schoeneweiss, 1981). Global-change-type drought events have been associated with increased damage syndromes caused by fungi (Desprez-Loustau et al., 2006) and herbivores (Ayres & Lombardero, 2000).

Trees may survive infrequent extreme events but ultimately die if frequency and duration of such events increase (Lebourgeois et al., 2010). But in almost every case a significant reduction of increment growth indicates a loss in productivity related to drought events (see e.g. Bigler et al., 2006, 2007; Eilmann et al., 2006; Klemmt et al., 2009; Utschig et al., 2004, among many others). And mortality as the final consequence of increased physiological drought stress is not necessarily triggered by secondary damages exclusively (compare e.g. Kölling et al., 2009a), but also directly by the reduction in vitality associated with physiological drought stress (Becker, 1989; Bert, 1993; Bigler et al., 2006, 2007).

I.1.2. Effects of increasing mean temperatures on tree vitality

Irrespective of total precipitation amount, warmer temperatures alone can increase water stress of forest trees (Angert et al., 2005; Barber et al., 2000). However, for tree species well within their distributional range, the main control of higher mean temperatures on vitality is exerted indirectly, through altered pathogen dynamics. In temperate regions, an increase in mean temperature generally has positive effects on the development cycle of poikilotherm organisms (like many pathogens), and increases their reproductive potential (Asante et al., 1991; Porter et al., 1991; Sharpe & DeMichele, 1977). Warmer winter temperatures additionally increase survival rates during winter (Marçais et al., 1996; Virtanen et al., 1998). This leads to a higher potential for forest damages through insects.

In contrast, tree species growing at or near the drier edge of their distributional limits may also be directly threatened by higher mean temperatures (Jump et al., 2006), as they are not adapted to even drier conditions. Their loss in vitality is then instigated by the deprivation in hydraulic integrity, as depicted above.

In the individual case, the effects of increased mean temperatures and more frequent extremes can not be separated unambiguously, as a number of complex interactions between site quality, temperature-dependent factors like pathogens and direct drought effects exist (Fensham & Holman, 1999; Lloret et al., 2004).

I.2. Assessing the drought susceptibility of forest trees – setting the scene

Given the loss in productivity and increase in mortality under climate change conditions, the future suitability of native tree species is questioned. A number of recent studies tackle this concern. These studies could basically be ascribed to either empiricism, expertise or simulation, based on the methodology used.

I.2.1. Simulation studies

Simulation approaches to the drought response of trees and forest stands include dynamic succession models based on gap-phase dynamics (Bugmann, 1996; Bugmann & Cramer, 1998), individual tree based stand growth models incorporating climate-sensitive difference equations (Pretzsch & Dursky, 2002), and deterministic process models (Pastor & Post, 1988; Pedersen, 1998). Simulation models are best suited for equilibrium states in climate and site conditions (Lindner & Cramer, 2002), as the set of equations used to explain observed behavior is subject to specific boundary conditions and calibrated within those. Thus, the predictive power of especially process-based models—i.e. prediction under different boundary conditions not calibrated within—is questionable at least from a theoretical perspective (Hauhs & Lange, 2006). A substantial benefit can thus be gained through a broad range of site and climate conditions for an extended calibration, rendering a simulation model more applicable for climate impact research (Pretzsch et al., 2002).

I.2.2. Expertise

Expert knowledge is based on scientific insights and/or practical experiences, i.e. tree behavior under managed conditions. A typical *modus operandi* is a benchmarking approach based on some subjectively chosen criteria, either merely physiological (Auge et al., 1998; Niinemets & Valladares, 2006), or a combination of both physiological and practical knowledge (Roloff & Grundmann, 2008). Obviously, any expertise can only be as profound as the information available to the expert. Given the generally high uncertainty regarding tree reaction to summer drought subject to interaction with climatic and site boundary conditions, the scientific and practical value of these expert assessments might be rather questionable at the current state.

I.2.3. Empirical approaches

Among the empirical approaches, biogeographic techniques are becoming increasingly popular, particularly climatic envelopes (e.g. Iverson & Prasad, 1998; Iverson et al., 2008; Kölling, 2007; Talkkari & Hypén, 1996). For these statistical models of growth potential, climatic conditions (especially mean yearly temperature and mean yearly precipitation sum) are related to the potential or actual distribution of the individual tree species. These envelopes are then juxtaposed to the assumed future distributions of the respective climatic parameters to derive recommendations for forestry practice. Major drawbacks of this approach include ignoring the effects of climatic extremes, site-climate-interactions, intraspecific variability and adaptability (Bolte et al., 2008; Hamann & Wang, 2006). Furthermore, the mere presence or absence of a species does not tell anything about the vitality of the population at point.

The opposite extreme in terms of observational scale in empirical studies are studies on tree physiology under drought stress. Typically, the impact of drought on tree water status and/or on photosynthetic activity is captured, using various methods and combinations thereof, including sap flow measurements, measurements of transpiration rates and leaf gas exchange, and the indirect measurement of stomatal control on photosynthesis using stable carbon isotope (δ^{13}C) methods (e.g. Aasamaa et al., 2004; Auge et al., 1998; Maier-Maercker, 1998; Rennenberg et al., 2004). Owing to the methodological effort, usually only a small number of trees or saplings are considered for investigation, and the considerable reduction of natural influence factors in controlled experiments hampers the upscaling of results to adult trees, let alone ecosystems (Diamond, 1983). Therefore, the results drawn from excessive studies in model ecosystems should be interpreted with care, and generalization is most probably not advised (compare, e.g. Rennenberg et al., 2004, and the response by Ammer et al., 2005).

A compromise between the two extremes—models built from large sets of presence/absence data vs. conclusions drawn from a few, extensively studied individuals—can be found in the form of vitality assessments. The present dissertation could be ascribed to this class of studies. Vitality *per se* is not straightforward to define, the term is commonly associated with stress-tolerance, longevity, growth, and reproduction (Dobbertin, 2005). And as vitality cannot be measured directly, some proxy for vitality has to be captured instead, like tree growth or crown transparency (see Dobbertin, 2005, for an overview). If that parameter is easily measured, a large number of contrasting sites over a vast investigation area can be incorporated in the study. For example Huang et al. (2010), Miyamoto et al. (2010), and Büntgen et al. (2007) used tree growth as an indicator for vitality on large networks of sites.

I.3. Towards a dendroecological drought impact assessment

The approach followed in this dissertation is based on the assumption that parameters derived from tree-rings can act as surrogate variables for tree vitality. Large amounts of tree-ring data can be collected and evaluated in a relatively short time-span, which enables the incorporation of many sites with contrasting climatic and site conditions into the study. As both a broad spatial resolution and the direct connection to tree vitality is permitted by the approach followed, the present study is believed to suffer from neither the short-term nature and limited inter-site transferability of controlled ecophysiological experiments, nor from the lack of performance information in presence/absence modeling. And apart from the ease of data collection, a major advantage of tree-rings is their archiving nature, which allows for a retrospective analysis of tree vitality.

I.3.1. Tree-rings as environmental archives

Most gymnosperms and dicotyledon angiosperms in seasonal climates produce one tree-ring per year. The ring formation is started with earlywood in spring and early summer, usually characterized by thin cell walls and large lumen. In late summer, when growing conditions become less favorable, cambial activity slows and latewood is formed, with compact lumen and more flattened cells, rendering latewood appearance distinctively darker in most cases (Fritts, 1976). Following Liebig's law of the minimum, tree-ring growth cannot proceed faster than permitted by the most limiting factor (Fritts, 1976). Because of the limitation of tree-growth by environmental factors, series of tree-rings can be used as archives of a tree's reaction to these factors: as an integrating proxy for the ecophysiological processes that control allocation of carbon to shoot development (Dobbertin, 2005; Spiecker, 2002).

According to Cook (1990), the variance in tree-ring growth contributed by climatic influence will increase when trees grow at or near their climatic range. Well within the distributional range of a species, other factors might contribute more to the annual variability of tree-growth (Leal et al., 2008). Usually, latitudinal and altitudinal treeline sites are most sensitive to temperature variations, whereas lower treeline and forest border sites are most sensitive to precipitation (Luckman, 2006). The trees used in this study are located on neither treeline or border. Thus, the limiting factors are not uniform and easy to identify across the investigated populations. Under these circumstances, the variance in annual tree-ring growth related to climatic influences may fall below 30% (e.g. Büntgen et al., 2007; Rozas et al., 2009) compared to over 60% in sensitive sites used for climate reconstruction (e.g. Esper et al., 2010). Furthermore, the correlation patterns derived from growth/climate relations may be complicated to interpret (Friedrichs et al., 2008; Leal et al., 2008).

The greatest methodological challenge of this dissertation is therefore the extraction of quantitative information about the limiting factors of tree growth. It is achieved using a variety of different approaches, including dendroclimatic calibration, pointer year analysis, and a newly developed approach based on multivariate benchmarking using dendroclimatic archetypes. The former, direct approach of calibration is based on the assumption of multiple linear relationships between climate and tree growth. The main assumption of the latter, indirect approach is based on the hypothesis that universal patterns of tree growth can be identified. These are consistent across species and sites, i.e., about the same pattern representing drought resistance may be found in any tree, but to a varying degree. The distinctness of the respective patterns can then be used as a comprehensible, indirect measure for drought tolerance.

I.3.2. Focus on economically most important species

For this dissertation, Norway spruce (*Picea abies* (L.) H. KARST.), Scots pine (*Pinus sylvestris* L.), silver fir (*Abies alba* MILL.), common beech (*Fagus sylvatica* L.), and common oak (*Quercus robur* L.) as the major native forest tree species of Southern Germany are selected for two reasons: first, the abundance is high and allows for representative sampling, and second, the behaviour of these species under severe drought conditions and the site dependency of their climate-growth coupling is still uncertain.

A number of studies suggests the threatening of spruce growth under future climate scenarios for the investigation area (Kölling et al., 2009a,b; Leitgeb & Englisch, 2006; Profft et al., 2007). Spruce has been artificially grown far outside its natural montane and subalpine distribution for economical reasons (Schmidt-Vogt, 1988). Given a quota of still around 45% spruce in Bavaria's forests today (Brosinger & Tretter, 2007) two urgent questions arise: where the limits for growing spruce are under future climate conditions, and which species might be able to replace spruce in large parts of Bavaria. The call for substituting unstable monospecific spruce stands with sustainable mixed forests is unequivocal (e.g. Kölling et al., 2009b,a; Rothe & Borchert, 2003), but substantial uncertainties remain regarding alternative species. For instance, beech is discussed divisively (compare Hanke, 2004, and Rennenberg et al., 2005, but also Ammer et al., 2005). Even pine, which has had the reputation of a drought-resistant species for a long time (e.g. Cotta, 1849), shows a remarkable liability to drought-induced mortality in recent studies (Bigler et al., 2006; Pichler & Oberhuber, 2007; Rebetez & Dobbertin, 2004).

In addition to the five economically most important native tree species, Douglas fir (*Pseudotsuga menziesii* (Mirbel) Franco) was selected as a possible alternative to fir. Douglas fir has been successfully cultivated in Southern Germany since around 120 years, and the abundance is high enough to incorporate the species alongside the native species under investigation.

I.3.3. Consideration of site quality

Most studies dealing with the impact of drought (and climate in general) on tree growth focus on climatic parameters alone as predictors of tree growth (e.g. Abrams et al., 1998; Adams & Kolb, 2004; Battipaglia et al., 2009; Ogaya et al., 2003). However, the modification of local climate by site quality, like soil texture, is usually not taken into account. The soil water actually available to a tree at a certain time is a function of both climate and soil properties. Thus, incorporating the local soil water balance should enable to refine the climate-growth coupling specific to the very site.

This is achieved by modeling the soil water balance as a function of time for the stands under investigation. It is then tested, whether the modification of climate by the soils has any effect on the growth signals carried in the tree-ring series.

I.3.4. Consideration of tree-size

Studies on growth reaction to climate and drought tend to focus on dominant or codominant trees only, and quantitative data about the reaction of trees of different species is disproportionate to data about different size groups.

Research on size-dependent physiological patterns in trees is a relatively recent development (Thomas & Winner, 2002). As developing trees increase both their size and structural complexity, trees of different dimension may react differently to exogenous factors (e.g. Szeicz & MacDonald, 1995), finally leading to heterogeneous growth responses to changes in resource availability on stand level. According to Schwinning & Weiner (1998), depending on the respective limiting factor (e.g. light, water, nutrients) the division of resources may be completely size asymmetric, whereby the larger plants receive most of the contested resources. The opposite borderline case is a complete symmetric division of resources, what means that all plants get the same amount of resources irrespective of their size. Limitation of light is mostly associated with asymmetric resource distribution, as light is "pre-emptable" by the tall trees in a stand. In contrast, scarcity of water and nutrients causes rather symmetric resource distribution as they represent a less directional resource. In this case the amount of resources and growth increases proportional to size. A number of studies show that the mode of competition can change spatially along ecological gradients (Pretzsch & Biber, 2010a) and temporally with stand development (Weiner & Thomas, 1986). Other studies reveal a change from size-symmetric competition in dry years when belowground resources are scarce to size-asymmetry in moist years when light becomes the limiting factor (Wichmann, 2001).

Despite this theoretical framework being challenged for more than 25 years by now, findings on how water stress affects growth of trees of different size are still rare and not conclusive for either coniferous or deciduous species. While a greater growth reduction as a response to drought was found for suppressed trees in *Pinus strobus* (Vose & Swank, 1994), *Picea abies* (Brakel & Visser, 1996) and *Pinus sylvestris* (Pichler & Oberhuber, 2007), the opposite pattern was observed for *Pinus nigra*, in conjunction with a faster recovery of dominant trees (Martin-Benito et al., 2008). Orwig & Abrams (1997) found different patterns between sites with different water availability for *Quercus alba*, *Carya glabra* and *Nyssa sylvatica*, indicating that understory trees exhibit greater growth reductions on mesic versus dry-mesic sites, while He et al. (2005) found greater growth reductions in adult *Acer rubrum* and *Betula papyrifera* trees compared to saplings, with no difference found for *Betula alleghaniensis* and *Acer saccharum*.

The present dissertation addresses the question of size-dependent reactions to drought by investigating three species that represent different paradigms of coping with drought stress: avoidance (Scots pine), tolerance (common oak) and intolerance (Norway spruce). Scots pine is characterized as a drought avoiding species due to its strategy of immediate stomata closure in combination with a deep rooting system (Richardson, 2000). Early stomata closure is necessary as Scots pine is a relatively cavitation prone conifer (Martínez-Vilalta et al., 2004). In contrast, common oak maintains a relatively high stomatal conductance and photosynthetic rate under drought conditions (Epron & Dreyer, 1993), what can be ascribed to deep rooting (Rosengren et al., 2005) and low susceptibility to air embolism (Cochard et al., 1992). Norway spruce has a relatively shallow root system (Rosengren et al., 2005), and has repeatedly been described as a drought intolerant species (Innes, 1991; Lu et al., 1995, 1996; Strand, 1997).

Tree-ring series are employed to compare growth patterns of dominant and suppressed trees with respect to climate and climatic extremes. The approach followed also incorporates measurements of wood δ^{13}C as a more specific measure for drought stress, as wood δ^{13}C can be employed as a proxy for stomatal regulation and thus photosynthetic rate during the wood formation (Farquhar et al., 1989). There is evidence from wood δ^{13}C that under average climatic conditions larger trees decrease photosynthetic rate due to an altered hydraulic architecture (Yoder et al., 1994), but to the candidate's knowledge no study exists where this relationship is tested under both average and drought conditions.

I.3.5. Consideration of root-shoot allocation patterns

Most studies analyze the productivity of forest trees with a focus on above-ground vegetation parts (summarized in Boisvenue & Running, 2006), thus neglecting 10 to 40% of the total biomass, produced below-ground (Vanninen et al., 1996; Litton et al., 2007). Simultaneously, increasing biomass allocation towards above- and/or below-ground structures is a key trait for adapting to changes in resource availability (Weinstein et al., 1991; Dech & Maun, 2006). The adjustment of allocation patterns aims for an optimization of resource uptake under given environmental constraints. Thus, disregarding below-ground responses may result not only in deficits in the understanding of plant internal ressource allocation, but also in misrepresentation of plant performance and competitive ability (Matyssek et al., 2005).

Analysis on root growth dynamics is, therefore, fundamental to a comprehensive understanding of carbon storage and biochemical dynamics of forest ecosystems (Litton et al., 2007). Despite the demand for integrated research on above- and below-ground compartments being widely acknowledged, there are only few experimental studies on whole-plant biomass allocation of adult trees *in situ* (Comeau & Kimmins, 1989; Körner et al., 2005; Wang et al., 2000). Two alternative frameworks for resource allocation among different plant organs have been put forward: according to the optimal partitioning theory (OPT), a plant invests in order to gain access to the limiting resource (Bloom et al., 1985), whereas according the allometric biomass partitioning theory (APT) resource allocation patterns change solely with plant size (Enquist & Niklas, 2002; Müller et al., 2000). This means that—dependent on the theory under consideration—an increase in water limitation of tree growth may lead to either no change in allocation patterns (APT), or to the allocation of resource to the roots, to gain improved access to the soil water (OPT).

The main implication of these uncertainties for the questions tackled with this dissertation is that the whereabouts of carbon that is not allocated to stem growth under stress conditions remains widely unknown. To address this shortcoming, on a subset of sites chosen for this dissertation a precipitation gradient is established to represent a unreal time series of increasing drought stress under climate change conditions. Tree-ring series of stems and roots are then used to establish allometric relations for the allocation of carbon between above- and below-ground compartments.

I.4. Research objectives and hypotheses tested

Based on the framework and prerequisites outlined above, three leading research objectives were refined and connected to four main hypotheses:

1. Quantification of climatic constraints on tree-growth in temperate forests along a multidimensional gradient of sites, with a focus on differences resulting from tree species, tree size, regional climate and soil characteristics.

   Hypotheses tested:

   H1 The long-term limitation of tree-growth by climate and water availability is subject to species, site and tree-size.

   H2 The short-term impact of severe drought events on tree-growth is subject to species, site and tree-size.

2. Identification of universal, cross-species growth patterns with a connection to either drought resistance or drought susceptibility, which can be employed as ecological benchmarks.

   Hypothesis tested:

   H3 Growth reaction of forest trees to summer drought can be explained by universal reaction patterns that are valid across sites and species.

3. Quantification of possible changes in carbon allocation between shoot and root with increasing water stress.

   Hypothesis tested:

   H4 With increasing water stress, trees allocate relatively more carbon to the roots to increase their water uptake capabilities.

These hypotheses were operationalized as follows:

H1 Calculation of climate/growth relationships and relationships between growth and soil water balance features for stand-wise tree-ring chronologies from different species and a variety of sites (species and site effects) and individual tree-ring chronologies (size effects).

H2 Quantification of impact and recovery in connection with severe drought events on stand-wise tree-ring chronologies (species and site effects) and on individual tree-ring chronologies (size effects). Quantification of stomatal control on photosynthesis in drought vs. non-drought years among different groups of tree-sizes.

H3 Development of a benchmarking procedure based on multivariates extremes and application to stand-wise tree-ring chronologies.

H4 Application of allometric analyses on tree-ring series of roots and shoots of spruce trees growing along a precipitation gradient.

II. Material and methods

The main idea behind the study was to collect a large data set of tree-ring series from different species, originating from a standardized and strict sampling protocol. The information contained in the tree-rings—either as mere ring width or as recorded in the isotopic composition of the wood—is then extracted with various methods and correlated to climatic and soil water data. To tackle the research questions regarding tree size effects on growth reaction to climate and the allocation of biomass to roots vs. shoots, a subset of the sampled sites was used, as the methodological efforts were considerably higher in these cases.

II.1. Sampling procedure

II.1.1. Sampling design

The dissertation focuses on the six economically most important tree species in Bavaria, Southern Germany: *Picea abies* (L.) H. Karst., *Pinus sylvestris* L., *Abies alba* Mill., *Pseudotsuga menziesii* (Mirbel) Franco, *Fagus sylvatica* L. and *Quercus robur* L. Tree-ring cores were taken on various sites according to a protocol for site selection as follows: presence of as many of the target species in spatial proximity as possible (site homogeneity), closed canopy stands with as little strata as possible (structural homogeneity), mature stands not yet in rejuvenation (homogeneity of age), and no thinning operations directly before or after severe drought events (homogeneity of diameter increment). In total, 143 populations of trees were sampled on 48 sites in total, 40 in Bavaria, Southern Germany, 5 in Baden-Wuerttemberg, Southern Germany, and 3 in Vorarlberg, Western Austria. The per-species replication depth was 38 populations for spruce, 21 for pine, 26 for silver fir, 8 for Douglas fir, 24 for beech and 23 for oak. Tab. II.1 gives an overview over the sampled sites, the location of the sampled populations within the investigation area is depicted in fig. II.1.

Table II.1.: Sampled sites and tree species. Species are abbreviated as PA (*Picea abies*), PS (*Pinus sylvestris*), AA (*Abies alba*), PM (*Pseudotsuga menziesii*), FS (*Fagus sylvatica*) and Q (*Quercus spp.*).

#	**Geological unit**	**Location**	**Species**	**Latitude** [°]	**Longitude** [°]	**Altitude** [m a.s.l.]
1	Alps	Bad Laterns (Austria)	PA, AA	47.27713	9.77775	1300
2	Alps	Tilis (Austria)	PA, AA	47.26527	9.64265	700
3	Alps	Viktorsberg (Austria)	PA, AA	47.30153	9.67568	1000
4	Franconian Lower Triassic	Bad Brueckenau, Oehrberg	PA, PS, AA, PM, FS, Q	50.23703	9.93233	400
5	Franconian Lower Triassic	Graefendorf, Brombusch	FS, Q	50.12727	9.71603	250
6	Franconian Lower Triassic	Graefendorf, Gerlitzenschlag	PA, PS	50.11558	9.71623	315
7	Franconian Lower Triassic	Graefendorf, Kleinemass	FS, Q	50.13735	9.71692	250
8	Franconian Lower Triassic	Graefendorf, Lindenfuerst	FS, Q	50.15202	9.71937	260
9	Franconian Upper Triassic	Heideck	PA, PS, AA, FS, Q	49.13610	11.04392	460
10	Franconian Upper Triassic	Stadtwald Rothenburg	PA, AA, PM, FS, Q	49.32550	10.22712	475
11	Franconian Upper Triassic	Karlstadt, Muehlbach	FS	49.96480	9.74437	260
12	Franconian Upper Triassic	Veldensteiner Forst	PA, AA, FS	49.93948	11.31627	460
13	Franconian Upper Triassic	Castell, Schwanberg Alter See	Q	49.72562	10.27073	430
14	Franconian Upper Triassic	Castell, Schwanberg, JU	FS, Q	49.72562	10.27073	430
15	Franconian Upper Triassic	Alte Veste Zirndorf	PA, PS, AA, PM, FS, Q	49.45358	10.96467	360
16	Franconian Upper Triassic	Rothenburg, Sommerleite	PA, PS, AA, FS, Q	49.31187	10.36585	440
17	Franconian Upper Triassic	Roth, Hartmannshof	PA, AA	49.49365	11.56452	420
18	Franconian Upper Triassic	Pegnitz, Maximiliansgrotte	PA, PS, AA, PM, FS	49.62643	11.59482	440
19	Molasses	Unterer Blomberg	PA, AA, FS	47.74697	11.51140	740
20	Molasses	Hohenpeissenberg	PA, AA	47.80500	11.02260	910
21	Molasses	Taubenberg Nordhang	PA, AA, FS	47.83500	11.77190	730
22	Molasses	Taubenberg Suedhang	PA, AA, FS	47.82740	11.77130	730
23	Quaternary gravel	Forstenrieder Park	PA, PS, Q	48.07438	11.47720	570
24	Quaternary gravel	Eglharting frisch	PA	48.09192	11.87425	560

continued on next page

Table II.1 – continued

#	**Geological unit**	**Location**	**Species**	**Latitude** [°]	**Longitude** [°]	**Altitude** [m a.s.l.]
25	Quaternary gravel	Eglharting maessig frisch	PA, PS, Q	48.09192	11.87425	560
26	Quaternary gravel	Hoehenkirchen-Siegertsbrunn	PA, PS, AA, PM, FS	48.02173	11.78602	590
27	Tertiary	Hoeglwald	PA	48.50000	11.18333	540
28	Tertiary	Kranzberg/Thalhausener Forst	PA, Q	48.40533	11.71452	475
29	Tertiary	Schiltberg Nordhang	PA, PS, AA	48.45157	11.27092	470
30	Tertiary	Schiltberg Ruecken	PA, PS, AA, FS, Q	48.45282	11.25147	470
31	Tertiary	Schiltberg Suedhang	PA, PS, AA	48.44787	11.26020	470
32	Tertiary	Weissenhorn, Boeckeler	PA, Q	48.29347	10.29613	530
33	Tertiary	Weissenhorn, Steinbruch	PA, AA, FS	48.32198	10.24690	530
34	Tertiary	Weissenhorn, Stangengehau	FS	48.32100	10.24600	530
35	Tertiary	Weissenhorn, WB	Q	48.32760	10.24462	540
36	Tertiary	Weissenhorn, WG	AA	48.32823	10.26195	520
37	Upper Palatinate basins	Neuersdorf, Binsenschlag	PA, PS	49.56600	12.04848	440
38	Upper Palatinate basins	Neuersdorf, Haeckelschlag	PA, PS, AA, FS	49.56600	12.04848	440
39	Upper Palatinate basins	Neuersdorf, Sauhoehe	AA	49.56837	12.03350	500
40	Upper Palatine forest	Schnaittenbach, Freudenberg	PA, PS, AA, PM, FS, Q	49.46998	12.01937	580
41	Western Jurassic	Kelheim, Kalklehm frisch	PA, Kle, FS, Q	48.83640	11.91138	470
42	Western Jurassic	Kelheim, Kalklehm trocken	PA, PS, Q	48.83640	11.91138	470
43	Western Jurassic	Kelheim, Loess frisch	PA, PS, PM, FS, Q	48.83640	11.91138	470
44	Western Jurassic	Kelheim, Loess wechselfeucht	PA, FS	48.83640	11.91138	470
45	Wuerttembergian Upper Triassic	Heilbronn Bergfeld	PA, AA, FS, Q	49.18168	9.36983	305
46	Wuerttembergian Upper Triassic	Heilbronn Ilsfeld	PA, PS, AA, PM, FS, Q	49.03065	9.26713	310
47	Wuerttembergian Upper Triassic	Heilbronn Klingenrain	PA	49.18600	9.33283	285
48	Wuerttembergian Upper Triassic	Heilbronn Taschenwald	PA, PS, AA, FS, Q	49.16872	9.10285	230

II.1.2. Tree sampling

General tree sampling

On each site, at least 13 vital and undamaged dominant trees of all relevant species were cored at breast height. Each tree was cored at least two times, from northwestern and southeastern direction. That way the trees were cored 45° displaced from the main wind direction to prevent bias in diameter estimation due to reaction wood. For coring, a drilling machine (BDF 452 RFE, Makita, Anjo, Aichi, Japan) was used in conjunction with hardwood corers (Suunto, Finland) or softwood corers (Haglöfs, Sweden). For transport, drying and storage purposes, cores were put into specially constructed groove boards.

Tree sampling for study on size effects

To study the effects of tree size on growth reaction to climate and drought, on one site (Forstenrieder Park, #23 in table II.1), each twenty trees across all diameter classes of spruce, pine and oak were sampled. In addition to the usual two cores, a replicate sample was taken to gain enough material for isotope analysis.

To determine the sapwood area for these trees, an additional fourth core was taken on a hot and dry summer day. Sapwood length l_s was measured directly to the nearest 1 mm as the wet part of the core. Sapwood area as was then computed as the difference between basal area $(\text{diameter}/2 - l_b)^2\,\pi$ and heartwood area $(\text{diameter}/2 - l_s - l_b)^2\,\pi$, where l_b is bark thickness (Wullschleger & King, 2000).

Tree sampling for study on root-shoot-allocation patterns

For the study of root versus shoot growth, a precipitation gradient of three sites was established from Zirndorf (#15 in table II.1, 369 mm average precipitation sum during growing season) via Kranzberger Forst (#28, 492 mm average precipitation sum) to Siegertsbrunn (#26, 694 mm average precipitation sum). Additional root sampling was carried out on spruce trees on these sites (Nikolova, unpublished). From each sample tree, the three largest horizontal roots were selected on the windward site to assure comparable ages and forces caused by wind action on growth of the root cambium. The roots were excavated from the soil and cored once from the upper surface of the root at positions about 30 to 50 cm from the trunk edge. This distance was determined according

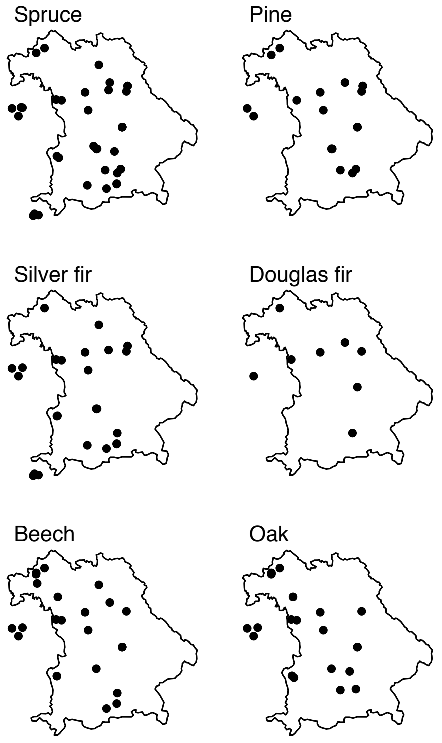

Figure II.1.: Location of the sampled population. The lines represent the political borders of Bavaria, Southern Germany.

to Krause & Morin (1999), who found the number of missing or discontinuous rings in roots to be lowest close to the trunk edge.

For the trees that were subject to root sampling, tree height was measured using the Vertex III ultrasonic hypsometer (Haglöf, Sweden). The individual tree h/d ratio, calculated as the tree height (h in m) divided by the tree diameter at breast height (d in cm), describes the individual form stability against wind-throw, with trees of a h/d ratio > 80 classified as relatively unstable (Mayer, 1984, p. 182). Unstable trees develop towards a slender, cone-shaped form, indicating wood formation on stem at breast height to have a lower priority than growth in height to improving the light supply.

II.1.3. Soil sampling

For each stand, at least one soil profile was recorded. When the homogeneity of the soil properties was doubtful, additional soil cores were taken. This way it is ensured that the employed stands grow on uniform substrate. Up to 1 m soil depth, soil texture and compaction were recorded for each horizon, following KA5 (AG Boden, 2005).

II.2. Climatic data

Climatic data was obtained in daily and monthly resolution from the German Weather Service (DWD, Deutscher Wetterdienst). In total, 29 station series from climate stations and 35 series from precipitation stations were used. The data series were tested for homogeneity, and single missing data were estimated by nearby stations. To obtain a realistic set of climate data for each site, data from nearby climate and precipitation stations were interpolated by inverse distance weighting (Shepard, 1968). Based on samples $u_i = u(P_i)$ for $i = 0, 1, \ldots, N$, the interpolated value u at a given point P is found as

$$u(P) = \sum_{i=0}^{N} \frac{w_i(P)}{\sum_{j=0}^{N} w_j(P)} u_i \tag{II.1}$$

with weights

$$w_i(P) = \frac{1}{\mathcal{D}(P, P_i)^r} \tag{II.2}$$

with known points P_i, the unknown point P and a distance metric $\mathcal{D}$ (here: Euclidian distance). The power parameter r defines the smoothness of the interpolation, and was set to 1 to downweight the influence of remote points.

This way, monthly time series of precipitation sums and temperature means were obtained for dendroclimatic calibration. For hydrological modeling, daily time series of daily minimum temperature, daily maximum temperature, global radiation, wind speed, vapour pressure, and daily precipitation sum were interpolated for each site.

II.3. Water balance modeling

II.3.1. Brook90-LWF

The hydrological model Brook90-LWF was used to model the soil water balance. This model is a modification of the model Brook90 (Federer et al., 2003) by Hammel & Kennel (2001). Brook90 is a one-dimensional, spatially-lumped physical process model representing the vertical water exchange in the soil. The modeled processes are the potential evaporation and the movement of soil water. Here, the modified Penman-Monteith potential evapotranspiration after Shuttleworth & Wallace (1985) is used. This expansion uses two discrete terms to separate total potential evapotranspiration νE into evaporation from the soil νE_s and transpiration from the canopy νE_c:

$$\nu E_s = \left(\Delta A_s + \rho c_p D_0 / r_{sa}\right) / \left(\Delta + \rho \left(1 + r_{ss}/r_{sa}\right)\right) \tag{II.3}$$

$$\nu E_c = \left(\Delta \left(A - A_s\right) + \rho c_p D_0 / r_{ca}\right) / \left(\Delta + \rho \left(1 + r_{cs}/r_{ca}\right)\right). \tag{II.4}$$

In the above formulæ, ρ is the air density, A_s is available soil energy, D_0 is the vapor pressure deficit in the canopy, r_{sa} is the aerodynamic resistance between substrate and canopy, r_{ca} is the boundary layer resistance of the vegetation, and r_{ss} is soil resistance. r_{aa} is the aerodynamic resistance above the canopy, and r_{sa} is the aerodynamic resistance between substrate and canopy source height; both are functions of constants and several parameters that are directly or indirectly supplied as model input, such as leaf area index, wind speed, vegetation height, eddy diffusitivity decay constant, reference height, von Karman's constant, and roughness length of substrate. D_0 is merely a function of vapor pressure deficit at reference height D_R, and is thus replaced by D_R. In Brook90-LWF, D_R is calculated from vapor pressure and air temperature.

The the movement of soil water is described as a Richards-model (Jury et al., 1991):

$$\frac{\delta \theta}{\delta t} = \frac{\delta}{\delta z}\left(K \frac{\delta \psi}{\delta z}\right) + S_r \tag{II.5}$$

with volumetric soil water content θ, time t, soil depth z, soil hydraulic conductance K, water potential ψ and sink term S_r for water consumption by roots.

Substantial modifications of the original model by Hammel & Kennel (2001) are the application of the Mualem–van Genuchten parametrization of the hydraulic functions (van Genuchten, 1980), an adapted time control for the hydraulic parameters, stand development over time, development of fine root distribution over time, and temperature-dependent phenology.

II.3.2. Parametrization of hydraulic functions

In Brook90-LWF, the original parametrization of the hydraulic functions after Clapp & Hornberger (1978) is replaced by the Mualem–van Genuchten parametrization

$$\psi_{\mathcal{M}}(\Theta) = -\frac{1}{\mathcal{A}}\left[\Theta^{\mathcal{N}/(1-\mathcal{N})} - 1\right]^{1/\mathcal{N}} \tag{II.6}$$

$$K(\Theta) = K_s\Theta^{\mathcal{L}}\left[1 - \left[1 - \Theta^{\mathcal{N}/(1-\mathcal{N})}\right]^{1-1/\mathcal{N}}\right]^2 \tag{II.7}$$

$$\Theta = \frac{\theta - \theta_r}{\theta_s - \theta_r} \tag{II.8}$$

to represent the saturation Θ, and water potential and hydraulic conductivity as functions of Θ. θ_s is the water content at saturation, θ_r is the residual water content, K_s is the hydraulic conductivity at saturation, and $\mathcal{A}$, $\mathcal{L}$, $\mathcal{M}$ and $\mathcal{N}$ are empirical parameters. The advantage of this parametrization is that a number of modern pedotransfer functions can be employed to derive soil hydrological parameters from other parameters that are easier to obtain under field conditions. For this study, soil hydraulic parameters were derived through the pedotransfer function of Schaap & Leij (1998). This function is a regression model based on a hierarchical neural network calibrated with numerous soils in Europe and the USA that takes soil texture classes as input to predict $\mathcal{A}$, $\mathcal{L}$, $\mathcal{M}$ and $\mathcal{N}$ for the Mualem–van Genuchten parametrization.

II.3.3. Water balance modeling in mixed stands

A general shortcoming of soil water balance models is the incapability to describe complex forest stands. E.g., Brook90 is designed for non-stratified, mono-specific stands. Thus, for the approach of this dissertation, the problem of modeling soil water balance in mixed stands arises. To mitigate this shortcoming, only stands with a homogeneous age-distribution were selected, and it was paid attention to select stands without a complete intermixture of the species involved, but rather with bands of one species – to avoid interactions among different species. Consequentially, the water balance of mixed stands was

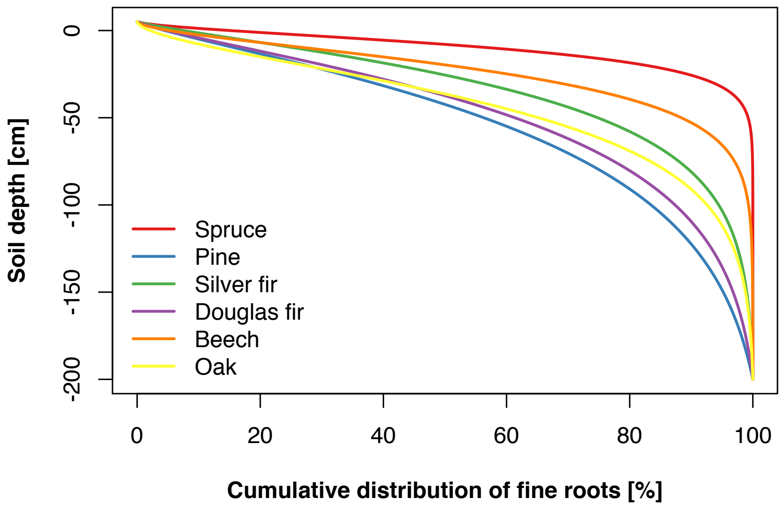

Figure II.2.: Cumulative fine root distribution of the species under investigation assembled from published data.

modeled as the arithmetic mean of hypothetical pure stands of the species encountered (Hammel & Kennel, 2001).

II.3.4. Vegetation parameters

In mixed forest stands, species-specific profiles of the fine root distribution with depth are almost impossible to obtain, for each single fine root encountered in the soil profile would have to be attributed to a certain species. Therefore, for all six species under investigation, a typical vertical distribution of fine roots was assembled from published data (Weis et al., 2009) and used for all parametrizations (see Fig. II.2).

Specifications of leaf area index (LAI) and maximum stomatal conductance (GLMAX) were taken from Breuer et al. (2003). The minimum stomatal conductance (GLMIN) was set to 2% of GLMAX for coniferous species, and to 20% of GLMAX for deciduous species. For stem area index (SAI), measured values from the Höglwald were used (Wendelin Weis, pers. comm.). Constant values were used for all stands (Tab. II.2).

II.3.5. Implementation details

To streamline the use of Brook90-LWF for this dissertation, the original, Microsoft Access based input generator was circumvented by a custom input generator written in R (R Development Core Team, 2009) and Unix Bash. This way, climate and parameter input

Table II.2.: Vegetation parameters used for water balance modeling: leaf area index (LAI), stem area index (SAI), maximum stomatal conductance (GLMAX) and minimum stomatal conductance (GLMIN).

Species	LAI	SAI	GLMAX [mm/s]	GLMIN [mm/s]
Spruce	6,0	3,0	3,5	0,07
Pine	2,0	1,25	4,0	0,08
Silver fir	6,0	3,0	4,0	0,08
Douglas fir	9,0	5,0	4,25	0,09
Beech	6,0	2,0	4,0	0,80
Oak	4,5	1,5	4,5	0,90

files were created automatically based on the coordinates of the sites, the species involved, and the stand age derived from tree-ring series. The various workstations running the simulations for all 143 site–species combinations were monitored and synchronized using a custom messaging system implemented using the Twitter API.

II.3.6. Output parameters

Two output parameters of Brook90-LWF were used for further analysis: soil water content θ, integrated over the first 100 cm of soil, and a modified transpiration deficit. Usually, transpiration deficit is calculated as the difference between actual transpiration and potential transpiration (Rossi et al., 2007). Under non-drought conditions, this difference is 0, indicating that the transpiration by the forest stand is not limited by soil water supply. As time series of transpiration deficit were needed for regression analysis, the more homoscedastic ratio of actual to potential transpiration was employed for this dissertation. A ratio < 1 indicates temporary water shortage.

II.4. Tree-ring measurement

The increment cores of each tree were mounted and smoothed with a chisel. Ring-widths were measured to the nearest 0.01 mm on each core using a measuring table (LINTAB 5; Rinntech, Heidelberg, Germany) with a stereoscope (MZ 6; Leica, Wetzlar; Germany) and the TSAP-Win software package (Rinn, 2003). Crossdating accuracy was checked both visually by on-screen curve comparison in TSAP-Win and statistically using program COFECHA (Holmes, 1983). COFECHA compiles a crossdating accuracy report based on leave-one-out interseries correlations for shifted series segments of a given length (here: 50 year segments shifted by 25 years). The correlation of the series segment left out with the mean series of the remaining series is reported for time lags of -10 years to +10 years for the identification of measurement errors like missed or double rings. Cores that could not successfully be crossdated even after several measurements were omitted from further analysis.

II.5. Representation of tree-ring series

The tree-ring series are represented according to a linear aggregate model of unobserved components (Cook & Kairiukstis, 1990):

$$X(t) = \hat{X}(t) + \tilde{X}(t) + \delta D_1(t) + \delta D_2(t) + E(t) \tag{II.9}$$

where $X(t)$ is the observed tree-ring width series, $\hat{X}(t)$ is the age- or size related long-term growth trend, $\tilde{X}(t)$ is the tree growth signal related to climate, $D_1(t)$ and $D_2(t)$ are disturbance pulses caused by local endogenous disturbance and standwide exogenous disturbance, respectively. The unexplained year-to-year-variability unrelated to the other components is summarized in $E(t)$. $X(t)$ is non-stationary, because $\hat{X}(t)$ is a process reflecting geometrical constraints and effects of aging. The target component in equation II.9 is $\tilde{X}(t)$, and a number of steps are required to get from $X(t)$ to a standardized series of tree-ring indices that best reflects $\tilde{X}(t)$.

II.5.1. Tree-ring standardization

Standardization of a tree-ring series $X(t)$ usually is achieved by estimating the long-term growth trend $\hat{X}(t)$, and to carry out subsequent analyses on the remainder of the curve fitting procedure—the ring width indices (RWI) $I(t)$: $I = X/\hat{X}$. Out of the various different possibilities for tree-ring standardization (see Cook & Kairiukstis, 1990, for an overview), a frequency domain approach was chosen for this dissertation for two reasons: first, the long-term growth signal of trees from closed canopy stands is usually not dominated by a simple age-related trend that could be captured by a biologically motivated deterministic function, and second, the research questions tackled with this dissertation do not aim at long-term growth trends that should be preserved by more conservative methods. Instead, it was aimed at removing as much low-frequency variation as possible, to strengthen the climatic signal in the resulting index series. Therefore, every tree-ring series has been subject to low-pass digital filtering, in the form of cubic smoothing splines that are fit to $X(t)$ to obtain $\hat{X}(t)$. Following de Boor (1978), for a given series of N tree-rings taking values $X(t_j)$ at times t_j with $j = 1 \ldots N$, the smoothing spline fit $\hat{X}(t)$ is found as the instance of a function $f(t)$, that minimizes

$$\Xi = \lambda \sum_{j=1}^{N} \left[f(t_j) - X(t_j)\right]^2 + (1-\lambda) \int_{t_1}^{t_N} \left[\ddot{f}(t)\right]^2 dt. \tag{II.10}$$

Minimizing equ. II.10 is a compromise between a close fit of the data (first term), and obtaining a smooth curve (second term). For the use of smoothing splines as low-pass filters, λ is chosen on the basis of the desired filtering to obtain an effective frequency response ϕ at a frequency ζ. Following Cook & Peters (1981), the frequency response $\phi(\zeta)$ for a cubic smoothing spline is given by

$$\phi(\zeta) = 1/\left(1 + \frac{\lambda\left(\cos 2\pi\zeta + 2\right)}{6\left(\cos 2\pi\zeta - 1\right)^2}\right). \tag{II.11}$$

To obtain λ for a frequency 50% cut-off at $\zeta_{0.5}$, equ. II.11 can be rearranged to

$$\lambda = \frac{6\left(\cos 2\pi\zeta_{0.5} - 1\right)^2}{\cos 2\pi\zeta_{0.5} + 2} \tag{II.12}$$

In this dissertation, a $\zeta_{0.5}$ at 2/3 of the curve length is applied for all series, as this is empirically supported as a good compromise between overfitting (i.e. removing an excessive amount of variance) and underfitting (i.e. retaining a high amount of low-frequency variability) (Cook & Kairiukstis, 1990).

II.5.2. Autoregressive modeling

Due to persisting effects of carbon storage and remobilization across years, series of tree-ring indices are characterized by a reasonable amount of serial autocorrelation. Serious amounts of serial autocorrelation violate assumptions of statistical techniques, such as OLS regression, as the variance structure is influenced by a latent variable. To be able to remove the autocorrelation structures from the tree-ring series, the RWI series $I(t)$ were considered AR(n) processes of the form

$$I(t) = c + \sum_{i=1}^{n} \tau_i I(t-i) + \epsilon(t) \tag{II.13}$$

with order n chosen via Aikaike's Information Criterion (Venables & Ripley, 2002), usually ranging between 1 and 3, which is in line with satisfactory AR(1)–AR(3) models for various coniferous and deciduous species in North America (Cook, 1985; Monserud, 1986; Knutson & Pyke, 2008) and Europe (Birrong & Schönwiese, 1988; Dittmar & Elling, 1999). The autocorrelation structure $\hat{I}(t) = \sum_{i=1}^{n} \tau_i I(t-i)$ is then removed from $I(t)$ by subtraction, a process that is also called prewhitening.

II.5.3. Chronology building

The averaging of the index series $I(t)$ from all trees per species and stand to a site chronology $\bar{I}(t)$ aims at the removal of the disturbance pulses $\delta D_i(t)$ in equation II.9. This site chronology is then considered the common climatic signal of tree growth for the population under investigation. Tukey's biweight robust mean was used as averaging procedure (Mosteller & Tukey, 1977), with the biweight mean of m observations for year t_i computed by iteration as

$$\bar{I}(t_i) = \sum_{j=1}^{m} w_j(t_i) I_j(t_i) \tag{II.14}$$

and the symmetric weights function $w(t)$ given as

$$w(t_i) = \begin{cases} 0 & \text{if } \dfrac{I(t_i) - \bar{I}(t_i)}{6S^*(t_i)} \geq 1, \\ 1 - \left[\left(\dfrac{I(t_i) - \bar{I}(t_i)}{6S^*(t_i)} \right)^2 \right]^2 & \text{otherwise.} \end{cases} \tag{II.15}$$

$S^*(t_i)$ is a robust estimate of the standard deviation of the frequency distribution (here: the median absolute deviation, Cook & Kairiukstis, 1990), and the median of $I(t_i)$ is used as an initial approximation for $\bar{I}(t_i)$ in the iteration process. According to equation II.15, outliers which surpass the estimated mean by more than 6 standard deviations are omitted from the averaging procedures, and all other values are downweighted in relation to their distance from $\bar{I}(t_i)$. Cook (1985) showed a remarkable reduction of error variance resulting from using a biweight mean over the arithmetic mean for closed-canopy forest tree-ring data. As a similarly serious outlier contamination can be presumed for the data set used in this dissertation, a substantial mitigation of the corruption of the estimated common signal can be expected from the above procedure.

II.6. Descriptive tree-ring statistics

II.6.1. Mean sensitivity

Mean sensitivity (MS) is a measure for variance in a tree-ring series $X(t)$ that—unlike the common coefficient of variation—depends on the year-to-year variability, and is therefore employed as a general measure for variability due to exogenous factors. MS is calculated as the mean of the yearly sensitivities S_i for all years of a series:

$$\mathrm{MS} = \frac{\sum_{i=2}^{n} |S_i'|}{n-1} \tag{II.16}$$

with

$$S_{i+1} = 2\frac{X(t_{i+1}) - X(t_i)}{X(t_{i+1}) + X(t_i)} \tag{II.17}$$

and the length of the original series n.

II.6.2. Mean interseries correlation

The mean interseries correlation (Rbar) is a measure for agreement among all series to be averaged to a site chronology. It is calculated as the arithmetic mean of all pairwise Pearson's correlation coefficients for the given set of tree-ring series.

II.6.3. Expressed population signal

The uncommon variance in tree-ring series expressed in the terms $\delta D(t)$ and $E(t)$ in equation II.9 will decrease in direct proportion to the number of series $I_i(t)$ to be averaged to $\bar{I}(t)$. For single series, the variance in $I(t)$ is the sum of the common signal, Rbar, and the remaining noise, $1 - \text{Rbar}$. Averaging of N tree-ring series reduces the noise to $(1 - \text{Rbar})\,/N$, while the common signal will remain unaffected. The expressed population signal EPS (Wigley et al., 1984) is then defined as ratio between the common signal and the total variance of the chronology $\bar{I}(t)$

$$\text{EPS} = \frac{\text{Rbar}}{\text{Rbar} + (1 - \text{Rbar})\,/N}. \tag{II.18}$$

EPS thus quantifies how $\bar{I}(t)$ represents a hypothetical perfect chronology, and is used as a quality criterion for chronology building and interpretation.

II.6.4. Gleichläufigkeit

Gleichläufigkeit (GLK) after Eckstein & Bauch (1969) is a measure for the agreement of two tree-ring series X_1 and X_2, that is based on the sign test of the differenced series:

$$\text{GLK}(X_1, X_2) = \frac{1}{n-1} \sum_{i=1}^{n-1} |G(X_1(t_i)) + G(X_2(t_i))| \tag{II.19}$$

with

$$G(X(t_i)) = \begin{cases} \frac{1}{2} & \text{if } \delta X(t_i) > 0 \\ 0 & \text{if } \delta X(t_i) = 0 \\ -\frac{1}{2} & \text{if } \delta X(t_i) < 0 \end{cases} \tag{II.20}$$

derived from the differenced series $\delta X(t_i) = X(t_{i+1}) - X(t_i)$. In comparison to Pearson's correlation coefficient, the correlation by GLK is not influenced by low-frequency properties of the time series. The mean GLK of a set of series is the arithmetic mean of the GLK values for all pairwise comparisons.

II.7. Impact of drought events on tree growth

II.7.1. Drought impact from tree-ring indices

RWI-ratios of drought and post-drought years to average years were used to analyze the impact of drought on tree growth and the recovery thereof (e.g., Fekedulegn et al., 2003). Drought years were selected *a priori* based on information on Central European wide drought events (Bréda et al., 2006; Kahle, 1994; Raspe et al., 2004): 1947, 1976 and 2003. Time series of stand-wise soil water content further approved the selected extreme events based on statistical criteria (data not shown). Means of RWI values $I(t_i)$ for sets of drought and post-drought years t_i are related to means of sets of reference periods prior to drought events:

$$\mathrm{IS} = \frac{1}{3}\sum_i \frac{\frac{1}{5}\sum_{j=1}^{5} I(t_{i-j})}{I(t_i)}; \text{ with } i = 1947, 1976, 2003. \tag{II.21}$$

for the short-term impact on tree growth (IS), and

$$\mathrm{IL} = \frac{1}{3}\sum_i \frac{\frac{1}{5}\sum_{j=1}^{5} I(t_{i-j})}{\frac{1}{3}\sum_{k=0}^{2} I(t_{i+k})}; \text{ with } i = 1947, 1976, 2003. \tag{II.22}$$

for the long-term impact on tree growth (IL), that also incorporates the recovery from a drought event.

IS and IL are compared to the actuarial expectation of their distribution by means of statistical hypothesis testing via Student's t-test.

II.7.2. Drought impact from wood δ13C

For the study site Forstenrieder Park, the impact of severe drought on tree physiology subject to tree size is assessed using isotopic analysis of wood samples from increment cores.

δ^{13}C is used as a proxy for stomatal control over photosynthesis, as a measure for how the intrinsic water use efficiency of a tree is increased under adverse climatic conditions. This technique has been applied on the data subset of pine, spruce and oak used to evaluate size-specific reactions to drought (see section II.1.2).

All cores of the chosen trees were used for isotopic analysis after they had been successfully measured and crossdated. As the earlywood of tree-rings is formed primarily from carbon fixed in the previous year (Hill et al., 1995), δ^{13}C analysis was carried out on latewood only (e.g. Lipp et al., 1991).

The years 2003 and 2002 were chosen for isotope analysis. Whereas 2003 was a European wide drought year (see section II.7.1) and also a remarkably hot and dry year on this site (fig. II.3), the year 2002 resembled average conditions of temperature, precipiation and soil water content (fig. II.3) on this site and is thus employed as a template for average drought stress.

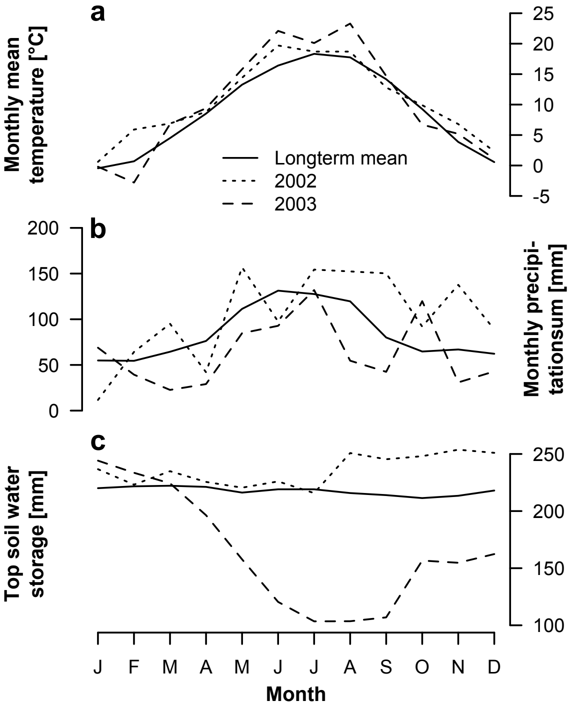

Figure II.3.: Comparison of a) temperature, b) precipitation and c) top soil water storage (integrated over 40 cm) of a drought year (2003) and a non-drought year (2002) with the long-term mean at the sampling site Forstenrieder Park.

Latewood of 2002 and 2003 of each core was carefully separated using a razor blade. For each tree, the yield from the three cores was pooled into one sample of latewood per tree. For a small fraction of samples (< 2%) earlywood and latewood could not be separated due to very small ring-widths (< 0.1 mm). As latewood covered the major part of the tree-rings in these cases, the whole annual ring was used and treated as latewood (Battipaglia et al., 2009). The samples were milled to fine powder with a ball mill. For oak, Loader et al. (2003) found the highest correlation between untreated oak sapwood and climate, thus all oak samples were used without any further preparation. Regarding spruce and pine samples, it has been argued that a variable and possibly higher amount of extractives in conifer wood might lead to biased estimates of δ^{13}C (Borella et al., 1998). As in this case δ^{13}C of cellulose was very closely correlated to the corresponding whole wood samples ($R^2 = 0.86$, $p < 0.001$), the subsequent analysis of spruce and pine wood was carried out using whole wood samples only.

The samples were combusted in an elemental analyzer (NA 1110; Carlo Erba, Milan) interfaced (ConFlo III; Finnigan MAT, Bremen) to an isotope ratio mass spectrometer (Delta Plus; Finnigan MAT). Carbon isotope data are presented as δ^{13}C relative to the international VPDB standard: $\delta^{13}\text{C} = \left(R_\text{sample}/R_\text{standard}\right) - 1$; where R_sample and R_standard are the ratios of ^{13}C/^{12}C in the sample and standard. All samples were measured against laboratory working standard gases, which were previously calibrated against IAEA secondary standards (IAEA CH_6 for ^{13}C). The accuracy of calibration was ±0.06‰ SD. Wheat flour as solid internal laboratory standard (SILS) was calibrated against these references. One SILS was measured after every tenth sample. The precision for sample repeats was better than 0.2‰ for δ^{13}C.

II.8. Long-term relationships between climate and tree growth

II.8.1. Response function analysis

A general problem of dendroclimatic calibration approaches using climatic data in monthly resolution—and thus the derivation of long-term relationships between climate and tree growth—is the pronounced intercorrelation of the climatic variables used (Cropper, 1984). This phenomenon is also signified as multicollinearity. One assumption of the linear regression model $\boldsymbol{y} = \boldsymbol{X}\beta + \epsilon$ is based on the assumption that the predictor variables are not significantly correlated. Using climatic data with a high amount of multicollinearity violates this assumption and leads to imprecise and unstable estimates $\boldsymbol{b} = \left(\boldsymbol{X}'\boldsymbol{X}\right)^{-1}\boldsymbol{X}'\boldsymbol{y}$ of regression coefficients and incorrect rejection of variables, the latter possibly leading to over-fitted models in turn (Fritts, 1976).

An alternative to multivariate and stepwise regression in paleoclimatic calibration (with a focus on tree-ring data) has been presented by Fritts (1971) in the form of *response function analysis*, where the response variable is regressed against the principal components of the set of predictor variables. This technique has the drawback that classical measures of significance may lead to overestimation of significance of the regression coefficients (Guiot, 1991; Morzuch & Ruark, 1991), eventually promoting over-fitted response functions as well. As a solution Guiot (1991) proposed bootstrapping (Efron & Tibshirani, 1997) to obtain more accurate results.

Prior to analyzing the whole data set, a simulation experiment has been carried out to test robustness of parameter estimation, explaining power and overfitting liability of response functions in direct comparison to possible alternatives: multivariate linear regression, ridge regression and stepwise procedures. Response functions clearly exhibited the advantage of the best match regarding the simulated correlation structures, and a similarly good avoidance of overfitting with increasing amounts of multicollinearity. A detailed description of the simulation experiment can be found in appendix A.

The procedure used in this dissertation is laid out as follows: let $\boldsymbol{y}$ be a $n \times 1$ vector of tree-ring indices, and $\boldsymbol{X}$ the $n \times k$ matrix of standardized climatic predictor variables. The original variables $\boldsymbol{X}$ are orthogonalized so that

$$\boldsymbol{y} = \boldsymbol{X}\boldsymbol{V}\boldsymbol{V}'\boldsymbol{b} + \epsilon = \boldsymbol{Z}\boldsymbol{a} + \epsilon \tag{II.23}$$

with $\boldsymbol{V}$ being the $k \times k$ matrix of normalized eigenvectors of $\boldsymbol{X}$, and $\boldsymbol{Z}$ being the $n \times k$ matrix of principal components $\boldsymbol{XV}$ of $\boldsymbol{X}$ and the $k \times 1$ vector $\boldsymbol{a} = \boldsymbol{V}'\boldsymbol{b}$ the linear transformation of the original regression coefficients $\boldsymbol{b}$. $\boldsymbol{a}$ can be transformed back to the original parameter space because $\boldsymbol{V}$ is an orthogonal matrix and thus $\boldsymbol{b} = \boldsymbol{V}\boldsymbol{a}$.

Usually, the method further involves partitioning $\boldsymbol{V}$ into $[\boldsymbol{V_1} \vdots \boldsymbol{V_2}]$ where $\boldsymbol{V_1}$ is a $k \times r$ matrix of important eigenvectors (high eigenvalues) and $\boldsymbol{V_2}$ a $k \times s$ matrix of eigenvectors that are deemed unimportant (low eigenvalues). This step ensures that the resulting matrix is farther from being singular, thus further reducing the amount of multicollinearity. Equation II.23 can be rewritten as

$$\boldsymbol{y} = \boldsymbol{X} \left[\boldsymbol{V}_1 \vdots \boldsymbol{V}_2 \right] \boldsymbol{a} + \epsilon, \tag{II.24}$$

and $\boldsymbol{a}$ can correspondingly be written as $[\boldsymbol{a}_1 \vdots \boldsymbol{a}_2]'$, where $\boldsymbol{a}_1$ is a $r \times 1$ vector associated with $\boldsymbol{V}_1$, and $\boldsymbol{a}_1$ a $s \times 1$ vector associated with $\boldsymbol{V}_2$, so that

$$\boldsymbol{y} = \boldsymbol{X}\boldsymbol{V}_1\boldsymbol{a}_1 + \boldsymbol{X}\boldsymbol{V}_2\boldsymbol{a}_2 + \epsilon = \boldsymbol{Z}_1\boldsymbol{a}_1 + \boldsymbol{Z}_2\boldsymbol{a}_2 + \epsilon. \tag{II.25}$$

There has been some discussion in the literature on about how many eigenvectors to retain; for an overview see Fritts (1991). In this dissertation, the PVP criterion is used (Guiot, 1991), i.e. eigenvectors are sorted according to descending eigenvalues and r is then the number of eigenvectors whose associated eigenvalues have a cumulative product greater than 1.

The estimators of the response function are obtained by application of ordinary least squares on a modified model that has been simplified by taking out the unimportant components $\boldsymbol{Z}_2$ so that

$$\boldsymbol{y} = \boldsymbol{X}\boldsymbol{Z}_1\boldsymbol{a}_1 + \epsilon^*. \tag{II.26}$$

with $\epsilon^* = \boldsymbol{Z}_2\boldsymbol{a}_2 + \epsilon$. The $r \times 1$ vector $\boldsymbol{a}_1$ is padded with $s - r$ zeros to obtain a $k \times 1$ vector $\boldsymbol{a}_1^*$. This vector can be used to obtain an estimator of $\boldsymbol{b}$ by translation back to the original parameter space via $\boldsymbol{V}\boldsymbol{a}_1^* = \boldsymbol{b}^*$. $\boldsymbol{b}^*$ is a $k \times 1$ vector, indicating that all of the original variables have been retained.

Bootstrap resampling (Efron & Tibshirani, 1986) is used to calculate response coefficients on 1000 samples drawn at random with replacement from the calibration set. Median coefficients are judged significant at the 0.05 level when their absolute values exceed half the difference between the 97.5th quantile and the 2.5th quantile (Guiot, 1991).

Motivated by the vast amount of data to be analyzed, an efficient computer program for bootstrapped response function analysis of proxy data was written as a package bootRes (Zang, 2009) for R (R Development Core Team, 2009), and made publicly available[1].

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[1] on the Comprehensive R Archive Network: `http://cran.r-project.org/web/packages/bootRes/`

II.8.2. Dimensionality reduction of response function coefficients

As climatic predictor matrices $\boldsymbol{X}$ in equation II.23, multivariate monthly time series of precipitation and temperature from previous July to current September were used for all 143 tree-ring chronologies. This way, a complex result matrix $\boldsymbol{R}$ is obtained from the individual $\boldsymbol{b}^*$ (143 observations $\times$ 32 response coefficients). To facilitate the interpretation of the underlying variance structure in growth response to climatic influences, principal component analysis (PCA) is applied to this parameter matrix to reduce the dimensionality of $\boldsymbol{R}$ (Huang et al., 2010). Thus, $\boldsymbol{R}$ is decomposed into the orthogonal matrices $\boldsymbol{RVV'}$ (loadings, summarizing the information about the response parameters) and $\boldsymbol{R}\,(\boldsymbol{RVV'})$ (scores, summarizing the information about the observations).

The equilibrium circle with radius $\sqrt{\frac{d}{p}}$ (with p total and d reduced dimension in ordination space) is used to identify meaningful scores and loadings in reduced space (Legendre & Legendre, 1998). All components (scaled to their standard deviations) outside this circle contribute more to the reduced ordination space than it would be the case for a uniform distribution of all components to all axes of the entire ordination space.

II.8.3. Dendroclimatic benchmarking through archetypes

Benchmarking is defined as the comparison of observations with some defined or selected best performers with regard to some (probably complexly defined) property. Here, the property aimed at is complex for sure: tree-growth over time. Hence, the question about possible benchmarks for drought-tolerance and drought-intolerance imposes a challenge on the statistical approach for identifying these benchmarks.

For instance, clustering techniques aim at finding groups of similar characteristics, allowing for the comparison of more homogeneous groups with one another. In this dissertation, archetypal analysis (Cutler & Breiman, 1994) is proposed as an alternative method when multivariate extremes rather than means within groups are demanded, and applied to an ecological data set for the first time. Archetypal analysis is based on the assumption that each point in a multivariate data set can be represented as a convex combination of a few (not necessarily observed) points on the boundary of the data scatter—the archetypes. These archetypes thus typify extremes in the data and can be employed as benchmarks for comparing the individual observations relative to these extremes.

The chronologies chosen for setting up the archetypes were combined into one multivariate data matrix $\boldsymbol{I}$, with m years as parameters and n chronologies as observations. Preliminary studies have shown that the inclusion of all species into archetypal analysis may lead to overly complex results, and the multivariate extremes thereof might be non-straightforward to interpret (Kathrin Klein, unpublished diploma thesis, HSWT). The choice of chronologies for the procedure—spruce and oak data exclusively—is based on knowledge gained from other analyses carried out for this dissertation and is detailed in section III.4.1. Archetypal analyis was then carried out on $\boldsymbol{I}$ in order to find a set of pure types, or more specific, to find hypothetical chronologies that resemble chronologies of hypothetical pure types of trees.

Archetypal analysis (Cutler & Breiman, 1994) aims at representing each point in $\boldsymbol{I}$ as a convex combination of l archetypes a_j:

$$\boldsymbol{I} = \boldsymbol{A}'\alpha \tag{II.27}$$

with constraints

$$0 \leq \alpha_{ij} \leq 1 \; \forall i, j, \; \sum_{i=1}^{l} \alpha_{ij} = 1, \;\; i = 1 \ldots n, \; j = 1 \ldots l.$$

At the same time, these archetypes themselves can be represented as a convex combination of the data:

$$\boldsymbol{A} = \boldsymbol{I}'\beta \tag{II.28}$$

with constraints

$$0 \leq \beta_{ji} \leq 1 \; \forall j, i, \; \sum_{j=1}^{m} \beta_{ji} = 1, \;\; j = 1 \ldots l, \; i = 1 \ldots n$$

The algorithm alternates between finding the best α for a given $\boldsymbol{A}$

$$\underset{\alpha_i}{min}\frac{1}{2} \parallel \boldsymbol{I} - \boldsymbol{A}\alpha_i \parallel_2, \tag{II.29}$$

and finding the best $\boldsymbol{A}$ for a given α

$$\underset{\beta_i}{min}\frac{1}{2} \parallel \tilde{\boldsymbol{A}} - \boldsymbol{I}\beta_j \parallel_2 . \tag{II.30}$$

The complex least squares problems associated with these steps are solved using a penalized version of the non-negative least squares algorithm by Lawson & Hanson (1974), which is implemented in the package archetypes (Eugster & Leisch, 2009) for R (R Development Core Team, 2009), that is used for this dissertation.

The obtained archetypes matrix $\boldsymbol{A}$ is a $l \times m$ matrix, resembling l hypothetical tree-ring chronologies. Each column of $\boldsymbol{I}$ has a corresponding α-value for each j, indicating the contribution of each archetype to the very observation.

A measure for the summarizing power of l archetypes is given by the RSS function

$$\text{RSS}\,(l) = \sum_{i=1}^{n} \parallel \boldsymbol{I} - \boldsymbol{A}\,(l)\,\alpha_i\,(l) \parallel . \tag{II.31}$$

The initial choice of l is thus not conclusive, but must be made according to either the reduction in RSS with increasing number of archetypes, or according to their meaning, which can only be assessed *a posteriori*. Therefore, an exploratory and interactive way of selecting l is recommended (Porzio et al., 2008).

The hypothetical tree-ring chronologies, from here on referred to as archetypes, are used in like manner as real tree-ring chronologies in further analysis. After having found these archetypes as multivariate extremes, the next question is the identification of the best and worst performers among them, with regards to the initial problem of susceptibility to drought.

As a measure for drought sensitivity, the amount of variance in (hypothetical) tree-growth explained by either summer precipitation (June, July and August precipitation sum, JJAP), or summer temperature (June, July and August temperature means, JJAT) was used. Ordinary least squares regression was employed to calculate the correlation between the archetypes and seasonal climate targets for each site-specific climate time-series. The ratio of significantly positive correlations (JJAP) or significantly negative correlations (JJAT) with the archetype's RWI to the number of sites (40) is considered a measure of overall drought susceptibility of the respective archetype, as it reports on how many real sites this hypothetical set of trees would have displayed remarkable drought-related growth patterns.

The benchmarking procedure itself was carried out as the sequential correlation of all tree-ring chronologies with the benchmarks derived from archetypal analysis.

II.9. Correlation of tree-ring indices with water balance features

Within the yearly course of the soil water content, many days are characterized by saturated conditions. So, typically the early spring months have no variation in soil water content due to saturation, and transpiration deficit ratios equal 1 for large parts of the year. These circumstances impede the use of response functions to analyze growth/water-balance relationships with monthly data for a numerical reason: the matrix $\boldsymbol{X}$ of predictor variables cannot be transformed to $\boldsymbol{X}\boldsymbol{V}\boldsymbol{V}'$ because of singularities that render the correlation matrix ill-conditioned.

Thus, standard OLS regression is applied to quantify the relationships between tree growth and water balance features in a bivariate manner. For this purpose, meaningful targets (like transpiration deficit during growing season) have been assembled.

II.10. Allometric analysis

Allocation patterns between shoot and root are assessed using allometric analysis on spruce trees along a precipitation gradient (Nikolova, unpublished, see section II.1.2). As a surrogate variable for resource allocation, the allometric exponent γ is used, derived from

$$\delta r_i = g\,\delta s_i^{\gamma} \tag{II.32}$$

where δr_i and δs_i are the root and stem radii for year i and g is the allometric factor (Pretzsch, 2009). Equation II.32 is applied in its logarithmic representation

$$\ln \delta r_i = \ln g + \gamma x \ln \delta s_i \tag{II.33}$$

to reduce the effect of outliers, and to better meet the statistical assumptions of normal distribution and homoscedasticity (Pretzsch, 2010). The allometric exponent γ can be understood as a distribution coefficient for the growth resources between root and stem organs: when shoot increases by 1%, root increases by γ%. This set value is used to quantify the long-term root-shoot allometry on tree and stand level and to analyse its relationship to water supply.

Further, the value pairs δr_i, δr_{i+1} and δs_i, δs_{i+1} from the consecutive years are employed to calculate the period-wise slope γ'. It represents the distribution key of biomass allocation between root and shoot of individual trees in a given period, e.g. one year.

$$\gamma' = \frac{\ln \delta r_{i+1} - \ln \delta r_i}{\ln \delta s_{i+1} - \ln \delta s_i} = \frac{\ln \delta r_{i+1} / \delta r_i}{\ln \delta s_{i+1} / d\delta s_i} \tag{II.34}$$

For infinitely small time steps, γ' corresponds to γ. To compute the scaling exponents γ for each tree after plotting the root and stem data on natural logarithm (ln-ln) scale, ordinary least square regression (OLS) was applied.

II.11. Generalized additive modeling

All bivariate regression models in this dissertation are—when no indiciation for nonlinearity was given—ordinary least squares regression models (OLS), or—when nonlinear relationships were assumed—generalized additive models (GAM).

In GAM (Hastie & Tibshirani, 1986), the common linear model $y = b_0 + \beta_1 x$ that linearly relates the response y to the predictor x is generalized to an additive model

$$g(E(y)) = b_0 + h(x) \tag{II.35}$$

where $h(x)$ is a function of the predictor x, usually a smoother, and $g(E(x))$ is a link function that relates the expected values of the response distribution to the predictors.

The response distribution is chosen from the exponential family, and here—as it is dealt with approximate normal distributions only—a Gaussian error distribution was used, rendering $g(E(x))$ the identity link. As $h(x)$, penalized regression splines were used that, unlike the cubic smoothing splines used for tree-ring standardization, were not fitted according to a certain frequency response, but based on the number of knots which define the spline base (Wood, 2008). The number of knots determines the curvature of the fitted curve and is found using generalized cross-validation (GCV) (Gu & Wahba, 1991) to prevent overfitting due to too many knots (which add to the degrees of freedom used for the model). The GCV aided fitting procedure aims at minimizing the term $nD/\,(n-F)^2$ with total deviance D, the number of observations n, and the number of effective degrees of freedom F, and thus tries a compromise between close data fitting and overly complex models. The R package mgcv (Wood, 2004) has been used for fitting GAM.

III. Results

From December 2006 to June 2009, about 3,500 increment cores were taken, of which 2,860 passed the quality tests and were used for further analysis. This amounts to approximately 272,000 single tree-ring widths from 1,430 trees in total. All chronologies employed for further analyses had an EPS above 0.85 (Wigley et al., 1984).

The sampling sites represent a large part of the climatic envelope of Bavaria, and—as both are quite similar—of Germany as well (fig. III.1). The main sampling was carried out at the warm and dry end of the gradient, mainly represented by the large number of sites located in the Franconian and Wuerttembergian triassic (see also tab. II.1).

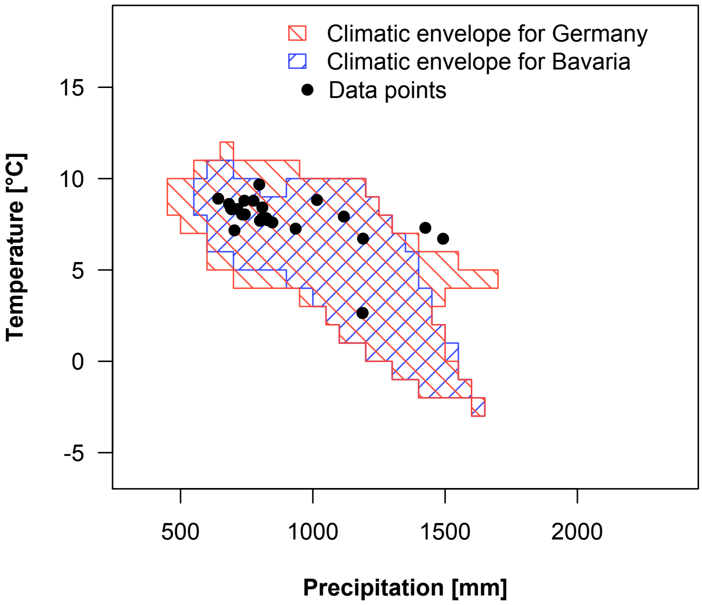

Figure III.1.: Location of sampled sites in climatic envelopes of Bavaria and Germany. The climatic envelopes are redrawn after Kölling (2007). The two outliers are data points in Vorarlberg near the Bodensee.

III.1. General characterization of tree-ring series

III.1.1. Tree-ring widths

The mean tree-ring widths are lowest for oak and pine, and highest for Douglas fir (tab. III.1). Mean tree-ring widths do not follow any spatial pattern, nor do they significantly correlate with climatic parameters (data not shown). Oak had a remarkably high minimum tree-ring width, indicating that even under adverse conditions a considerable increment growth can be achieved.

Table III.1.: Summary of measured tree-ring widths and sensitivities. Different small letters indicate significant differences at $p < 0.05$ (actual p for individual tests adjusted with Bonferroni correcture for multiple tests).

Species	min. TRW [mm]	mean TRW [mm]	max. TRW [mm]	mean sensitivity [%]
Spruce	0.09 ab	2.44 a	12.35 a	19 a
Pine	0.01 b	1.88 a	13.49 a	17 a
Silver Fir	0.01 ab	2.39 a	11.61 a	19 a
Douglas Fir	0.01 a	3.12 b	12.92 b	18 a
Beech	0.09 b	2.24 ac	9.65 ac	20 a
Oak	0.21 ab	1.76 d	9.32 c	20 a

III.1.2. Mean sensitivity

MS is remarkably indifferent among the different species (tab. III.1), if the average values across the study area are compared. However, in map view, a clear differentiation of MS among the individual populations can be observed, with MS peaking in North-Western Bavaria (fig. III.1.2, left panel). The highest MS have been encountered on dryer sites in the Franconian upper triassic, especially for spruce, silver fir and beech. MS significantly decreases with increasing precipitation sums (fig. III.1.2, right panel).

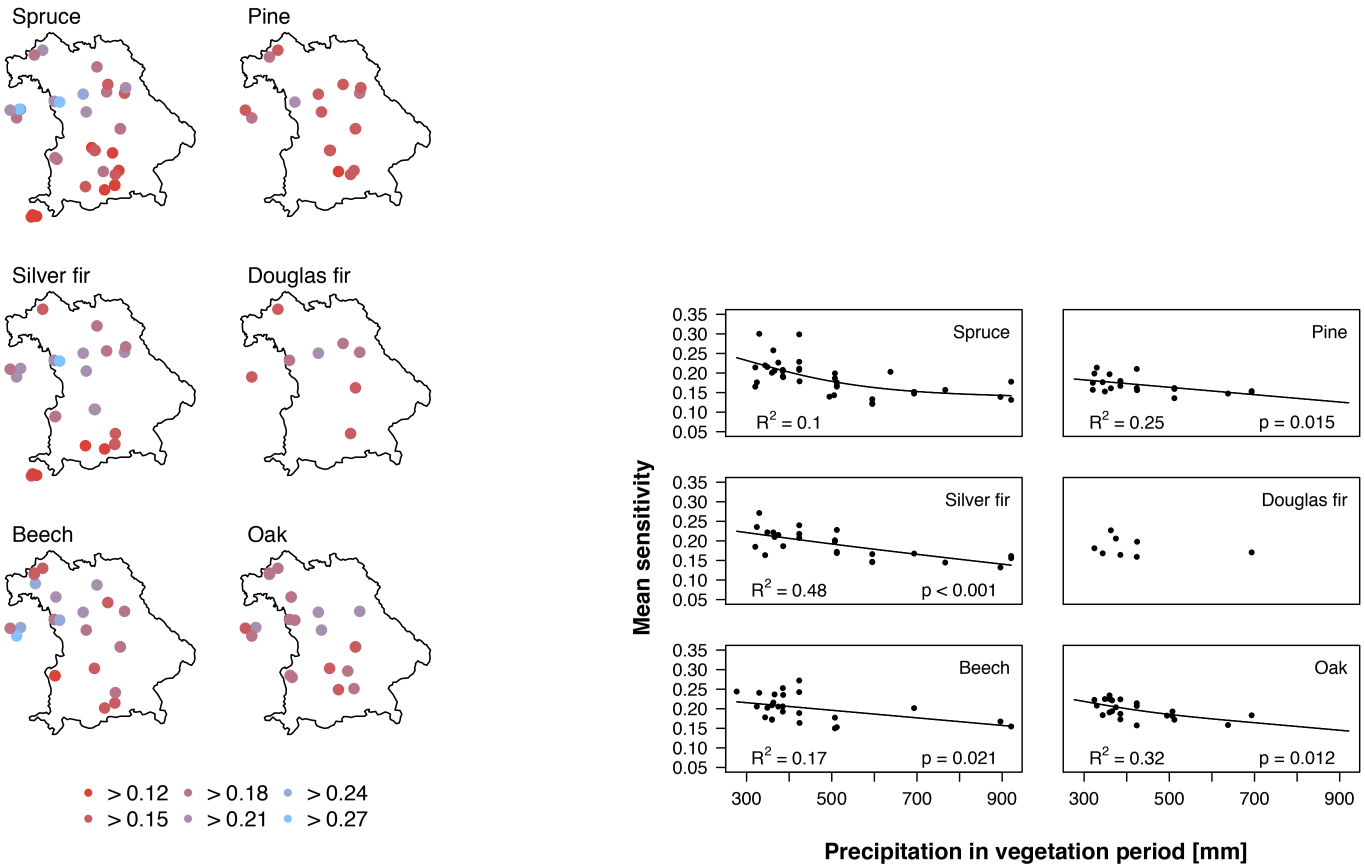

Figure III.2.: Map view of mean sensitivity (left panel), and relationships between mean sensitivity and average precipitation sum in growing season (April to September, right panel). The regression lines represent generalized additive models, whose coefficients of determination and overall significances are given below the lines.

III.2. Species and site effects on climate and drought response

The results in the following sections represent the findings from the full data set of all 143 populations and refer to research objective 1 (see section I.4).

III.2.1. Impact of extreme drought events

Short-term impact of drought events

132 out of the 143 populations under investigation exhibited a short-term decline in increment growth (IS) associated with the drought years of 1947, 1976 and 2003 (fig. III.3a). The relatively strongest decline is found for spruce in Northern Bavaria and in North-Eastern Wuerttemberg, i.e. the driest regions of the investigation area.

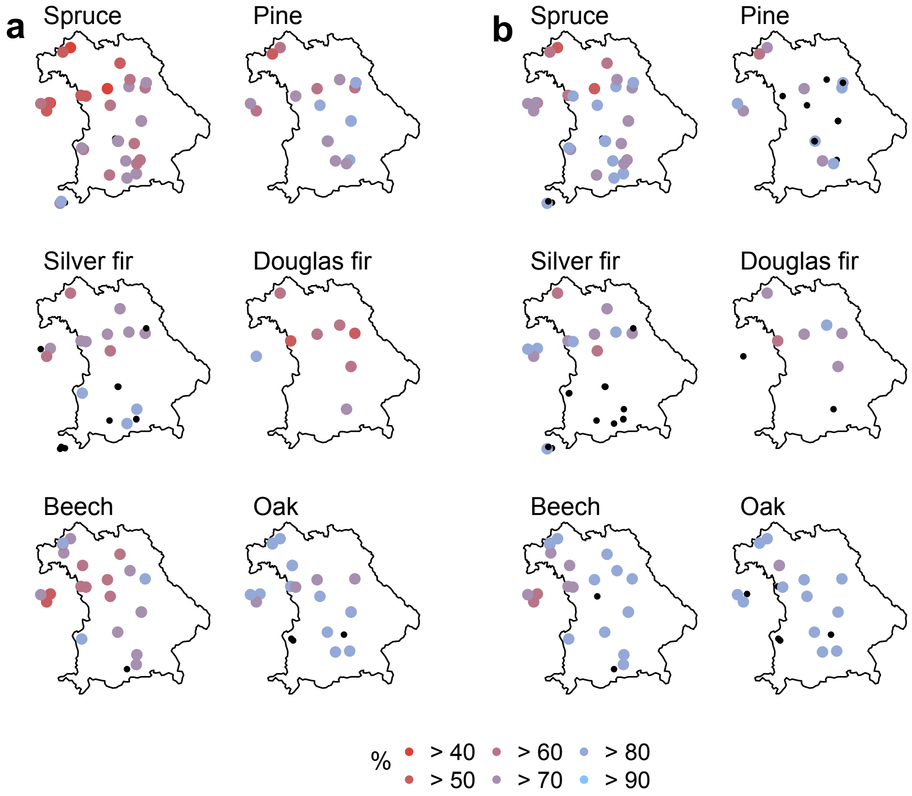

Figure III.3.: Map view of short-term growth impact of drought events (IS, panel a) and long-term impact (IL, panel b). Shown is the reciprocal value for IS and IL as percentage, to illustrate the increment growth in drought years relative to average years.

For spruce, silver fir and beech, IS significantly decreases with higher amounts of precipitation during the vegetation period ($p < 0.05$, fig. III.2.1a). A threshold at around 500 mm is implied for spruce and silver fir, with stronger impact of drought events on tree growth below. In direct comparison of spruce and silver fir, silver fir reacted remarkably more moderately to drought events. From 500 mm precipitation sum during the vegetation period onwards, silver fir seems to be able to resist even extreme dry years without considerable growth decrease. Of all species under investigation, oak exhibits the most moderate reaction to drought events.

Long-term impact of drought events

When the two consecutive years after a drought events are considered additionally to assess the ability to recover from drought stress (IL), yet 127 out of the 143 populations under investigation exhibited a long-term growth decrease associated with drought events (fig III.3b). The pattern already observed for IS is validated, with the strongest reaction of spruce (again in Northern Bavaria), and the weakest reaction of oak (with only about half of the sites showing long-term growth decrease in oak altogether).

Silver fir shows a noticeably fast recovery, especially in Southern Bavaria, and also pine is able to recover fast on most sites and exhibits minor long-term growth reductions only. Beech recovers nearly as fast as oak, except for one site (a low altitude site in the Keuper region), where drought events seem to be much more critical for beech than for oak. Douglas fir shows remarkably weaker long-term growth reactions to summer drought than spruce. The coupling of growth decrease with regional climate seems to be dampened for the long-term growth impact: only silver fir exhibits a significant relationship between IL and mean precipitation sum during the vegetation period ($p < 0.05$, fig. III.2.1b).

Neither IS nor IL are significantly correlated with the modeled soil water storage for the corresponding years 1947, 1976 and 2003 (data not shown). Even a coarse classification of soil water storage into three classes does not yield a viable gradation of drought impact with regard to soil water status (fig. III.5).

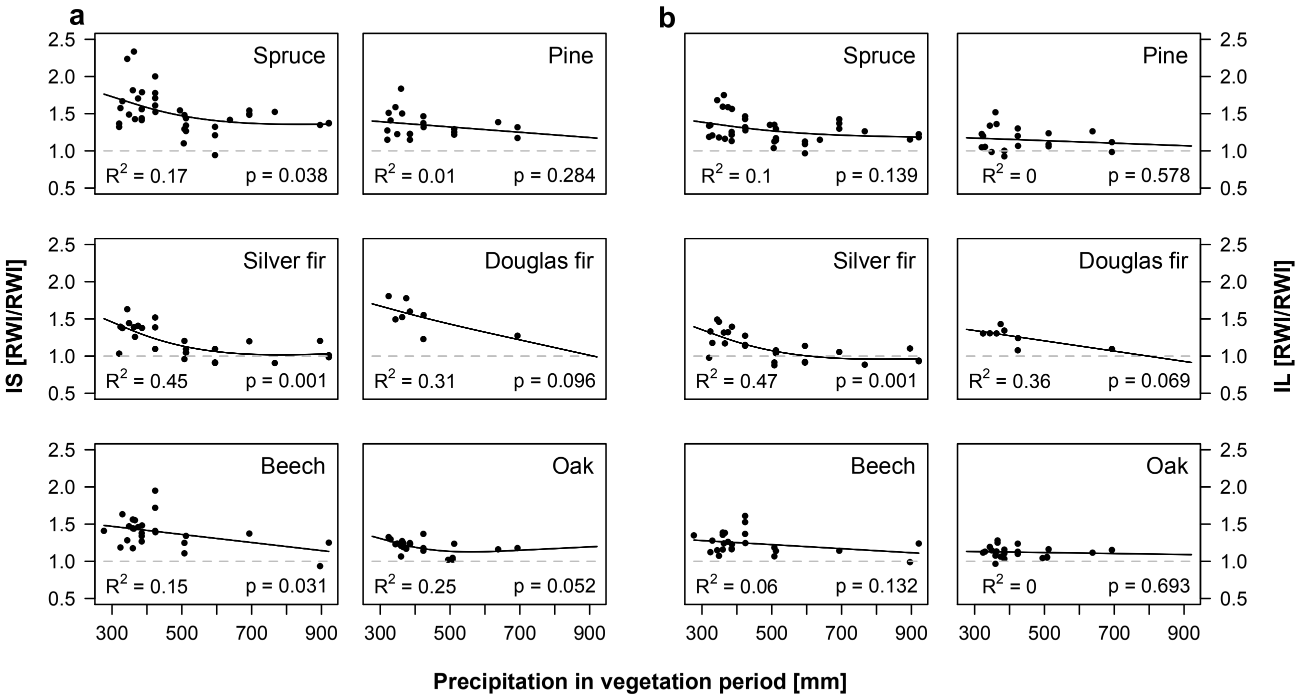

Figure III.4.: Correlation between precipitation during vegetation period (May through September) and IS (left panel), and IL (right panel). The regression lines represent generalized additive models, whose coefficients of determination and overall significances are given below the lines. The dashed horizontal line stands for an IS or IL of zero, representing no growth decrease associated with severe summer drought.

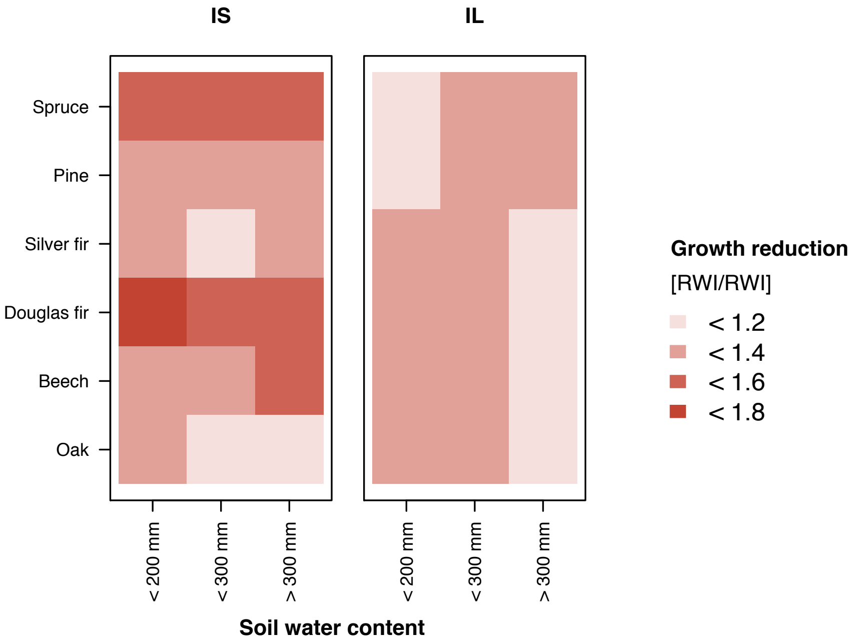

Figure III.5.: Growth decrease associated with severe drought events (IS, left panel, and IL, right panel) subject to the modeled soil water storage integrated over the first 100 cm of soil (average for 1947, 1976 and 2003).

Variability in growth reaction to summer drought

On single tree level, a remarkable variability of IS and IL can be observed for all species: for many populations the coefficient of variation for these impact measures based on the single trees chronologies is higher than the coefficient of variation based on the site chronologies for the whole investigation area (fig. III.6). This means that the growth reaction of the sampled trees of individual populations varies more than the average reaction of all populations investigated. Especially for the coniferous species spruce, pine, silver fir and Douglas fir, some populations with a very high inner differentiation of drought impact can be found. Oak shows the lowest differentiation on the level of the investigation area, but interestingly, all individual stands depicted a higher inner differentiation.

For none of the species under investigation a relationship between inner differentiation of drought impact and climatic or site factors could be established (data not shown).

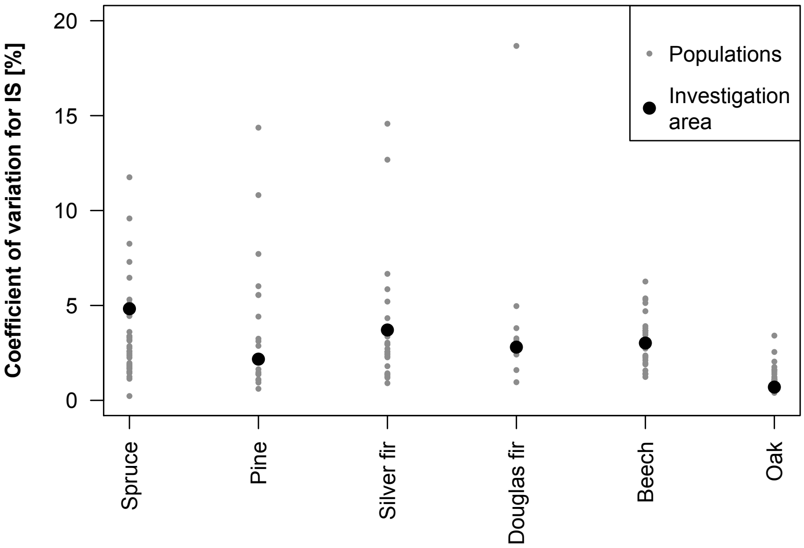

Figure III.6.: Comparison of the coefficients of variation for the short-term drought impact on tree growth (IS) on population (tree chronology) and investigation area (site chronology) level.

III.2.2. Long-term growth limitations

Limitations by temperature and precipitation

Growth/climate relationships show a growth limitation by low summer precipitation for all species and almost all sites. Especially June precipitation is often a key factor (fig. III.7). As far as temperature is concerned, high summer temperatures limit tree growth in most cases, with June being the most important summer month. Therefore, all tree species are sensitive to summer drought on most of the sites.

From fig. III.7, a difference between the species can be derived, too: spruce, Douglas fir and beech often show a strong growth limitation by high summer temperatures, whereas oak reacts indifferently to summer temperatures. And for the coniferous species a longer period of limitation by summer precipitation can be observed (June to August, or June to Juli), whereas the deciduous species show remarkable correlations with summer precipitation only in June.

A more condensed representation of the growth/climate relationships is provided by the PCA of the response coefficients (fig. III.8). The first axis of the PCA shows a high positive loading of high summer temperatures and a high negative loading of high summer precipitation amounts (fig. III.8, upper part); this axis is therefore explained with the feature “summer drought”.

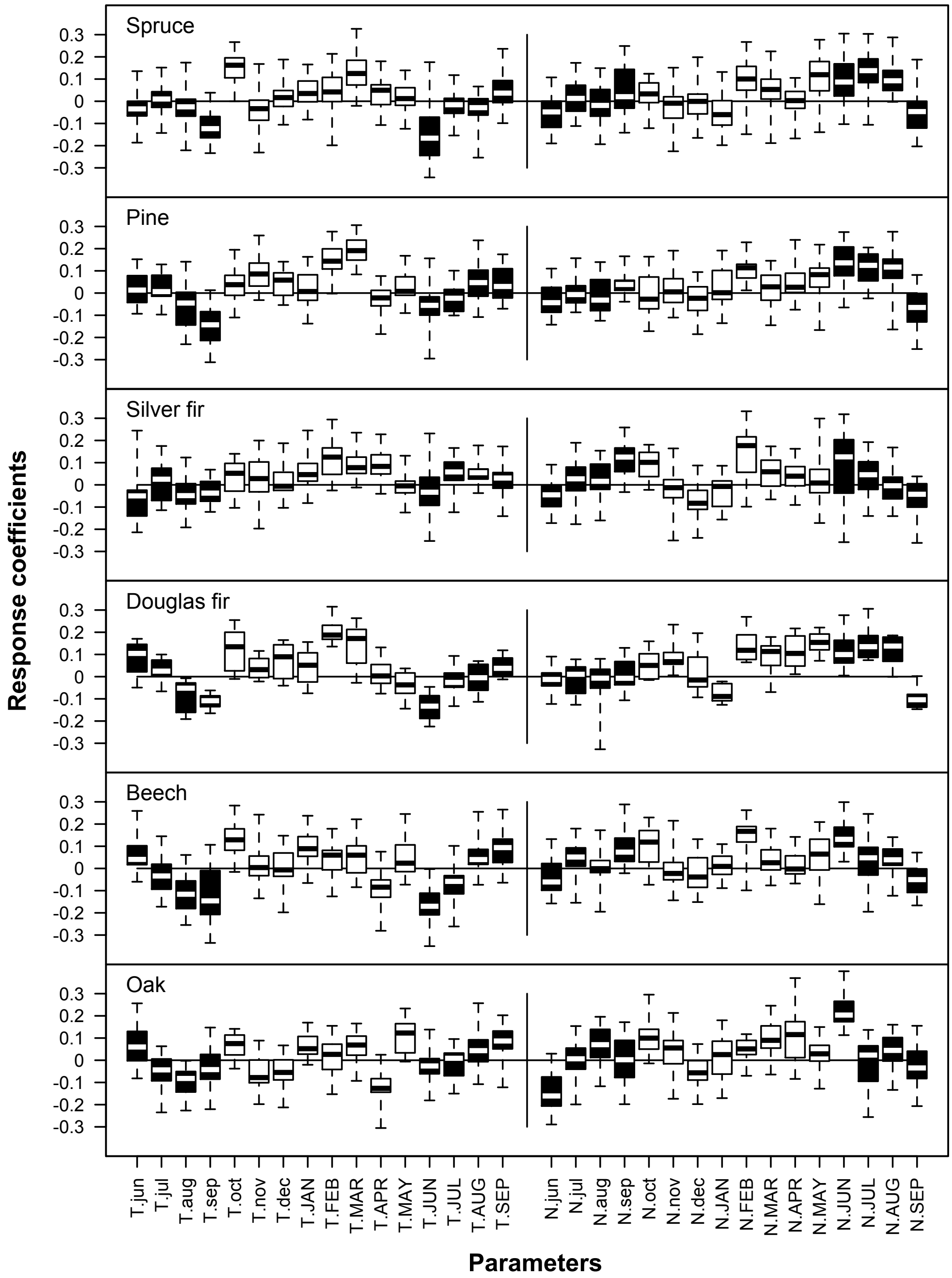

Figure III.7.: Box plots of the response coefficients for the species under investigation. Black boxes represent summer months, all caps month names stand for the current year, lower-case month names stand for the previous year.

PCA shows a good separation of the species in this space of ecological demands (fig. III.8, lower part): especially spruce, pine and Douglas fir are clearly separated from oak. This suggests a clear differentiation regarding the species' demands for mainly sufficient summer precipitation and favorable summer temperatures.

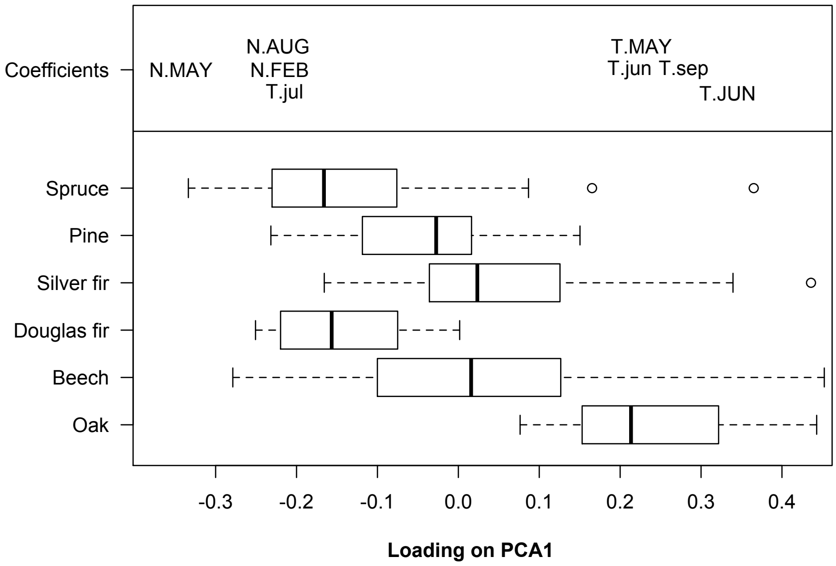

Figure III.8.: Representation of the first axis of a PCA of the response coefficients, in terms of coefficients (upper part) and species loadings (lower part). In the upper part, only coefficients outside the equilibrium circle for PCA1 are shown.

The map view of the PCA scores reveal a noticeable growth limitation of spruce by high summer temperatures and low summer precipitation typically in the warmer and drier regions of the investigation area (fig. III.9). These regions are almost identical to the most critical regions for growth decline associated with extreme summer drought (fig. III.3). The main areas of drought sensitivity are the triassic area and the Upper Palatinate Basins for all species under investigation.

Limitations by transpiration deficit

In general, no improvement of the growth/climate relationships is realized when feature sizes from soil water balance modeling (like soil water storage) are employed instead of temperature and precipitation data only. Although the modelled features are not merely functions of precipitation (for spruce see fig. III.10, left panel), they do not improve the overall explanatory power (fig. III.10, right panel). Consequently, only transpiration deficit is taken into further consideration as explanatory variable for tree growth, as this feature provides a clear connection to the species used for parametrization—via the ratio

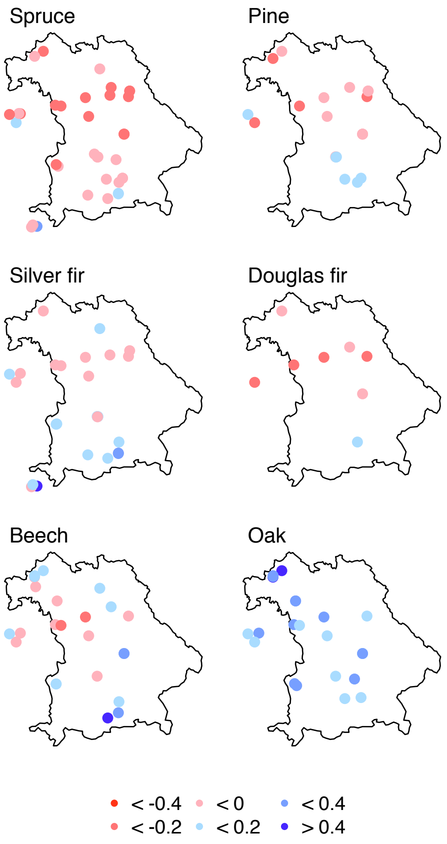

Figure III.9.: Map view of the population loadings on the first axis of a PCA of the response coefficients. A more reddish color stands for a stronger correspondence between a population and the first axis representing the feature “summer drought”.

between potential and actual transpiration—which is not a quality of the basic climatic data.

The areas with the strongest limitation of tree growth by transpiration deficit during summer for spruce and pine are found in Eastern Franconia (spruce) and in Upper Palatinate (spruce and pine, fig. III.11). Silver fir and oak show only weak correlations between long-term tree growth and transpiration deficit, with insignificant correlations over large parts. Thus, no critical region can be identified in the investigation area for these species. Beech and Douglas fir exhibit the strongest correlations in the western triassic (Keuper), but with a small total number of strong correlations only. Of all species under investigation, spruce exhibits the strongest and—in terms of area affected—most important relationship between tree growth and site water balance.

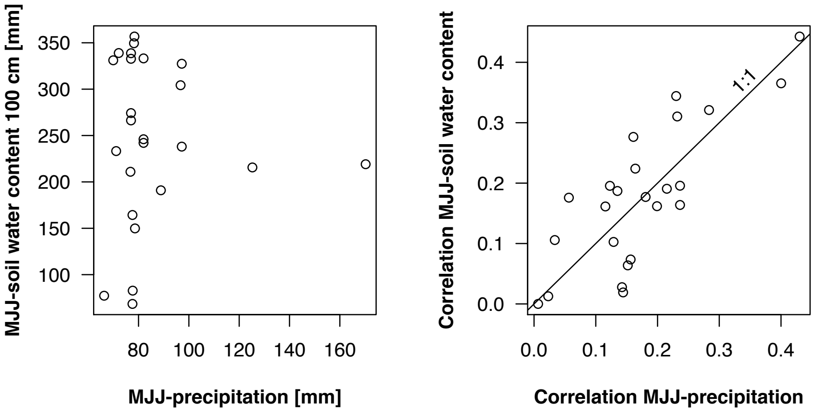

Figure III.10.: Comparison of the variance in tree-ring growth explained by precipitation and soil water storage. Left panel: Correlation between early summer precipitation (May, June, July) and the mean soil water storage over the first 100 cm of soil for the same time span. Right panel: Comparison of the explained variance in tree-ring growth for spruce by early summer precipitation and early summer soil water storage.

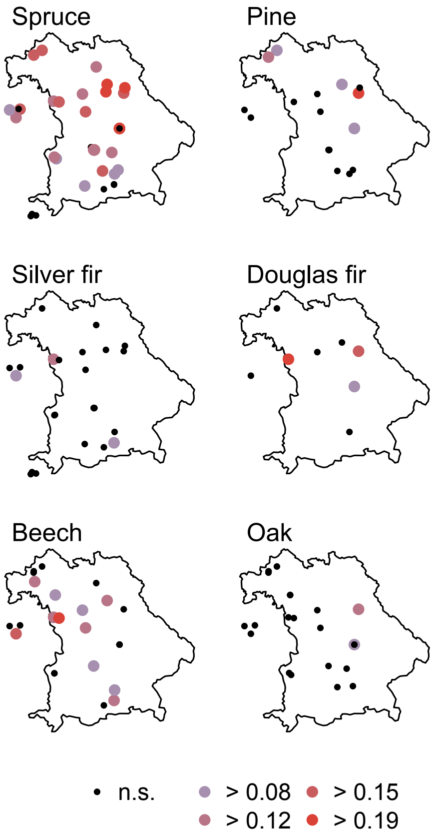

Figure III.11.: Map view of the explained variance (R^2) in tree-ring growth by transpiration deficit. The smaller black points indicate correlations insignificant at a significance level of 0.05.

III.3. Effects of tree size on climate and drought response

The results presented in the following section refer to research objective 1 (see section I.4) and are based on the subset of pine, spruce and oak trees across all diameter classes sampled at Forstenrieder Park (site #23 in tab. II.1, see also section II.1.2).

III.3.1. Classification of trees according to diameter

Diameter reconstruction based on raw tree-ring widths allowed for the definition of 2 size groups for pine, spruce and oak at Forstenrieder Park: a group of suppressed trees, defined as the trees with the smallest diameters for at least the last 25 years, and a group of dominating trees, defined as the trees with the greatest diameters for at least the last 25 years (fig. III.12).

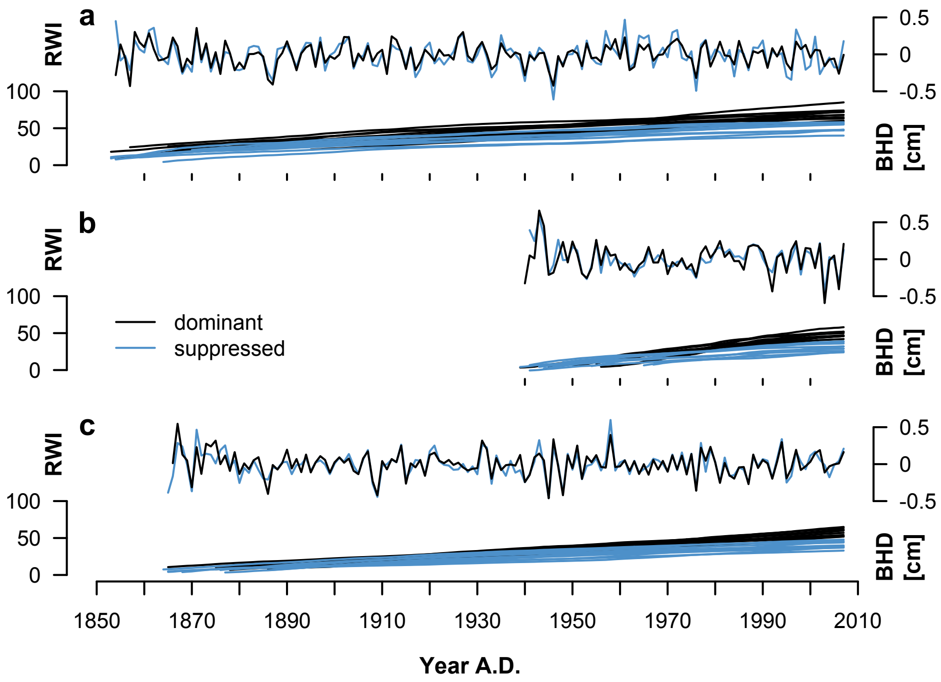

Figure III.12.: Class chronologies for suppressed and dominant trees of pine (a), spruce (b), and oak (c), and reconstructed diameters at breast height for single trees. The asynchronous first years of each chronology are due to diverging juvenile growth patterns of single trees, and have not been used for calculations.

Table III.2.: Characterisitics of class chronologies and employed trees (*BHD* diameter at breast height, *Rbar* interseries correlation, *MS* mean sensitivity, *AC* autocorrelation). Different small letters indicate significant differences at $p < 0.05$.

Group	BHD [cm] min–max (mean)	Chronology length [a]	Rbar	MS	AC	EPS
Pine dominant	60–85 (70.0)	155	0.53	0.22a	0.72a	0.87
— suppressed	40–58 (51.8)	155	0.53	0.29b	0.76a	0.85
Spruce dominant	42–58 (49.0)	69	0.69	0.25a	0.65a	0.93
— suppressed	24–39 (31.0)	69	0.63	0.23b	0.74b	0.91
Oak dominant	52–64 (58.0)	143	0.67	0.21a	0.54a	0.91
— suppressed	33–48 (40.8)	144	0.62	0.22a	0.75b	0.90

III.3.2. Size-specific tree-ring chronologies

The length of the chronologies per diameter class was identical or differed by one year (oak) (Tab. III.2). EPS was at or above the critical value of 0.85 (Wigley et al., 1984), and Rbar also indicated a good agreement between the radii (Tab. III.2). Dominant and suppressed chronologies differed in mean sensitivity (MS) for pine and spruce, with significantly higher MS in suppressed pine trees, and significantly higher MS in dominant spruce trees. The suppressed trees exposed a stronger autocorrelation in comparison to the corresponding dominant trees, with significant differences in spruce and oak.

III.3.3. Impact of extreme events

Impact of drought events on tree growth

Pine trees of both diameter groups showed a significant decrease in growth associated with drought years (fig. III.13a), and dominant trees experienced a significantly higher growth decline during these events, cutting down growth to nearly 50% of average growth. These differences only occurred in the drought years, in the years following drought events, both dominant and suppressed pine trees exhibited significantly reduced diameter increment, but no differences between diameter groups.

Drought events affected growth of spruce trees for only one year (fig. III.13b). In the drought years, increment growth of both dominant and suppressed trees differed significantly from average growth, with a (not significant) greater growth decline in suppressed

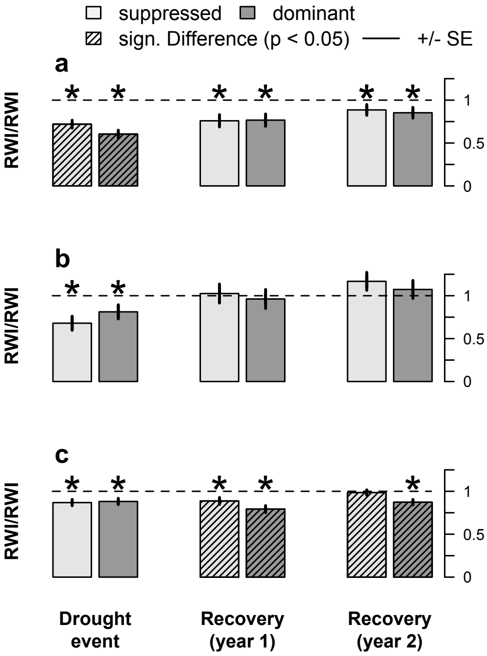

Figure III.13.: Ratio between ring width index (RWI) of drought years (1947, 1976 and 2003) and a reference period of five years prior to drought, resp. post drought years (recovery, year 1 and 2) and the same reference period for a) pine, b) spruce and c) oak. Asterisks denote significant growth reductions as deviations from 1 ($p < 0.05$), hatched bars indicate significant differences between diameter classes ($p < 0.05$).

trees. In the years following drought events, growth of spruce trees did not show any lasting influence of drought stress in either diameter group.

Oak trees showed significant decreases of increment growth in drought years, with no significant difference between the diameter groups (fig. III.13c). However, significant differences could be observed for the recovery of tree growth: in both years following drought events, suppressed oak trees depicted a stronger recovery of increment growth in comparison to dominant oak trees. In the second year after drought events, growth of suppressed oaks had fully recovered and did not differ significantly from average growth.

Impact of drought events on stomatal control on photosynthesis

For the relatively moist year 2002 with optimal growth conditions, a significant negative relationship between latewood δ^{13}C and diameter was found in pine, indicating an overall stronger stomatal regulation of photosynthesis in suppressed pine trees (less negative δ^{13}C, fig. III.14a). No relationship between diameter and 2003 latewood δ^{13}C could be observed for pine. The ratio of latewood δ^{13}C for 2002 and 2003 was related to diameter (fig. III.14a, right): this ratio gets more positive with increasing diameter in pine, indicating that bigger trees show a stronger increase of stomatal control than smaller trees, which in turn explains the evened relationship for 2003.

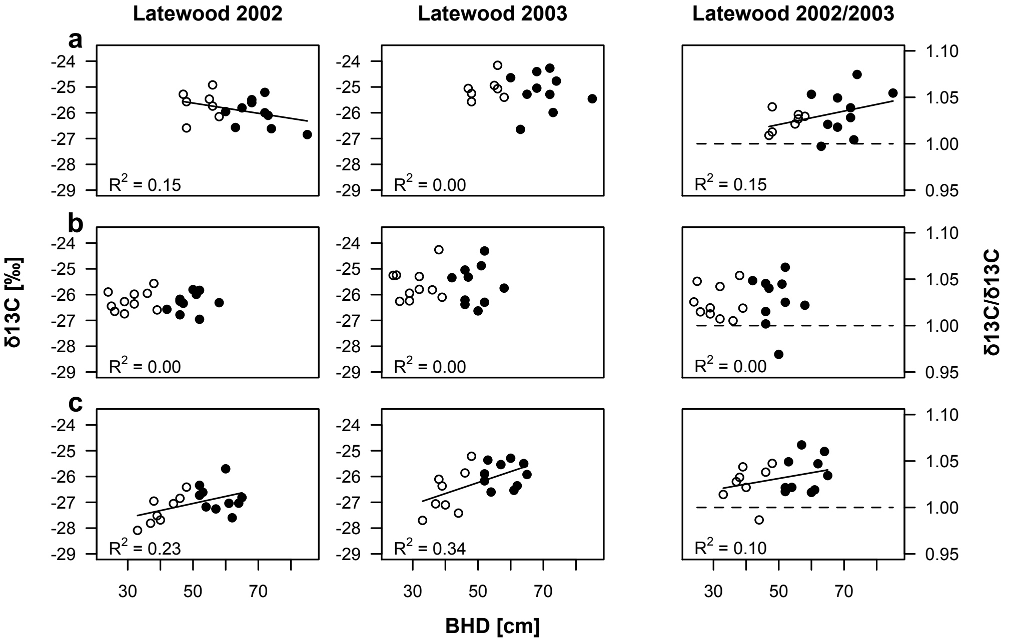

Figure III.14.: Relationship of latewood δ^{13}C for the non-drought year 2002 (left side), latewood δ^{13}C for the drought year 2003 (middle) and the relative increase in δ^{13}C from 2002 to 2003 (right side, measured as the ratio between latewood δ^{13}C for 2002 and 2003) to tree diameter at breast height (BHD) for (a) pine, (b) spruce and (c) oak. The horizontal bars in the rightmost charts indicate the state of no change in carbon isotope discrimination between 2002 and 2003. Dominant trees are represented by filled dots, suppressed trees by hollow dots.

On the opposite, the relationship between 2002 latewood δ^{13}C and diameter of oak depicts a stronger stomatal regulation in dominant trees. In the extreme drought year 2003 oak showed an even steeper relationship between latewood δ^{13}C and diameter (fig. III.14c), indicating that dominant trees exhibited a stronger increase in stomatal control of photosynthesis under drought conditions. Like in pine, the ratio of latewood δ^{13}C for 2002 and 2003 gets more positive with increasing diameter in oak, marking a stronger effect of severe drought stress on bigger trees (fig. III.14c, right).

For spruce no relationship between 2002 or 2003 latewood δ^{13}C, or the ratio between latewood δ^{13}C for 2002 and 2003 and diameter could be observed (fig. III.14b).

All species exhibited a significant increase in latewood δ^{13}C from 2002 to 2003 (paired *t*-test, all $p < 0.001$).

III.3.4. Long-term growth limitations

In general, high May temperatures and low June and July temperatures promoted growth in both diameter groups of pine (fig. III.15a). No significant differences between diameter groups could be observed with respect to growth reaction to temperature. Pine showed the highest demand for precipitation in April, June and July, with suppressed trees exhibiting a significantly more positive response to June precipitation.

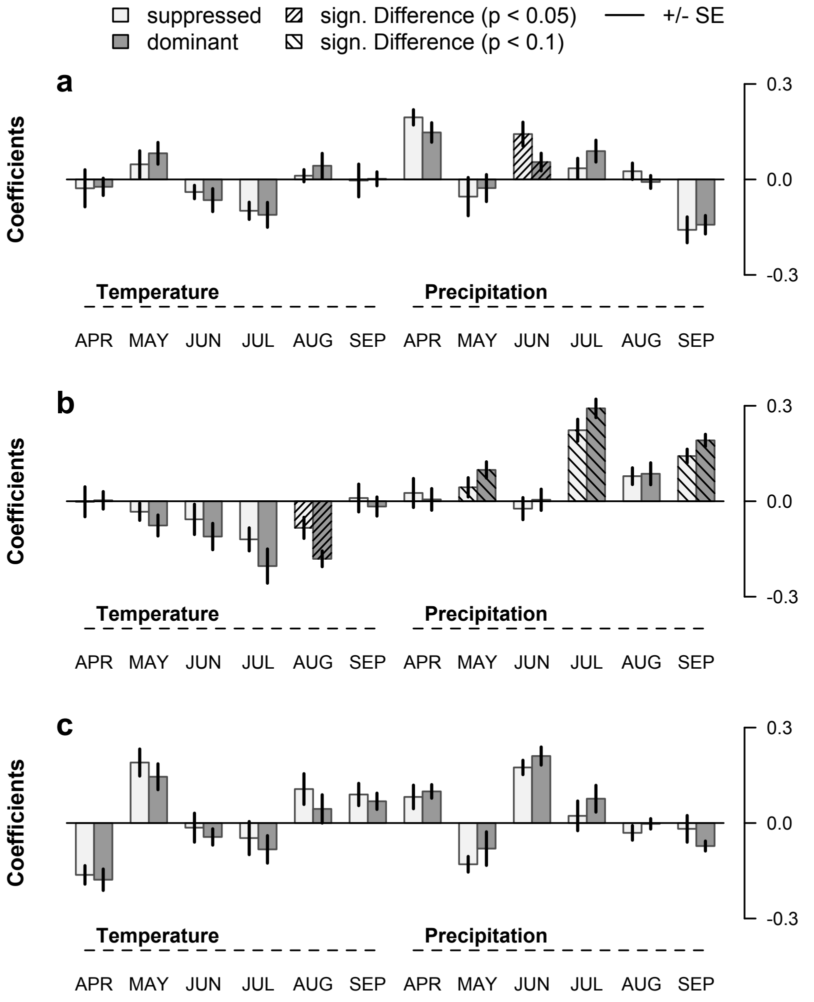

Figure III.15.: Growth/climate relationships for (a) pine, (b) Norway spruce and (c) oak. The height of the bars represents the corresponding coefficient of a response function for monthly temperatures and precipitation. The calibration period is 1948 – 2007 (60 years). The error bars represent the standard error of the parameter observations for all trees of a given diameter group.

High temperatures limit growth of spruce throughout the growing season (fig. III.15b). Dominant trees generally displayed a stronger limitation by high summer temperatures, with a highly significant difference in August. High amounts of precipitation in July and September foster growth of spruce, with relationships being significantly more positive in dominant trees.

Oak trees of both diameter groups profit from a wet and cold April, a dry but a warm May, and a wet June (fig. III.15c). Dominant trees tended towards a stronger limitation by summer precipitation and warm temperatures throughout the growing season, but no significant differences could be observed.

III.3.5. Ontogeny of hydraulic architecture

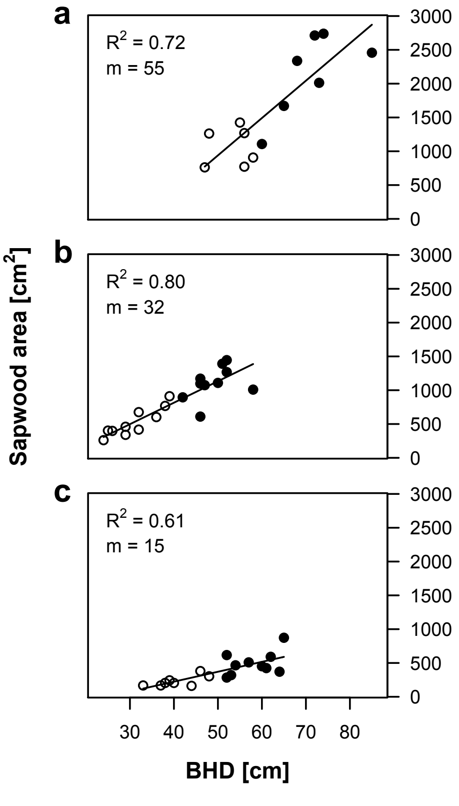

Figure III.16.: Relationship of sapwood area to diameter at breast height (BHD) for (a) pine, (b) spruce and (c) oak. The value of the parameter *m* gives the slope of the regression line. Dominant trees are represented by filled dots, suppressed trees by hollow dots.

Remarkable differences in the relationship between increasing diameter and increasing sapwood area between species could be observed: in all species diameter at breast height was highly significantly correlated with sapwood area at breast height, but the slopes of the regression lines differed significantly between all species (significance tested with species and the interaction of species with diameter as dummy variables in pair wise regression models, fig. III.16). The steepest slope was found for pine (fig. III.16a), signifying that this species increases sapwood area faster with growing diameter than the other species under investigation. The shallowest slope was found for oak (fig. III.16c), this species builds up a relatively small amount of sapwood per unit of diameter.

III.3.6. Effects of drought on modes of competition

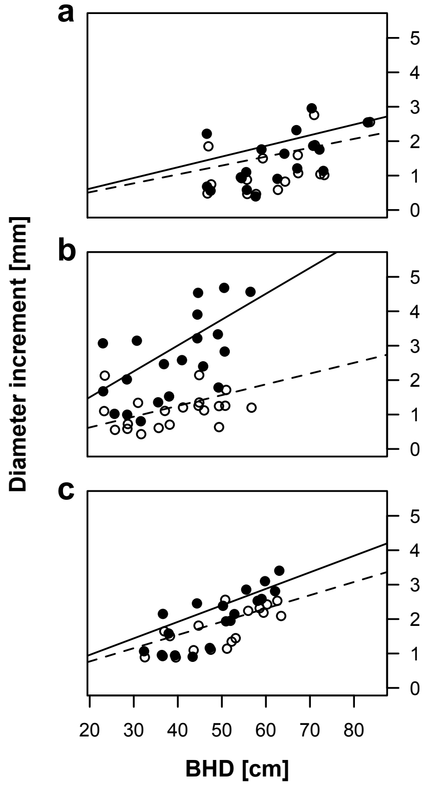

Figure III.17.: Relationship of diameter at breast height (BHD) and diameter increment for pine (a), spruce (b) and oak (c) for the moist year 2002 (filled dots, full line) and the dry year 2003 (hollow dots, dashed line). All models are significant at $p < 0.001$, all R^2 are higher than 0.82. For spruce and oak, the slope for 2002 is significantly steeper than for 2003 ($p < 0.001$ and $p = 0.011$ resp.).

There was a statistically significant positive relationship between diameter at breast height and diameter increment for all species and both the moist year 2002 and the dry year 2003 (fig. III.17). For 2002, all regression slopes were steeper than in 2003, indicating a stronger asymmetric competition under moist conditions, as taller trees grew disproportionately more than smaller trees. Under dry conditions, a shallower slope indicates a more symmetric competition. These differences in regression line slopes were statistically significant for spruce and common oak (regression lines tested for significantly different slopes using the interaction of year with diameter as dummy variable in per species regression models).

III.4. Archetypal patterns of tree growth

The results presented in this section refer to research objective 2 (see section I.4), and are based on the full data set of 143 tree-ring chronologies.

III.4.1. Data set for calculation of archetypes

As from the above results a clear distinction between drought tolerance, mainly represented by oak, and drought intolerance, mainly represented by spruce, could be derived, these two species were used exclusively to set up the archetypes to be used for benchmarking. This means, that extreme—or "pure"—types of spruce and oak growth were to be identified, and in further steps used as benchmarks for drought tolerance and intolerance. The multivariate data matrix $\boldsymbol{I}$ in equation II.27 thus consists of 36 spruce and 23 oak chronologies.

III.4.2. Summarizing power of archetypes and choice of l

From the RSS function (figure III.18) the ideal number of archetypes l to be used for the analysis is not conclusive. Aiming at RSS minimization, either three or six archetypes could be used, as a further increase in l does not directly reduce the RSS function. However, choosing six archetypes increases the reduction of RSS by less than 10%, for the prize of higher complexity of the results and a probably more difficult interpretation of the archetypes, as only two different species are present in the data set. Therefore in the following sections, solutions for l = 2 and l = 3 are explored.

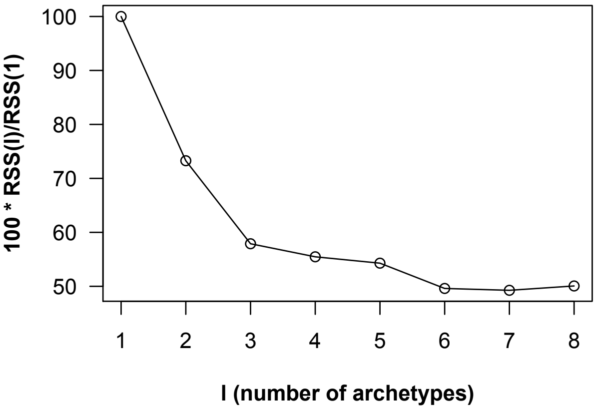

Figure III.18.: RSS-function for archetypes with $l = 1 \ldots 8$. See section II.8.3 for the definition of the RSS-function.

III.4.3. Ecological interpretation of archetypes

For l = 2, archetypes provide a clear separation of the two species through archetype contribution α (figure III.19). This leads to the connotation of a spruce archetype and an oak archetype, whose contribution to each single chronology is represented by α_1 and α_2, respectively.

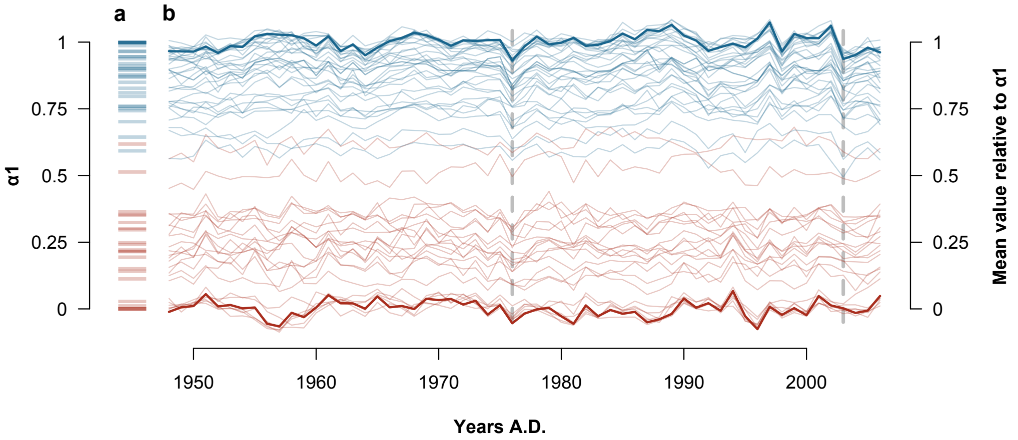

Figure III.19.: (a) α_1 of spruce chronologies (blue lines) and oak chronologies (red lines) for l = 2, and (b) individual tree-ring chronologies for spruce (blue curves) and oak (red curves)—centered to a mean value of α_1—plotted together with archetypes for l = 2 (thick curves). The extremely dry years 1976 and 2003 are indicated by vertical dashed grey lines.

As a consequence, the patterns represented by the archetypes with regard to drought susceptibility are diverging: the spruce archetype typifies trees with a strong growth limitation by both summer temperatures, indicated by a high percentage of significantly negative correlations with JJAT, a high percentage of significantly positive correlations with JJAP, and higher averages of explained variance by JJAT and JJAP (table III.3, upper part). At the same time, the oak archetype shows no significant correlations with either JJAT or JJAP on any site, and significantly less variance in RWI of the oak archetype is explained by climatic parameters. Regarding extreme drought events, the spruce archetype is characterized by a stronger decrease in RWI in the dry years 1976 and 2003 (figure III.19b, dashed vertical lines).

The α_j can therefore act as indicators for drought susceptibility (α_1) and drought insusceptibility (α_2). However, for l = 2 these α_j lack any further explanatory power. They are not significantly correlated with parameters that would help to obtain supplementary information, such as altitude and mean climatic conditions at the individual sites. Nevertheless, the highest values for α_2 are found at the cool and wet end of the precipitation and temperature gradient (fig. III.20a). This means that the two spruce populations that

Table III.3.: Comparison of percent significant negative correlations with all June-July-August-temperature series (JJAT) and significant positive correlations with June-July-August-precipitation series (JJAP) of archetypes, and of percent explained variance in archetype RWI by JJAT and JJAP (mean value and standard deviation, different letters per group and column indicate significant differences at $p < 0.05$ by t-test)

l	Groups	% Sign. JJAT	% Sign. JJAP	% Variance JJAT	% Variance JJAP
2	Archetype 1	72.5	65.0	9.7 ± 4.8^a	8.0 ± 3.0^a
	Archetype 2	0	0	2.4 ± 2.3^b	1.7 ± 1.4^b
3	Archetype 1	60.0	10.0	8.9 ± 4.0^a	2.9 ± 3.0^a
	Archetype 2	42.5	80.0	6.0 ± 4.0^b	13.4 ± 6.9^b
	Archetype 3	0	0	2.4 ± 2.2^c	1.8 ± 1.5^c

are most similar to the ideal oak are found on wet and cool sites. In turn, α_1, i.e. the contribution of the "pure" spruce growth signal, of the oak chronologies depicts the highest values at dry end of the gradient, with the maximum value found at a dry and warm site (fig. III.20b).

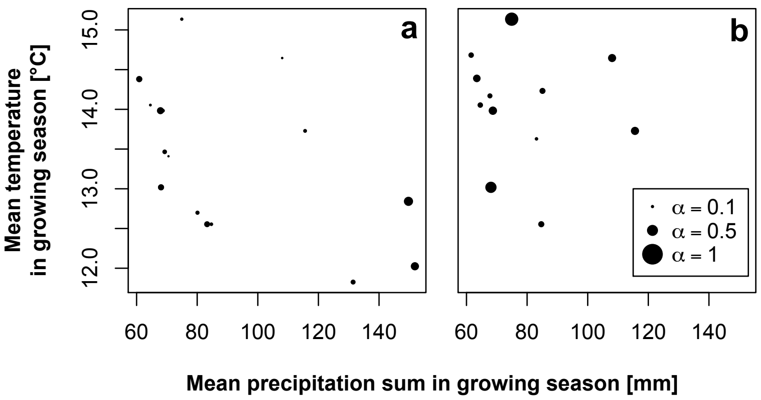

Figure III.20.: α_2 for $l = 2$ for the spruce chronologies (a) and α_1 for the oak chronologies (b) plotted in an ecological space spanned by mean precipitation sum and mean temperature for the growing season.

Increasing l to 3 leads to a considerably improved explanatory power of the archetypes (figure III.18). The RSS function is decreased by more than 15%, indicating an increase in summarizing power. The oak archetype for $l = 2$ is very closely correlated to one of the archetypes for $l = 3$ (archetype 1, r = 0.90). Thus, the main changes from two to three archetypes consist in splitting up the spruce archetype into two new archetypes: in most years, the archetype related to oak growth does not noticeably change its position when l is increased from 2 to 3, whereas the archetype related to spruce growth for $l = 2$ is replaced by two archetypes for $l = 3$ in many cases (fig. III.21).

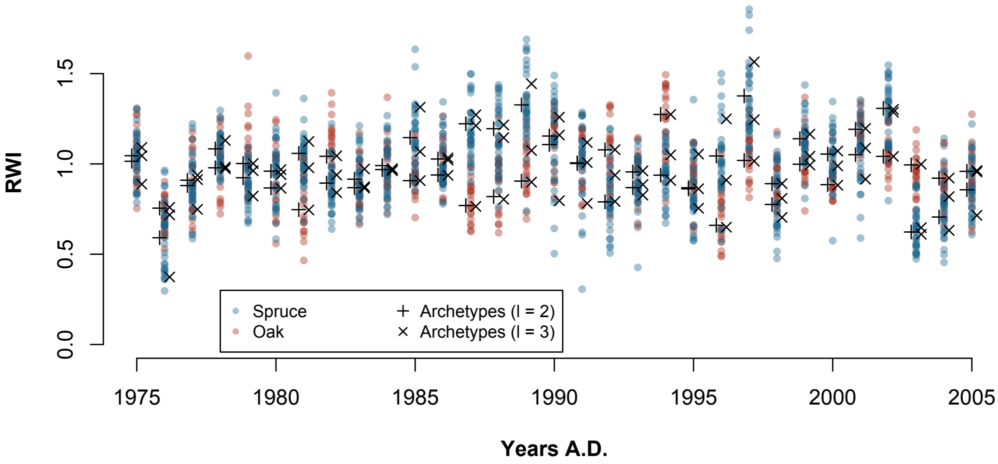

Figure III.21.: Time-series of spruce and oak chronologies (shown is a subset of the total time span used for the analysis), with archetypes for $l = 2$ and $l = 3$.

In terms of drought sensitivity, the two spruce archetypes exhibit two different patterns: one spruce archetype (archetype 1 in table III.3) is strongly associated with growth limitation by high summer temperatures, but not with growth limitations by low summer precipitations. The other spruce archetype (archetype 2 in table III.3) exhibits a weaker coupling with summer temperatures, but a very strong one with summer precipitations. For $l = 3$, the archetype related to oak has not changed in terms of growth limitation in comparison to $l = 2$ and does again not display any significant correlation with either JJAT or JJAP. From the latter, it is concluded that already for $l = 2$ a hypothetical extreme performer was found for oak growth which does not change when l is increased.

The meaning of $\boldsymbol{A}$ for $l = 3$ is discussed using a ternary plot of α (figure III.22). While the oak chronologies still are associated with a high α_3 for the oak archetype (AT3) throughout, the spruce archetypes can be best interpreted as a high altitude spruce archetype (AT1) and a low altitude spruce archetype (AT2).

III.4.4. Archetypal patterns of spruce growth as ecological benchmark

Consequently, the $l = 3$ configuration is used for benchmarking, and archetype 2 is employed as a benchmark for drought intolerance (extreme low altitude spruce growth patterns). By means of correlation, all tree-ring chronologies can be subject to benchmarking. The map view reveals spatial patterns of drought intolerance that are quite similar to

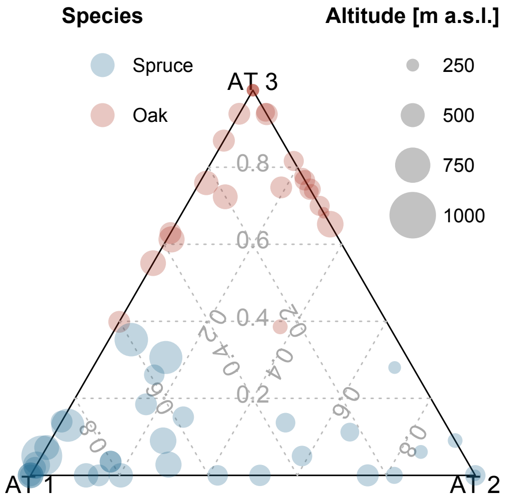

Figure III.22.: Ternary plot of the α values for three archetypes.

the patterns encountered above (fig. III.23), with a main area of drought susceptibility in the northern part of the investigation area, mainly in the Franconian and Wuerttembergian upper triassic. In terms of differences between species, spruce populations show the most distinct similarity to the archetypal low altitude spruce, but populations of the other coniferous species as well as of—surprisingly—beech represent a remarkably close resemblance of the archetypal spruce. Oak exhibits the least overall resemblance of the archetypal spruce, and has therefore the least share of drought related tree performance patterns.

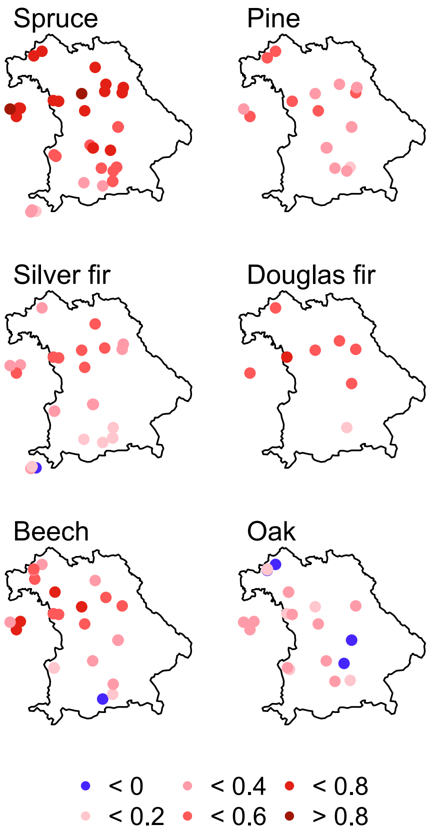

Figure III.23.: Correlation of individual site chronologies with drought intolerance benchmark (archetype 2 for *l* = 3).

III.5. Changes in root-shoot-allocation patterns along a precipitation gradient

The results laid out in this section refer to research objective 3 (see section I.4) and are based on root and shoot tree-ring series sampled along the precipitation gradient from Zirndorf via Freising to Siegertsbrunn (see also section II.1.2).

III.5.1. Comparison of growth patterns between stems and roots

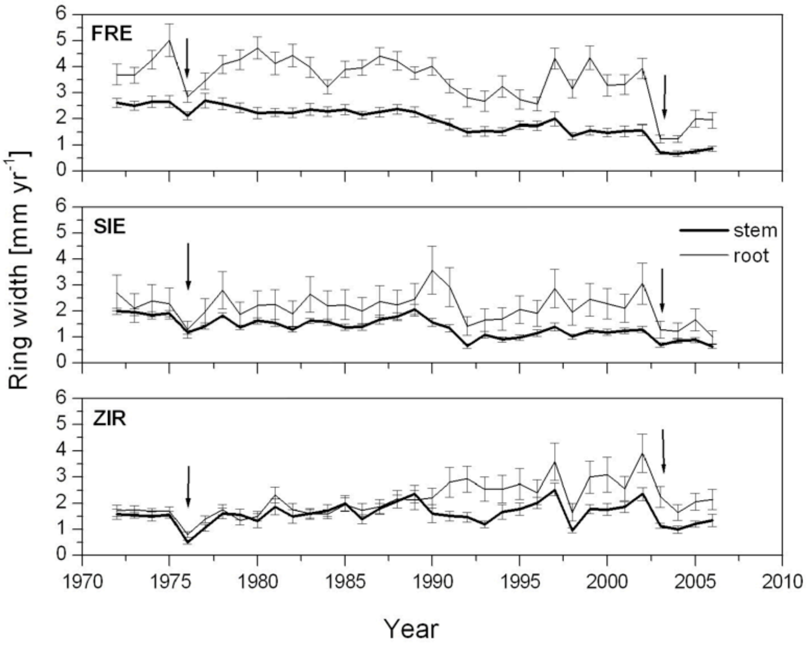

Figure III.24.: Average tree-ring widths (± standard error) for roots and stems of spruce for the study sites Freising, Siegertsbrunn and Zirndorf in 1972–2006. Arrows indicate the extremely dry years 1976 and 2003.

The mean tree-ring chronologies of spruce trees growing in Freising had, in general, larger annual stem and root increments compared to the spruce trees from the other two locations (i.e. Siegertsbrunn and Zirndorf; fig. III.24). At each study location, two abrupt declines occurred in the annual radial growth of both stem and root, corresponding to the extremely dry years 1976 and 2003 (fig. III.24). During these two dry years the annual increment of both analyzed tree compartments exhibited reductions of 20 to 40% relative to the previous year's growth. Overall, the reduction in growth was more pronounced after the extremely warm and dry 2003, and recovery was still not complete at the end of the study period in 2006. However, in the years with average climate conditions, mean tree-ring widths in the roots were greater compared to those of the stems at breast height, which was related to the eccentric form of the root-rings (c.f. also Krause & Morin, 1995).

Chronologies of shoots at Freising and Siegertsbrunn had significantly greater MS than the corresponding chronologies of roots (0.27 and 0.33 versus 0.21 and 0.26, respectively; t-test, $p < 0.001$), whereas the MS of shoots at the dryer site Zirndorf was relatively high but similar to that of roots (i.e. 0.32; cf. fig. III.25). Only at Zirndorf a significant correlation was detected between MS and tree form stability ($p < 0.05$; fig. III.25). The sensitivities of root and shoot growth of the form stable trees at this dry location were relatively low but similar to the MS of the trees from the intermediate location Freising, whereas the non-stable trees showed greater MS.

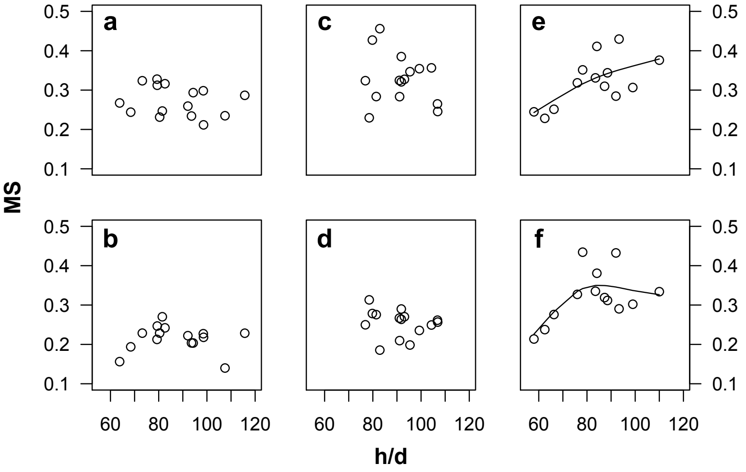

Figure III.25.: Mean sensitivities (MS) of the root and shoot chronologies at each study site as related to the individual tree form stability (h/d ratios < 80 indicate high form stability) for Freising (shoot, a, and root, b), Siegertsbrunn (shoot, c, and root, d) and Zirndorf (shoot, e, and root, f). Correlation lines show the significant relationships at $p < 0.05$.

III.5.2. Below-ground vs. above-ground reactions

There was no temporal offset between below- and aboveground growth reactions to climate conditions in the spruce trees from all studied locations (fig. III.26). By far the highest values for GLK (fig. III.26a) derive from non-lagged series of shoot and root growth. GLK is not influenced by individual long-term growth trends, whereas the correlation between curves also factors in these low-frequency dynamics and leads to more uniform values. Nonetheless, the lagged correlation between shoot and root growth also indicates the best agreement when the series are not lagged (fig. III.26b), albeit the differences are not as pronounced as the differences in GLK. Median GLK is higher at Siegertsbrunn (71% agreement between curves) and Zirndorf (68% agreement), and lower at Freising (59% agreement), whereas median correlation is higher for Freising (R^2 = 0.59) and Siegertsbrunn (R^2 = 0.56), and lower for the driest site Zirndorf (R^2 = 0.40).

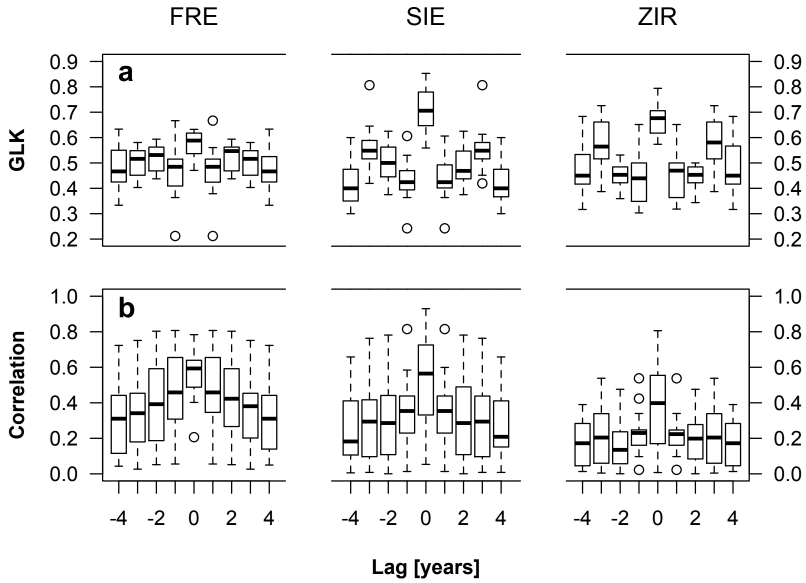

Figure III.26.: Gleichläufigkeit (GLK) of above- and belowground growth (a) and median Pearson's coefficient of correlation (b) as calculated for the same root and lagged (from -4 to +4 years) shoot series of individual spruce trees in Freising (FRE, left column), Siegertsbrunn (SIE, middle column) and Zirndorf (ZIE, right column).

III.5.3. Root-shoot allometry

The allometric exponent γ, that represents the long-term root-shoot allometry on tree level, was found to range between 1 and 3 in Freising and Siegertsbrunn, and between 1 and 5 in Zirndorf (data not shown). Regarding site effects, Tab. III.4 reveals similar mean γ values for both Freising and Siegertsbrunn (2.16 and 2.13, respectively). In the long term, spruce trees growing in Zirndorf (mean γ = 2.86) allocated significantly more ($p < 0.001$) growth resources to roots than to stems compared to spruce trees from the other two study locations. The differences in the site quality are similarly evident in the variation coefficient (CV) of the slope γ' assessed for each study location (Tab. III.4). It

Table III.4.: Characteristic values for the allometric slopes γ and γ' of spruces growing at Freising, Siegertsbrunn and Zirndorf. Letters indicate significantly different values between the study sites ($p < 0.05$).

Site	γ		γ'		**CV of** γ' **%**	
	mean	SD	mean	SD	mean	SD
Freising	2.16^a	0.12	2.24^a	0.13	21.1^a	3.5
Siegertsbrunn	2.13^a	0.17	2.20^a	0.16	30.8^{ab}	3.9
Zirndorf	2.86^b	0.33	3.07^b	0.33	39.6^b	7.0

amounts to 21.1% in Freising, 30.8% in Siegertsbrunn, and 39.6% in the water-limited site Zirndorf. However, the differences in CV are significant only between Freising and Zirndorf (Tab. III.4; $p < 0.05$). Our results suggest that spruce trees growing under permanent water limitation change their allocation patterns to above- and/or below ground structures with a stronger oscillation than spruce trees growing under non-limited soil conditions.

Among all study locations, spruce trees in Zirndorf in general had the highest form stability against wind-throw (mean h/d of 83), showed the highest exponent γ (Tab. III.4), and thus the highest relative allocation of growth resources to roots.

IV. Discussion

The results presented draw a clear picture of species ranking and regional differences with respect to drought susceptibility. Similar spatial patterns of drought tolerance and intolerance could be obtained for all species, with spruce generally being the most drought prone species. Furthermore, striking differences in ontogeny of climatic limitation among species were found, and evidence for adaptive capability to increased drought stress by means of increased allocation of biomass towards roots was given. In the following sections, the results are discussed with regard to the initial hypotheses (section I.4).

IV.1. Species effects on growth reaction to climate and drought

IV.1.1. Spruce

Of all species under investigation, spruce depicts the strongest impact of drought on tree growth—in the long term and in the short term. Regarding the long-term growth/climate coupling, spruce shows the strongest dependence of sufficient summer precipitation and moderate summer temperatures. Lower growth rates connected to dry and warm summers in central Europe have also been observed by Mäkinen et al. (2002) and Spiecker (1990). This confirms the classification of spruce as a drought-intolerant tree species by climatic envelopes (most notably Kölling, 2007), simulation studies (e.g. Pretzsch & Dursky, 2002), ecophysiological studies (e.g. Cochard, 1992), and expert assessment (e.g. Niinemets & Valladares, 2006). The comparably slow recovery of spruce growth after extreme drought confirm the prolonged growth reductions in spruce as a consequence of drought observed by Kahle & Spiecker (1996) and Mäkinen et al. (2002).

Large parts of the radial increment take place during June (Deslauriers et al., 2003), which explains the high sensitivity of spruce regarding high June temperatures. A preconditioning of growth by high temperatures in previous late summer—which was also observed here—is by some authors explained by increased cone production associated with dry conditions, that leads to a decreased carbon allocation towards shoot growth (Chalupka et al., 1975; Andreassen et al., 2006). On the other hand, Seifert & Müller-Starck (2009) could not verify a relationship between increased cone production and decreased increment growth for Bavarian spruce. Therefore, the aftermath of summer drought is the most probable explanation for the negative influence of high previous summer temperatures on tree growth in the subsequent year.

IV.1.2. Pine

Following climatic envelope models, pine has to be considered a critical species with regard to predicted climatic changes (Brosinger & Tretter, 2007), and the species' natural geographical distribution suggests its unsuitability for warm and dry climates as well (Walentowski et al., 2007). On the other hand, pine is rated rather drought-resistant in dendroecological studies (Oberhuber et al., 1998; Bouriaud & Popa, 2009). The present results lead to a more favorable rating of pine in comparison to spruce: pine shows a smaller growth decrease in connection with severe summer drought events, and the recovery from drought is faster. When long-term growth/climate relationships are considered, pine exhibits a remarkably lower negative influence of dry and warm summers, as can be seen from the results of the response functions and the low correlation between tree growth and transpiration deficit. A stronger impact of spring and early summer precipitation on pine growth as opposed to late summer precipitation has also been observed by Thabeet et al. (2009).

A potential ecophysiological explanation for these differences between pine and spruce can be found in the species' diverging strategies for water use: in contrast to spruce, pine is able to exert a tight control on transpiration by decreasing stomatal conductance. This can prevent impeririling expansive embolisms (Cochard, 1992; Cochard et al., 2004; Irvine et al., 1998). Moreover, in case of enduring summer drought, pine has the advantage of an earlier onset and termination of growth in the year (Pichler & Oberhuber, 2007), rendering this species less limited by (late) summer drought than spruce.

IV.1.3. Silver fir

Silver fir exhibits far less growth decline in connection to drought years than spruce (and pine), and a quicker recovery. From all coniferous species under investigation, it shows the least limitation of growth by summer drought. This is well in agreement with the results of Elling et al. (2009) who found that silver fir generally is a drought resistant species, and that severe growth declines in silver fir in the past are most probably due to the preconditioning by air pollution (mainly SO_2, Elling, 1993). Owing to a drastically reduced concentration of air pollutants since the mid 1980ies, the drought year of 2003 lead to only minor growth decreases (Elling et al., 2009).

The smaller susceptibility of silver fir to dry and warm summers in comparison to spruce is consistent with other dendroecological studies from Central Europe (Bouriaud & Popa, 2009; Becker, 1989; Desplanque et al., 1999), as well as with climatic envelope models (Kölling, 2007). Major factors for the resistance of silver fir are a deep rooting system (Elling et al., 2009) enabling a superior water uptake, and a more efficient utilization of spring precipitation in comparison to spruce (Becker, 1989; Desplanque et al., 1999; Bouriaud & Popa, 2009).

IV.1.4. Douglas fir

Douglas fir exhibits a dendroclimatic profile rather similar to that of spruce, characterized by remarkable growth limitations by high summer temperatures and low amounts of summer precipitation. But the partially strong decline in increment growth associated with severe drought events is connected to the generally highest growth rates, and the recovery from drought was quick even on the most affected sites.

The observed patterns of growth/climate coupling confirm the evaluation of Kölling (2008), whereupon Douglas fir may profit from a prolonged growing season in Southern Bavaria, but is most probably not suited for the warmer areas (like the triassic), where climatic conditions for growing Douglas fir are out of range under present conditions already.

The results presented here should be interpreted more cautiously than for the other species, as no information about the provenance of the populations was available. In contrast to the native tree species under investigation, genetic diversification of Douglas fir was not as strongly interrupted by glacial ages (Halliday & Brown, 1943). Therefore, a stronger connection between genotype and growth conditions at the origin of seed material exists in Douglas fir, that may e.g. manifest as differences in drought tolerance (Hermann & Lavender, 1968; Martinez Meier et al., 2008).

IV.1.5. Beech

Considering the divisively discussed suitability of beech as a tree species for future climatic conditions (compare, e.g., Rennenberg et al., 2004, and the response by Ammer et al., 2005), the present results superficially show that questions like that should not be approached using a small number of trees or populations only. Beech exhibited a remarkably wide spectrum of possible reactions to summer drought. Throughout the investigation area, beech showed a more distinct limitation of tree growth by summer drought than oak, and the growth decline associated with severe drought events is stronger. Recovery from extreme drought is quick, though. A significant limitation of beech growth in low altitude stands by low summer precipitation and high summer temperature has also been observed by Dittmar et al. (2003).

The most distinct differences to oak are found on sites that resemble viticulturally favorable climatic conditions by today already—i.e. the north-western part of the investigation area. Here the impact of drought on tree growth of beech is far more pronounced as it is for oak.

A particularly strong increase of beech growth under recent conditions as compared to yield tables (Pretzsch, 1999) suggests a benefit through increasing average temperatures besides other factors, and the best height growth is achieved in the warmer regions of Bavaria (Felbermeier, 1994). Somewhat contrarily, the present results demonstrate that in the warmer regions of the investigation area (Northern Bavaria, North-Eastern Wuerttemberg) high summer temperatures exert a stronger limitation on beech growth. Furthermore, some northern populations also exhibit a remarkably close resemblance of "spruce-like" growth patterns related to drought intolerance. These findings suggest, that other external factors modify the impact of climate on tree growth, resulting in complex species-climate-site interactions.

Interestingly, populations with severe impact of extreme drought events on tree growth are not necessarily those with a stronger general growth/climate coupling. This gives further evidence that different mechanisms control beech growth under drought conditions, particularly physiological drought stress versus physiological response to increased tropospheric ozone concentrations (Löw et al., 2006).

IV.1.6. Oak

Of all species under investigation, oak shows the greatest resistance to extremely dry summers. The growth decline associated with extreme drought years is low and transient in general. This finding is in contrast to longer lasting effects of drought events found for various oak species in other studies (Jacobi & Tainter, 1988; Jenkins & Pallardy, 1995; LeBlanc & Foster, 1992). Also, only a weak coupling between tree growth and summer climate or transpiration deficit could be established. These findings suggest only a minor limitation of oak growth by warm and dry summers in the investigation area, and the high potential to recover from severe drought events in short time implies an exceptional growing suitability under conditions of more frequent dry summers under future climate regimes. Friedrichs et al. (2008) also found only a weak coupling between summer temperatures and growth of common oak in Central-West Germany, with the highest response of oak growth to precipitation in spring. This signifies the importance of water supply in spring, when the vessels are formed (Gonzalez & Eckstein, 2003).

The differences to beech can be explained by diverging water balance strategies in case of drought stress: oak maintains a higher leaf conductance and higher photosynthetic activity (Backes & Leuschner, 2000), whereas beech tends to an early closure of stomata and restriction of photosynthesis to avoid embolisms, to which this species is particularly prone (Cochard et al., 2005). In comparison, beech further has a more shallow rooting system than oak (Lebourgeois et al., 2005), which could be an additional disadvantage in case of scarce soil water resources.

IV.2. Site effects on growth reaction to climate and drought

Regional climate characteristics (particularly precipitation during the growing period) influence the primary growth decline associated with drought events and the general growth/climate coupling, with generally stronger impact of dry summers in the northern half of the investigation area. This is also confirmed by the strong correlation between MS and precipitation sum during the growing period, which emphasizes the sensitivity of radial growth to water limitation (Klemmt et al., 2009; Mäkinen et al., 2003; Neuwirth et al., 2004). The areas with high MS are similar to the areas with strong growth/climate couplings, indicating that a considerable part of the year-to-year variance is due to climatic forcing of tree-growth. Regarding a possible refinement of local climate to the amount of water that is actually available to the trees as soil water, no advancement could be achieved.

Douglas fir and oak showed a rather plausible differentiation of growth decline with regard to the modelled soil water storage—in terms of a stronger decline on dryer sites. For the remaining species, this is not the case. This means that no clear relationship with site quality (i.e. other than climate alone) could be established.

Non-conclusive relations between site quality and drought impact have also been observed by Orwig & Abrams (1997), suggesting that complex interactions between site, climate and species might hamper the establishment of site-specific drought assessment. For instance, a rather asymmetric competition in mesic stands usually not limited by soil moisture (c.f. Pretzsch & Biber, 2010b) may lead to fewer drought adaptations of the individuals. Consequently, mesic sites may be more affected by severe drought than xeric sites, where enduring scarceness of soil resources renders the individual tree more adapted to drought conditions. A potential source of differentiation in the form of altered root-shoot-ratios of xeric vs. mesic sites is discussed in section IV.6.

IV.3. Sources of unexplained variability

Despite the present results allow for some spatially explicit predications about the growing suitability of the six species in the investigation area—like the obvious threat of spruce in Franconia and Upper Palatinate—, the strong variability in growth reaction to summer drought has to be emphasized. This variability hampers the deduction of clear, climatic or site-related thresholds for silvicultural choices. Variability on population level does not correspond to site-conditions, thus a causal relation of the form "more environmental stress on the long-term—more degrees of freedom in the reaction to extremes" is not likely. But—besides the complex interactions between site and species discussed above—the genetic diversity on the level of the investigation area might play an important role. For Douglas fir, the general drought susceptibility is controlled by the genotype (see section IV.1.4), and for beech different provenances exhibit different traits connected to drought tolerance, like e.g. the ratio of root to shoot biomass (Tognetti et al., 1995). Genotypic variations like these are often found in species with a large natural distribution area (Rose et al., 2009). Different provenances could therefore explain some of the basic noise in the data set presented in this dissertation, which leads to weak relationships between growth reactions and site characteristics.

But also on population level, genetic diversity or the spatially or temporally inhomogeneous distribution of resources might lead to an increased variability in reaction to drought stress. In every population there are individuals with higher or lower potential for adaption. This can be explained by a varying quality of information stored in the genome of the individuals—reflecting the different environmental experiences of their ancestors (Levins, 1968). Furthermore, small-scale disturbances like wind-throw or thinning can lead to changes in growth behavior of individuals that might then override the climatic component of the growth signal (Jump et al., 2006).

The following section discusses the influence of size effects on growth reactions to climate and drought. These might—in general—be an additional source for variance within the sampled populations. As according to the sampling protocol for the main data set only (co)dominant trees were chosen, it is believed that this effect is rather negligible for the variance discussed here.

IV.4. Size effects on tree reaction to climate and drought

IV.4.1. Size dependent chronology characteristics

As the age of the diameter group chronologies was identical or differed by only one year for all three species and as tree-rings were measured to the pith for all samples, the differences found between diameter classes can indeed be ascribed to size rather than age effects. The expressed population signal (EPS) value of < 0.85 (Wigley et al., 1984) for all group chronologies and high values for mean sensitivity (MS) indicate a common signal corresponding to regionally effective limitation factors. Suppressed trees in all species have a higher inertia in growth as indicated by the higher autocorrelation, which can be explained by a higher importance of growth limiting factors that do not vary much in time, like root and crown competition (Martin-Benito et al., 2008).

IV.4.2. Differences in growth/climate relationships between diameter groups

Differences in growth/climate relationships between diameter groups could basically be ascribed to two diverging mechanisms: On the one hand, there is evidence that suppressed trees experience greater water stress because of greater root competition for soil moisture (Abrams & Mostoller, 1995; Jacquart et al., 1992; Kloeppel et al., 1993). This may lead to a stronger climatic signal in tree-ring patterns of suppressed trees. In this study, suppressed Scots pine trees showed a higher demand for precipitation in June, indicating a stronger root competition for water among the suppressed individuals. The higher MS of suppressed pine trees also gives evidence for a stronger climatic signal in suppressed Scots pine trees. Martin-Benito et al. (2008) found a lower MS of tree-ring width of dominant *Pinus nigra* trees, where a deeper rooting system may offset regular drought stress to later in the summer, when the latewood is formed, rendering a large part of the tree-ring less influenced by short-term climatic fluctuations.

On the other hand, the Limitation-Caused Matter Partitioning (LCMP) hypothesis states that the mode of competition is heavily influenced by the prevailing limiting factor (Pretzsch & Biber, 2010a). While limitation of light is mostly associated with asymmetric resource distribution as light is "pre-emptable" by the tall trees in a stand, scarcity of water and nutrients causes rather symmetric resource distribution as they represent a less directional resource and the access of a plant depends more on size than on spatial position. A significant change in the mode of competition for spruce and oak was observed, from an asymmetric (under moist conditions, steep slope in the diameter-increment growth relationship) to a more symmetric resource partitioning (under dry conditions, more shallow slope). Moreover, suppressed trees are more likely to be influenced by stand dynamics such as crowding, gaps and overtopping (Phipps, 1982) and may therefore hold a stronger ontogenetic and non-climatic signal in their tree-ring patterns as dominant trees. Also, trees growing under shade of their neighbors face a different microclimate than dominant trees, due to lower direct solar radiation and wind speed, leading to a reduced transpiration (Bréda et al., 2006). A stronger climatic signal ascribed to reduced competition in bigger trees is the basic assumption of the commonly applied sampling protocol for dendroecological studies, where selection occurs among the dominant trees of the stands under investigation (Fritts, 1976; Cook & Kairiukstis, 1990). Data from spruce trees at Forstenrieder Park confirm this alternative mechanism, as dominant trees generally depicted a greater influence of temperature and precipitation throughout the growing season. Additionally, a higher MS in dominant spruce trees corroborates this perception. Oak does not show any distinctive differences in growth/climate relationships at this sampling site, equally no significant differences in MS between diameter classes indicate a quite similar amount of long-term climatic signal.

IV.4.3. Reaction to extreme drought events: differences in growth reaction across diameter classes

Pine trees of both diameter groups showed prolonged reductions in tree-ring growth associated with drought events. Prolonged reductions of increment growth in Scots pine in connection with extreme summer drought were also reported for Austria (Pichler & Oberhuber, 2007) and the French Mediterranean region (Thabeet et al., 2009). Prolonged growth reductions can possibly be caused by leaf, branch and root dieback, xylem cavitation, and changes in carbon allocation patterns within trees (Orwig & Abrams, 1997). The reduced reduction of growth in drought years in suppressed pine trees is in accordance with findings in deciduous species (Liu & Muller, 1993) and *Pinus nigra* (Martin-Benito et al., 2008), and might be explained by drought hardening due to higher concentrations of abscisic acid (Chandler & Robertson, 1994), which plays a substantial role in drought resistance (e.g. Schachtman & Goodger, 2008). However, in Norway spruce a tendency to greater growth reductions in suppressed trees was found (not significant), which is in accordance with Brakel & Visser (1996) who also found greater growth reductions in understory *Picea abies*.

In oak, in the year of drought both diameter classes exhibited a significant radial growth reduction with no differences between dominant and suppressed trees, whereas for dominant oaks it took one year longer to recover to average growth conditions after a drought event. This is in accordance with longer lasting effects of drought events on dominant oak trees found by Orwig & Abrams (1997).

IV.4.4. Reaction to extreme drought events: differences in latewood δ13C across diameter classes

Pine, spruce and oak showed a significant increase in $\delta^{13}C$ from 2002 to 2003. The $\delta^{13}C$ signal in wood or wood components is commonly used as a proxy for stomatal control of photosynthesis during the formation of the wood (McCarroll & Loader, 2004; Panek & Waring, 1997). Thus this finding can be interpreted in terms of a stronger limitation of photosynthesis in dry versus average years, which is in accordance with the theory on stable carbon isotope discrimination along the photosynthetic pathway (Farquhar et al., 1989).

Under average conditions the latewood of suppressed pine trees exhibited a stronger reduction in the discrimination of $\delta^{13}C$ than the latewood of dominant pine trees. This observed pattern could be interpreted in terms of a stronger limitation of photosynthesis in suppressed pine trees under average, non-drought conditions. In contrast, in the drought year the relative increase in $\delta^{13}C$ is higher in the dominant trees. According to hydraulic limitation hypothesis (Ryan & Yoder, 1997) trees of greater size experience a stronger limitation in photosynthesis due to a stronger stomatal regulation required to maintain a species-specific minimum water potential in leaves. Under average conditions, the Scots pine trees in this study fail to corroborate this hypothesis by displaying the opposite behavior. However, a number of studies report on compensations that reduce the impact of tree height on the conducting system (for an overview, see Ryan et al., 2006). These compensations include a decreased ratio of leaf area to sapwood area and a reduction of minimum midday leave water potential, and work against a hydraulically driven reduction in total tree photosynthesis (Ryan et al., 2006). The amount of sapwood increased much faster with diameter in pine compared to oak. Leaf area was not measured directly, but based on field observations it is assumed that in pine sapwood area was relatively increased in relation to leaf area, because bigger pine trees tended towards a lessened crown volume. This is also confirmed by Scots pine (like all *Pinus spp.*) being prone to xylem cavitations and physiologically adopted to maintain water potentials within relatively narrow limits (Martínez-Vilalta et al., 2004).

According to Oren et al. (1999) plants have three options to decrease the gradient of water potential under water limiting conditions: increase resistance to xylem embolism to reduce loss of the hydraulic conductivity of the sapwood, decrease the leaf-to-sap area ratio, and/or decrease stomatal conductance. Martínez-Vilalta et al. (2004) found that none of these strategies serves as a sufficient predictor of drought resistance in *Pinaceae*, yet a range of traits is used to minimize the gradient of water potential through the xylem. The present results imply that these traits may be effective on different time scales: whereas the increase in xylem is a long-term adaptation to increasing drought stress with increasing tree dimension, on a short-term timescale a reduction of stomatal conductance is an additional strategy, as indicated by the relative stronger increase in δ^{13}C in the drought year in dominant trees. On the other hand, under average conditions, δ^{13}C reflects the relative competitive advantage of dominant trees.

In common oak, under average and drought conditions, dominant trees depict a stronger limitation of photosynthesis. In contrast to pine, oak is not a cavitation prone species (Cochard et al., 1992). Thus, the comparably small increase in sapwood area with increasing dimension reflects a hydraulic architecture that scales efficiently because of a generally minimized risk of vessel cavitation. The relationship of latewood δ^{13}C in the non-drought year 2002 suggests that dominant oak trees cannot take advantage of their competitive bonus, such as a deeper and more developed rooting system. The lack of differences in growth/climate relationships also promotes that view, as dominant and suppressed trees seem to face the same climatic limitations throughout the growing season.

IV.5. Universal patterns of tree growth

The use of two archetypes for the analysis of the oak/spruce data subset leads to extremes that are well matched against current conceptions of the ecology of the species involved and the fundamental results of this study: a drought prone spruce (see section IV.1.1) and a drought resistant oak (see section IV.1.6). However, increasing l to 3 leads to a considerably improved explanatory power of the archetypes, and to a splitting of the spruce archetype into one archetype associated with high altitudes, and one archetype associated with low altitudes. This separation, integrated with the differentiating results from the climate-growth relations of the archetypes, corroborates findings from the literature on Norway spruce. E.g., Dittmar & Elling (1999) showed that with increasing altitude, the correlation between precipitation and RWI changes from positive to negative, with a drop of overall correlation in a transitional zone. A decrease in the importance of summer precipitation and a decreasing negative effect of warm summer temperatures for growth of Norway spruce with increasing altitude was also found by Andreassen et al. (2006), Leal et al. (2008) and Mäkinen et al. (2002).

From the ambitions of this part of the dissertation, the identification of rather stable and physiologically well explained archetypes enables one to use these multivariate extremes as complexly defined benchmarks for drought tolerance and drought intolerance. Therefore, the contribution of these archetypes to a given real tree-ring chronology is a comprehensible measure of drought tolerance versus drought susceptibility of the underlying population of trees.

The power of this method—that is solely based on intrinsic growth patterns—becomes even clearer when the patterns derived with this benchmarking approach are compared to the patterns generated using additional data (climate, water balance): the low altitudinal spruce archetype employed for benchmarking shows a remarkably good agreement with short-term growth reduction IS ($R = 0.73$), IL ($R = 0.65$), population scores on PCA1 of response coefficients ($R = 0.88$), and long-term growth limitation by transpiration deficit ($R = 0.63$). That means that a high score on any of these parameters is related to a high amount of "spruce-like" growth patterns in the respective tree-ring series.

Furthermore, the fact that the spruce data could be represented by a linear combination of a high and a low altitudinal extreme performer suggests a smooth gradient between the two. This means that there is no evidence for clear climatic thresholds triggering a switch in the modality of general growth/climate relationships. And anecdotally, the oak populations with the highest values for "archetypal oak growth" are located in an area that has had an excellent reputation for growing oak for many centuries (and long before sophisticated multivariate statistical methods evolved): the Spessart mountains (e.g., Behlen, 1823).

IV.6. Above- vs. below-ground growth reactions

IV.6.1. Growth of stems and roots as depending on water supply

During the extremely dry years 1976 and 2003, growth of stem and coarse roots in Norway spruce was characterized with abrupt decline, independent of the study location. However, the MS of both root and stem chronologies were lower at the moist sites Freising and Siegertsbrunn than at the driest site (i.e. Zirndorf; c.f. fig. III.25). Therefore, a relationship between mean climatic conditions (particularly precipitation sum) and sensitivity of root growth similar to the relationship observed for shoot growth (section III.1) can be assumed.

Spruce trees from Zirndorf showed the highest below-ground MS, suggesting that Norway spruce overcomes shortage in soil moisture by also enhancing the sensitivity in root cambial activity. Several studies showed that the disturbance in growth of a root system begins at fine-root scale (Joslin et al., 2000; Meier & Leuschner, 2008), and reflects on the coarse-root construction (Coutts, 1987).

Under naturally limited conditions with patchy resource supply, as during the drought events of 1976 and 2003, the morphological fine-root adjustments in Norway spruce may take longer time to complete than the duration of the patch of a given quality. This view is supported by the observation of costly and morphologically conservative fine-root structures of spruce (Bolte & Villanueva, 2006; Nikolova, 2007), and a little and slow transport of new carbon to roots (Andersen et al., 2010). In such a case, soil resource acquisition might not be optimized by the plants' own structures, and the potential benefits of the resource supply would not be realized (Hutchings & John, 2004). The lack of adequate morphological adjustment within fine roots to patchy environmental benefits may therefore have contributed to the poor root and stem growth of Norway spruce at all locations during the dry years 1976 and 2003. Moreover, the form unstable spruce trees at Zirndorf reacted to permanent soil resource limitation by enhancing the sensitivity in both stem and root growth. These results provide additional evidence that the high-frequency reallocation of growth resources within the relatively unstable and generally less productive trees imply a costly morphological adjustment in response to drought stress in spruce.

In this study, the highest values for GLK for non-lagged above- and below-ground series indicated that roots and shoots react to environmental constraints in the same year, and that there is no relative delay in one of the compartments. This is in contrast to asynchronous growth rates in the annual stem increment and annual fine-root production reported by Côté et al. (2003) for deciduous species. However, the present results point out that the synchronicity in the below- and above-ground reactions of trees to climatic signals may be species-specific. Here, general scarcity of soil water could synchronize the growth patterns of root and shoot to improve the acquisition of the limiting resource (Hutchings & John, 2004). Thus, the growth of root and shoot on the water-limited site Zirndorf is not only more prone to fluctuations as depicted by the higher sensitivity, but growth also becomes more synchronous. The lower correlation between non-lagged above- and belowground series for Zirndorf in comparison to Freising and Siegertsbrunn is most probably due to the stronger water limitation of the trees, imposing a greater degree of freedom to individual growth trends between root and shoot. A more independent low-frequency growth pattern eventually leads to lower correlation coefficients.

IV.6.2. Allocation patterns between stems and roots under different site conditions

According to the allometric partitioning theory (APT), resource allocation patterns between different organs change solely with plant size, being insensitive to habitat characteristics (Enquist & Niklas, 2001; Enquist, 2002). The allometric slopes assessed in the study trees, however, seem to indicate rather site-specific biomass allocation patterns in line with the optimal partitioning theory (OPT), i.e. improving plant access to soil water. Along the precipitation gradient, the most water-limited spruce stand Zirndorf showed the highest relative allocation of growth resources to coarse roots in a long and in a short term. Under restricted water supply, spruce trees at this site are evidently diverting more of their fixed carbon to the roots than to the shoot. The highest level coefficient of variation for α' was also detected at Zirndorf, which is in line with several recent studies that showed increased variation in growth of conifers in central Europe and Fennoscandia to be mainly related to decrease in water supply (Kahle, 1994; Kahle & Spiecker, 1996; Mäkinen et al., 2001).

V. Conclusions

Silvicultural practices of the future will have to gauge risks and uncertainties—and to integrate these aspects into a framework for sustainable long-term planning (Nitschke & Innes, 2008). Given the need to somehow assess these risks, like the risk of growing spruce under future climate conditions, evidence based on a broad data base is needed. In this context, the present dissertation contributes to the understanding of magnitude and variability of the growth reaction of economically important tree species to summer drought.

Of all species under investigation, spruce shows the most distinct growth reaction to summer drought, and archetypal spruce growth patterns are clearly associated with drought susceptibility. These findings confirm recent efforts to change pure spruce stands to more stable mixed stands, motivated by the predicted climatic change (e.g. Kölling et al., 2009a). On the other hand, the strong relationship between drought impact on spruce growth and the regional climatic conditions also demonstrates that spruce may maintain a leading role on suitable sites. Furthermore, the high variability on population level suggests that natural adaptability and selection may spare a sweeping change in stock.

Oak showed itself to be least critical in terms of drought impact on tree growth, but also the more productive silver fir can very well replace spruce on many sites.

The differences among diameter groups of different species regarding the impact of drought stress on growth and tree physiology lead to the conclusion that the influence of hydraulic limitation with increasing tree dimension is not uniform among species and environmental conditions. So, drought effects, irrespective of acute or chronic nature, can alter the size-growth relationship and thus forest dynamics and structure. Furthermore, the ontogeny of hydraulic architecture appears to be a key modifier of the distribution of resources among the individuals of a stand.

The results presented further indicate that the relative root-shoot allocation of growth in spruce follows site-specific allometry predicted by the optimal partitioning theory. This indicates that trees are able to mitigate the effects of increasing summer drought by structural adaption to a certain extend. Nevertheless, from a economical point of view, an increased investment in belowground structures is not appealing, and even more so, when the biomass production aboveground still does not approach that of more productive sites.

A major finding of this study is the high variability on regional and population level. This causes individual trees from a population to resist drought years nearly unaffected. However, the trade-offs that might emerge from one or another genotype are not conclusively assessable. For instance, Sthultz et al. (2009) showed that an increased resistance of a genotype to herbivores can be associated with an increased vulnerability to drought stress. A lopsided selection of seed material may therefore—under novel regimes we are not able to predict sufficiently—have costly consequences. This realization corroborates the postulation of a silvicultural practice that also aims at maintaining the genetic diversity, as a key trait for adaption to changing environmental conditions (Schaberg et al., 2008).

VI. Outlook and future research perspectives

In the present dissertation, a variety of methods has been applied to extract climate- and particularly drought-related signals from tree-rings. The fact that consistent results could be obtained renders this dissertation a significant contribution to the discussion of tree suitability under climate change conditions. Nevertheless, some shortcomings of the current approach—or more generally, dendroecology as a whole—have been identified with regard to the research questions tackled. In the following chapter some ideas for further research are discussed, concerning one of the core methods of this dissertation—dendroclimatic calibration—and one of the main findings—the large variability in growth reaction to drought.

VI.1. Enhancing the dendroclimatic calibration toolset

VI.1.1. Improvement of chronology development

The first step of chronology development is also one of the most critical for all subsequent analyses: the removal of an age- and disturbance-related long-term growth trend. Most of the currently employed techniques are based on statistical or deterministic smooth functions (Cook & Kairiukstis, 1990). A major shortcoming of these methods is that variance on larger time scales is removed. Thus, capturing long-term effects of climate on tree growth is not possible with the approach followed in this dissertation. Regional standardization curves (RCS) can mitigate this problem (Esper et al., 2002; Büntgen et al., 2008). But due to utilizing the same RCS for all curves, end problems may occur especially with longer curves (Biondi & Qeadan, 2008). Possible alternatives include theory-based modeling of the long-term trends of ageing and growing (Biondi &

Qeadan, 2008), or the flexibilization of RCS detrending, e.g. by means of quantile regression. From the perspective of research focusing on trees from managed temperate forest the latter approach seems more appealing, because data-adaptive procedures offer more flexibility.

VI.1.2. Temporal instability of growth/climate relationships

The relationships between climate and tree growth are not constant over time, owing to age effects (Carrer & Urbinati, 2004, 2006), management effects or changes in the climate regime (D'Arrigo et al., 2008). For some applications of tree-ring series, e.g. for climate reconstruction, this limitation is an obstacle. But for ecological studies on trees, time-dependent growth/climate coupling provide the unique opportunity to study the impact of e.g. management strategies on climatic limitation of tree growth. For a managed spruce stand it could be shown that selective thinning changes growth/climate relationships in a threefold way (Zang, unpublished, data provided by Tröndle & Häberle): after thinning, general limitation by precipitation decreases; at the same time, a positive preconditioning of warmer October temperatures abruptly ends with thinning; and third, sensitivity with regard to high summer temperatures abruptly increases after thinning (fig. VI.1).

These preliminary results demonstrate the potential of time-dependent growth/climate relations as a tool for assessing the mitigating effects of management options with regard to climate sensitivity of temperate forests.

VI.1.3. Non-linearity of growth/climate relationships

Linear relationships between climate and tree growth are almost exclusively used in dendroclimatic calibration. But a considerable number of experimental studies have found non-linear relationships between climatic predictors and tree growth (Fritts, 1976; Gates, 1980; Kramer & Kozlowski, 1979; Lyr et al., 1992; Schoettle, 2004). These findings are affirmed by empirical studies (Case & Peterson, 2005; Graumlich & Brubaker, 1986; Laurent et al., 2003; Oberhuber et al., 2008; Pichler & Oberhuber, 2007), for instance to that effect of an inversion of positive correlations between temperature and tree growth into negative correlations in very warm years (Case & Peterson, 2005; Oberhuber et al.,

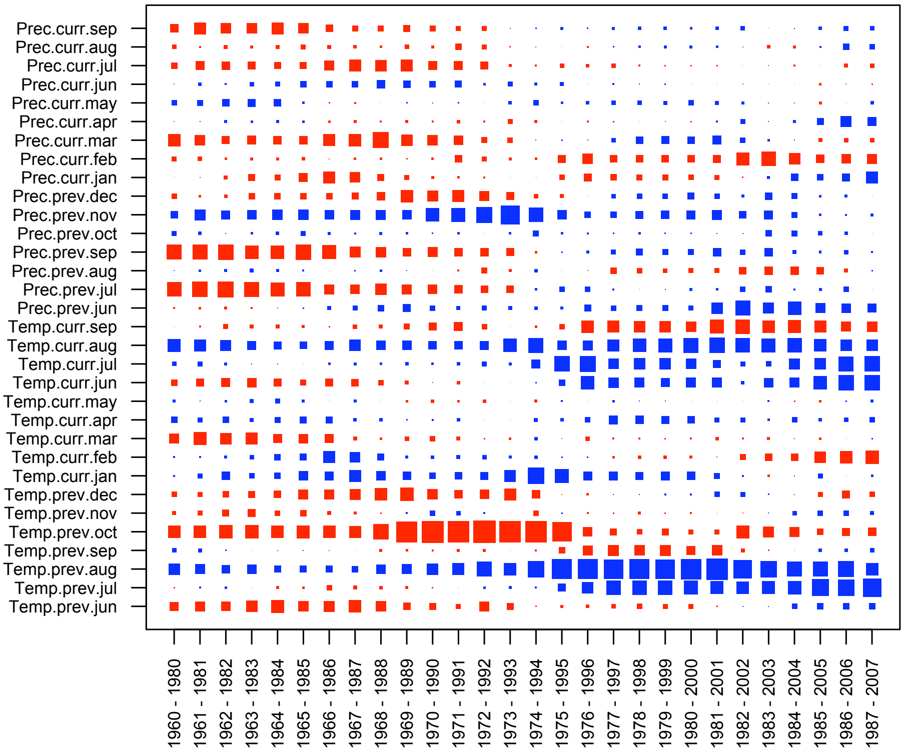

Figure VI.1.: Time-dependent growth/climate relations for a managed spruce stand subject to past thinning operations (Freising, Kranzberger Forst, raw tree-ring series provided by Tobias Tröndle and Karl-Heinz Häberle). Shown are the coefficients for shifted response functions. The size of the squares corresponds to the absolute value, the sign is coded with blue for negative influence and with red for positive influence. Selective thinning has been carried out in this stand in 1975. The parameters are abbreviated as "prec" for precipitation and "temp" for temperature, "cur" for current year and "prev" for previous year.

2008; Pichler & Oberhuber, 2007). Furthermore, non-linear growth/climate relationships are discussed as thresholds (Büntgen et al., 2006) or time-dependent reactions with regard to current warming trends (Carrer & Urbinati, 2006).

A framework for integrating non-linear responses into growth/climate models exists in the form of neural networks (Woodhouse, 1999). This family of models allows for different types of functional relationships, like linear, non-linear or threshold-functions. Yet, an initial requirement would be to establish physiologically profound non-linear relationships. A promising approach for that are generalized additive models, which have successfully been applied to bivariate problems in this dissertation already.

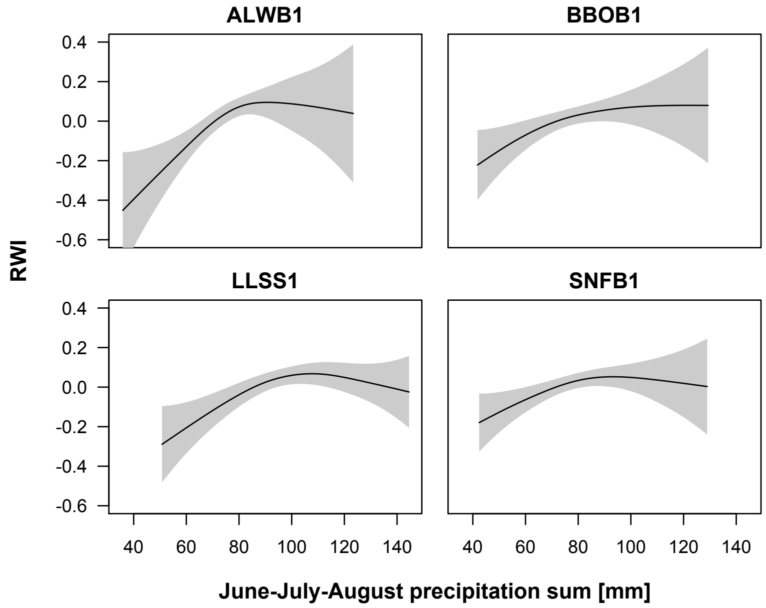

Figure VI.2.: Nonlinear relationships between tree-ring growth and summer precipitation. Shown are generalized additive models for spruce from Heideck (ALWB1, Franconian upper triassic), Bad Brückenau (BBOB1, Franconian lower triassic), Schiltberg (LLSS1, tertiary) and Schnaittenbach (SNFB1, Upper Palatine forest). The shaded area contributes to the 95%-confidence interval.

Fig. VI.2 shows nonlinear tree growth response to precipitation of several spruce populations from this dissertation's data set. A threshold of about 80–100 mm precipitation sum during summer (June, July and August) can derived, above which the increase in tree-ring width with increasing precipitation sum strongly flattens. The distinct nonlinear fashion of these relationships questions the currently most prominent employment of exclusively linear assumptions for growth/climate relationships.

VI.1.4. Calibration performance

The fact that multicollinearity in the climatic data hampers dendroclimatic calibration has been addressed in this dissertation, and response functions have been confirmed as a suitable workaround. However, principle component decomposition may—for ill-defined—problems not necessarily result in a perfect orthogonalization of the problem at hand.

A promising alternative to PCA can be found in the maximum entropy formalism (Beirlant et al., 1997). Maximum entropy based approaches have been shown to outperform alternative regression-based approaches (Paris & Howitt, 1998), but have not yet been applied for dendroclimatic calibration. From a theoretical perspective, the extension of the maximum entropy formalism without any exogenous assumptions (maximum entropy Leuven estimators, Paris, 2001) seems particularly apt for calibration purposes.

VI.2. Dealing with variability on population level

The high amount of variability on population level imposes further challenge on future research: what controls this variability, and to which extend can it be maintained by management strategies. A possible way to tackle this question is a combination of both tree-ring and genetic analyses to gain insight into the genetic microstructure of (sub)regional populations.

Knoke et al. (2005) recently put forward an economical approach to risk assessment in temperate forests based on portfolio theory, which—contrarily to classical economical calculus—suggests a mixture of species to minimize risks while maximizing returns. In a wider sense, this mindset could also be applied to intraspecific diversity, i.e. the variety of possible reactions to disturbances or climatic extremes. A better understanding of distribution, variability and possible interconnectivity (see also chapter V) of species traits might therefore contribute to a more precise risk assessment.

A better understanding of intrapopulation diversity with regard to reactions to climate and drought would also require a modified sampling: the trees used for this dissertation were all healthy and undamaged, and—even more important—they are the ones that survived *all* preceding drought episodes. Therefore, a strong sampling bias towards genetically drought-adapted individuals has to be assumed. A more integrative approach would need to incorporate also the more susceptible, and probably already dead trees. It has been shown that it is possible to utilize living and dead trees for dendroecological research alike (Bigler et al., 2006, 2007; Bigler & Veblen, 2009), but for the investigation area no such data are available yet.

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This dissertation is dedicated to the memory of Prof. Dr. Wolfram Elling who unexpectedly died during the dissertation project. He introduced me to the science of tree-rings and has been a steady source of enthusiasm for the subject.

A. Dendroclimatic calibration in presence of multicollineary—A simulation experiment

Background

Serious amounts of multicollineary in the predictor matrix $\boldsymbol{X}$ lead the violation of one assumption of the linear regression model $\boldsymbol{y} = \boldsymbol{X}\boldsymbol{b} + \epsilon$: that the predictor variables are not significantly correlated. Using climatic data with a high amount of multicollinearity is therefore problematic and may lead to imprecise and unstable estimates of regression coefficients $\boldsymbol{b} = (\boldsymbol{X}'\boldsymbol{X})^{-1}\,\boldsymbol{X}'\boldsymbol{y}$ and incorrect rejection of variables.

To evaluate existing alternatives for multivariate dendroclimatic calibration in the presence of multicollinearity in the climate data, a simulation experiment was carried out.

Material and Methods

36 tree-ring chronologies of Norway spruce (*Picea abies* (L.) H. KARST.) were used to calculate realistic residuals of growth/climate relations, i.e. the part of the growth signal unrelated to climatic influences. For this purpose, linear models of RWI (see section II.5) and June-July-August-temperature and June-July-August-precipitation have been constructed. The predicted values have been subtracted from the observed values, and the resulting residuals have been stored.

Real monthly time series of temperature and precipitation have been further manipulated by randomly adding noise (decreasing the amount of multicollinearity) or by adding random amounts of artificially generated autocorrelation (increasing the amount of multicollinearity). This modified climate data ($\boldsymbol{X}$) has then been used to model artificial tree-ring series. For this purpose, a random set of climatic parameters $\boldsymbol{x}$ was drawn from the modified climate data and combined to a error free initial RWI series using random correlation coefficients. In the next step, residuals from the first step were added to obtain artificial RWI series $\boldsymbol{y}$ with realistic error structures.

A calibration subset of each the modelled tree-ring series and the modelled climate series were then subject to four derivatives of linear modeling: ordinary least squares, response function analysis, stepwise regression and ridge regression.

Starting from the simple linear model $\boldsymbol{y} = \boldsymbol{X}\boldsymbol{b} + \epsilon$ with tree-ring series $\boldsymbol{y}$, predictor matrix of climate data $\boldsymbol{X}$, correlation coefficients $\boldsymbol{b}$ and error component ϵ, stepwise regression aims at finding $\boldsymbol{b}$ using a subset of $\boldsymbol{X}$. Here, Akaike's Information Criterion is used to find the optimal subset $\boldsymbol{X}_S$ by means of model comparison for different alternatives.

The main assumption of ridge regression is that for an ill-defined problem (like the inverse of $\boldsymbol{X}'\boldsymbol{X}$ when $\boldsymbol{X}$ is affected by high amounts of multicollinearity), additional assumptions are necessary to obtain a stable solution of $\boldsymbol{b}$: $\boldsymbol{b}_{\boldsymbol{R}}$. Thus, $\boldsymbol{b}_R$ is obtained by adding a constant term (i.e. a multiple of the unity matrix) to $\boldsymbol{X}'\boldsymbol{X}$: $\boldsymbol{b}_R = (\boldsymbol{X}'\boldsymbol{X} + k\boldsymbol{I})^{-1}\boldsymbol{X}'y$.

Response function analysis is carried out on the principle components of $\boldsymbol{X}$ to obtain a set of regression coefficients that is later transformed back into the original parameter space. The rationale and the method itself are laid out in detail in section II.8.1.

The amount of multicollinearity present in $\boldsymbol{X}$ was quantified using the condition number $\kappa_X = \sqrt{\lambda_{max}\lambda_{min} - 1}$ with maximum and minimum eigenvalues λ_{max} and λ_{max} of $\boldsymbol{X}$.

The relationships established using the four different methods were then expanded to a validation subset of each the modelled tree-ring series and the modelled climate series, and the performance of the models was assessed using three measures: score (i.e. the number of $\boldsymbol{x}$ correctly identified as significant), root mean square error (i.e. the deviation of predicted from observed values), and overfit (i.e. the ratio of the number of parameters judged significant by the model and the number of parameters used to construct the artificial tree-ring series). A flow chart of the simulation experiment is provided with fig. A1. In total, 1000 simulation runs were performed.

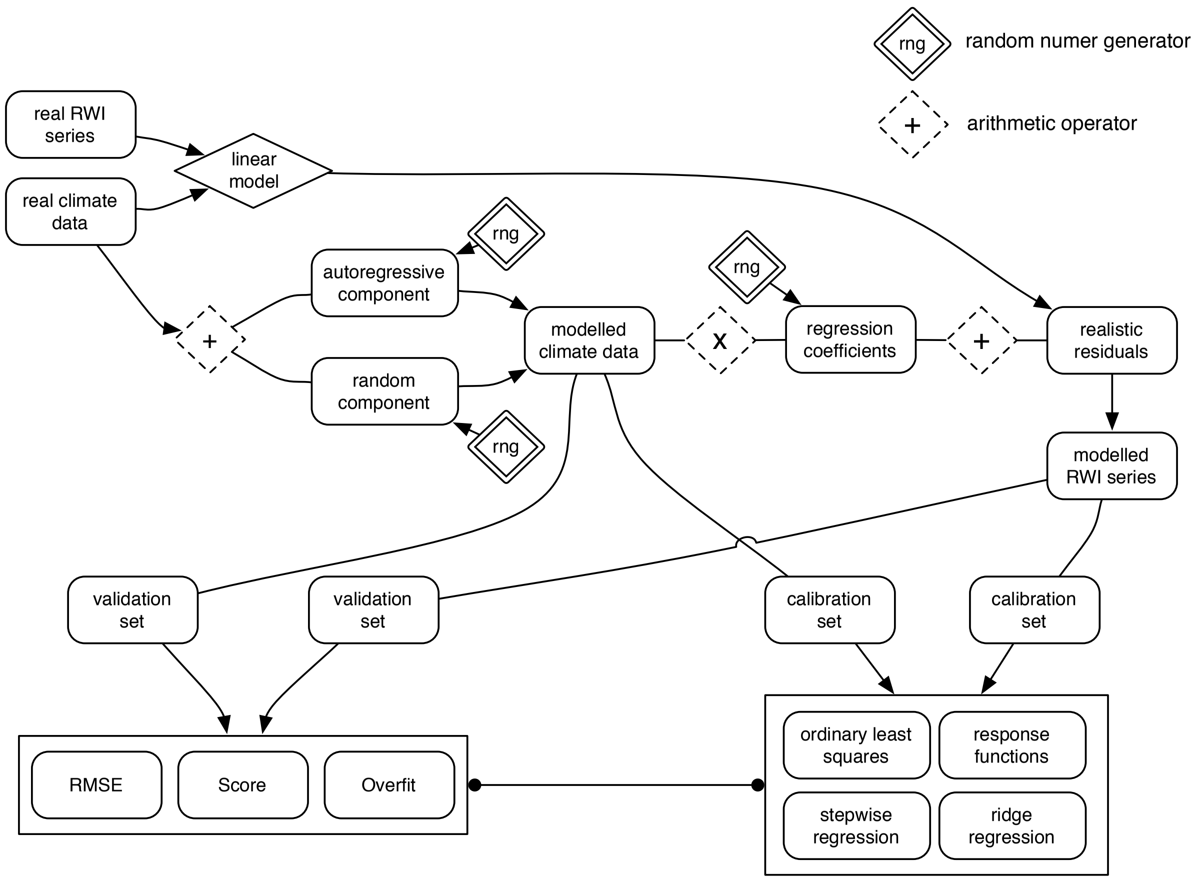

Figure A.1.: Flow chart of calibration simulation experiment.

Results

All models tend to underfitting, i.e. less parameters are judged significant, although they have been used to model the artificial tree-ring series (fig. A.2. However, some cases of serious overfitting have been observed as well: the maximum observed values of overfit are 3.0 for stepwise regression (corresponding to 3 times more parameters judged significant by the model than used for modeling the input data), 2.5 for OLS regression, 2.0 for ridge regression, and 1.5 for response functions. For higher amounts of multicollinearity, the desired value of 1 for overfitting is achieved more often by response functions.

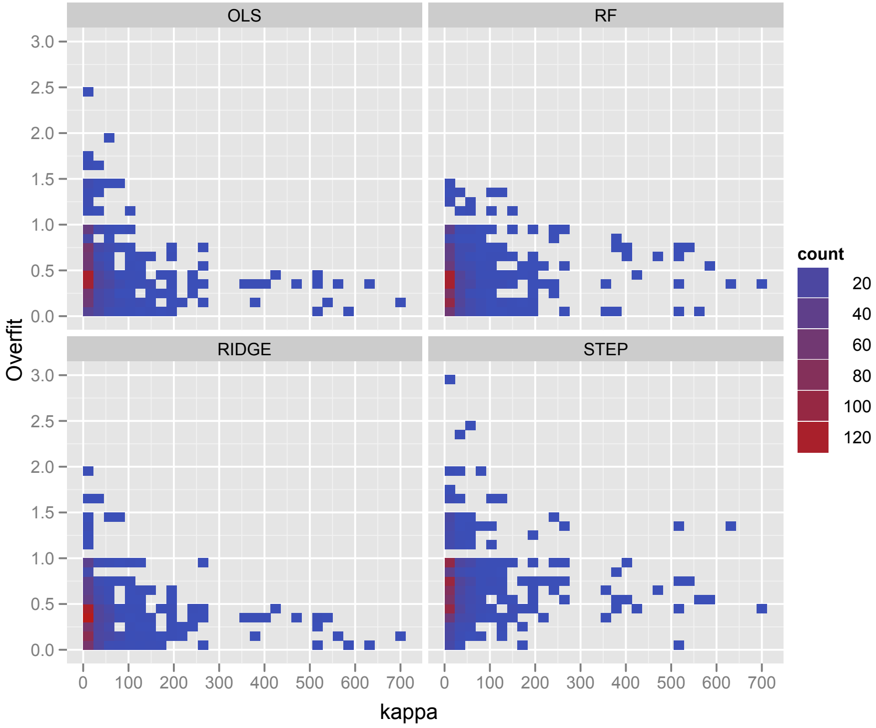

Figure A.2.: Overfit in relation to multicollinearity (κ). The squares are colored relative to the density of observations at point.

Mean RMSE was significantly higher for ridge regression and stepwise regression, but no clear relation to κ_X could be observed for any approach (data not shown).

All methods gain a better score (i.e. matching of the true parameters) at the cost of a higher overfitting in a similar manner (fig. A.3). But owing to the generally better performance of response functions in terms of overfitting, a full match of the initial model parameters was associated with a slight overfit at most.

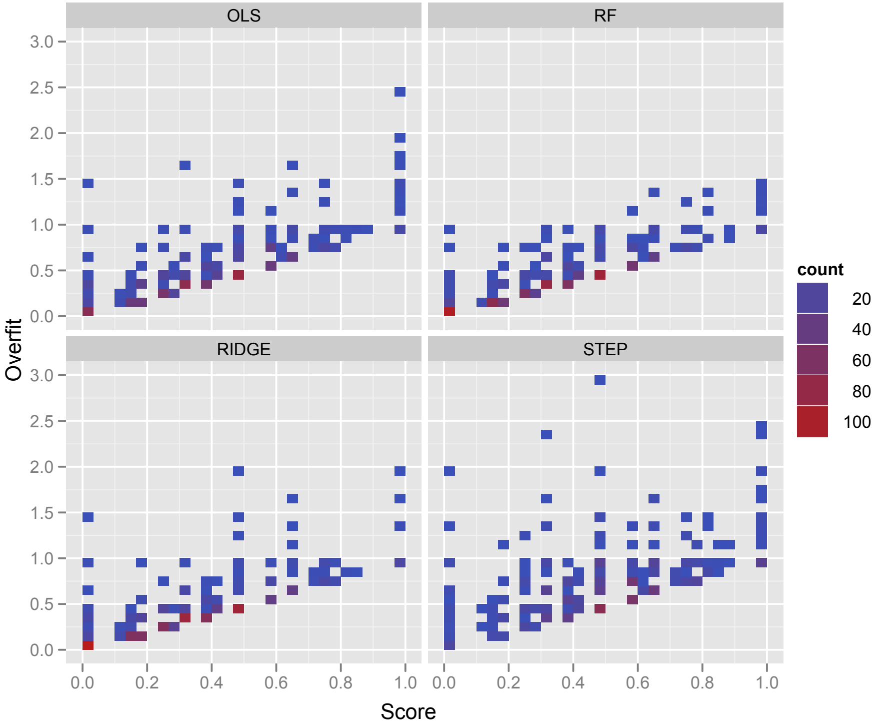

Figure A.3.: Overfit in relation to score. The squares are colored relative to the density of observations at point.

Implications

Given the overall worse performance of stepwise and ridge regression in terms of RMSE, this two methods are not taken into further consideration for data analysis in this dissertation. Ultimately, response functions provided the closest fit to the data without excessively overfitting the relationships between climate and tree growth. Therefore, this method is eventually chosen over OLS regression for this dissertation.

B. Original research papers

B1 Multivariate extremes as ecological benchmarks: archetypal analysis of tree-ring network data

Christian Zang

Draft close to submission.

Abstract: Archetypal analysis is proposed for finding multivariate extremes in ecological data sets. The procedure is based on the assumption that each observation in a data set can be represented as a convex combination of a few archetypes of the same dimensionality as the individual observations. These archetypes represent extreme performance rather than group averages and can for example be applied for benchmarking purposes. This study uses archetype analysis to identify patterns of extreme performance in tree-growth with respect to summer drought, based on tree-ring data from Norway spruce (*Picea abies* (L.) H. Karst.) and common oak (*Quercus robur* L.), comprising 59 site chronologies from 40 different sites in Southern Germany. It is shown for two and three archetypes, respectively, that these are characterized by oppositional growth/climate relationships with regard to summer drought. These findings are well in line with general ecophysiological characteristics of the species involved. The drought resistant archetype can be used as a benchmark for assessing the drought susceptibility of individual populations.

B2 Size dependent responses to summer drought in Scots pine, Norway spruce and common oak

Christian Zang, Hans Pretzsch, Andreas Rothe

In review. Manuscript submitted to *Tree Physiology*, 21.02.2011.

Abstract: In this study we provide a detailed analysis of tree growth and water status in relation to climate of three major species of forest trees in lower regions of Bavaria, Southern Germany: Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*) and common oak (*Quercus robur*). Tree-ring chronologies and latewood δ^{13}C were used to derive measures for drought reaction across trees of different dimensions: growth reduction associated with drought years, long-term growth/climate relations and stomatal control on photosynthesis. For Scots pine, growth/climate relations indicated a stronger limitation of radial growth by high summer temperatures and low summer precipitation in suppressed as opposed to dominant trees. This is corroborated by a stronger stomatal control on photosynthesis for suppressed pine trees under average conditions. In dry years, however, dominant pine trees exhibited stronger growth reductions. For Norway spruce, a significantly stronger correlation of tree-ring width with summer temperatures and summer precipitation was found for dominant trees. Additionally, for Norway spruce there is evidence for a change in competition mode from size-asymmetric competition under conditions with sufficient soil water supply to a more size-symmetric competition under dry conditions. Suppressed oak trees showed a weaker stomatal control on photosynthesis under both dry and average conditions, which is also reflected by a significantly faster recovery of tree-ring growth after extreme drought events in suppressed oak trees. The observed patterns are discussed in the context of the Limitation-Caused Matter Partitioning hypothesis and possible modifications by the species-specific ontogenesis of hydraulic architecture.

B3 **Combining tree-ring analyses on stems and coarse roots to study the root-shoot allometry of individual trees along environmental gradients. A case study on Norway spruce (*Picea abies* [L.] Karst.)**

Petia Simeonova Nikolova, Christian Zang, Hans Pretzsch

In review. Manuscript resubmitted with minor revisions to *Trees – Structure and Function, 01.02.2011.*

Abstract: We show the potential of a new method combining tree-ring analyses on stems and on coarse roots of individual trees in order to advance the understanding of growth dynamics in forest trees. To this end, we studied the root-shoot allometry of trees and its dependency on site conditions and tree form stability. Along a gradient in water supply in Southern Germany from dry to moist sites we selected 43 Norway spruce trees (*Picea abies* (L.) H. Karst.) aged 65-100 years. Increment cores were taken from stem and main roots revealing the trees' above- and below- ground growth course in the last 34 years. We apply annual growth rates of root and stem and their allometric relationship as surrogate variables for a tree's resource allocation to above- and below- ground organs. The mean sensitivities of both stem and root chronologies were found to be site-specific, and increased from the moist to the driest site. Significant correlation between the sensitivity of root and stem growth and tree form stability was detected only at the driest site. At all study locations, no temporal offset between above- and below- ground growth reactions to climate conditions was found in Norway spruce. The more the sample trees were limited by soil moisture, the higher was the long-term root-shoot allometry. The results from our study suggest that the root-shoot allometry depends on the specific site conditions according to the optimal partitioning theory (the more restricted the below ground resources, the more organic matter allocation into the below ground organs).

B4 **Zur Baumarteneignung bei Klimawandel: Ableitung der Trockenstress-Anfälligkeit wichtiger Waldbaumarten aus Jahrringbreiten**

Christian Zang, Andreas Rothe, Hans Pretzsch

In review. Submitted to *Allgemeine Forst- und Jagdzeitung*, 16.02.2011.

Abstract: Die prognostizierte Zunahme extremer Trockenperioden im Rahmen des Klimawandels stellt die Frage nach der Trockenresistenz der heimischen Baumarten. Das extreme Trockenjahr 2003 führte in weiten Teilen Bayerns zu erheblichem Wasserstress der Waldbäume, und nach aktuellen Szenarien kann diese Sommertrockenheit als ein Vorgeschmack auf künftige Trockenereignisse verstanden werden. Um eine vor allem für die forstliche Praxis weiterführende Antwort auf die künftige Anbaufähigkeit der heimischen Hauptbaumarten zu geben, wurden etwa 1500 Bäume (Fichte, Kiefer, Tanne, Douglasie, Buche und Eiche) auf 48 Standorten in ganz Bayern (und z.T. in angrenzenden Gebieten) jahrringanalytisch untersucht. Es wurden zum einen Maße für den Zuwachseinbruch im Zusammenhang mit extremen Trockenjahren betrachtet, und zum anderen wurden die Jahrringbreiten mit Klimavariablen und Kenngrößen des Bodenwasserhaushaltes in Beziehung gesetzt. Die Herstellung von Klima-Wachstums-Beziehungen erfolgte mit Hilfe von Hauptkomponentenregressionen auf der Basis monatlicher Klimadaten. Von allen untersuchten Baumarten hat Fichte am stärksten auf Trockenjahre reagiert. Tanne war deutlich weniger anfällig als Fichte. Eiche zeigte von den untersuchten Baumarten die größte Widerstandsfähigkeit, Buche, Kiefer und Douglasie reagierten schwächer als Fichte aber stärker als Eiche. Dies bestätigt die Bemühungen, Fichtenbestände angesichts des prognostizierten Klimawandels in stabilere Mischbestände umzubauen. Der Zusammenhang zwischen Zuwachsreaktion und Klima- bzw. Standortvariablen war bei allen Baumarten allerdings erstaunlich schwach. Es besteht zwar die Tendenz, dass die Anfälligkeit mit abnehmenden Niederschlägen zunimmt, diese wird jedoch von der hohen Variabilität der Einzelbaumreaktion überlagert. Generell zeigt sich aber eine gute Trennung der Baumarten nach ihren klimatischen

Ansprüchen, vor allem Eiche und Fichte sind durch den Aspekt "Sommertrockenheit" stark differenziert. In den trockeneren Regionen des Untersuchungsgebietes (Keuperregionen, Oberpfälzer Becken) ist die Limitierung des Baumwachstums durch warme und trockene Sommer vor allem bei Fichte stärker ausgeprägt als in niederschlagsreicheren Regionen (Schotterebene, Alpenvorland).

B5 Species response to springwater acidity: is the delineation of niche attributes a matter of spatial scale?

Christian Zang, Volker Audorff, Carl Beierkuhnlein

Draft close to submission.

Abstract: **Aim:** To determine the effects of different spatial sampling scales on species' niche characteristics. **Location:** Helocrenic springs in siliceous mountain ranges in central Germany and northwest Czech Republic (49.9° - 50.8° N, 10.6° - 12.8° E). **Methods:** The probability of bryophyte and tracheophyte species occurrence in respect to pH is modeled, using generalized additive models (GAM). To compare species optima and amplitudes, those were derived separately for two spatial scales, in an entire spring and a subplot-based within-spring approach. **Results:** Species occurrence is driven by an acidity gradient, which determines nutrient availability. The pH value acts as leading representative of this gradient, and controls the potential species pool (calculated from the amplitudes of the species response curves), regardless of observation scale. Lowest species numbers are found in acidic, highest in circumneutral springwaters. The hypothesized independency of niche characteristics from sampling scale was corroborated only for the pH optima. Contrary, a smaller plot size (i.e. grain) narrowed pH amplitudes significantly. **Main conclusions:** Both, dispersal limitation and niche mechanisms are less scale-dependent in springs than in other habitat types. We assign these findings to two special features of springs. (1) They are groundwater-dependent aquatic biotopes encircled by terrestrial habitats. Similar to islands, dispersal vectors to the spring habitats are limited also on the larger scale. (2) Helocrenic springs are characterized by certain small-scale within-site variability. Thus environmental factors constitute the niche characteristics also on the smaller scale. **Nomenclature:** Frahm & Frey (2004) for bryophytes; Oberdorfer (2001) for tracheophytes.

B6 Paleoclimatic calibration of proxy data in R – the package bootRes for bootstrapped response function analysis

Christian Zang

Draft close to submission.

Abstract: Proxy data are often used for the reconstruction of ancient climate conditions. To derive paleoclimatic transfer functions, proxy data have to be calibrated against modern climate data. The high degree of multicollinearity in climatic data of monthly resolution violates the assumption of independent predictor variables in standard ordinary least squares regression. Bootstrapped response function that obtain parameter estimates via regression against the principle components of the predictor variables are a common solution to that problem. Package bootRes for R implements an interface for bootstrapped correlation analysis and tackles some shortcomings of currently available software packages used for obtaining paleoclimatic transfer functions from proxy data.

C. Peer-reviewed abstracts for conference volumes

C1 Variabilität in der Zuwachsreaktion auf Trockenstress

Christian Zang, Andreas Rothe and Hans Pretzsch

Forstwissenschaftliche Tagung 2010. Göttingen, Germany, September 2010. Accepted as poster contribution.

Abstract: Im Rahmen eines vom Bayer. Staatsministerium für Ernährung, Landwirtschaft und Forsten finanzierten Forschungsprojekts wurde von 2006–2009 die Reaktion von Waldbäumen auf Sommertrockenheit mit dendroökologischen Methoden untersucht. Anhand eines großen Datensatzes der ca. 1500 Einzelbäume umfasst, kann gezeigt werden, dass sich die Variabilität der Reaktion auf Trockenstress innerhalb der standörtlich homogenen Kollektive in der gleichen Größenordnung bewegt wie die Variabilität zwischen den einzelnen edaphisch und klimatisch differenzierten Standorten. Insbesondere die Fichte zeigt auf trockenen Standorten eine große Spielbreite möglicher Reaktionen auf Trockenstress, so dass die Ableitung standortstypischer Reaktionsmuster kaum möglich ist. Diese Variabilität wird als Vorteil hinsichtlich der Anpassung an den Klimawandel verstanden, dahingehend, dass die Populationen bereits heute über ein beträchtliches Potential zur internen Kompensation von Extremereignissen besitzen.

C2 Auswirkungen des Trockensommers 2003 auf das Jahrringwachstum von Fichte, Tanne, Kiefer, Douglasie, Eiche und Buche in Bayern

Andreas Rothe and Christian Zang

Forstwissenschaftliche Tagung 2010. Göttingen, Germany, September 2010. Accepted as oral contribution.

Abstract: Im Rahmen eines vom Bayer. Staatsministerium für Ernährung, Landwirtschaft und Forsten finanzierten Forschungsprojekts wurde von 2006–2009 die Reaktion von Waldbäumen auf Trockenjahre (insbesondere den Trockensommer 2003) anhand dendroökologischer Methoden untersucht. Das Projekt umfasste 47 Standorte in ganz

Bayern und die wichtigsten Wirtschaftsbaumarten Fichte, Tanne, Kiefer, Douglasie, Eiche und Buche. Insgesamt wurden rund 1500 Bäume jahrringanalytisch untersucht. Weiterhin wurden Klima- und Standortfaktoren erhoben bzw. gemessen und der Wasserhaushalt mittels eines hydrologischen Models berechnet. Im Rahmen des Vortrags sollen folgende Ergebnisse des Projekts dargestellt werden: 1) Zuwachseinbruch und Erholung der untersuchten Baumarten nach Trockenjahren (insbesondere 2003), 2) Einfluss von Klima und Standort (Wasserhaushalt) auf die Baumreaktion, und 3) Variabilität der Reaktion auf Einzelbaum- und Populationsebene

C3 **It's all in the mix – Dendroecological archetypes provide a new perspective on inherent growth patterns**

Christian Zang, Andreas Rothe and Hans Pretzsch

Worlddendro 2010. Rovaniemi, Finnland, June 2010. Accepted as oral contribution.

Abstract: Archetypal analysis is based on the assumption that each point in a multivariate data set can be represented by a convex combination of a set of equally dimensioned archetypes that do not necessarily need to be observed in reality. By applying archetypal analysis on a data set of 32 Norway spruce (*Picea abies* (L.) H. Karst.) and 22 common oak (*Quercus robur* L.) chronologies from Southern Germany, we derived two growth patterns that represent two archetypes of growth dynamics. These patterns are designated to a hypothetical ideal oak or spruce, respectively. As common oak and Norway spruce are often associated with different strategies of coping with climatic constraints, the derived archetypes may as well be interpreted in terms of drought tolerance (oak) and drought intolerance (spruce). We found the oak archetype to be characterized by a lower mean sensitivity and a weaker dependence on both temperature and precipitation, whereas the spruce archetype shows a higher mean sensitivity and a stronger growth limitation by summer and autumn temperatures and summer precipitation. Despite the algorithmic complexity of the method, the mixing ratio of the two archetypes in each chronology provides a comprehensible measure of tolerance and intolerance. We prove this method to be more effective in terms of species separation than more established grouping approaches like fuzzy *c*-means clustering. Furthermore, the derived archetypes are hypothetical chronologies and can be interpreted as such. We see this as an advantage over classical PCA, where interpretation of principal components of higher order is generally not as intuitive. In a spatially explicit approach we show that archetypal analysis can be used to derive site specific species rankings with respect to drought tolerance.

C4 **Effects of drought on growth and water availability of *Picea abies* (L.) Karst., *Pinus sylvestris* L. and *Quercus robur* L. trees of different social classes**

Christian Zang, Klaus Kagerer, Andreas Rothe and Hans Pretzsch

Eurodendro 2009. Cala Milor, Mallorca, Spain, October 2009. Accepted as oral contribution.

Abstract: We investigated tree-ring chronologies and late wood δ^{13}C to determine the influence of extreme drought events like the heat wave of 2003 on radial growth and water availability of spruce, pine and oak trees of different crown classes in southern Germany. Climate-growth-relationships were calculated with bootstrapped response functions of total monthly precipitation and mean monthly temperature. The impact of severe drought events on tree growth was computed using bootstrapped super epoch analysis. Additionally we measured latewood δ^{13}C to assess stomatal response to drought. General climate-growth-relationships differed between species, depicting different critical periods for water supply and temperature throughout the year. In contrast to pine and oak, growth of spruce was significantly correlated with high precipitation in current summer. These relationships are consistent between crown classes. Regarding the impact of drought events, growth of spruce trees was reduced the most but recovered quickly, whereas in oak growth was reduced the least but recovered slowly. In spruce and oak a higher impact but faster recovery was found in the dominant trees, whereas dominant pine trees exhibited a lower growth reduction in combination with a slower recovery compared to suppressed pine trees. These differences are discussed as effects of root competition and shading that differ across crown classes. While the change in late wood δ^{13}C in 2003 is correlated with the reduction in diameter growth in spruce and pine, oak showed a drought- related isotope signal lagged one year. The latter findings are interpreted as differences in storage strategies between species independent of crown class.

C5 **Reaktion verschiedener Baumarten auf extreme Sommertrockenheit in Bayern: Erkenntnisse aus Zuwachsuntersuchungen und Holzisotopie**

Christian Zang, Andreas Rothe and Hans Pretzsch

Forstwissenschaftliche Tagung 2008. Freiburg, Germany, September 2008. Accepted as poster contribution.

Abstract: Die vorhergesagten globalen Klimaänderungen gehen mit einer erhöhten

Frequenz und Intensität von Dürreereignissen in den Sommermonaten einher. Die Reaktion der Wirtschaftsbaumarten auf zunehmende Sommertrockenheit wird deshalb in kommender Zeit von besonderem ökonomischem und ökologischem Interesse sein. Die Hitzewellen von 1976 und 2003 boten bereits einen Vorgeschmack auf künftige Extremereignisse, und ermöglichen es dadurch die Trockenheitsempfindlichkeit verschiedener Baumarten mit einem vergleichsweise geringen methodischem Aufwand zu untersuchen. Als Indikator für die Trockenheitsempfindlichkeit der Baumarten dient die Zuwachsreaktion (Durchmesserzuwachs) mittelalter Bäume, in Kombination mit einer physiologischen Abschätzung des Trockenstress über die Holzisotopie (δ^{13}C). Die Beurteilung der Intensität der Trockenheit erfolgt anhand hydrologischer Modelle. Ziel ist es hierbei, (semi-)quantitative Kenngrößen für die Sensitivität einzelner Baumarten abzuleiten. Im Gegensatz zu einzelnen sehr intensiven Fallstudien werden in diesem Projekt zahlreiche Standorte in ganz Bayern einbezogen, mit insgesamt rund 50 Einzelflächen auf ca. 10 Standortsgruppen. Das Spektrum zu untersuchender Standorte reicht hierbei von mäßig trockenen bis mäßig frischen Standorten in Regionen, die bei einer Klimaänderung als besonders gefährdet betrachtet werden (z.B. Schotterebenen, Tertiäres Hügelland, Keuperlandschaften, nördliche Oberpfalz) bis hin zu frischen Standorten in weniger gefährdeten Regionen (z.B. Jungmoräne, Fränkische Platte, Alpenraum). Die Untersuchungen konzentrieren sich dabei auf die Hauptbaumarten Fichte, Tanne, Douglasie, Kiefer sowie Buche und Eiche. Das Forschungsprojekt wird vom Bayer. Ministerium für Landwirtschaft und Forsten gefördert (Laufzeit 2006–2009).

C6 **Drought responses of different tree species in Bavaria: Evidence from tree-ring growth and wood δ13C**

Christian Zang, Andreas Rothe and Hans Pretzsch

Adaptation of Forests and Forest Management to Changing Climate with Emphasis on Forest Health: A Review of Science, Policies and Practices. Umeå, Sweden, August 2008. Accepted as oral contribution.

Abstract: Global change climate is predicted to yield increases in both frequency and intensity of drought. Hence, the growth reaction of forest trees to increasing drought will be of considerable economical and ecological interest. The European heat waves of 1976 and 2003 provided a foretaste of future drought events and thus give the opportunity to investigate drought-sensitivity of different tree species on a variety of sites with a comparable small methodological effort. We use increment growth and wood isotopic signature (δ^{13}C) to derive measures of susceptibility and resilience with respect to these drought events. Our investigations focus on the commercially most important species in Bavaria: *Picea abies* (L.) H. Karst., *Pinus sylvestris* L., *Abies alba* Mill., *Fagus sylvatica* L.and *Quercus robur* L. – and on *Pseudotsuga menziesii* (Mirbel) Franco, as a possible alternative to *Picea abies*. The diversity of investigated sites ranges from regions with wine climate in north western Bavaria to colder and humid sites in the south, with a variety of soil types being covered as well. For *Picea abies* we could derive clear patterns of drought impact on tree growth along environmental gradients: on the large scale (across Bavaria) drought impact follows the climatic gradient with a higher impact under drier conditions, whereas on the site scale (subsites with different soil conditions) this pattern is inverted. Consequently the impact of drought on tree growth can be interpreted as a tradeoff between the species' autoecological limits and the individual site-specific adaptation. Further, a site-specific ranking of tree species regarding susceptibility and resilience with respect to global-change-type drought events could be obtained.

C7 **Effects of increased drought on choice of commercial forest trees in Bavaria**

Christian Zang, Andreas Rothe and Hans Pretzsch

Eurodendro 2008. Hallstadt, Austria, May 2008. Accepted as poster contribution.

Abstract: According to global and regional prognoses for climatic change, the Northern Hemisphere will face more frequent and prolonged droughts. Thus rethinking site-specific choice of commercial forest trees is one of the most urgent tasks on the forester's agenda on one hand, on the other hand still one of the most uncertain ones. A number of studies already have dealt with trees' reaction to drought, but no reliable implications for silvicultural practice in a given region could be obtained yet. While climate change as a complex phenomenon cannot be simulated under field conditions, we believe that at least the aspect of increasing drought can be captured on stand scale: several events of summer drought have been monitored during the past decades, that are quite similar to those predicted by prognoses. We use these extreme years as observational experiments that provide us with the unique opportunity to investigate how different, species-dependent strategies in response to water deficits will lead to different sensitivities to changes in water availability, finally leading us to conclude site-specific recommendations for species choice in Bavaria. We compare the results of different species in growth rate (measured via radial increment) and intrinsic water use efficiency (which we infer via carbon isotope discrimination) among a gradient of sites in Bavaria, ranging from humid mountain regions to dry regions with wine-climate, covering a great range of substrates as well. Our

study focuses on *Picea abies* (L.) H. KARST., *Pinus sylvestris* L., *Abies alba* MILL., *Fagus sylvatica* L. and *Quercus robur* L. as the economically most important species in Bavaria, and on *Pseudotsuga menziesii* (MIRBEL) FRANCO which currently is being discussed as an alternative to Picea abies under climate change conditions. As far as our conception of drought is concerned, we do not focus on meteorological drought alone but also take soil hydrology into account. Therefor we use a regionalised version of the hydrological model Brook90 to derive soil water characteristics in the rhizospere in fine temporal resolution, allowing us to aggregate sensitive hydrological parameters to correlate with radial increment and wood δ^{13}C. This poster documents work in progress, focuses on our methodology and gives some preliminary results to discuss.

D. Student projects

D18 **Michelangelo Olleck** (in progress, Diploma) Auswirkung von Streunutzung auf die Wuchsdynamik von Alteichen im Spessart

D17 **Sergej Groh** (in progress, Diploma) Wachstumsreaktionen von Fichte, Kiefer, Tanne und Buche auf Sommertrockenheit im Oberpfälzer Becken

D16 **Martin Hostenkamp** (in progress, Diploma) Klima-Wachstums-Beziehungen von Fichte und Tanne entlang eines Höhengradienten im Vorarlberg

D15 **Florian Forstner** (2010, BSc.) Wachstumsmuster der Lärche entlang eines Höhengradienten im Nationalpark Berchtesgaden

Short abstract: ARIMA modeling has—among other methods–been used to separate climate related patterns of larch (*Larix decidua* MILL.) growth from patterns resulting from other exogeneous factors, especially insect outbreaks. The patterns of irregular growth depression for alpine larch were not in agreement with reported panalpine outbreaks of larch budmoth, and the growth/climate relationships followed no clear trend along the altitudinal gradient. Thus it is concluded, that the larch populations used for this study are not suitable for neither climate nor insect outbreak reconstruction purposes.

D14 **Johannes Riepl** (2010, Diploma) Reaktion der Fichte (*Picea abies* (L.) H. Karst.) auf Klimaveränderungen entlang eines Höhengradienten im Nationalpark Berchtesgaden

Short abstract: Growth/climate relations of spruce (*Picea abies* (L.) H. KARST.) were studied along an altitudinal gradient. Across all elevations, spruce trees depicted only weak correlations between tree growth and climatic variables. Despite a warming trend already visible in the temperature series for the investigational area, no effect of warming on tree growth could be observed.

D13 **Lingyun Ma** (2010, MSc.) The impact of climate change on silver fir (*Abies alba* Mill.) growth along elevational gradients in the Bavarian Alps

Short abstract: Growth/climate relations and sensitivity of silver fir growth have been studied to assess the effects of increasing temperatures on tree growth. Fir growth is favoured by higher winter temperatures, and significantly influenced by extreme drought events in the higher altitudes. It is concluded that an further increase in temperatures will at first foster tree growth for silver fir in the Berchtesgaden region.

D12 **Jan Kraft** (2010, Diploma) Einfluss von Hagelschaden auf den Radialzuwachs von Fichten

Short abstract: Tree-ring series of spruce trees from a stand with hail damage and a control stand were compared in order to evaluate the impact of hail on radial growth. The damaged stand showed a significant growth decline in comparison to the control stand for one decade after the hail event. The amount of initial damage, measured as cambial damage from cross-sectional disks, was significantly related to recovery time, i.e. the time a tree needed to approach its pre-damage growth rate.

D11 **Alexandra Schade** (2010, Diploma) Auswirkungen von Streunutzung auf die Zuwachsleistung von Waldkiefern im Forstbetrieb Burglengenfeld in der Oberpfalz

Short abstract: The impact on litter removal on absolute tree growth and growth-climate coupling of Scots pine (*Pinus sylvestris* L.) is evaluated on two adjacent plots: one with repeated litter removal, and one control plot without litter removal. In terms of growth-climate coupling, no significant differences could be observed. Also, no impact of litter removal on absolute tree-ring width was found. A diverging growth trend between the two plots could not unambiguously be ascribed to the effects of litter removal.

D10 **Stefan Kraus** (2010, Diploma) Einfluss von Klima, Störungen und Konkurrenz auf das Jahrringwachstum in Buchen- und Eichenbeständen am Schwanberg, westlicher Steigerwald

Short abstract: Wavelet analysis and pointer year analysis were used to disentangle growth signals deriving long-term climate fluctuations and short term impact of extreme climatic events. As a main result, a significant correlation between a long-term (> 30 a amplitude) precipitation signal and oak growth was observed, whereas on higher frequencies no correlation could be detected.

D9 **Kathrin Klein** (2009, Diploma) Zuwachsreaktion von Fichte, Tanne, Kiefer, Douglasie, Buche und Eiche im Kreis Heilbronn im Hinblick auf extreme Trockenjahre

Short abstract: Archetype analysis, pointer year analysis and response function analysis were used to derive a ranking of six dominant tree species in the wine-growing region in north-eastern Baden-Wuerttemberg: *Picea abies* (L.) H. KARST., *Pinus sylvestris* L., *Abies alba* MILL., *Pseudotsuga menziesii* (MIRBEL) FRANCO, *Fagus sylvatica* L. and *Quercus robur* L.. *P. abies*, *P. sylvestris* and *Quercus robur* are characterized by similar traits in terms of a low productivity, low growth inertia and a high degree of long term growth trends, as reflected by archetype analysis. Due to a lower overall productivity, the relative impact of extreme drought on growth of *P. abies* is not as pronounced as in regions with higher amounts of precipitation.

D8 **Klaus-Jürgen Kagerer** (2009, Diploma) Auswirkungen von extremen Trockenereignissen auf Fichte (*Picea abies* (L.) Karst.), Kiefer (*Pinus sylvestris* L.) und Stieleiche (*Quercus robur* L.) verschiedener sozialer Klassen im Forstenrieder Park

Short abstract: Growth reaction to summer drought was evaluated for trees of *Pinus sylvestris* L., *Picea abies* (L.) H. KARST., and across all diameter classes. Remarkable differences were found regarding long-term growth/climate relationships and growth reduction associated with drought events, with a stronger impact on summer drought on dominant pine trees, dominant spruce trees and dominant oak trees.

D7 **Ludwig Abele** (2008, Diploma) Reaktion von Fichte, Eiche, Buche, Douglasie und Tanne auf Lösslehm-Standorten im Hienheimer Forst auf klimatische Extremjahre

Short abstract: On a loess covered site in the western jurassic of Bavaria, the most distinct growth reductions associated with summer drought were found for spruce and Douglas fir. For beech, a remarkable difference between a terrestric site and a stagnic site could be observed, with higher drought impact on the terrestric site.

D6 **Marcus Engel** (2008, Diploma) Reaktion von Fichte, Eiche, Buche, Douglasie und Tanne auf Kalkverwitterungslehm-Standorten im Hienheimer Forst auf klimatische Extremjahre

Short abstract: A similar species ranking with regard to drought events like in the preceding study could be found on a residual loam site in the western jurassic of Bavaria. Here, pine showed a remarkably high resilience with regard to extremes on both xeric and mesic sites.

D5 **Katja Kneer** (2008, Diploma) Einfluss von Trockenjahren auf das Wuchsverhalten von Fichte, Tanne, Buche und Eiche auf wechselfeuchtem Standort im Forstbetrieb Weißenhorn

Short abstract: This thesis contributes to the understanding of growth reaction to climate and drought on groundwater-influenced sites (stagnic luvisols) versus terrestric sites (luvisols). All species under investigation (*Picea abies* (L.) H. Karst., *Abies alba* Mill., *Fagus sylvatica* L. and *Quercus robur* L.) showed significant growth reductions with respect to drought events on both types of soil. However, drought impact was more severe on groundwater-influenced sites.

D4 **Malte Hauss** (2007, Diploma) Dendroökologische Studien an Fichte und Kiefer, Sibirien

Short abstract: Tree-ring series of *Pinus sylvestris* L. from Siberia were assessed for their dendroclimatic potential. The climatic signal transported in the growth signal was found to be rather weak; instead, the series provided a record of past land use activities like repeated grazing.

D3 **Klaus Limmer** (2007, Diploma) Literaturstudie zur Baumarteneignung bei Klimawandel

Short abstract: This literature review aims at the compilation of different methods currently employed to derive species recommendations for a changing climate. Among the most frequent approaches are biogeographic techniques, small-scale experimental manipulations and modelling approaches. A considerable number of studies uses a combination of several methods.

D2 **Stefanie Meyer** (2007, Diploma) Der Trockensommer 2003: Auswirkungen auf das Baumwachstum im tertiären Hügelland

Short abstract: The growth reactions of *Picea abies* (L.) H. Karst, *Pinus sylvestris* L. and *Abies alba* L. growing in the Bavarian tertiary uplands (i.e. outside the natural distribution range of *P. abies*) were compared with respect to climate and extreme drought events. Tree-ring widths were correlated with temperature, precipiation and modelled soil water storage. Growth of *P. abies* showed the strongest correlation with soil water storage and the strongest influence of climate parameters. Summer drought strongly affected growth of *P. abies*, whereas *A. alba* showed only a small influence of summer drought on tree growth.

D1 **Hans Feist** (2007, Diploma) Untersuchungen zur Zuwachsreaktion von Fichte, Kiefer und Eiche auf Trockenjahre und daraus resultierende Folgerungen für die Eignung bei Klimawandel im Ebersberger Forst

Short abstract: Growth/climate and growth/soil water relations are used to derive a site specific assessment of the vulnerability of *Picea abies*, *Pinus sylvestris* and *Quercus robur* to summer drought on two luvisols with differing textures in Southern Bavaria. Different parametrizations of a soil hydrological model are used to quantify the effect of differing resolution depth in vegetation and soil parameters on simulating the soil water balance. All species performed nearly equally well, and the sites are not critical for growing *P. abies*. For similar soils, the influence of vegetation parameters (like LAI) on modelled soil water content is very low in comparison to climate as master variable.

Erklärung

Ich erkläre an Eides statt, dass ich die der Fakultät Wissenschaftszentrum Weihenstephan für Ernährung, Landnutzung und Umwelt der Technischen Universität München vorgelegte Arbeit mit dem Titel

Growth reaction of temperate forest trees to summer drought—a multispecies tree-ring network approach

unter der Anleitung und Betreuung durch Prof. Dr. Dr. Hans Pretzsch ohne sonstige Hilfe erstellt und bei der Abfassung nur die gemäß § 6 Abs. 5 angebenen Hilfsmittel benutzt habe.

Ich habe die Dissertation in dieser oder ähnlicher Form in keinem anderen Prüfungsverfahren als Prüfungsleistung vorgelegt.

Ich habe den angestreben Doktorgrad **noch nicht** erworben und bin **nicht** in einem früheren Promotionsverfahren für den angestrebten Doktorgrad endgültig gescheitert.

Die Promotionsordnung der Technischen Universität München ist mir bekannt.

München, den